

**COMMUNITY STRUCTURE**

**OF**

**CLIFF-TOP COASTAL HEATHLANDS**

**IN**

**BOTANY BAY NATIONAL PARK, SYDNEY**

**Robert Nigel Fullerton**

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Submitted to the University of Technology, Sydney in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

## **Declaration of originality**

I hereby declare that the contents of this thesis, unless where otherwise cited, are the product of original research conducted by the author. I also hereby declare that the contents of this thesis have not been previously submitted for any award.

Robert Nigel Fullerton

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## Abstract

This thesis examines community structure of cliff-top coastal heathlands in Botany Bay National Park, Sydney. Community properties of floristic composition, structure and species richness are investigated. This investigation is made in order to assess the justification for contemporary pre-emphasis in local studies on individual community properties. It is also made in order to assess the relative and independent contributions of individual properties to variance in overall community structure. It is also made in order to assess the relative utility of multi-property classifications in summarising community structure of cliff-top coastal heathlands.

First, the presence of determinable structure in each property is assessed through multivariate classification of respective data sets. Secondly, a new model of community structure is developed in which the hypothesis that community structure is a function of common (shared) and independent (unique) variance in each of the three properties is assessed. This is achieved through application of variance partitioning using correspondence analysis techniques. Thirdly, a matrix combining variance in all three properties is classified. This classification is compared with those of individual properties in order to assess the hypothesis that more ecologically cohesive classifications than those of single properties are obtainable. The ecological significance (environmental relativity) of all classifications and variance components is assessed through examination of relationships with variance in 20 environmental factors which encompass variation in maritime factors, soil physical factors, soil nutrition factors and effects of time since fire.

Classifications of individual properties showed the presence of determinable structure in each. Eleven floristic complexes, nine structural complexes and eighteen species richness complexes were recognised. Nineteen community complexes were recognised from the classification of the combined property matrix. All complexes were shown to differ significantly with respect to multiple environmental factors.

Variance partitioning showed the presence of both independent and common variance components with respect to properties compared pairwise. These were all shown to differ in magnitude. Examination of environmental correlates showed ecological differentiation of all properties and most variance components. Maritime and fire factors provide a major axis of environmental differentiation for most properties and

variance components. A second major axis was resolved with respect to physical soil factors. With the exception of variance in species richness, major soil nutrients were generally of secondary importance to community structure. Low soil nutrients may demarcate heathlands from other vegetation types. However, this study shows elevated importance of other major areas of environment for community structure within cliff-top coastal heathlands.

Comparisons of environmental homogeneity characteristics between all classification systems showed the classification of the combined property matrix to be more ecologically robust than those of structure or species richness. Homogeneity characteristics of the combined classification remained statistically inseparable from that of floristic composition. However, studies provided some evidence suggesting greater robustness of the combined classification with regard to fine-scale variance in community structure.

This thesis shows that variance in all major community properties of the studied vegetation to be of ecological significance. It also shows that this significance is differential with respect to properties and their variance components. Pre-emphasis on individual properties in syntheses of local systems thus involves the loss of ecological information. I thus conclude that if adequate ecological syntheses of cliff-top coastal heathlands are to be obtained which are appropriate to their scale of distribution and functioning in the Sydney area then inclusion of attributes of multiple properties is required. Equally, multiple sources of environmental variation need to be examined.

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## CHAPTER 1: INTRODUCTION

### 1.1 WHAT ARE HEATHLANDS?

The term "heathland" refers to a vegetation type characterised by a distinctive structural formation. Heathlands are defined as having an upper stratum consisting of sclerophyllous shrubs not exceeding 2 m in height (Specht 1970). Types of heathland may be identified according to height and foliage projective cover of the upper stratum, co-dominance of life forms in the upper stratum and by habitat (Specht 1970, 1979a,b). The principal types most commonly referred to include wet heathland (seasonally waterlogged, but may also be seasonally dry), dry heathland (on deeper, freely draining soils, not seasonally waterlogged), open heathland (foliage projective cover of 30%-70%) and closed heathland (foliage projective cover of 70%-100%) (e.g. Siddiqi *et al.* 1972; Specht 1970, 1979a,b; Clemens & Franklin 1980; Groves 1981a; Myerscough & Carolin 1986; Adam *et al.* 1989a; Enright 1989). This approach to the classification of heathlands succeeds approximately two centuries of confusion regarding the precise meaning of the term "heath". As detailed by Specht (1979a), confusion has arisen due to widely varying interpretation of the term across language groups, and due to concurrent application of the term "heath" to both taxonomic units found in heathlands and to the vegetation type. The term itself is of Germanic origin and originally referred to uncultivated strips of land, irrespective of the plant communities present (Specht 1979a).

## 1.2 DISTRIBUTION OF HEATHLANDS.

### 1.2.1 Global and Australian distribution.

Heathlands have a world-wide distribution and are united by: 1) their evergreen sclerophyllous nature, 2) their ecological restriction to soils very low in plant nutrients and 3) the presence of the families Diapensiaceae, Empetraceae, Epacridaceae, Ericaceae, Grubbiaceae, Prionotaceae and Vacciniaceae (Specht 1979a). Heathlands are found from the tropics to the sub-arctic and from lowland to sub-alpine regions (Specht 1979a).

The distribution of heathlands in Australia reflects the global pattern. Heathlands are found across the top of Australia and south into more temperate regions, being best developed in higher rainfall areas south of the Tropic of Capricorn (Specht 1979a). Sub-alpine heathlands are found mainly on peaty soils at high altitudes in New South Wales, Victoria and Tasmania (Specht 1970). Principal areas of lowland heathlands occur in regions along the eastern-central, south-eastern and southern coastlines, and in the south-western corner of Western Australia (Specht 1970, 1979a).

Australian heathlands are amongst the most floristically diverse in the world (Specht 1979b, 1981a). There are upwards of 3,700 typical heathland species in Australia (Specht 1979a). The most diverse region is the south-west corner of Western Australia, where 50% of the typical species may be found (Specht 1979a). The second most diverse region is that of Sydney, New South Wales, where 751 species have been recorded (Specht 1979a, 1981a; Fairley & Moore 1989).

### 1.2.2 Distribution of heathlands in the Sydney Area.

In the Sydney region heathlands comprise part of what is referred to as the Hawkesbury Sandstone Vegetation (Benson & Howell 1990). This includes a number of vegetation types situated on poor sandy soils derived from Hawkesbury Sandstone (Benson & Howell 1990). The distribution of heathlands in the region is principally coastal. Heathlands are seen to occupy headlands and sea-cliffs within the region. Prior



to white settlement heathlands constituted the predominant vegetation type of the coastal margins (Benson & Howell 1990). Since this time, most of this heathland vegetation has been destroyed or degraded by urbanisation (Benson & Howell 1990). Heathlands situated on sea-cliffs in the area, however, have been relatively less affected by virtue of inclusion in reserves and the inappropriate nature of the substrate for urban development. It is these heathlands which provide the focus for this study. Casual inspection of the coastline around Sydney reveals that most of the remaining heathlands on sea-cliffs are contained within the National Parks system. Four National Parks in the area have oceanic sea-cliff boundaries within which heathlands are contained. These include Royal National Park and Botany Bay National Park to the south, Sydney Harbour National Park, and Bouddi National Park to the north. Location of these parks in the area is indicated in Fig. 1.1.

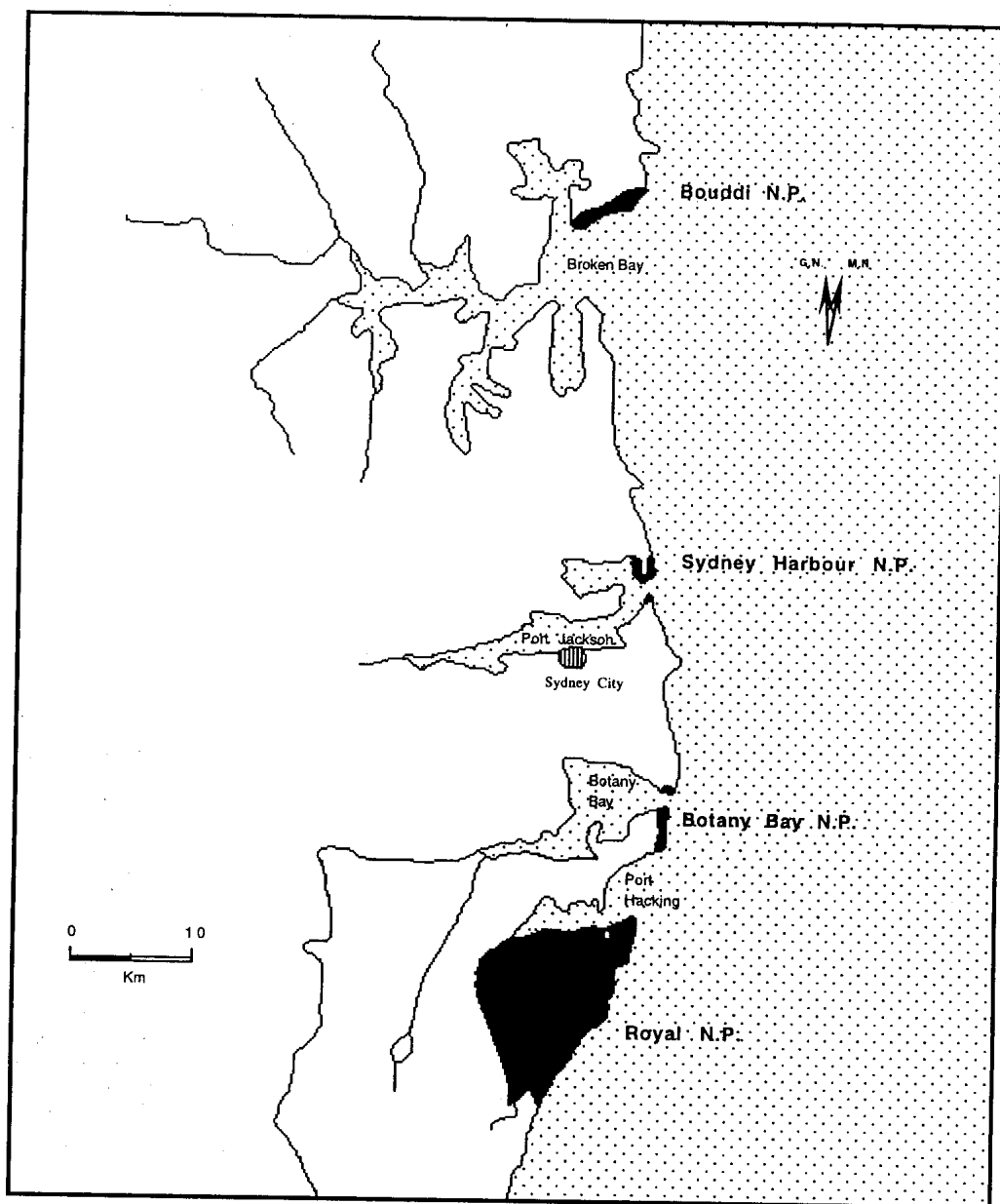


Fig. 1.1 National Parks in the Sydney area containing cliff-top coastal heathlands.

### 1.3 TERMINOLOGY

Heathlands of sea-cliffs are, by virtue of their location, coastal heathlands. The term "coastal heathlands", though, has no clear definition. Specht (1979a, 1979b) in his reviews of heathlands makes no clear distinction between heathlands of "lowland areas" and heathlands of "coastal lowland areas". For the purpose of this thesis, the term "coastal heathlands" refers to heathlands within the general vicinity of the contemporary coastline. This definition is implicit in most studies of such heathlands but is rarely if ever expressed (e.g. Siddiqi *et al.* 1972; Clemens & Franklin 1980; Enright 1989). Further, I suggest and adopt the term "cliff-top coastal heathlands" as a suitable descriptor for what are recognisable as heathlands of sea-cliffs. This is a reasonable habitat descriptor given the importance of maritime influences on vegetation in this environment (Adam *et al.* 1989a,b).

The usage of some contemporary ecological terms in this thesis also requires some clarification. The term 'floristic composition' is used to refer to the species composition of vegetation. The term 'structure' is used to refer to the physical architecture of vegetation. The term 'species richness' is used to refer to the number of species per unit area of vegetation. The term 'community structure' has been used to refer to these properties collectively. It should be noted that the terms structure and community structure are thus used with different meanings. However, this distinction is made clear in the context of usage in this thesis.

The term 'ecological significance' is also used throughout this thesis. Except where otherwise stated this term has been used in relation to community properties (or their variance components) having demonstratable relationships with environment.

#### 1.4 PREVIOUS STUDIES OF CLIFF-TOP COASTAL HEATHLANDS IN THE SYDNEY AREA.

Previous studies of the vegetation of cliff-top coastal heathlands in the Sydney area may for convenience be classified as either autecological or synecological. Only those of a synecological nature are addressed here. Synecological studies may be categorised as:

- (1) mainly descriptive broad-scale studies with little ecological/environmental reference;
- (2) studies as in (1) but which integrate either directly or indirectly information regarding ecological/environmental relationships; and
- (3) site-specific studies where the smaller scale enables greater emphasis on community structure and underlying regulatory factors.

A review of the relevant published literature from the twentieth century reveals that few synecological studies have been conducted in cliff-top coastal heathlands of the Sydney area. Several general descriptions of Sydney's vegetation were made in the eighteenth and nineteenth centuries. However, the emphasis of vegetation science in these earlier periods was on the botany and systematics of the newly discovered Australian flora (see Benson & Howell 1990). It has not been until more recent times that comprehensive studies of a synecological nature, inclusive of cliff-top coastal heathland vegetation, have been conducted.

Johnson & Briggs (1965) provide a map and general key to the vegetation of the Kurnell headland. Along the cliff-top margins they noted the presence of what they termed 'low cliff-heath'. This was noted as occurring in a narrow band along the exposed cliff-tops, intergrading with low-medium scrub at a short distance inland. Noted species occurring in the low cliff-heath included *Baeckea imbricata*, *Westringia fruticosa*, *Actinotus helianthi*, *Correa alba* and *Darwinia fascicularis*. They also noted the unspoilt condition of these heathlands with the exception of invasive patches of *Stenotaphrum secundatum*.

All national parks indicated in Fig. 1.1 have been surveyed at a general level for major plant communities, as reported by Specht *et al.* (1974) in their assessment of conservation of major plant communities in Australia and Papua New Guinea. This consisted of a listing of major alliances at particular localities, based on either direct survey or on indirect information. In the case of what is now Botany Bay National Park two alliances were listed, these being an *Acacia-Banksia* alliance and a South-coast heath (*Correa alba-Monotoca scoparia-Conospermum* sp.) alliance. My early reconnaissance suggests that these alliances are not currently present, the vegetation possibly being altered by fire. This highlights the need for caution in interpreting what is "static" information derived to describe a dynamic system.

Armstrong *et al.* (1976) mapped the vegetation of La Perouse. They recognised two heath communities. The first was termed a 'cliff-heath', being constituted by very low open heath occupying cliff-tops. Noted species included *Westringia fruticosa*, *Banksia integrifolia*, *Lomandra longifolia*, *Monotoca elliptica* and *Baeckea imbricata*. The second heath community was described as a 'sand heath' on aeolian sand over sandstone in protected positions behind a *Banksia integrifolia* scrub.

Benson (1978) conducted a brief survey of the native vegetation of the Long Bay rifle range. Although immediately adjacent to sea-cliffs, no heathlands were recorded. Rather, in cliff-top areas three low-open scrub communities were noted including a *Banksia ericifolia-Allocasuarina distyla* community, a *Melaleuca nodosa-Banksia ericifolia* community and a *Hakea teretifolia-Banksia ericifolia* community.

Urwin (1979) reported on a descriptive survey of the Kurnell Peninsula. General attributes of structural formation and floristic composition were recorded. Three structural types and five community types were recorded. Further details are provided in the research site description (Chapter 2).

According to Groves (1981a), large scale mapping and numerical classification of heathlands has been completed for a number of areas of the Royal National Park. However, results of this work do not appear to have been published.

These studies may be placed in category one as defined above. These studies are not of direct relevance to my research due to differences in scale and/or purpose. However, they provide useful reference in providing descriptions of a little studied vegetation type.

Of increasing relevance are those previous studies which may be classified as belonging to category 2. While being mainly descriptive, they place the observed structure within a general framework of environment and/or ecological process.

A principal early study of coastal vegetation of the Sydney area was that of Hamilton (1918). This study described the vegetation and general features of the environment from Turrimetta Head (Collaroy) in the north to Port Hacking in the south. Noted associations between species were not summarised and are too numerous to effectively summarise here. However, a number of salient aspects of the structure of coastal vegetation in the area emerged from this study. Among these were arborescent retardation and nanism in vegetation in positions exposed to the ocean. Structural variation in individual species such as *Banksia integrifolia* was also observed, as were marked distributional zonations in species in exposed positions. These early observations are testament to the strong influence of maritime gradients on vegetation in exposed coastal environments. It is also important that a significant proportion of species noted in this study were alien species. A significant component of coastal vegetation today may be comprised of aliens. If so they may have been naturalised for some time. This points to the need to account for alien species in synecological studies, in order that the niche dynamics of these species be better understood with respect to the native vegetation.

Pidgeon (1937, 1938, 1940, 1941) reported on an investigation of the vegetation and environment of the central coastal area of New South Wales. Cliff-top coastal heathland vegetation was briefly described as a variant of the recognised scrub seral community located on soils derived from Hawkesbury sandstone. Extreme nanism along with 'diminution and toughening of foliage' were cited as characteristic physiognomic attributes of this variant. Shrubs were noted as being closely packed where found over continuous substrate. However, on rocky parts of headlands and on cliff ledges a more open structure was observed. Considerable complexity of floristic structure was noted for this community. This was characterised by a lack of uniformity in the distribution of many species at both local and landscape scales. While many species were observed as being widespread throughout the area, distributional disjunctions of many species were observed to occur over small areas. Further, many species were observed to occur alternatively as either community dominants or community subordinates in such areas. Despite this, 'co-dominance of many species exhibiting a highly

integrated social growth' was observed as a characteristic community structure. In cliff-top areas, the number of species co-dominating was cited as being lower than elsewhere, with a 'pre-dominance of the hardiest sclerophylls'. It is clear that the considerable spatial complexity of this vegetation is a reflection of both what species are present and how the vegetation is physically constructed. It follows that there is a need to account for both floristic and structural components if this complexity is to be effectively resolved.

Adam *et al.* (1988) reported on a phytosociological survey of saltmarsh vegetation along the central coast of New South Wales. They recognised in excess of 25 saltmarsh communities. Many of these were recorded as occurring in sea-cliff environments in association with heathlands/shrublands. Not only was spatial proximity noted but a number of saltmarsh species were recorded as occurring throughout the shrub-based communities. Composition of cliff-top saltmarshes was noted as varying according to exposure to maritime influences.

Adam *et al.* (1989a) report on a phytosociological survey of the vegetation of sea-cliffs and headlands in New South Wales. A variety of survey techniques, data types and analytical techniques were used. Fifteen communities were recognised of which five were true heathlands. Species/community/environment relationships were suggested through the above analyses, general observations and limited soil sampling. Maritime factors and soil nutrition were suggested as comprising the principal environmental gradients. It is worth noting that while broad-scale similarities in sea-cliff vegetation were recognised, the details of the "disposition" of communities and species were said to be site-specific.

Benson & Howell (1990) recognised "about 30 different plant communities for the Sydney area". However, this information was not presented, instead being condensed into eight major vegetation types. Heath and scrub were described together within one grouping. Although alluded to, no distinction was made between coastal and cliff-top coastal heathlands (*also* see 1.3 Terminology). In describing vegetation of individual municipalities, however, they do note stunting of heathland in windswept cliff-top environments. Also, they provide a short list of species typical of my research area (see Chapter 2). While this publication is mainly descriptive, general environmental reference is made. Their description of individual municipalities shows

that local vegetation structure is largely influenced by environmental factors, principally edaphic, which vary substantially at the same scale. This is despite recognition of the influence of environmental factors operating at larger temporal and spatial scales.

McRae (1990) reported on a vegetation survey of Bouddi Peninsula. Fifteen vegetation communities were mapped, including five heathland communities. These communities were related to physiographic habitat factors, including geology, geomorphology, climate and soil. Also, 359 species from 94 families were recorded. Although height and coverage of individual species was recorded in this study these data was not presented. Also, the format of the floristic list provided does not allow for comparison of floristic patterns between individual communities. Despite this, it is of interest that in the heathland communities considerable complexity in structural formation was recorded, height and coverage of strata varying substantially both within and between communities. Also, considerable intergrading was apparent between the heathlands and other formations/sub-formations (*sensu* Specht 1970). Gradients in structural formation appeared to be related to similar environmental factors influencing the floristic composition component, mainly drainage characteristics, physical soil properties and exposure to maritime influences. However, relationships between structural formation, floristic composition and environment were only addressed through extensive descriptions, which obscured analytical interpretation. The collected data would have allowed quantitative analysis of relationships between the three components.

Benson & Howell (1994) described and mapped the vegetation of the Sydney area. Three map units included cliff-top coastal heathlands. These units were coastal clay heath, coastal dune heath and coastal sandstone heath. The coastal clay heath developed on Narrabeen strata north of Long Reef and along the coastline of Bouddi National Park consisted of an open heath community dominated by *Allocasuarina distyla* and a grassland community dominated by *Themeda australis*. The open heaths were noted as occurring in sandier soils of lower nutrient content than those on which the grasslands occurred. The coastal dune heath was noted as occurring at Bouddi National Park, at North Head and in the eastern suburbs, on perched Pliocene dune sands and Holocene marine sands. This map unit was an open heath community dominated by *Banksia aemula* and an open scrub community dominated by *Monotoca elliptica*, *Banksia integrifolia* and *Leptospermum laevigatum*. The last-mentioned



community was noted as being largely restricted to the marine Holocene sands. The coastal sandstone heath was amongst the most spatially extensive of the mapped units along cliff-top margins, and was noted as being developed on Hawkesbury sandstone headlands. This unit contained a variety of floristically rich structural forms including open heaths, closed heaths, open scrubs, closed scrubs and sedgelands. Fire and soil moisture were cited as principal factors underlying structural differences. Unlike the survey of Adam *et al.* (1989a), the role of exposure to maritime influences in regulating community structure was not emphasised.

Previous studies of principal interest to my research are those which fall under category (3). Only three published studies approach this level with respect to cliff-top coastal heathlands of the Sydney area.

The first is that of Siddiqi *et al.* (1972), who investigated the macrostructure of heathlands of Mourawaring Point in Bouddi National Park. They employed a hierarchical divisive monothetic classification procedure using presence/absence data, and identified nine final groupings of sites. These were subsequently interpreted as representing three main vegetation groups based on divisions of an edaphic catenary sequence. The three main vegetation groups were sand heath, groundwater heath and peaty swamp. The sand heath was divided into a "dry" sand heath and "wet" sand heath. Both types were located on deep sandy profiles, and were distinguished on the basis of water table depth. Floristically, the sand heaths were characterised by presence of *Banksia aemula*, the wet sand heath being characterised by the presence of *Banksia ericifolia*. The groundwater heath was characterised by shallower profiles with increased amounts of silt and/or clay. Three sub-groups were identified, based on the presence of *Banksia ericifolia*, *Allocasuarina distyla* and *Allocasuarina nana* respectively. The third vegetation group identified was peaty swamp, consisting of sites in and bordering swamps. This group was characterised by the presence of *Baeckea imbricata*.

This study was successful in terms of the stated aims of examining macrostructure of heathlands within a relatively small area. A broad range of environmental variables was recorded and their correspondence with identified vegetation groups effectively discussed. Irrespective of purpose, I suggest that finer scale resolution of community structure may have been possible had a polythetic method been

utilised on data with a higher information content. As recognised by the authors, techniques for this were available at the time. Also, each of the identified groups had a high percentage of exclusive species (>30%). This was explained in terms of competitive exclusion. However, this explanation was limited by a lack of quantitative abundance/cover data, and analysis through polythetic classification may have refined their explanation.

The second site-specific study is that of Siddiqi *et al.* (1976a). This may be considered as a supplement to the last study, and investigated regeneration one year after fire in the same heathlands. Regeneration was shown to be greatest in the "dry" sand heath and least in the groundwater heaths. An inverse relationship was demonstrated between regeneration and soil depth in groundwater heaths. Aspects of the influence of fire on community structure are a subject of my investigation, and further consideration of the study of Siddiqi *et al.* (1976a) is made in the relevant chapters of this thesis.

The third site-specific study is that of Clemens and Franklin (1980) who describe community structure of cliff-top coastal heathlands of North Head in Sydney Harbour National Park. Particular reference was made to fire and other disturbances. An agglomerative polythetic classification procedure was used to analyse quantitative cover data from areas last burnt in 1969. Two heath types were recognised: *Leptospermum* heath and *Restio-Leucopogon* heath, based on the exclusiveness of *Leptospermum laevigatum* on one hand and *Restio fastigiatus* and *Leucopogon microphyllus* on the other. Of these two heaths, the *Restio-Leucopogon* heath displayed higher species richness (26 vs. 13) as well as a higher percentage of exclusive species (ca. 58% vs. 15%). Despite this fact, all species in the *Leptospermum* heath occurred in the *Restio-Leucopogon* heath (except *Leptospermum laevigatum*). Of these species, approximately half occurred at high constancy in both heaths.

Some results of soil analyses were included in this study, and heath types were shown to be demarcated on the basis of physical soil structure. The recognised heaths were suggested as being equivalent to the "wet" sand heath and ground water heath respectively as recognised by Siddiqi *et al.* (1972). Through consideration of fire histories of all vegetation, it was shown that floristic differences between the two heaths could not be accounted for by fire alone, due to the "confounding" effect of other

factors. While this may have been the case, it appears to be inherent in this result that differences in complex environmental states or gradients existed that separated the two heaths. A multivariate approach to linking environment to vegetation may have allowed for the nature of these complex differences to be identified hence also allowing for more precise elucidation of the nature of confounding.

Although not addressing the synecology of the current cliff-top vegetation directly, a site-specific study relevant to my research was reported recently by Johnson (1994). This study investigated swamp profiles in the immediate vicinity of my research site for the purpose of reconstructing environmental changes over the past 2,400 years. A general description of vegetation was provided for the area (see Chapter 3). This study provided evidence that my research site was subject to Aboriginal burning practices for many centuries prior to white settlement. It was suggested that such burning was of low intensity and has favoured maintenance of shrub-based floristic and structural elements. However, it was also suggested that understorey/disturbance elements have also been favoured. This indicates that past burning practices may have had a substantial effect in promoting diversity of structural formation as well as floristic diversity. Also of importance, this study showed inexplicably high levels of magnetic susceptibility in surface layers of the studied swamps. It was suggested, amongst other things, that this may be attributable to inputs of magnetic aerosols from nearby industry. Given this, and potentially significant inputs of nutrients from salt-spray (see Ingham 1950), it may be possible that substrates in the area are relatively nutrient enriched compared with cliff-top environments elsewhere.

It is evident from this review that much scope exists for research into cliff-top coastal heathlands of the Sydney area. Understanding of the community ecology of these heathlands may also be said to be still in its infancy. There is hence a need for synecological emphasis in research into these heathlands. This is despite the suggestion that synecological studies alone remain unsatisfactory in the sense that more questions are likely to be raised than answered (Siddiqi *et al.* 1972). This is only in part correct and should not detract from any community level investigation. A synecological approach may be considered to be essential in studies of areas where little prior research exists. My investigation is not an exception, and has through necessity a significant exploratory function.

## 1.5 COMMUNITY STRUCTURE OF CLIFF-TOP COASTAL HEATHLANDS: SOME NEW HYPOTHESES.

A community may be defined as "an assemblage of species populations which occur together in space and time" (Begon *et al.* 1986). Community ecology is concerned with the study of the properties of these assemblages, in other words community structure. It is also concerned with the study of biotic and abiotic interactions associated with components of community structure.

Commonly studied properties of plant communities include floristic composition (e.g. Siddiqi *et al.* 1972; Bridgewater 1976, 1978, 1981; Russell & Parsons 1978; Holton & Johnson 1979; Clemens & Franklin 1980; Brown & Hopkins 1983; Adam *et al.* 1989b; Gibson *et al.* 1991; Hill 1991; Keith & Myerscough 1993; Pharo & Kirkpatrick 1994; Taggart 1994), species richness (e.g. Parsons & Cameron 1974; Rice & Westoby 1983; Gentry & Dodson 1987; Specht & Specht 1989a,b; Huntley 1993; Kohn & Walsh 1994) and structure or physiognomy (e.g. Dansereau 1951; Webb 1959, 1968, 1978; Webb *et al.* 1970, 1976; Barkman 1979, 1988a,b, 1990; Fox 1979; Cowling & Campbell 1980; Gillison 1981; Sato 1994). Patterns in these properties are commonly, but variously, related to environment (e.g. Auclair & Goff 1971; Zobel *et al.* 1976; Burgman 1988; Enright 1989; Druitt *et al.* 1990; Allen *et al.* 1991; Le Brocque & Buckney 1995). Environment may be seen as the abiotic substrate with which properties of plant communities interact and on which properties interact with one another.

Variance in plant community structure may thus be seen as encompassing the variance in each of the properties above. By extension, variance in community structure may also be seen as being a product of either coincident variance in different properties, variance in properties which is independent of that of other properties, or a mixture of both. If this extended definition is to be enumerated in an ecological context then it follows that the variance in internal organisation of each defining property (i.e. independent and common variance components), if present, need to be identified along with respective environmental correlates.

In light of the above I suggest that ecological syntheses may be categorised as either primary, secondary or tertiary. Primary syntheses may be seen as those which address single properties only. Secondary syntheses may be seen as those

which address multiple properties but which do not seek to inter-relate properties directly. Tertiary syntheses may be seen as those which seek directly to identify the nature of variance in properties including that which is common (shared) and that which is independent (unique). This thesis provides syntheses at the secondary and tertiary levels for cliff-top coastal heathlands in Botany Bay National Park, Sydney.

As outlined earlier few studies have been conducted into community structuring of cliff-top coastal heathlands in the Sydney area at the scale at which they occur and function. There is hence little known of the community structure of this vegetation in the Sydney area. This is despite the previously published studies, as reviewed in the previous section (e.g. Siddiqi *et al.* 1972; Clemens & Franklin 1980). All these studies have addressed a single property (i.e. floristic composition) and the relationships of this property with environment. Inclusion of additional components would have allowed for more complete ecological syntheses of community structure to be obtained.

Previous studies of vegetation elsewhere which have inter-related different properties have variously shown that higher order syntheses of community structure are ecologically relevant and convey a higher level of understanding of communities than studies which address individual properties (e.g. Gimingham 1961; Webb 1968; Auclair & Goff 1971; Zobel *et al.* 1976; Naveh & Whittaker 1979; Burgman 1988; Keith & Myerscough 1993). However, comprehensive community studies of heathland vegetation which are inclusive of multiple properties are largely still lacking.

In addition to the need for studies including multiple properties, a need also exists for studies which place equivalent emphasis on each included property with regard to its 'ecological primacy'. Contemporary community ecology studies at smaller spatial scales have predominantly placed emphasis on floristically recognised communities as being the 'principal ecological units' (e.g. Siddiqi *et al.* 1972; Clemens & Franklin 1980; Enright 1989; Bowman *et al.* 1990; Keith & Myerscough 1993; Enright *et al.* 1994; Pharo & Kirkpatrick 1994). From a functional perspective, however, other properties of community structure may have equivalent ecological relevance. In cliff-top coastal environments, for instance, it is known that classifications of vegetation based on floristic attributes exhibit considerable lack of concordance with those based on structure

(Bridgewater 1978; Adam *et al.* 1989a). This in part occurs as a result of structural plasticity in a number of plant species in response to exposure to maritime influences (see Boyce 1954; Parsons 1981). Further, there is evidence for the existence of structurally and/or physiologically distinct ecotypes within communities exposed to maritime influences (see Boyce 1954, Auld & Morrison 1992). This scenario of non-concordance implies that overall community structure of cliff-top coastal heathlands may be as much a function of independent variation in individual properties as of relationships between properties. It also implies, by extension, that different community properties and their common and independent variance components may be underlain by different environmental factors.

I envisage that both common and independent variance components of multiple properties could be isolated and examined through the use of contemporary multivariate variance partitioning techniques (see ter Braak 1987; Bocard *et al.* 1992; McIntyre & Lavorel 1994; Okland & Eilertsen 1994). I suggest that this approach would provide a framework whereby community structure could be examined in detail and the relative importance of the above variance components assessed. If this is to be achieved, however, separate properties need to be elucidated on an independent basis. If this requirement is not met then resolved patterns of complexity will be biased and potentially misleading. I suggest this requirement is not satisfied in systems which seek resolution of vegetation types in terms of multiple properties but which pre-emphasise particular properties through *a priori* placement in a classification hierarchy (e.g. Beadle & Costin 1952; Johnston & Lacey 1984; Outhred *et al.* 1985). I also suggest that this requirement is not satisfied in studies which compare alternative properties of vegetation between communities recognised on the basis of single properties (e.g. comparing structure between communities recognised on the basis of floristic composition, or alternatively, comparing floristic composition between communities recognised on the basis of structure). I suggest pre-emphasis on individual properties negates valid resolution of community structure.

Pre-emphasis on the floristic component of community structure may not be considered unreasonable given the contemporary definition of 'community' as furnished in the first paragraph of this section. However, pre-emphasis with this, or other properties, has in part been due to traditional usage of attribute types depending on the

spatial scale being considered. At broader spatial scales (e.g. continental) structural attributes of vegetation have been predominantly used for both descriptive/classificatory studies and for evolutionary/form-behavioural studies (see Dansereau 1951; Mooney 1974; Beard 1978; Cowling & Campbell 1980; Box 1981; Cowling & Witkowski 1994). The rationale behind the use of structural attributes lies essentially in the fact that structural attributes are more general than floristic attributes (species) and are hence of greater utility at broad spatial scales. However, at broad spatial scales these attributes are also considered more stable indicators of biotope conditions (see Mooney 1974; Beard 1978). Conversely, at local spatial scales, floristic attributes have generally been considered to be more sensitive as ecological indicators of communities. However, it appears that the perceived sensitivity is largely attributable to the fact that in general, many floristic attributes (species) are considered in studies at this scale, hence allowing for many variants (combinations) of such attributes to be amenable to ecological interpretation. However, species are found together for many diverse reasons including chance events (see Simberloff 1982; Grubb 1986; Schoener 1986; Fowler 1990; Walter and Paterson 1994, 1995). So while community patterns may be resolvable in terms of floristic composition alone such patterns may be largely incidental. I suggest that inclusion of multiple properties in community studies and provision of equivalent emphasis to each allows not only for effective and valid resolution of individual properties, but also for more ecologically robust definition of communities.

In view of the above suggestions four hypotheses are put forward. The first hypothesis is that;

*major community properties of cliff-top coastal heathlands, including those other than floristic composition, display interpretable variation in internal organisation at local spatial scales*

Address of this hypothesis has been approached through formulation of a secondary synthesis of community structure as previously described. Emphasis is thus on detection of pattern in community properties independently. This hypothesis is examined through a multivariate classificatory approach.

While a secondary synthesis of community structure, as defined, does not involve comparisons of individual properties, it is implied that a secondary synthesis has the capacity to recover independent patterns which remain undetectable or which are distorted through enumeration of individual properties (primary syntheses). Such effects would be manifest in classifications by a lack of congruence in the information summary provided by separate classifications. I thus compare classifications of individual properties numerically in order to determine differential summaries of vegetation pattern.

The second hypothesis put forward is that;

*community structure of cliff-top coastal heathlands is a function of both common variance between major properties and variance which is uniquely attributable to individual properties.*

Address of this hypothesis constitutes formulation of a tertiary synthesis of community structure. This formulation is new in community ecology and is implemented through application of contemporary gradient analysis techniques. Through this application variance components are quantified, and visualised through biplot construction.

The third hypothesis put forward is that;

*major properties of cliff-top coastal heathlands and their common and independent variance components are underlain by different environmental gradients.*

Address of this hypothesis establishes the ecological significance of both community syntheses and is designed to show that pre-emphasis on individual properties necessarily involves the loss of relevant ecological information. The utility of both secondary and tertiary syntheses is assessed in this context. Major areas of environmental variation of known importance to cliff-top coastal heathlands are examined. The applicability of existing ecological models for cliff-top coastal heathlands are thus assessed for their applicability at local spatial scales.



The fourth hypothesis put forward is that;

*more ecologically robust community classifications are possible by consideration of attributes of multiple properties in the one framework as opposed to classifications based on attributes of single properties.*

Through address of these four hypotheses the community structure of cliff-top coastal heathlands in Botany Bay National Park, Sydney is enumerated in detail. As outlined above this is done in a way in which the adequacy of contemporary approaches to community structure studies are evaluated with respect to the new approaches presented in this thesis.

## CHAPTER 2: RESEARCH SITE DESCRIPTION

### 2.1 LOCATION

The research site is located within the Kurnell section of Botany Bay National Park, Sydney (Fig. 2.1). This section of the park is located at the most easterly extent of the Kurnell Peninsula, approximately 18 km SSE of the Sydney central business district. The Kurnell Peninsula is a broad sand isthmus separating Botany Bay and the Georges River in the north from Port Hacking in the south (Urwin 1979; Benson & Howell 1990; Johnson 1994). The site extends in a band approximately 150 m wide from Cape Solander south to Cape Bailey Lighthouse, oceanic sea-cliffs forming the easterly boundary.

### 2.2 TOPOGRAPHY, GEOLOGY AND SOILS

The topography is generally restricted. Relief contours are indicated in Fig. 2.1. The easterly margins of the entire site and most of the area contained north of Tabbagai Gap are characterised by flat to gently seaward sloping sandstone platforms. The relief gradient is approximately 0.07. Greatest relief is observable north of Tabbagai Gap. Microtopographic features in these areas include localised depressions, drainage lines and terraces. The relief gradient associated with these features exceeds 0.07, but occurrences are localised. Sudden breaks in relief generally do not exceed 1 m.

South of Tabbagai Gap sand dunes encroach towards the cliff-line. The area of exposed sandstone platform is hence reduced and topography becomes more variable. Within the site (Fig. 2.1) these dunes are generally oriented parallel to the cliff-line. However, localised diversity in both aspect and relief of the dunes is seen to occur, possibly being the result of "blow-outs" (see Johnson 1994). In addition to the above small flat areas of impeded drainage are found between the dunes and platform areas. This feature is probably the result of dune sands and other material having accumulated in microtopographic depressions according to obstructions presented by the underlying bedrock.

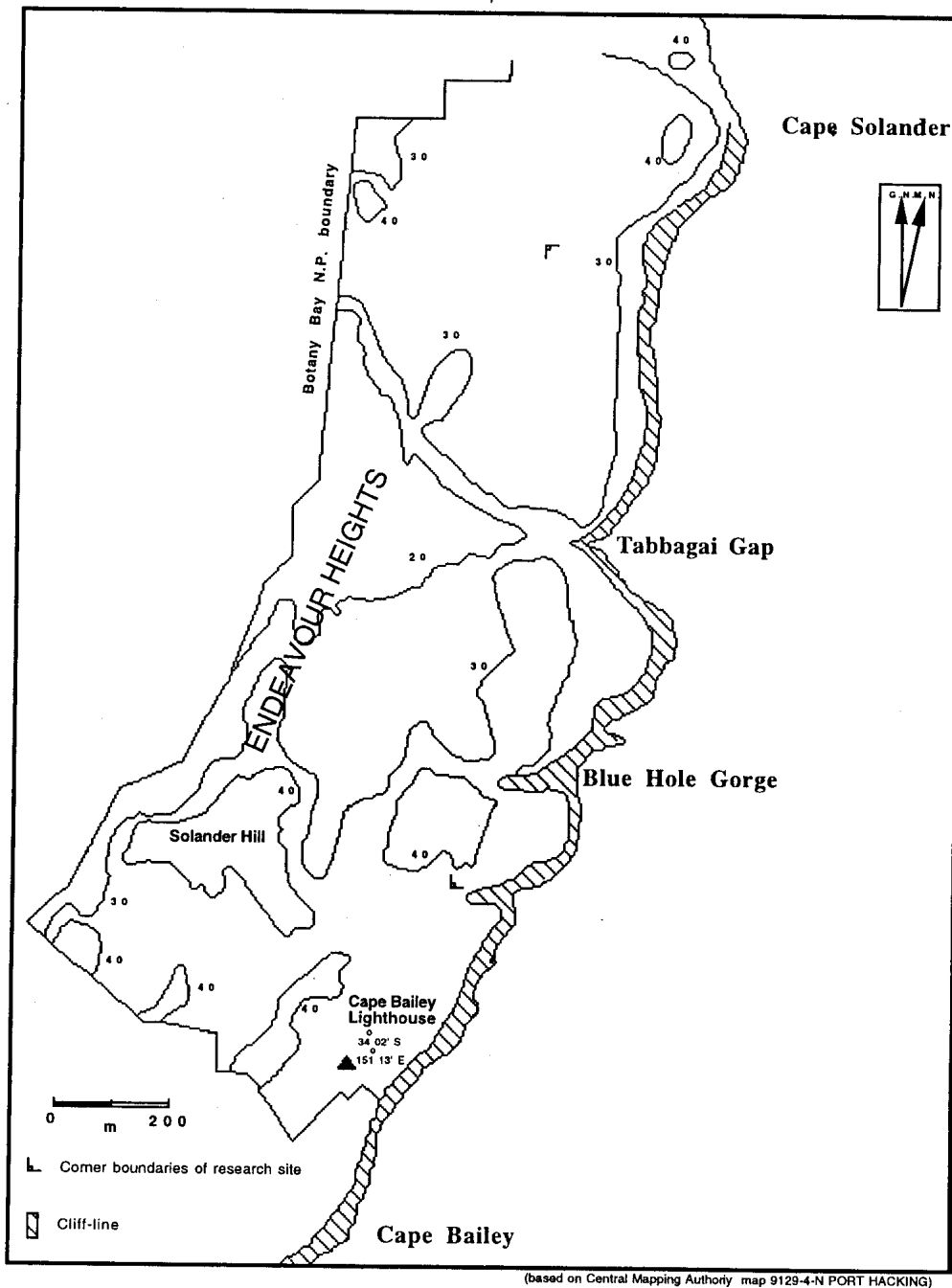


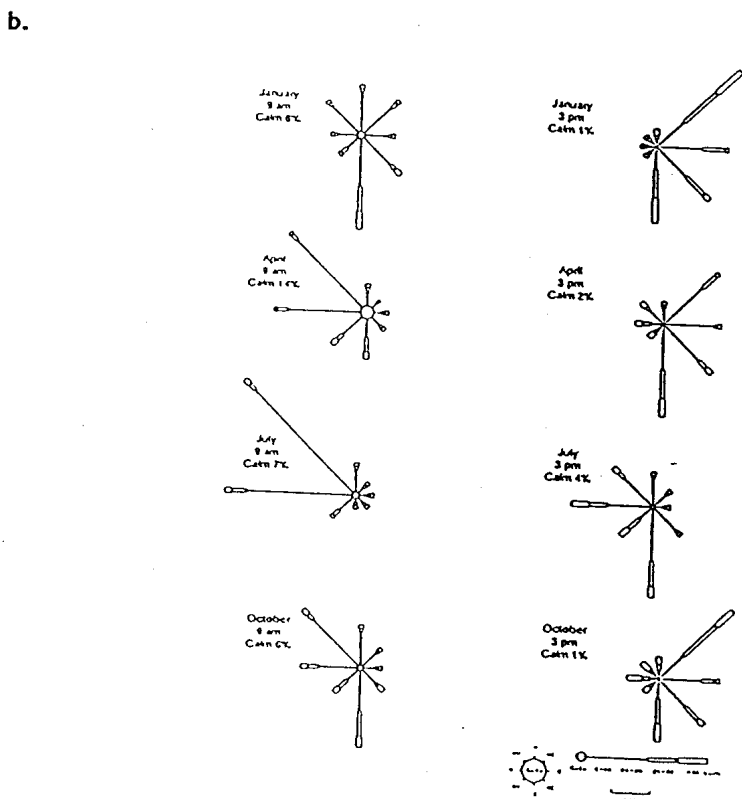
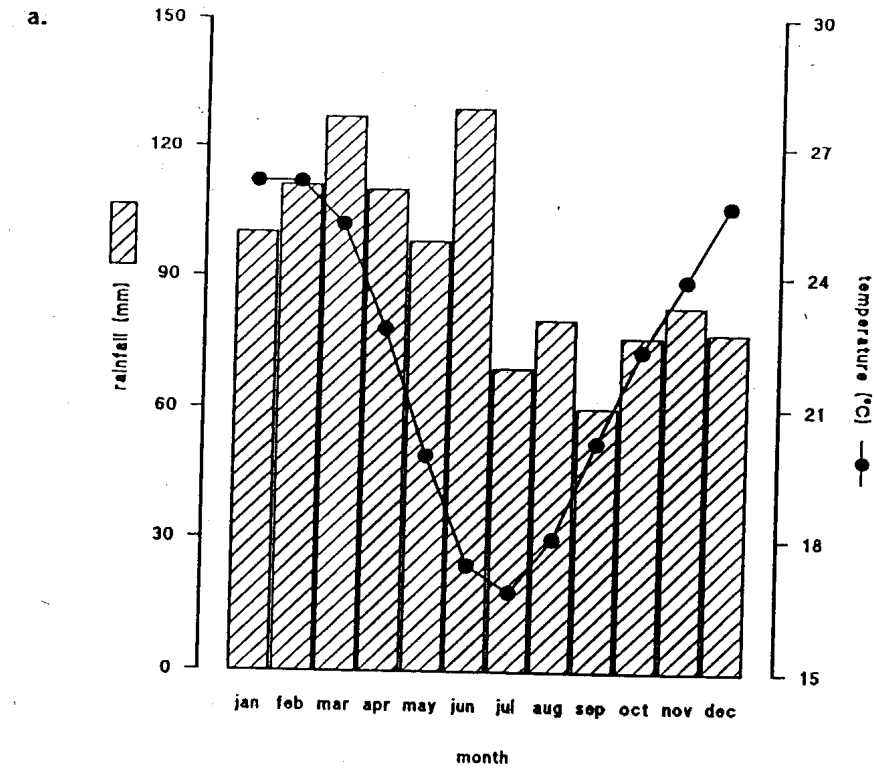
Fig 2.1 Research site location in Botany Bay National Park, Sydney.

Two geological features characterise the site. The first is the sandstone platform on which much of the vegetation is located. This is a Hawkesbury Sandstone outlier of Triassic origin (Benson & Howell 1990) which was separated from the mainland by water prior to the Holocene (Johnson 1994). The second feature is the sand dunes which are prevalent on the western side of the site south of Tabbagai Gap. Within the site, these dunes overlie the sandstone platform. They comprise the easterly margin of what Urwin (1979) describes as the early dune land unit. As outlined by Urwin (1979) and more recently by Johnson (1994) this land unit was derived from deposition of marine sands from Bate Bay which is to the south west of the site. As outlined by Johnson (1994), the dunes comprising this unit are relatively deep, highly podzolised, high in organic matter and low in calcium. In addition to the above features, several thin shale strata outcrop just to the north of Blue Hole Gorge. These appear to be weathering *in situ*.

Soils represented in the area are indicated by Corbett (1972) as including acid peats (on sand and sandstone), sandy lithosols, yellow podzolics and sand podzols. On platform areas to the north of Tabbagai Gap shallow acid peats (on sandstone) and shallow sandy lithosols occur. These also occur on platform areas south of Tabbagai Gap, but the depth is greater due to the proximity of sand dunes. Deep sand lithosols, yellow podzolics and sand podzols occur in the sand dune area and to a lesser extent in the transitional areas between dunes and platform. Podzolised profiles within the site often occur as buried profiles underneath shifting dune sands. The swamps in the site are associated with deep acid peats on sand and sandstone (see Johnson 1994).

### 2.3 CLIMATE

A climate profile for Sydney Airport is provided in Fig. 2.2. Sydney Airport is located approximately 10 km NW of the research site, on the north west shoreline of Botany Bay. It is the closest weather station to the site having complete and long term records.



(Anon. 1991)

**Fig. 2.2** Climate profile of Sydney Airport. a. Mean monthly rainfall and mean daily temperature (3 pm) based on all available data to 1993. b. Seasonal wind roses (9 am and 3 pm). Lengths of arms and arm segments are proportional to the relative frequency of days on which the given conditions were recorded, based on all available data to 1987.

As indicated in Fig. 2.2a, mean maximum daily temperature (3 pm) ranges from approximately 26°C during summer months to approximately 17°C over the winter months. The decline in temperature between these periods is relatively uniform. Mean maximum daily temperature falls beneath 20°C over the period of May to September. No highly seasonal pattern emerges with respect to rainfall, although rainfall is lower in the second chronological half of the year than in the first (Fig. 2.2a).

Seasonal wind roses are presented in Fig. 2.2b. Salient features include a relatively low frequency of calm conditions at any time, and the prevalence of onshore afternoon winds except in winter when afternoon winds are predominantly offshore. Also, winds strengthen between morning and afternoon. There is an apparent switch from offshore to onshore winds between morning and afternoon, except in summer when a significant southerly component is apparent in the mornings, and in winter when winds remain predominantly offshore. It should be noted that onshore windspeeds experienced at the site are probably greater than those represented in Fig. 2.2b. The cliff-tops bordering the site in the east are approximately 30m above sea-level. Onshore winds impinging on the heathlands may hence be expected to have a higher velocity due to reduced frictional effects imposed by the sea surface.

## 2.4 VEGETATION

The vegetation contained within the site consists of a range of heathlands and associated herbfields. Of the heathlands, those located on the sandstone platform are mainly tall closed heathlands *sensu* Specht (1970). Structurally dominant species in these heathlands include *Baeckea imbricata*, *Melaleuca armillaris*, *Hakea teretifolia* and *Westringia fruticosa*. Urwin (1979) described the vegetation on these platform areas as open heath. He noted *Westringia fruticosa*, *Acacia* spp. and *Kunzea ambigua* as dominants occurring in various associations. He also noted pockets of a *Banksia ericifolia* dominated open heath and swamplands dominated by *Gahnia sieberiana*, *Scirpus littoralis* and a *Restio* sp. Benson & Howell (1990) cited the typical presence in these areas of *Westringia fruticosa*, *Leptospermum laevigatum*, *Baeckea imbricata*, *Acacia longifolia*, *Correa alba*, *Actinotus helianthi*, *Pimelia linifolia* and *Eriostemon*

*buxifolius*. They also noted the presence of thickets of *Allocasuarina distyla*, *Banksia ericifolia* and *Hakea teretifolia* interspersed with more open heath in which *Melaleuca nodosa* and *Isopogon anemonifolius* occur. Johnson (1994) noted canopy dominants as including *Allocasuarina distyla*, *Banksia serrata*, *Banksia ericifolia*, *Westringia fruticosa*, *Kunzea ambigua* and an *Acacia* sp. One of the most abundant canopy dominants in these heathlands, *Baeckea imbricata*, was not noted.

Heathlands located on the sand dunes south of Tabbagai Gap (Fig. 2.1), may be described currently as open heathlands *sensu* Specht (1970). These heathlands were subject to an extensive fire on the 28th July 1991, but are regenerating rapidly. Structurally dominant species in these heaths include *Banksia serrata*, *Correa alba* and *Aotus ericoides*. Other prevalent species in these heathlands include *Pimelia linifolia*, *Gonocarpus teucroides*, *Actinotus helianthi* and the graminoid *Lepidosperma squamatum*. Urwin (1979) described vegetation in this area as open heath/scrub, with canopy dominants in the heath including *Allocasuarina distyla* and *Banksia serrata*, and those in scrub including *Allocasuarina distyla* and *Leptospermum laevigatum*. He also recorded the presence of swamplands dominated by *Gahnia/Scirpus* spp. Johnson (1994) noted these same formations, but also noted the presence of grasslands dominated by *Themeda australis* and shrublands dominated by *Eucalyptus botryoides* and *Banksia integrifolia*.

Relatively flat areas exist south of Tabbagai Gap, which are situated between the sand dunes on the western side of the site and the sandstone platform areas to the east. These areas represent the easterly extent of the 1991 fire. The vegetation of these areas is complex. In areas which escaped burning, closed heathlands remain. A swamp herbfield is also located in this area which remained unburnt. Dominant species in the swamp include *Leptocarpus tenax* and *Baumea juncea*. Johnson (1994) cites *Gahnia/Scheonoplectus* spp. as being dominants in nearby swamps. However, these genera appear to be absent from my research site. In non-swamp areas which were burnt, a range of herbfields currently persist. Due to impeded drainage, much of these herbfields have a significant graminoid component. However, they also support components of both the burnt open heathlands and unburnt closed heathlands.

The western half of the research site north of Tabbagai Gap (Fig. 2.1) was subject to fire on the 19th March 1992. Here, herbfields and low shrublands

representing regenerating closed heathlands are found. Unlike those to the south, however, these are located on shallow substrate associated with the sandstone platform. While containing elements of their unburnt counterparts, they also include a number of species not currently found elsewhere. In addition to the platform areas, a small dune area exists just north of Tabbagai Gap. This was also burnt in the same fire. The dwarf heathlands and herbfields found in this area currently contain components of both the adjacent closed heathlands and the open dune heathlands to the south burnt in the earlier fire.

Much of the tall closed heathlands found on the platform and associated areas along the eastern half of the site have remained unburnt in recent times. Official records do not extend back past 1991. However, information from unsubstantiated sources suggest that these heathlands may have remained unburnt for at least 20 years.

In addition to swamp herbfields and herbfields associated with regenerating burnt heath, a third type is represented in the research site. This type occurs principally to the north of Tabbagai Gap on bare frontal (cliff-top) strips of sandstone platform. Scattered throughout this area are accumulations of recently deposited sands. These are unconsolidated and are apparently derived from weathered platform. The substrate of these deposition areas is very shallow, conforming to microtopographic depressions or obstructions. Maritime herbs such as *Samolus repens* and graminoids such as *Zoysia macrantha* colonise these depositions. Shrub seedlings are also occasionally present. These herbfields correspond approximately to several cliff-top saltmarsh communities described previously by Adam *et al.* (1988).



## CHAPTER 3: CLIFF-TOP COASTAL HEATHLANDS IN BOTANY BAY NATIONAL PARK, SYDNEY: FOUNDATIONS OF A SECONDARY SYNTHESIS OF COMMUNITY STRUCTURE.

### 3.1 INTRODUCTION

In this chapter foundations of a secondary synthesis of community structure are constructed. Multivariate classification is applied to attributes quantifying floristic composition, structure and species richness. This is done to detect the presence and nature of variation in internal organisation of these major properties. In this chapter this organisation is interpreted with respect to attributes used in respective classifications and with respect to some general environmental factors which are quantified fully in later chapters. This interpretation is also made with respect to ecological models which may be considered *a priori* as being of importance for community structure of cliff-top coastal heathlands. The detection and interpretability of patterns in these contexts is taken as an initial indicator of the need to address multiple properties in examining community structure of cliff-top coastal heathland communities. This is also assessed quantitatively by assessing the congruence of individual classifications.

A brief background to each community property is provided below. A background to the rationale for adopting a classificatory approach to a secondary synthesis of community structure is also provided. This background is followed by details of research objectives and hypotheses.

#### 3.1.1 Background

##### 3.1.1.1 Floristic composition as a community property

Recognition of community types on the basis of floristic attributes has been the primary approach taken to analysis of coastal heathland vegetation in the Sydney area. Previous studies have indicated that coastal heathland vegetation of the Sydney

area is not only species-rich, but displays diversity in terms of both the number and floristic composition of recognised types (e.g. Siddiqi *et al.* 1972; Clemens & Franklin 1980; Keith & Myerscough 1993). Further, these studies have shown this to be the case at local spatial scales.

Previous site-specific studies of cliff-top coastal heathlands in the Sydney area were reviewed in Chapter 1. These studies, particularly those of Siddiqi *et al.* (1972) and Clemens & Franklin (1980), showed clearly that heathland communities can be demarcated within local landscapes. However, the demarcations were not unequivocal. In the study of Clemens & Franklin (1980), much of the distinctiveness of the recognised heaths was attributable to sub-ordinate species with low constancy values. This is notwithstanding the exclusive presence of the dominant, *Leptospermum laevigatum*, in one of the heaths. However, it was also apparent that much of the difference in community structure between the two heaths could be attributed to quantitative differences in constancy/cover of a sub-set of dominant species. Complexity of the vegetation in this instance would hence appear to be characterised by specificity of sub-ordinates and more continuous variation in dominants.

Notwithstanding differences in data type and analytical techniques, a similar pattern was also recovered in the study of Siddiqi *et al.* (1972). However, in this instance substantial environmental heterogeneity in the landscape would appear to have, first, added to the diversity of community types present, and secondly, sharpened discontinuities in the distribution of structurally dominant species.

Further evidence for complexity in floristic composition comes from studies of coastal heathlands away from cliff-tops in the area. These are briefly reviewed below.

Buchanan (1980) described the swamp and moist shrubland vegetation of the Lambert Peninsula in Ku-ring-gai Chase National Park, Sydney. Four swamp types and two types of moist shrubland (including true heaths) were recognised. These types were shown to represent a partitioned vegetation gradient corresponding to a gradient of soil moisture. The graminoid component, typical of swamps, was shown to become less abundant but more diverse along this gradient from wetter to drier substrates. Shrublands, a term used loosely in this study, were situated at the driest end of this gradient. Notwithstanding description of the other vegetation types as swamps, all types had a significant proportion of shrub species. Abundance of shrubs increased in the

opposite direction to that of graminoids. Swamps and shrublands were separated on the abundance and height of some larger species. Of interest was that of the characteristic species listed for swamps five out of seven were shrub species. Also, it is apparent from the table of typical species provided that pattern diversity of shrubs across the whole data set was equivalent to that of graminoids. The descriptions of individual types make it apparent that this type of diversity also occurred *within* individual types, with patterns of complexity in floristic composition characterising each individual type. I suggest that this indicates that complex patterns of floristic composition with respect to both shrubs and graminoids are a characteristic feature of both swamps and related shrublands (including heaths).

Outhred *et al.* (1985) reported on a classification of the vegetation in Kuring-gai Chase National Park. They recognised 23 community types, of which one corresponded to wet closed heath. This community type was shown to be closely affiliated with three other shrub-based community types. This study covered a single area which was much larger than that within which cliff-top coastal heathlands commonly occur in the Sydney area. Concordantly, sampling methodology used in this study may have been too coarse to resolve organisation of floristic composition more typical of that of cliff-top coastal heathlands.

Keith & Myerscough (1993) examined floristics and soil relations of upland swamp vegetation on the Woronora Plateau south of Sydney. They resolved five communities of which two were heathlands, cyperoid heath and restioid heath. These heaths were comprised of similar species, but were separated in terms of differential frequency of relatively well demarcated sets of species. This pattern was related to edaphic factors dictated by toposequences which were symmetrical around small and large valley swamps.

Studies which recognise community types provide inventories of ecological diversity by the simple fact that vegetation is classified into 'coherent' units. However, recognition of complex types also provides a framework within which finer levels of detail can be resolved, as well as allowing for functional aspects to be examined in more detail. As evidenced by these studies, this level of investigation has remained largely descriptive. Buchanan & Humpries (1980) point out that for Hawkesbury sandstone vegetation floristic structure can vary over very short distances as a result of small

variations in microtopography and soil properties. I hence suggest that vegetation classifications in restricted areas should effectively resolve small-scale complexity in floristic composition and provide badly needed insights into the ecological foundations of such complexity.

### 3.1.1.2 Structure as a community property

Structure as a community property is a function of both the morphological attributes of species and of the spatial positioning of individuals as a result of ecological interactions (see Tilman 1994). At a fundamental level structure may be characterised as the vertical and horizontal extent of vegetation (i.e. height and coverage). This characterisation is commonly but variously extended to include details of the vertical stratification of vegetation and growth forms of constituent species (e.g. Richards *et al.* 1940; Dansereau 1951; Webb 1959, 1968; 1978; Specht 1970, 1979b, Webb *et al.* 1970, 1976; Gillison 1981; Walker & Hopkins 1990). Structure may hence be best viewed as the physical architecture of vegetation.

By virtue of its physical nature structure may be seen as a more general property of communities than floristic composition. However, it is important to recognise the integral nature of structure and floristic composition in overall community structure. Both properties must be related by the simple logic that one could not exist without the other. However, the relationship between floristic composition and structure is unlikely to be one of direct concordance. Structure may not be, or may be only partially constrained taxonomically. It follows that if structure is to be validly classified then the classification must be made independently of floristic composition.

Schemes for the classification of structure have traditionally been developed for application at broad spatial scales (see Beard 1978). This can be attributed to the more general nature of structure compared with floristic composition. The large number of floristic attributes (species) which characterise vegetation at broad spatial scales are considered to preclude effective floristic classifications (Beard 1978). The use of structural attributes for classifying vegetation at broad spatial scales is also founded on observations of repeated convergences in structure in response to climate-substrate-successional combinations (e.g. Cowling & Campbell 1980; Box 1981; Rice & Westoby

1983; Cowling & Witkowski 1994). Classifications of structure are hence considered stable indicators of biotope conditions at these scales (Mooney 1974; Beard 1978).

Arguably, the most widely accepted structural classification scheme in Australia is that of Specht (1970). This classification scheme was developed for use at a continental scale, and is based on foliage projective coverage (FPC) and height/life-form of the uppermost stratum of vegetation. Four (Specht 1970) to five (Specht 1981b) broad FPC categories are provided ranging from very sparse (0-10%) to dense (70-100%). Similarly, a number of height categories are provided and are based essentially on the life form classification of Raunkiaer (1934). Heathlands fall within the category of "shrubs 0-2m". Two heathland sub-formations are allowed for, these being, open heath (30%-70% FPC) and closed heath (70%-100% FPC). This structural classification scheme has been applied extensively in the classification of vegetation in Australia at a variety of spatial scales (e.g. Hopkins & Robinson 1981; Benson 1981, 1986; Burgman & Thompson 1982; McRae & Cooper 1985; Myerscough & Carolin 1986; Clark & Benson 1987; Keith & Benson 1988; McRae 1990; Benson & Howell 1994; Keith 1994).

While the classification scheme of Specht (1970) is effective in demarcating major structural formations on the basis of one stratum, it cannot by definition resolve formations with more than one significant stratum. This is notwithstanding the additional but subjective "triplet" notation proposed by Specht (1970) to demarcate between similar structural formations on the basis of the general character of additional strata. In view of the inability of Specht's (1970) classification scheme to accommodate attributes of multiple strata, I suggest that it is likely to be of questionable utility in ecological studies due to the insufficient recovery of structural detail. I suggest that this limitation applies irrespective of the spatial scale at which it is implemented. These suggestions are supported by many habitat studies of insects, birds and mammals, conducted at a variety of scales, which have shown 'secondary' structural attributes (e.g. height and coverage of sub-canopy strata) to be significant habitat factors (e.g. MacArthur & MacArthur 1961; MacArthur *et al.* 1962; Recher 1969; Murdoch *et al.* 1972; Abbott 1976; Fox & Fox 1978, 1981; Fox 1979; Rotenberry & Weins 1980; Kikkawa 1982; Rotenberry 1985; Chan 1990; MacNally 1990; Recher *et al.* 1991; Brown & Stillman 1993).

In order that structural classifications be made more ecologically informative there is a need for classifications to include and place equivalent weighting on additional structural attributes. Optimally, these should be functional attributes (*sensu* Gillison 1981; also see Hopkins 1981; Johnson 1981). In the past, descriptive systems have been implemented which have supplemented life-form and foliage stratification attributes with additional attributes such as leaf size, leaf shape, bark type, amounts of dead wood, type of branching and periodicity of vegetative organs (e.g. Richards *et al.* 1940; Dansereau 1951; Gillison 1981). By virtue of higher information content such systems provide a more complete summary of structure than classification schemes such as that of Specht (1970). However, the choice of additional attributes is largely subjective, and such systems are often used with poor repeatability between workers (Gillison 1981). A further problem with such systems is the lack of significant classification frameworks whereby synopses of structure can be derived and stands compared on the basis of all attributes. Some descriptive and associated approaches have utilised alpha-numeric codes, symbols, profile diagrams or combinations of these for comparative purposes (e.g. Christian & Perry 1953; Gillison 1981). However, such systems would not appear to have been widely accepted.

A proximate problem for describing structure may thus be seen as the development of a system that would remove much of the subjectivity of attribute selection inherent in past descriptive systems but which would also be sufficiently sensitive to detect fine-scale differences of functional importance. I suggest that a suitable approach would be to quantify height and cover of all identifiable strata.

For heathland vegetation, previous community studies which have quantified structure have used height and coverage of a shrub stratum and herb stratum (e.g. Adam *et al.* 1989a, Keith & Myerscough 1993, Keith 1994; although see Gimingham 1961). This is despite reference in these studies to the existence of sub-shrubs as well as a structural separation between graminoids and other herbaceous forms. I envisage that quantification of height and coverage of additional strata would allow for finer scale resolution of structure within this vegetation type.

I suggest that five strata can be consistently recognised in cliff-top coastal heathland vegetation, including emergent, shrub, sub-shrub, graminoid and groundcover strata. The shrub stratum may be defined as the shrub stratum present which displays the

highest coverage. This definition, in part, retains the rationale of Specht (1970) that it is the tallest stratum which is in the principal position to utilise solar radiation in the community. However, in my system the shrub stratum need not be the tallest stratum present. Emergent and sub-shrub strata can be defined relative to the shrub stratum on the basis of lower coverage and differences in height proportional to the shrub stratum. Comparability of stands in this system derives from the fact that the same functional unit (the shrub stratum) is defined in the same way in all instances. Identification of the graminoid stratum is self-explanatory, but is extended in the proposed system to include all other herbaceous plants with similar growth forms. The groundcover stratum is defined to include all non-graminoid herbs, shrub seedlings and several shrub forms deemed to function as herbs.

In addition to quantification of height and coverage of recognisable strata, I further suggest that a measure of radiation attenuation through the stand being described be made. This is in part dependent on the amount of vegetation present, and has been used in past structural analyses of heathland vegetation (see Fox & Fox 1978, 1981; Fox 1979). Although in part redundant with cover, I envisage that such redundancy would aid in averaging out errors associated with estimation of cover. Inclusion of radiation attenuation as a structural attribute may also allow for parity checks to be made between workers describing/classifying the same vegetation.

One virtue of Specht's (1970) classification scheme is the simplicity and clarity of its two-way classification layout. However, where attributes of multiple strata are included in a classification such a simplistic layout becomes difficult to maintain. Further, I suggest that unmodified extension of the layout of Specht's (1970) classification scheme for classification of multi-stratal structure is in any case undesirable. First, this layout is maintained by imposing fixed and arbitrary attribute divisions, which may not be optimal for the resolution of structure. Significant differences in structural attributes may exist between stands within classes defined by fixed divisions, which would remain unresolved by Specht's (1970) classification scheme. Secondly, because of the likelihood of differing morphological and/or ecological constraints in attribute variance of different strata the use of fixed attribute divisions by Specht's (1970) classification scheme could not be readily extended across different strata. In view of these limitations, I suggest that, for effective classification of multistrata structure,

classification systems need to be able to not only accommodate attributes of multiple strata but also need to be sufficiently sensitive to resolve patterns of differences in all attributes accurately without constraints brought about by divisions which are either too broad or inappropriate.

I therefore suggest that numerical multivariate classification techniques provide appropriate methodology for the classification of structure. By virtue of grouping samples on the basis of similarity in multiple attributes, these techniques are clearly desirable where formations are to be recognised on the basis of attributes of multiple strata. By making greater use of the information content of collected attribute data, it may be reasonably expected that multivariate classification techniques would not only provide more informative classifications of structure than Specht's (1970) scheme but that they would also better reflect patterns of differences in attributes.

Despite this, relatively few studies have used multivariate classification techniques for structure. Webb *et al.* (1970, 1976) applied multivariate classification to a wide variety of structural attributes of Australian and New Guinean rainforest. Webb *et al.* (1970) similarly classified floristic composition, and compared floristic and structural classifications. They also examined the ability of both classifications to recover environmental information. They found that both classifications recovered comparable vegetation patterns and that both had similar efficiencies in recovery of environmental conditions. Importantly, they found the structural classification to be efficient at recovery of environmental conditions at lower hierarchical levels. This shows that use of structural attributes can provide ecologically meaningful and sensitive classifications.

Cowling & Campbell (1980) used average linking clustering to examine convergence in physiognomic attributes of climatically matched communities in Chile, California and South Africa. This enabled recognition of non-convergence in physiognomy of the South African communities compared with Chilean and Californian communities.

Gillison (1981) applied multivariate classification and other multivariate techniques to structural data collected along an edaphic gradient in a semi-arid woodland ecosystem in southern Queensland. The data included height, coverage of the tallest stratum, and data derived from description of functional attributes (leaf size, leaf angle,



leaf type and life-form) of three vegetation strata. Functional attributes were found to contribute most information to group formation.

In a habitat study of small mammals, Fox & Fox (1981) applied a series of multivariate classifications to data collected from a small area of heathland at Myall Lakes, New South Wales. These included two classifications of structure using different combinations of multiple structural attributes, and a classification of floristic attributes. They also classified the vegetation using the classification scheme of Specht (1970). Although showing that both floristic and structural attributes were important for predicting distributions of small mammals, they also showed that distributions were more closely correlated with multivariately defined classes than with groupings derived from application of Specht's classification scheme.

In a habitat study of birds, Kikkawa (1982) classified structure of a range of vegetation types in the tropical humid region of north Queensland. A large number of structural attributes were included in the multivariate classification, including those previously used by Webb *et al.* (1970). Attributes also included measures of both horizontal and vertical foliage density, and diversity. Discontinuities in bird distributions were found to correspond with recognised structural types. Also, the use of multiple structural attributes allowed for significant correlations to be identified between multivariate structural vectors and bird distributions.

Campbell (1986) classified data from a large number of plots covering montane fynbos areas of the Cape Floristic Region, South Africa. An ecologically meaningful classification was derived through a table sorting strategy, supplemented by multivariate classification, on a large number of predominantly structural attributes. Communities recognised within the fynbos vegetation type were shown to be demarcated on the basis of climatic factors as well as multiple factors quantifying soil nutrition and physical structure.

Komarkova & McKendrick (1988) used a single linkage (nearest neighbour) classification technique to analyse plant growth forms in Arctic communities. They classified percentage cover of different growth form types along with environmental data. They found this effectively recovered major landscape unit patterns in both vegetation and environment.

Haering & Fox (1995) reported on a study of habitat utilisation of two murid rodent populations in coastal heathland at Myall Lakes, New South Wales. They used agglomerative average linking to define 'macro-vegetation habitats' based on 19 structural variables. Variables included estimates of horizontal and vertical vegetation density of five strata as well as estimates of total vertical vegetation density and an associated coefficient of variation. Estimates of understorey height, cover of litter, twigs, sedges and bare ground were also included. Six macro-vegetation habitats were defined which were found to display an 'interlocking mosaic' pattern within the research site. Linkage with rodent capture data showed marked patterns in habitat selection by both populations.

These studies demonstrate that meaningful and fine-scale resolution of structure is possible through application of numerical multivariate classification to multiple structural attributes. They also serve to illustrate that there is no conceptual limitation to applying multivariate classification to structural attributes. At local spatial scales, where the predominant use of multivariate classification has been with floristic attributes, there is hence considerable scope for multivariate classifications of structure. I envisage that, not only would this property of community structure be better resolved but through comparison with similarly classified properties it would allow for greater insights into community structure and associated dynamics.

### 3.1.1.3 Species richness a community property

Species richness is amongst the most easily comprehended properties of community structure and may be defined simply as the number of species present in a community (Peet 1974). This is commonly expressed as the number of species in a sampling unit of known area (e.g. Glenn-Lewin 1975; Westman 1975; Peet 1978; Kruger 1979; Naveh & Whittaker 1979; Whittaker *et al.* 1979; Rice & Westoby 1983; Adam *et al.* 1989a; Lunt 1990; Keith 1994), a measure also known as species density (Whittaker 1975; Magurran 1988).

Although containing little information in itself, species richness is seen as a central component of many complex ecological processes such as evolution, resource

partitioning and competition (*see* Pielou 1975; Whittaker 1977; Peet 1978; Tilman 1982, 1986; Yodzis 1986; Brown 1988). Species richness has provided a useful attribute whereby some of these processes have been examined (e.g. Naveh & Whittaker 1979; Rice & Westoby 1983; Adam *et al.* 1989a). Species richness as a property of community structure may thus be seen as a 'summary property' which reflects the composite action of a variety of processes through time and space.

In view of the fact that species richness is expressive of a number of important ecological processes it may reasonably be expected that species richness would have found explicit use in definition of communities, or at least been investigated with respect to the influence of its variance on such definitions. However, there appear to be relatively few investigations of this nature (*although see* Austin & Grieg-Smith 1968; Austin 1981). Such investigations appear pertinent in view of the absence of any comprehensive theory of the community structure of vegetation (Roughgarden & Diamond 1986).

It was outlined in the introduction (Chapter 1) that Australian heathlands are amongst the most species-rich in the world. While undoubtedly correct as a generalisation it is also correct that there is substantial variability both between heathlands in different localities and within heathlands at particular localities (*see* Specht *et al.* 1958; George *et al.* 1979; Kruger 1979; Naveh & Whittaker 1979; Specht 1979a,b; Brown & Hopkins 1983; Adam *et al.* 1989a,b; Specht & Specht 1989a,b; Keith & Myerscough 1993; Keith 1994). I envisage that this variance could be highly influential in differentiation of communities within localised areas of cliff-top coastal heathlands. With the exception of the studies of Adam *et al.* (1989a,b), however, there appears to be little known of the species richness relationships of cliff-top coastal heathland vegetation. It hence appeared worthwhile to investigate these relationships for the cliff-top coastal heathlands in Botany Bay National Park, Sydney

While total species richness is a useful attribute for ecological analyses of community organisation, it ignores the species richness of different vegetation strata. Previous studies of various northern hemisphere forest vegetation have shown differential patterns of species richness for tree, shrub and herb strata across successional and environmental gradients (e.g. Whittaker & Woodwell 1969; Auclair & Goff 1971; Whittaker 1972, 1977; Glenn-Lewin 1975; Zobel *et al.* 1976; Peet 1978). In these

studies, greatest differences in richness patterns were generally recorded between tree strata on one hand and shrub and herb strata on the other hand.

In heathlands and related vegetation, finer scale strata/life-form divisions have enabled enumeration of species richness patterns which would have otherwise remained unresolved if only total species richness had been examined (e.g. Naveh & Whittaker 1979; Rice & Westoby 1983; Cowling 1990). These studies and others (see Campbell & van der Meulen 1980; Cowling & Gxaba 1990; Keith & Myerscough 1993) have generally shown a negative relationship between species richness and structural dominance of upper strata.

All the studies above show that investigation of broadscale evolutionary processes as well as contemporary environmental relationships of species richness can be greatly enhanced by consideration of structural (stratal/lifeform) dimensions of species richness.

Despite the above, little is known of the structural dimensions of species richness in cliff-top coastal heathlands specifically. Specht & Specht (1989b) showed significant inverse relationships between overstorey coverage and understorey species richness for a variety of heathland communities in Australia. Although not including cliff-top coastal heathlands, they cite retardation of canopy coverage as a result of sodium chloride accretions from the sea as a potential influence on understorey species richness (*after* Parsons 1981; Walker *et al.* 1981). They also cite canopy removal by fire and canopy growth retardation by low substrate nutrient status as factors which might also lead to elevated species richness of sub-canopy strata/life-forms (*after* Specht & Morgan 1981). In view of the prevalence of all these factors in cliff-top coastal heathlands (Adam *et al.* 1989a,b) it appears that investigation of stratal species richness patterns in the studied vegetation might lead to valuable insights into organisation of this property.

#### 3.1.1.4 A rationale for a classificatory approach to construction of a secondary synthesis of community structure

Data in community ecology is largely multivariate. That is, samples are characterised by many attributes. These attributes are commonly species abundances or associated measures. Analysis of such data is based at the fundamental level on a

geometric model in which samples are located in attribute space, or, attributes in sample space (Causton 1988).

Two broad categories of techniques are available for effective summary and analysis of multivariate data. The first category of techniques is known as classification, or clustering (Jongman *et al.* 1987). The second category of techniques is known as ordination, or alternatively, gradient analysis (Jongman *et al.* 1987). Classification techniques attempt to arrange samples into classes whereby members of one class display higher affinity with one another than with members of other classes (Grieg-Smith 1983, Jongman *et al.* 1987, Causton 1988). Ordination techniques attempt to arrange samples whereby those of high affinity are represented as proximate points and those of no or little affinity are represented as distant points in a continuous space (Jongman *et al.* 1987).

Ordination techniques have been developed in line with acceptance of the continuum concept of community structure (Grieg-Smith 1986; Causton 1988). A central tenet of this concept is that species are distributed individually according to their own genetic, physiological and life-cycle characteristics with no two species having identical distributions. A second central tenet is that communities intergrade continuously due to the scattered centres and broad overlap of species populations (Gleason 1939; Whittaker 1975, 1978a; Austin 1985). Communities may hence be seen as groups of species which respond similarly along environmental gradients (Schoener 1986, 1988). In seeking to arrange samples (or species) in a continuous multivariate space ordination techniques are thus seen as appropriate for this model of community structure.

Classification techniques, by virtue of constructing classes, have traditionally been linked with the organismal concept of community structure whereby communities are seen as integrated and discrete entities (see Goodall 1963; Daubenmire 1966; McIntosh 1967). This concept implies the existence of real units separated by discontinuities and has hence been seen in the past as diametrically opposed to the continuum concept (see Anderson 1965a). One criticism of the use of classification in recognition of community types is the artificial definition of types due to classification criteria being necessarily determined by the researcher (Whittaker 1978b). It is also maintained that class boundaries are similarly maintained and are often arbitrary (Whittaker 1978b, although see Goodall 1978).

It should be noted that the argument that community classifications are unnatural in the sense of being abstractions, may be equally applied to ordination techniques (Dansereau 1961). Notwithstanding this, discontinuities between vegetation units are observable in the field (Scott 1974; Whittaker 1975, 1978a). Further, a sound biological rationale exists as to how boundaries may be maintained (see Wilson & Agnew 1992) and how relatively discrete community types may come into being (see Anderson 1965a). It follows that, while classifications may be artificial in the sense of being abstractions, they may also be natural in the sense of recovering vegetation types which are spatially and/or ecologically coherent.

Ordination and classification may appear to be mutually exclusive by virtue of association with the two community structure concepts. Much of the early debate concerning these concepts, however, has been diffused; proponents of both concepts generally recognising that both concepts are abstract and that attributes of both are observable in the field (e.g. Scott 1974; Whittaker 1962, 1967, 1975, 1978a). Further, multivariate classification and ordination techniques are not inexorably linked with concepts of community structure (Goodall 1963; Anderson 1965a; McIntosh 1967; Anderson & Kikawwa 1986). As stated by Grieg-Smith (1983), "ordination techniques are not dependent on data being continuous any more than classification techniques are dependent on the existence of discontinuities in the data". Ordination and classification are complementary and can be used in an integrated fashion in the one investigation (e.g. Crawford & Wishart 1967; Noy-Meir 1971; Goodall 1978; Grieg-Smith 1983; Jongman *et al.* 1987; Feoli & Zuccarello 1991; Kent and Coker 1992).

In this chapter construction of a secondary synthesis of community structure is detailed. For this purpose the use of multivariate classification has been preferred. A principal reason for this preference was that multivariate classification techniques are multi-scale analyses. That is, in the case of divisive techniques (see Grieg-Smith 1983; Jongman *et al.* 1987), that successively finer scale divisions are produced with each successive sub-group division being based only on the respective individual subgroups which were discerned at the previous division. Conversely, most ordination techniques are 'single-scale' techniques in that all patterns present are scaled in terms of a single (or few) hypothetically constructed gradients (see Grieg-Smith 1983; Jongman *et al.* 1987). As a consequence of this fine-scale patterns may be subsumed by more prominent

patterns in the vegetation. In examining a vegetation type within a local area I anticipated that any patterns present would be of a relatively fine-scale. I also anticipated that patterns may occur at different scales. I thus considered that multivariate classification would be more appropriate than ordination in this phase of my research.

A second reason for the preference of multivariate classification was the contemporary emphasis on these techniques in analysis of heathland communities (e.g. Siddiqi *et al.* 1972; Clemens & Franklin 1980; Adam *et al.* 1989a). While algorithms employed differ across previous studies I envisaged that use of classification would enable in part a comparison with these studies.

In view of the nature of the vegetation under study (see Chapter 2) I anticipated that variance in individual properties would be characterised by both discontinuities (e.g. burnt dune heaths versus swamps), and more continuous variation (e.g. within platform heaths). I must thus point out that while classification has been used to detect variance in internal organisation of properties that some recognised communities ('complexes' in this study) may in fact represent partitions of continua. Therefore, recognised complexes should be considered as provisional.

### 3.1.2 Research objectives and hypotheses

The first research objective was to determine the presence and nature of variance in internal organisation of floristic composition, structure and species richness. This has been addressed through independent classification of each property in order to recognise what I term 'complexes'. The hypothesis assessed is that outlined in Chapter 1, this being that,

*major community properties of cliff-top coastal heathlands, including those other than floristic composition, display interpretable variation in internal organisation at local spatial scales*

The second research objective was to quantitatively determine the concordance between the separate classifications. The comparative information contents of the classifications have been examined in order to assess the advantage of a secondary synthesis of community structure over a primary synthesis. This may alternatively be seen as providing an assessment of the loss of information involved with pre-emphasis on particular properties, insofar as a secondary synthesis is concerned. The hypothesis assessed is thus that;

*the information content of individual property classifications is not contained in entirety in classifications of alternate properties.*

The third research objective was to examine the concordance of individual classifications with a subjectively based site reconnaissance used as an initial sampling stratification. This is done for two reasons. First, it enables assessment of the possibility that major local patterns in cliff-top coastal heathlands may be adequately summarised by rapid and simple traverses of the vegetation. Secondly, the site reconnaissance has been done in a way so as to classify the major physiographic features (e.g. dunes vs. swamps vs. sandstone platform). Assuming the most important and general factors influencing community structure are correlated with this classification, which is a reasonable assumption, then concordance of individual classifications with the reconnaissance provides an indirect measure of the likely functional significance of these classifications with respect to general environmental parameters. This examination is a precursor to more detailed examination of environmental correlates presented in Chapter 5. This research objective is addressed within the methodological framework adopted to address the second hypothesis above.



## 3.2 MATERIALS AND METHODS

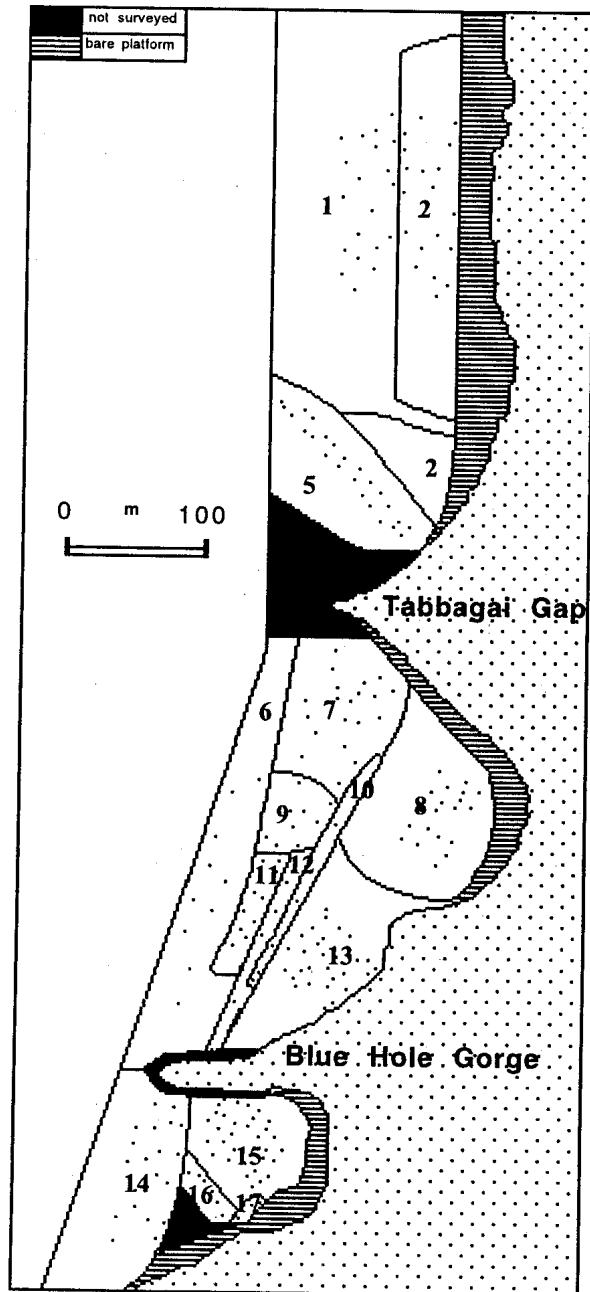
### 3.2.1 Field survey

#### 3.2.1.1 Reconnaissance

Reconnaissance consisted of repeated traverses of the site to a distance inland of approximately 150 m. Landscape segments supporting vegetation of apparent floristic and structural homogeneity were identified on a visual basis. General physiographic features of the landscape (see Chapter 2) were also used as a stratification factor (*viz.* swamps, sandstone platform, bare frontal sandstone platform, sand dunes and flat areas intermediate between dunes and platforms). The approximate area and location of these segments were determined using tape measure and compass. In this study these segments are referred to as reconnaissance zones. Seventeen reconnaissance zones were demarcated in the research site, at the locations shown in Fig. 3.1.

#### 3.2.1.2 General survey methodology

Quadrat sizes to be used in the main floristic survey were first determined. First, grids were defined in each reconnaissance zone to cover the largest possible area considered homogenous. These were oriented to be approximately parallel with the cliff-line with the grid margin closest to the cliff located to be approximately an exact multiple of 10m from the cliff-top. Three nested quadrat systems were then placed at randomly selected positions within each grid. The format of the systems used follows Smith (1966) with successive quadrat sizes being 0.125 m<sup>2</sup>, 0.25 m<sup>2</sup>, 0.5 m<sup>2</sup>, 1 m<sup>2</sup>, 2 m<sup>2</sup>, 4 m<sup>2</sup>, 8 m<sup>2</sup>, 16 m<sup>2</sup>, 32 m<sup>2</sup>, 64 m<sup>2</sup>, 128 m<sup>2</sup> and 256 m<sup>2</sup>, except in the case of reconnaissance zones 3 & 4. Reconnaissance zone 3 corresponded to islands of heathland scattered along the bare frontal platform area between Cape Solander and Tabbagai Gap. In this case five islands were selected at random and nested plot systems established but with a maximum plot area of 4 m<sup>2</sup>. Reconnaissance zone 4 corresponded to maritime herbfields established on areas of deposition of weathered material scattered in the same area. Five of these areas were selected at random and nested plot systems established with a maximum plot area



**Fig. 3.1** Reconnaissance zone and quadrat locations. Reconnaissance zones are identified by number (see text). Quadrats are shown as dots (quadrat centres). Quadrat identity can be ascertained from quadrat numbers (see text). Reconnaissance zones 3 and 4 cover the bare platform area to the north of Tabbagai Gap. Quadrat locations within these zones are not shown.

of 8 m<sup>2</sup>. Species-area curves were then constructed for each reconnaissance zone using data from the nested quadrat systems. Minimum sampling areas were then determined using the tangential procedure described by Mueller-Dombois & Ellenberg (1974). The sizes of square quadrats for use in each reconnaissance zone were then determined by taking the side length (in whole metres) that gave the area closest to but above the minimum sampling area as determined above.

Subsequently, all sampling grids were stratified in 10m segments away from the cliff-top. Five quadrats were then located within each 10 m stratum of each grid, with the exception of four reconnaissance zones where the grid dimensions and the nature of the vegetation necessitated use of fewer quadrats in some or all strata. Quadrats were located within grid strata by use of random co-ordinates.

This procedure was not used in the case of reconnaissance zones 3 & 4 due to the scattered nature of the vegetation. In these instances a line transect was traversed running parallel to the cliff-line and approximately 10 m in from the cliff-top. Metre marks were selected randomly, and quadrats established in islands closest to these marks. The procedure was continued until 10 quadrats of each vegetation type were located, 5 quadrats within the range 0 m to 10 m from the cliff-top and 5 quadrats in the range 10 m to 20 m from the cliff-top.

In all, 254 quadrats were located covering the 17 reconnaissance zones (Fig. 3.1). Sampling details are summarised in Table 3.1. These do not include nested quadrats which were used purely for determination of appropriate quadrat sizes. Also included in Table 3.1 is a classification of the structure of the reconnaissance zones according to the classification scheme of Specht (1970). This classification is included as a guide only and has been made entirely subjectively as part of the reconnaissance process. Species seen to commonly occur in reconnaissance zones are also noted.

### 3.2.1.3 Quadrat and species referencing

The 254 quadrats have been referred to by either 'quadrat number' or 'analysis number'. Quadrats were numbered to reflect their spatial arrangement, in the format x/y.z where, x = the reconnaissance zone number, y = the distance stratum and z

**Table 3.1 Sampling program details**

Zone areas are approximate total areas covered by recognised vegetation segments (see text).

Position: 1 - sand dunes, 2 - flat sandy or peaty areas usually of impeded drainage between sand dunes and sandstone platform, 3 - sandstone platform.

YSLF: years since last fire at commencement of survey.

Structural formation follows Specht (1970). Common species are identified by analysis number (see text).

Grid dimensions and area refer to sampling grids in which quadrats were located. Grid dimensions are breadth\*length of sampling grid where breadth refers to the length of the edges running perpendicular to the cliff-top.

Range sampled refers to the range of distance from the cliff-top which was sampled.

Recon. zone	Zone area (ha)	Position	YSLF (years)	Structural formation	Common species	Grid dimensions (m*m)	Grid size (ha)	Quadrat size (m <sup>2</sup> )	Quadrats (number)	Area sampled (m <sup>2</sup> )	Range sampled (m)
1	3.71	3	1.4	open sedgeland	145, 126, 25	40*120	0.48	16	20	320	60 to 100
2	1.60	3	20	tall closed heathland	89, 94, 111	40*120	0.48	25	20	500	20 to 60
3	scattered	3	20	closed heathland	74, 89, 94	N/A	N/A	1	10	10	0 to 20
4	scattered	3	20	open herbfield	12, 109, 110	N/A	N/A	1	10	10	0 to 20
5	0.90	1	1.4	open heathland	5, 20, 69	120*30	0.36	25	24	600	30 to 150
6	1.10	1	2.3	open heathland	51, 69, 114	20*200	0.40	25	10	250	130 to 150
7	0.83	3	20	tall closed heathland	94, 111, 121	50*100	0.50	25	20	500	100 to 150
8	0.83	1	20	tall closed heathland	74, 89, 94	40*60	0.24	64	20	1280	50 to 90
9	0.33	2	2.3	open sedgeland	25, 26, 90	30*50	0.15	25	9	225	90 to 120
10	0.33	2	20	closed heathland	74, 89, 94	10*100	0.10	25	5	125	60 to 70
11	0.33	2	20	sedgeland	25, 33, 128	20*50	0.10	9	10	90	80 to 100
12	0.33	2	2.3	open heathland	51, 69	10*100	0.10	25	5	125	70 to 80
13	1.10	3	20	closed heathland	74, 89, 94	60*60	0.36	25	30	750	0 to 60
14	1.10	1	2.3	open heathland	51, 114, 146	40*120	0.48	16	20	320	110 to 150
15	0.66	3	20	tall closed heathland	89, 94, 118	70*60	0.42	36	33	1188	30 to 100
16	0.22	2	2.3	open heathland	46, 54, 69	50*20	0.10	25	5	125	50 to 100
17	0.04	2	20	sedgeland	25	10*40	0.04	9	3	27	40 to 50
	<u>13.41</u>						<u>4.32</u>		<u>254</u>	<u>6445</u>	

= the number of the quadrat within the stratum from the most northern grid boundary. For cross-referencing in numerical analyses, quadrats have also been numbered by single integers termed analysis numbers. Further details and cross-referencing of quadrat and analysis numbers are provided in Appendix 3.1.

Species referred to are either referred to by their full name, by an abbreviation of the species name, or by analysis number. Species name abbreviations used are in the format xxx.yyy where, xxx = the first three letters of the genus name and yyy = the first three letters of the species name. Species names are cross-referenced to both species name abbreviations and analysis numbers in the research site floristic list provided in Appendix 3.2.

#### 3.2.1.4 Survey of floristic attributes

Floristic lists were compiled for each quadrat. All plants were identified in the field to the lowest taxonomic level possible using the identification key of Beadle *et al.* (1982) and the pictorial identification aids of Fairley & Moore (1989) and Robinson (1991). Samples of species were submitted to the National Herbarium of New South Wales to confirm the identification, or to identify species unable to be keyed satisfactorily in the field. Authorities for species names follow Harden (1990, 1991, 1992, 1993). Species remaining unidentifiable, or identifiable only to generic level, have been retained in the study and are identified by code.

The species present in each stratum (see below) were noted, and an estimate of foliage projective cover (see Specht 1970; Specht *et al.* 1974; Walker & Hopkins 1990) assigned to each species in each stratum. Estimates were made visually using 1% intervals to 10% and 5% intervals to 100%. Although visual estimates of cover have been criticised in the past for introduction of subjective bias (Mueller-Dombois & Ellenberg 1974; Kershaw 1985) they can be conducted rapidly enabling more samples to be included than if more exacting measurements are utilised (Gauch 1982). These estimates were hence considered appropriate given the relatively large number of quadrats.

The preference for use of foliage projective cover (cover) over other abundance measures has been made in my study for several reasons. First, cover has been shown to provide effective expression of the dynamic and competitive relationships between species in heathland vegetation ( see Gimingham 1961). Secondly, the nature of substrates and the prostrate nature of individuals in heathlands can make the identification of individual plants difficult. The use of cover over direct density measures was thus considered preferable from a logistical perspective. Thirdly, cover is known to vary with time since fire (see Kruger 1983). It may also be reasonably assumed to vary according to maritime influences (see Malloch 1971,1972; Parsons 1981; Specht & Morgan 1981; Adam *et al.* 1989a; Specht & Specht 1989b). I thus considered that cover would provide an appropriate functional response in the studied vegetation where these factors are of likely importance. Notwithstanding the preference for cover in this study it should be noted that cover is a function of both the size and density of individuals (Morrison *et al.* 1995). It is recognised that these components may reflect different ecological processes. However, in this study these components are not investigated. The composite measure, which is cover, is taken as the estimate of abundance. This is considered to be a function of both physiological tolerances dictated by environment and competitive interactions conditioned by such tolerances. I have thus considered the use of cover likely to reveal ecologically relevant aspects of community structure.

All floristic survey work was conducted during the period of August to December 1993. Reconnaissance zones were sampled in the order from the most recently burnt to the least recently burnt.

#### 3.2.1.5 Survey of structural attributes

The 254 quadrats were surveyed concurrently for structural attributes. For each quadrat, the presence/absence of five strata was first determined according to the identification system shown in Table 3.2. The shrub stratum was identified first, by placing a pole in the middle of the quadrat perpendicular to the slope of the substrate. The pole was marked in centimetre divisions and a cotton cord was attached to the pole so that it could be moved up and down and rotated around the pole. This was used to

**Table 3.2** Scheme for identification of strata of cliff-top coastal heathland vegetation.

Stratum <sup>1</sup>	Code	Growth form <sup>2</sup>	Height	Coverage
Emergent	(ES)	shrubs	>140%(SS)	<(SS), <50%
Shrub	(SS)	shrubs	<2.5m	highest of any shrub stratum
Subshrub	(SSS)	shrubs	<60%(SS)	<(SS)
Graminoid	(GS)	graminoids	any	any
Groundcover (GCS)		Herbs	any	any
		Shrub seedlings	<0.3m	any
		Herbaceous shrubs	<0.3m	any
		Prostrate shrubs	<0.3m	any

<sup>1</sup> If coverage of emergent stratum exceeds 50% it becomes the shrub stratum. The shrub stratum is determined prior to all others. As many subshrub strata as are required may be defined, the height of successive strata not exceeding 60% of the immediately preceding subshrub stratum. Graminoid and groundcover strata are determined independently of shrub based strata.

<sup>2</sup> Shrub - woody plant, not usually more than 6 m tall, apical dominance replaced at early stage by lateral branching; Graminoids - grasses and grass-like plants with similar growth form including members of the Poaceae, Restionaceae, Cyperaceae, Juncaceae, Centrolepidaceae, Liliaceae; Herbs - plants largely lacking secondary growth and with a growth form unlike graminoids; Shrub seedlings - seedlings or early regenerative shoots of shrubs emerging at ground-level; Prostrate shrubs - shrubs trailing on ground; Herbaceous shrubs - stem not exceeding 20% of total height, most growth herbaceous, no woody branching.

identify individuals within the quadrat of the same height. Foliage projective coverage was determined visually for individuals that occurred at particular heights.

Subsequently, all shrubs within  $\pm 40\%$  of the height of the initially identified stratum were included in the shrub stratum. Shrubs with a height above this limit constituted the emergent stratum. Shrubs below this limit constituted the sub-shrub stratum. Any number of sub-shrub layers were allowable on the basis of successive 40% height breaks with respect to the shrub stratum, but this was not necessary. It should also be noted that if the cover of the emergent layer was estimated to exceed 50% it was ascribed as the shrub stratum and those below were ascribed as sub-shrub strata.

Subsequently, the presence/absence of graminoid and groundcover strata was determined. As indicated in Table 3.2, the groundcover stratum was set to include shrub seedlings, herbaceous shrubs and prostrate shrubs under 0.3 m in height as well as herbs. This appeared reasonable in that many diminutive and/or prostrate shrubs, and shrub seedlings appeared to be primarily of an herbaceous nature. From a structural perspective it was considered that these forms were of functional equivalence.

After identification of strata a visual estimate of cover was made for each species occupying each stratum (see above). For each quadrat, species cover values were summed for each stratum to give an estimate of total coverage for respective strata. For each stratum five points were then located by random co-ordinate selection. The height of the individuals in the respective strata closest to each of the five points was recorded. These measurements were averaged to give an estimate of height of each stratum present.

In addition, a further five points were located in each quadrat by random co-ordinate selection. Photosynthetically active radiation was then recorded above the canopy and at ground level (plus height of sensor, ca. 4 cm) at each of the five points using a Li-cor light meter fitted with a quantum sensor. All radiation readings were made between 11 am and 1 pm under clear conditions in December 1993. Measurements were not made concurrently with recording of structural attributes but rather in a single three-day period near the end of the survey. Absolute differences between above canopy and ground level readings were subsequently converted to proportionate extinctions for each sample point. The five proportionate extinctions recorded for each quadrat were then



averaged to provide an estimate of proportionate extinction of photosynthetically active radiation associated with the structural assemblage within each quadrat.

#### 3.2.1.6 Survey of species richness attributes

All quadrats were surveyed concurrently for species richness. The total number of species present in each quadrat was recorded as was the number of species in each strata present i.e. shrub, sub-shrub, graminoid and groundcover strata.

#### 3.2.2 Numerical analyses

Quadrats were classified by two-way indicator species analysis using TWINSpan (Hill 1979a). Three classifications were performed, one for each of the properties. In the case of floristic composition untransformed cover values were used, the cover values for individual species being summed across strata. Cover data for the emergent stratum was omitted due to infrequent occurrence. In the case of structure, data quantifying height and cover of all strata, and proportionate extinction of photosynthetically active radiation, were classified. These data were range standardised from zero to one hundred prior to analysis. In the case of species richness, counts were 'spatially standardised' by dividing by quadrat size to obtain species  $m^{-2}$ . Other standardisations are available for equating species richness of quadrats of differing size (*see* Whittaker 1972, 1975; Peet 1978). However, most of these are based implicitly on the assumption of the existence of a single species-area relationship. This was known not to be the case with respect to the studied vegetation. Also, the preliminary nested quadrat data indicated that curvi-linear sections of species-area curves for particular reconnaissance zones were pre-dominately below the  $1m^2$  mark. The linear standardisation adopted was thus considered appropriate for the purposes of this study. I considered that any error associated with comparing arrays of quadrats of slightly different size subsequent to standardisation should be minimal. In any case, any error should be no greater than that introduced by considering a single quadrat size across

vegetation of differing spatial structure. To bring standardised species richness figures into a range of approximately 0 to 100 data were multiplied by 50 prior to analysis. This was done rather than range standardising in order to maintain additivity between total species richness and richness of individual strata.

Each classification performed using TWINSpan was performed in the same way. Cut values used were 0%, 5%, 10%, 20%, 30%, 40%, 50%, 60% and 70%. Minimum group size for division was set to 5. The resulting ordered two-way matrix and dendrogram were inspected. Complexes were defined at the lowest division levels where clear boundaries existed in the distribution of any one or more species and/or pseudospecies. However, in order to minimise inclusion of meaningless divisions in the process of complex recognition divisions where disjunctions in distributions of species and/or pseudospecies were considered minor were not considered. This was supported by familiarisation gained through the site reconnaissance. While these decisions were subjective they were constrained to the final division level of each classification. Any undue influence on interpretation of classifications may thus be considered to be minimal.

It should be noted that as a result of this analysis it was possible that the recognised complexes could contain quadrats of different sizes. While adjustments for this have been made with respect to species richness none were made with respect to floristic composition or structure. Complexes may vary in their spatial expansion, and grouping of quadrats of different size within complexes allows explicitly for recognition of this if it is accepted that they represent the same complex. Quadrats of differing size which have been grouped together have hence been considered as comparable in this study.

In the case of floristic composition, complexes were named according to the two species having the highest average FPC values. The order of the species in the complex name reflect the rank of the two species in terms of average FPC. If the species with the highest average FPC had an average FPC greater than twice that of the second species then only the first species name was assigned. Where any species names identifying complexes were duplicated between complexes irrespective of order, additional species names were introduced, these being the next highest ranked species. Structural and species richness complexes were named simply by identification codes.

The effectiveness of classifications in summarising internal organisation of properties was assessed by examining differences in mean levels of attributes between complexes of the respective classifications. Attributes examined were those used in the recognition of complexes i.e. floristic (species), structural and species richness attributes respectively. In the case of floristic composition this was done subjectively due to the large number of species involved. In the case of structure and species richness differences were assessed quantitatively using one-way analyses of variance. These analyses were followed by Tukey tests to compare pairs of means. Assumptions of the analyses were assessed (see Sokal & Rohlf 1981; Mead & Curnow 1986) and data transformations were made where required. By demonstration of differences between complexes it is implied that significant variation in internal organisation of respective properties exists in the vegetation. It should not be taken as implying the existence of ecologically integrated vegetation units which are distinct from one another (*viz.* the organismal concept of community structure) since such differences could equally be demonstrated for continua. However, the relationships of complexes are considered in this chapter in relation to major physiographic features as detailed in Chapter 2 and with respect to effects of fire. These may reasonably be assumed to create spatially discrete areas which are of differing functional significance to community structure. Consideration of these general patterns is made in this chapter in interpreting detected vegetation patterns. However, detailed consideration of environmental correlates is reserved for Chapter 5.

In seeking to identify vegetation patterns it should also be noted, that at local spatial scales, the influence of stochastic processes may be expected to have a potentially large influence. This, along with sampling error, may thus also be expected to give rise to a degree of spuriousness in detected patterns. However, the general survey methodology was designed to safeguard against potentially spurious patterns to the greatest practicable extent. By stratifying the vegetation prior to the main survey, by selecting appropriate quadrat sizes, by selecting the areas within strata (reconnaissance zones) considered to be most homogenous and by using a relatively high sampling intensity, I considered that vegetation patterns would be effectively abstracted and undue influences minimised.

To quantify concordance between the classifications and between the classifications and site reconnaissance, cross-tabulations were first made. These were

counts of quadrats occurring in complexes of the different classifications and reconnaissance zones. The percentage of information of one classification contained in the other was then calculated. Complexes in one property, all quadrats of which were contained within single complexes of the compared classification, were first identified. Complexes in the first property were then identified which had quadrats located predominantly within a single complex of the compared classification. Such complexes were identified as having greater than 50% of its quadrats located in a single complex of the compared property with the additional proviso that the next highest number of quadrats contained in any individual complex of the compared classification was not greater than half the initial figure. The number of common quadrats from these complexes were then tallied and added to the number of quadrats in complexes of the first property which were contained within single complexes of the compared classification. This number was then divided by the total number of quadrats (254) and multiplied by 100 to obtain a percentage. This figure was the percentage of information in the compared classification (as conveyed by clustering of quadrats) contained in the first classification. This procedure was used in each pairwise comparison of classifications and was computed reciprocally in each case. The same procedure was used to determine the information in each classification contained in the site reconnaissance.

### 3.3 RESULTS

#### 3.3.1 Multivariate classification of floristic composition

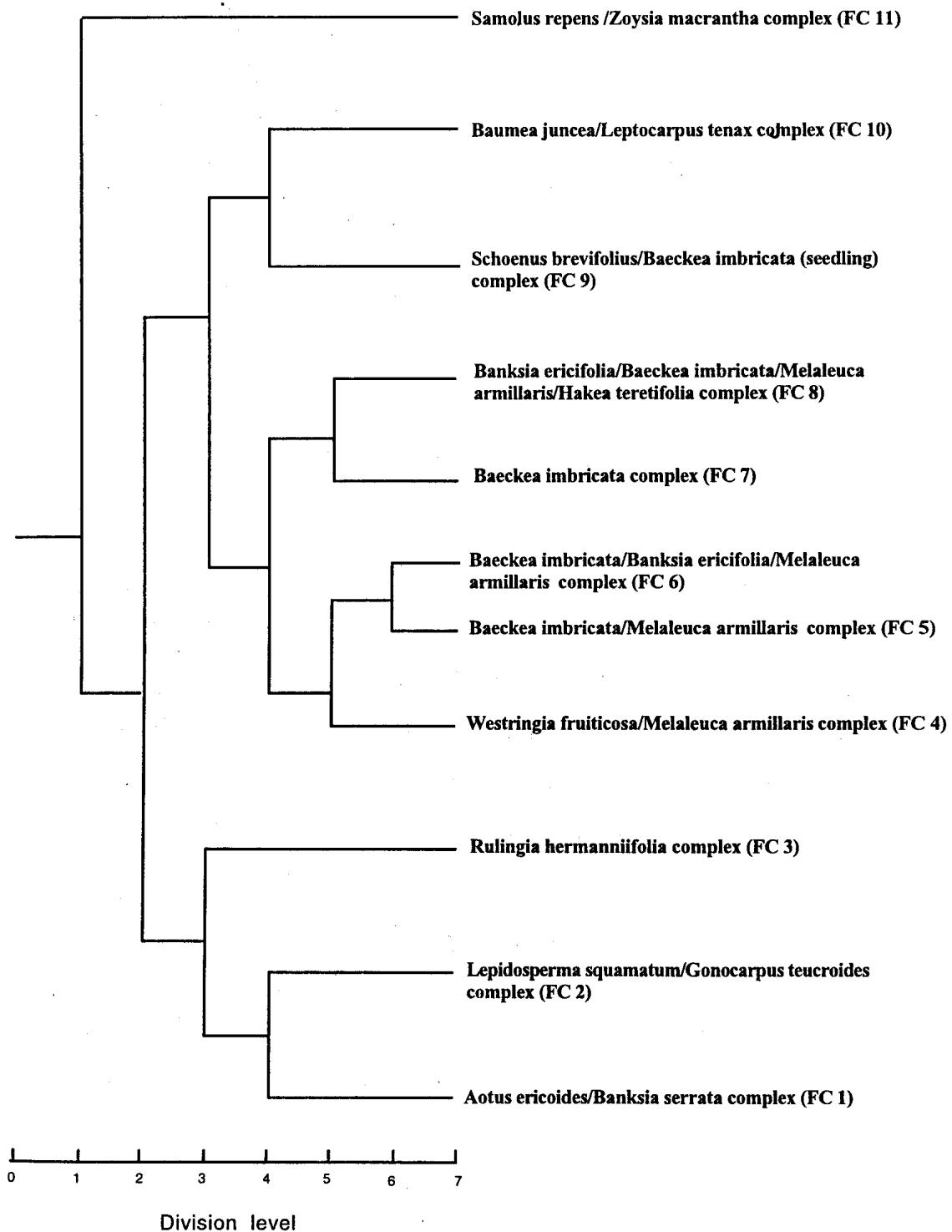
A total of 139 species from 45 families were recorded, 124 of these species being recorded in the surveyed quadrats. A full floristic list for the site is provided in Appendix 3.2.

From the indicator species analysis 11 complexes were recognised (Fig. 3.2). Quadrat membership of individual complexes is provided in Table 3.3. Mean FPC values for species in each complex are provided in Appendix 3.3. The recognised floristic complexes are briefly described below.

##### A. *Aotus ericoides/Banksia serrata* complex

This complex is the first of a group of three complexes recognised at the second division level which correspond to regenerating burnt heaths located on sand dunes and platform areas. With the exception of three quadrats, this complex corresponds with reconnaissance zones 6 and 14. Both of these zones cover the sand dunes to the south of Tabbagai Gap.

The vegetation of this complex is dominated by *Banksia serrata* and *Aotus ericoides*, which are common elements throughout the complex. With the exception of the occasional seedling, most *Banksia serrata* individuals appear to have resprouted since the July 1991 fire. This has apparently led to rapid establishment of structural dominance. However, this complex has an open structure except where groups of *Banksia serrata* have resprouted together. These groves occur throughout the complex, as do groves of *Aotus ericoides*. Groves of both species intergrade, the growth of both species appearing more vigorous where this occurs. Other common shrub species in this complex include: *Correa alba*, *Allocasuarina distyla*, *Melaleuca armillaris*, *Pimelia linifolia* and *Ricinocarpos pinifolius*. In more open inter-grove areas *Gonocarpus*



**Fig 3.2** Indicator species analysis dendrogram showing the recognised floristic complexes. Complex names and codes are indicated (see text).

**Table 3.3** Quadrat membership of the floristic complexes

Complexes are as indicated on the floristic classification dendrogram. Quadrats are identified by quadrat number (see text).

Complex	Complex code	Quadrats
<i>Aotus ericoides/Banksia serrata</i>	FC 1	6/14.1, 6/14.2, 6/14.3, 6/14.4, 6/14.5, 6/15.1, 6/15.2, 6/15.3, 6/15.4, 6/15.5, 14/12.1, 14/12.2, 14/12.3, 14/12.4, 14/12.5, 14/13.1, 14/13.2, 14/13.3, 14/13.4, 14/13.5, 14/14.1, 14/14.2, 14/14.3, 14/14.4, 14/14.5, 14/15.1, 14/15.2, 14/15.3, 14/15.4, 14/15.5, 15/6.2, 15/6.3, 15/7.4
<i>Lepidosperma squamatum/Gonocarpus teucrioides</i>	FC 2	5/4.1, 5/4.2, 5/5.1, 5/5.2, 5/6.1, 5/6.2, 5/7.1, 5/7.2, 5/8.1, 5/8.2, 5/9.1, 5/9.2, 5/10.1, 5/10.2, 5/11.1, 5/11.2, 5/13.2, 15/7.5, 15/8.4, 15/8.5
<i>Rulingia hermaniifolia</i>	FC 3	1/7.1, 1/7.2, 1/7.3, 1/7.4, 1/7.5, 1/8.1, 1/8.2, 1/8.3, 1/8.4, 1/8.5, 1/9.1, 1/9.2, 1/9.3, 1/9.4, 1/9.5, 1/10.1, 1/10.2, 1/10.3, 1/10.4, 1/10.5, 5/12.1, 5/12.2, 5/13.1, 5/14.1, 5/14.2, 5/15.1, 5/15.2
<i>Westringia fruticosa/Melaleuca armillaris</i>	FC 4	10/7.4, 10/7.5, 12/8.1, 12/8.2, 12/8.3, 12/8.4, 12/8.5, 13/1.1, 13/1.2, 13/1.3, 13/2.1, 13/2.2, 15/4.2, 15/4.3, 15/4.4, 15/4.5, 15/5.2, 15/5.3, 15/5.4, 15/5.5, 15/6.4, 15/6.5
<i>Baeckea imbricata/Melaleuca armillaris</i>	FC 5	3/1.1, 3/1.3, 3/1.5, 3/2.1, 3/2.2, 3/2.3, 3/2.5, 8/6.1, 8/6.2, 8/6.3, 8/6.4, 8/6.5, 8/7.1, 8/7.3, 8/7.4, 8/8.1, 8/8.4, 8/9.4, 10/7.2, 10/7.3, 13/1.4, 13/1.5, 13/2.3, 13/2.4, 13/2.5, 13/3.1, 13/3.2, 13/3.4, 13/3.5, 13/4.1, 13/4.2, 13/4.3, 13/5.1, 13/5.2
<i>Baeckea imbricata/Banksia ericifolia/Melaleuca armillaris</i>	FC 6	7/11.3, 7/11.4, 7/12.4, 8/7.5, 8/8.2, 8/8.3, 8/8.5, 8/9.1, 8/9.3
<i>Baeckea imbricata</i>	FC 7	2/4.2, 2/6.3, 3/1.2, 8/7.2, 8/9.2, 8/9.5, 10/7.1, 13/3.3, 13/4.4, 13/4.5, 13/5.3, 13/5.4, 13/5.5, 13/6.1, 13/6.2, 13/6.3, 13/6.4, 13/6.5
<i>Banksia ericifolia/Baeckea imbricata/Melaleuca armillaris/Hakea teretifolia</i>	FC 8	2/3.1, 2/3.2, 2/3.3, 2/3.4, 2/3.5, 2/4.1, 2/4.3, 2/4.4, 2/4.5, 2/5.1, 2/5.2, 2/5.3, 2/5.4, 2/5.5, 2/6.1, 2/6.2, 2/6.4, 2/6.5, 3/1.4, 3/2.4, 7/11.1, 7/11.2, 7/12.1, 7/12.2, 7/12.3, 7/13.1, 7/13.2, 7/13.3, 7/13.4, 7/14.1, 7/14.2, 7/14.3, 7/14.4, 7/15.1, 7/15.2, 7/15.3, 7/15.4, 15/4.1, 15/5.1, 15/6.1, 15/7.1, 15/7.2, 15/7.3, 15/8.1, 15/8.2, 15/8.3, 15/9.1, 15/9.2, 15/9.3, 15/9.4, 15/10.1, 15/10.2, 15/10.3, 15/10.4
<i>Schoenus brevifolius/Baeckea imbricata (seedling)</i>	FC 9	9/10.1, 9/10.2, 9/10.3, 9/11.1, 9/11.2, 9/11.3, 9/12.1, 9/12.2, 9/12.3, 16/6.1, 16/7.1, 16/8.1, 16/9.1, 16/10.1
<i>Baumea juncea/Leptocarpus tenax</i>	FC 10	11/9.1, 11/9.2, 11/9.3, 11/9.4, 11/9.5, 11/10.1, 11/10.2, 11/10.3, 11/10.4, 11/10.5, 17/5.1, 17/5.2, 17/5.3
<i>Samolus repens/Zoysia macrantha</i>	FC 11	4/1.1, 4/1.2, 4/1.3, 4/1.4, 4/1.5, 4/2.1, 4/2.2, 4/2.3, 4/2.4, 4/2.5

*teucroides* is common along with the sprawling *Bossiaea ensata*. Less common shrub species which occur in these open areas include *Zieria laevigata*, *Woollsia pungens*, *Philotheca salsolifolia*, *Conospermum ellipticum*, *Monotoca elliptica* and *Monotoca scoparia*. *Acacia myrtifolia* occurs in lower dune areas closer to the water table.

In addition to the dominant shrub species, the herb *Actinotus helianthi* and graminoid *Lepidosperma squamatum* are common elements in this complex. These species rank just behind the dominants in terms of average FPC. Other common herbs include *Xanthosia pilosa* and *Dampiera stricta*, which because of its stature has been considered part of the groundcover stratum. Other common graminoids include: *Entolasia stricta*, *Lomandra longifolia* and *Schoenus brevifolius*. The last-mentioned species is found in lower dune areas, occasionally with *Baumea juncea*; the other species occur throughout the complex.

#### B. *Lepidosperma squamatum*/*Gonocarpus teucroides* complex

This complex was recognised at the fourth division level where it was split from the previous complex. With the exception of three quadrats, this complex corresponds to reconnaissance zone 5, which covers a small conical dune just north of Tabbagai Gap. The vegetation on this dune was burnt in the March 1992 fire.

Dominant species in this complex include *Gonocarpus teucroides* and *Lepidosperma squamatum*, both of which were common in the previous complex and occur at similar foliage projective covers in this complex. However, *Banksia serrata* and *Aotus ericoides* are mostly absent from this complex. Other common shrub species in this complex include *Monotoca scoparia* and *Platysace lanceolata*, both having resprouted. The last-mentioned species also has seedlings represented. Other shrubs represented at early stages of vegetative development include: *Allocasuarina distyla*, *Melaleuca armillaris*, *Acacia suaveolens* and *Bossiaea ensata*. The small shrub *Hibbertia fastigata* is present and largely restricted to this dune.

In addition to *Lepidosperma squamatum*, other commonly occurring graminoids include: *Stipa mollis*, *Entolasia stricta*, *Hypolaena fastigiata* and *Lomandra glauca* ssp. *glauca*. The last-mentioned species is classified as a graminoid in this study.



This species is restricted to this complex. As in the previous complex, *Actinotus helianthi* and *Xanthosia pilosa* are commonly occurring herbs. Other prevalent members of the groundcover stratum include *Dampiera stricta* and seedlings of *Eriostemon buxifolius* ssp. *buxifolius*.

#### C. *Rulingia hermaniifolia* complex

This complex was recognised at the third division level and includes regenerating heathlands on sandstone platform burnt in the March 1992 fire. This complex corresponds to reconnaissance zone 1, plus quadrats towards the rear of reconnaissance zone 5. In this area the conical dune tapers into the platform areas.

The vegetation of this complex is floristically diverse, most species occurring in the groundcover stratum, with shrub development generally minimal and spatially patchy. Species occurring commonly as shrubs include: *Allocasuarina distyla*, *Banksia ericifolia*, *Hakea teretifolia*, *Dillwynia floribunda*, *Leptospermum squarrosus* and *Epacris obtusifolia* to a lesser extent. Burnt skeletons of the first three species occur densely in this complex. The adults present are small compared with individuals in unburnt areas. These adults are likely to be members of the same cohort as the seedlings present, localised conditions possibly having led to relatively faster vegetative growth.

The dominant species in this complex is currently *Rulingia hermaniifolia*. Foliage projective cover of this species varies substantially (2% to 45%) with a mean of 15% (see Appendix 3.3). Other prominent species include *Opercularia aspera*, *Opercularia varia* and *Dampiera stricta*. Unlike the dune complexes, regeneration in this heath appears to be mainly from seed. Seedlings of many species are represented including those of the previously mentioned species, as well as those of the following: *Eriostemon buxifolius* ssp. *obovatus*, *Dillwynia retorta*, *Cryptandra ericoides*, *Platysace lanceolata*, *Epacris longiflora*, *Epacris microphylla*, *Melaleuca nodosa*, *Baeckea imbricata* and *Leucopogon esquamatus*.

Commonly occurring graminoids include: *Baumea juncea*, *Schoenus brevifolius* and *Empodisma minus*. *Xanthorrhoea resinifera*, *Restio complanatus* and

*Lepidosperma quadrangulatum* are also represented but occur less frequently. The two last-mentioned species tend to occur as small populations throughout the complex.

#### D. *Westringia fruticosa*/*Melaleuca armillaris* complex

This complex was recognised at the fifth division level and is the first of a group of five complexes which correspond mainly to heathlands located on sandstone platform areas. These platform areas have remained unburnt in recent years. The quadrats come from reconnaissance zones 10, 12, 13 and 15. Two quadrats located at the southern most exposed end of a small sand ridge (reconnaissance zone 10) were included. All quadrats from reconnaissance zone 12 were included. These are located on the landward side of the abovementioned sand ridge and were burnt in the July 1991 fire. Quadrats included from reconnaissance zones 13 and 15 were located immediately adjacent to the cliff-top in positions of extreme exposure.

The dominant species in this complex are *Westringia fruticosa* and *Melaleuca armillaris*. However, co-dominance of these species is not uniform over the complex. In the burnt quadrats from reconnaissance zone 12 both species are present in small amounts; however, other shrub species more typical of dune areas are present with equivalent cover. These include: *Pimelia linifolia*, *Gonocarpus teucrioides*, *Chrysanthemoides monilifera* ssp. *rotundata*, *Correa alba* and *Aotus ericoides*. In the quadrats from reconnaissance zone 10 both species have increased covers; and *Monotoca elliptica* is also abundant. In quadrats from reconnaissance zone 13 *Melaleuca armillaris* is present; however, *Westringia fruticosa* assumes clear dominance and is present at high cover. In these areas *Stenotaphrum secundatum* also attains high cover. In quadrats from reconnaissance zone 15 both species are common elements, but are found in varying combinations with a large variety of other shrubs including: *Banksia ericifolia*, *Banksia serrata*, *Baeckea imbricata*, *Dillwynia floribunda*, *Dillwynia retorta*, *Darwinia fascicularis* ssp. *fascicularis*, *Epacris obtusifolia*, *Acacia sophorae*, *Acacia suaveolens*, *Correa alba* and *Conospermum ellipticum*.

E. *Baeckea imbricata*/*Melaleuca armillaris* complex

This complex was recognised at the sixth division level, and includes quadrats from reconnaissance zones 3, 8, 10 and 13. Those from reconnaissance zone 3 represent heathland islands scattered on frontal platform areas north of Tabbagai Gap. Interestingly, no quadrats from reconnaissance zone 2, which is immediately adjacent, were included in this complex. Quadrats from reconnaissance zone 10 are located at the northern end of a small sand ridge. Quadrats from reconnaissance zones 8 and 13 are located on platform areas where drainage appears to be particularly impeded.

The vegetation of this complex is similar to that of the last complex with similar mean foliage projective covers of *Melaleuca armillaris* and *Westringia fruticosa*. However, this complex is clearly differentiated from the previous one by the fact that *Baeckea imbricata* assumes clear dominance with covers generally two to five times higher than other species. Other shrub species present in this complex include *Banksia ericifolia*, *Melaleuca nodosa*, *Epacris obtusifolia* and *Hakea teretifolia*. However, these species are minor components of the complex in terms of both occurrence and cover.

Graminoids present in this complex include *Baumea acuta* and *Schoenus apogon* which persist beneath the canopy, *Baumea juncea* and *Juncus kraussii* which extend through the canopy, and *Themeda australis* which is abundant in patches where breaks in the canopy occur. As for other dense platform heaths the groundcover stratum is suppressed, with herbaceous non-graminoid components generally absent. However, seedlings of the dominant species occur throughout the complex.

F. *Baeckea imbricata*/*Banksia ericifolia*/*Melaleuca armillaris* complex

This small complex was recognised at the sixth division level. It includes quadrats from the front of reconnaissance zone 7 and from the rear of reconnaissance zone 8.

Foliage projective cover of *Baeckea imbricata* is reduced in this complex, and it co-dominates with *Banksia ericifolia* and *Melaleuca armillaris*. *Westringia fruticosa* is present but is less common than in the previous two complexes. *Hakea teretifolia* is a common component of this complex, as is an unidentified *Allosasuarina*

sp. Less common shrub species include *Melaleuca nodosa*, *Chrysanthemoides monilifera* ssp. *rotundata*, *Allocasuarina distyla* and a prostrate form of *Banksia integrifolia*. As with other platform heaths the groundcover stratum is suppressed, although two types of bryophytes occur commonly but at low covers. The graminoid *Themeda australis* is common in this complex, and reaches its highest mean foliage projective cover of 9% (see Appendix 3.3). *Baumea juncea* occurs commonly throughout the complex at low cover, as does *Imperata cylindrica* var. *major* and *Paspalidium distans*.

#### G. *Baeckea imbricata* complex

This complex was recognised at the fifth division level, and includes quadrats from reconnaissance zones 2 and 3 in the north and reconnaissance zones 8 and 13 in the south.

The vegetation is clearly dominated by *Baeckea imbricata*, which is present at near 100% cover in this complex. Other shrub species such as *Melaleuca armillaris*, *Banksia ericifolia*, *Hakea teretifolia*, *Allocasuarina distyla* and *Melaleuca nodosa* are present but generally occur at reduced covers.

The groundcover stratum is sparse, and consists primarily of *Baeckea imbricata* seedlings. Populations of *Drosera spathulata* appear where drainage appears to be particularly impeded. The graminoid *Baumea juncea* occurs commonly and in this complex reaches its highest cover values outside swamps. *Schoenus apogon* and the small lily *Thelionema umbulatum* are also common.

#### H. *Banksia ericifolia*/*Baeckea imbricata*/*Melaleuca armillaris*/*Hakea teretifolia* complex

This complex was recognised at the fifth division level, and is the most spatially extensive of the recognised complexes. The majority of quadrats from reconnaissance zones 2, 7 and 15 were included in this complex.

The vegetation of this complex is primarily a dense matrix of *Banksia ericifolia*, *Baeckea imbricata*, *Melaleuca armillaris* and *Hakea teretifolia*. In more open

areas *Banksia serrata*, *Darwinia fascicularis* ssp. *fascicularis* and *Allocasuarina distyla* are common. The former two species are more common in southern areas, with *Allocasuarina distyla* becoming more common northwards. A range of other shrub species are present in this complex at low cover, and occur primarily in interstices of the matrix. These species include: *Platysace lanceolata*, *Dillwynia retorta*, *Eriostemon buxifolius* ssp. *buxifolius*, *Melaleuca nodosa*, *Persoonia lanceolata*, *Monotoca elliptica*, *Mirbelia rubiifolia*, *Epacris obtusifolia*, *Leptospermum squarrosum* and *Callistemon linearis*.

As for the other platform heaths, the groundcover stratum is suppressed and consists primarily of seedlings of the dominant species. In wetter areas bryophytes and *Drosera spathulata* occur. In drier areas *Xanthosia pilosa* and *Actinotus helianthi* occur. The graminoid stratum of this complex is particularly rich, with most of the graminoid components already mentioned occurring in this complex. *Baumea juncea* and *Schoenus brevifolius* are common throughout, with a range of other species attaining high cover in interstices of the matrix. *Thysanotus juncifolius* occurs sporadically throughout the complex mainly in wetter parts.

Although extending further south, this complex may be considered an unburnt counterpart of the *Rulingia hermaniifolia* complex. A total of 44 shrub species are represented as either seedlings or adults in both complexes. Of these species 21 (48%) are represented in both complexes, 10 (23%) are represented in the *Rulingia hermaniifolia* complex but not in the *Banksia ericifolia/Baeckea imbricata/Melaleuca armillaris/Hakea teretifolia* complex and 13 (29%) are represented in the *Banksia ericifolia/Baeckea imbricata/Melaleuca armillaris/Hakea teretifolia* complex but not in the *Rulingia hermaniifolia* complex. A total of 21 shrub species occur as adults in the *Rulingia hermaniifolia* complex. Of these species 16 (76%) also occur as adults in the *Banksia ericifolia/Baeckea imbricata/Melaleuca armillaris/Hakea teretifolia* complex.

#### I. *Schoenus brevifolius/Baeckea imbricata* (seedling) complex

This complex was recognised at the fourth division level and corresponds with reconnaissance zones 9 and 16. Both of these reconnaissance zones are located in

areas of impeded drainage located between dune areas and platform areas. Both zones were burnt in the July 1991 fire.

Both reconnaissance zones are united by a high cover of the graminoid *Schoenus brevifolius* and by a groundcover stratum dominated by seedlings of *Baeckea imbricata*. However, the last-mentioned reconnaissance zone has a better developed shrub stratum, with common species including *Dillwynia floribunda*, *Sprengelia incarnata*, *Baeckea imbricata* and *Epacris obtusifolia*.

Notwithstanding the dominance of *Schoenus brevifolius* this complex has a diverse graminoid component, including *Empodisma minus*, *Entolasia stricta*, *Centrolepis strigosa* ssp. *strigosa*, *Isolepis cernua*, *Baumea acuta*, *Baumea juncea*, *Baumea rubiginosa*, *Lepyrodia muelleri*, *Juncus kraussii*, *Restio complanatus* and the lily *Thelionema umbulatum*. Of these species, *Baumea rubiginosa* and *Centrolepis strigosa* ssp. *strigosa* are more prevalent in reconnaissance zone 9, while *Restio complanatus* is more prevalent in reconnaissance zone 16. Also, with the exception of *Schoenus brevifolius* and *Baumea juncea*, these species appear to occur mainly in the form of small spatially discrete populations.

#### J. *Baumea juncea*/*Leptocarpus tenax* complex

This complex was recognised at the fourth division level at which it was divided from the previous complex. This complex is comprised exclusively of swamps, and corresponds to reconnaissance zones 11 and 17.

The graminoid *Baumea juncea*, which is present in much of the vegetation reaches its highest cover in this complex, in which it is the dominant species. In reconnaissance zone 17 it is the sole dominant. In reconnaissance zone 11 it is found in close association with *Leptocarpus tenax* and *Schoenus brevifolius*, and to a lesser extent with *Lepyrodia muelleri*. This complex lacks shrub species except for isolated occurrences of *Banksia ericifolia* and an *Allocasuarina* sp. However, seedlings of *Baeckea imbricata* and *Banksia ericifolia* are prevalent in the groundcover stratum. The groundcover stratum of this complex also includes a *Sphagnum* species, *Boronia parviflora*, *Goodenia paniculata*, *Goodenia dimorpha* var. *augustifolia*, *Myriophyllum*

*gracile*, *Myriophyllum criopatum*, *Hyrocotylee bonariensis*, *Selaginella uliginosa* and *Villarsia exaltata*.

#### K. *Samolus repens*/*Zoysia macrantha* complex

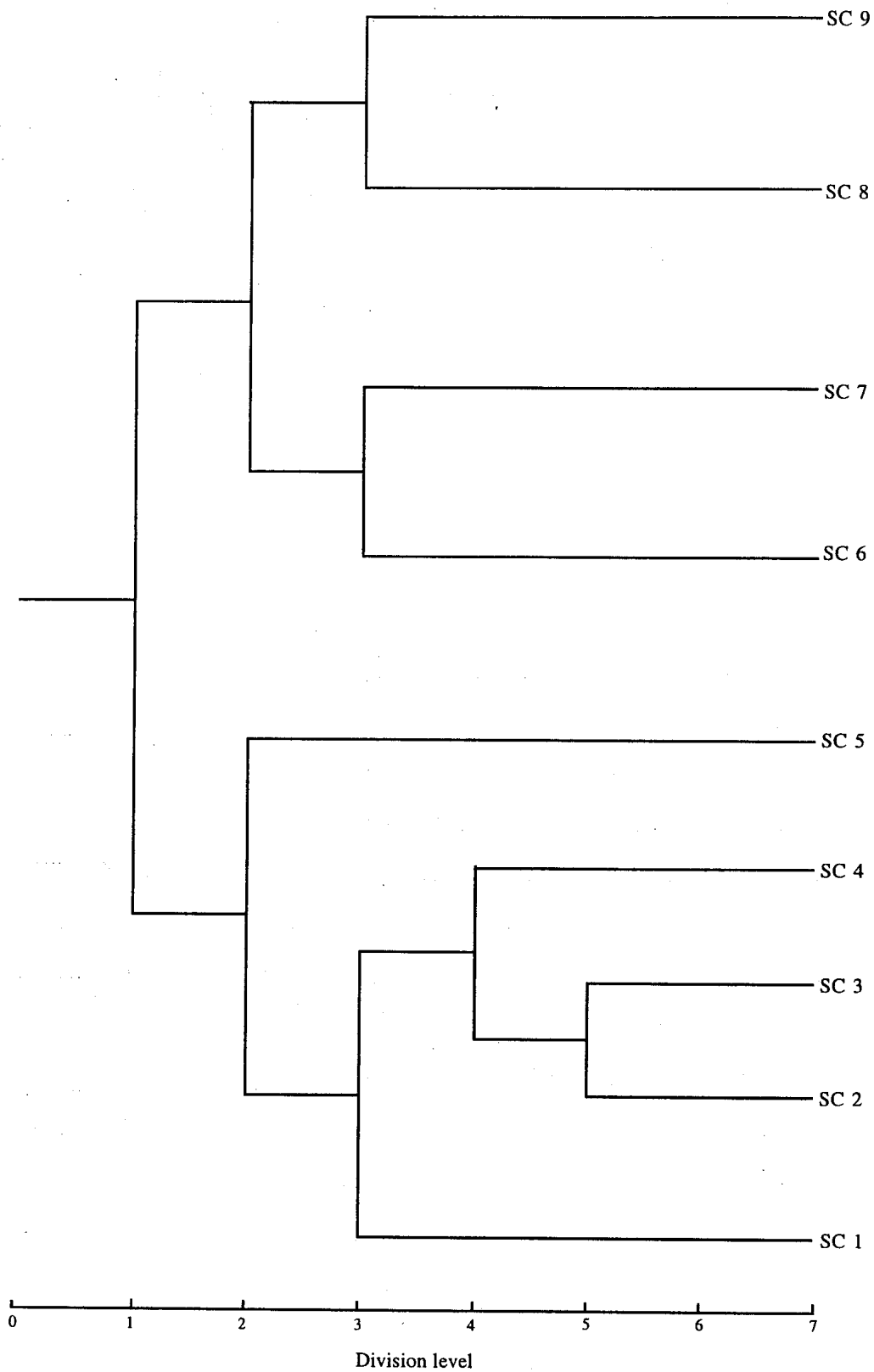
This complex was recognised at the first division level and is thus distinctive from the remaining vegetation. It corresponds to reconnaissance zone 4, and is located on shallow sandy deposits scattered throughout the bare frontal platform areas.

Dominant species in this complex include the creeping herb *Samolus repens* and the creeping graminoid *Zoysia macrantha*. These were found growing together in four of the ten quadrats used to sample this complex. However, where *Samolus repens* attained high cover *Zoysia macrantha* was not found. With the exception of a single quadrat the converse was not observed. Other common species in this complex include *Epaltes australis*, *Isolepis nodosa* and *Isolepis cernua*. *Plantago coronopus* ssp. *coronopus* is present, occurring as small colonies. In one quadrat seedlings of *Baeckea imbricata* had established. Interestingly deeper deposits to the south of the site were observed to support small shrubs of *Baeckea imbricata*.

#### 3.3.2 Multivariate classification of structure

From the indicator species analysis nine structural complexes were recognised (Fig. 3.3). Membership of quadrats in structural complexes (SCs) is shown in Table 3.4.

The first classification division (Fig. 3.3) separated quadrats comprising SCs 1 to 5 from those comprising SCs 6 to 9. As is evident in Table 3.5, the former group has been separated on the basis of greater height and cover of shrub and sub-shrub strata. However, this separation has also been based on the former group having significantly lower height and cover of the groundcover stratum as well as significantly higher



**Fig. 3.3** Indicator species analysis dendrogram showing the recognised structural complexes. Structural complexes are identified by code (see text).



**Table 3.4** Quadrat membership of the structural complexes.

Structural complexes are identified by code and follow the classification dendrogram. Quadrats are identified by quadrat number (see text).

Structural complex	Quadrats
SC 1	2/3.5, 2/6.2, 2/6.3, 2/6.4, 7/11.1, 7/11.2, 7/12.1, 7/12.2, 7/13.1, 7/13.2, 7/13.3, 7/14.1, 7/14.2, 7/14.3, 7/15.1, 7/15.2, 7/15.3, 7/15.4, 8/6.1, 8/8.1, 10/7.2, 13/3.1, 13/4.1, 15/6.1, 15/7.1, 15/7.2, 15/8.2, 15/10.1, 15/10.2
SC 2	2/4.2, 3/1.2, 3/1.3, 3/1.4, 3/2.2, 3/2.3, 7/11.3, 8/6.3, 8/6.4, 8/6.5, 8/7.3, 8/7.4, 8/8.5, 10/7.1, 10/7.3, 12/8.2, 13/1.4, 13/1.5, 13/2.4, 13/3.2, 13/3.3, 13/3.5, 13/4.2, 13/4.5, 13/5.3, 13/5.5, 13/6.1, 13/6.3, 13/6.4, 13/6.5, 15/4.1, 15/5.1, 15/5.2, 15/5.4, 15/6.3, 15/9.1, 15/9.4, 15/10.4
SC 3	2/3.3, 2/3.4, 2/4.1, 2/4.3, 2/4.4, 2/4.5, 2/5.3, 2/5.4, 2/5.5, 2/6.1, 2/6.5, 7/11.4, 7/12.3, 7/13.4, 7/14.4, 8/7.2, 8/8.2, 8/8.3, 8/8.4, 8/9.1, 8/9.2, 8/9.3, 8/9.4, 15/5.3, 15/7.3, 15/8.1, 15/8.3, 15/8.4, 15/9.2, 15/9.3, 15/10.3,
SC 4	2/3.2, 2/5.1, 2/5.2, 7/12.4
SC 5	2/3.1, 3/1.1, 3/1.5, 3/2.1, 3/2.4, 3/2.5, 6/14.1, 6/14.2, 6/14.3, 6/14.4, 6/14.5, 6/15.1, 6/15.2, 6/15.3, 6/15.4, 6/15.5, 8/6.2, 8/7.1, 8/7.5, 8/9.5, 10/7.4, 10/7.5, 12/8.3, 12/8.4, 13/1.3, 13/2.1, 13/2.2, 13/2.3, 13/2.5, 13/3.4, 13/4.3, 13/4.4, 13/5.1, 13/5.2, 13/5.4, 13/6.2, 14/12.1, 14/12.2, 14/12.5, 14/13.1, 14/13.2, 14/13.5, 14/14.1, 14/14.2, 14/14.5, 14/15.1, 15/4.2, 15/4.3, 15/4.4, 15/4.5, 15/5.5, 15/6.2, 15/6.4, 15/6.5, 15/7.4, 15/7.5, 15/8.5, 16/6.1
SC 6	5/4.1, 5/4.2, 5/5.1, 5/5.2, 5/6.1, 5/6.2, 5/7.1, 5/7.2, 5/8.1, 5/8.2, 5/9.1, 5/9.2, 5/10.1, 5/10.2, 5/11.1, 5/11.2, 5/12.2, 5/13.2, 5/14.2, 9/11.1, 12/8.5, 13/1.1, 13/1.2, 14/12.3, 14/12.4, 14/13.3, 14/13.4, 14/14.3, 14/14.4, 14/15.2, 14/15.3, 14/15.4, 14/15.5, 16/7.1, 16/8.1, 16/9.1, 16/10.1
SC 7	1/7.1, 1/7.2, 1/7.3, 1/8.1, 1/8.2, 1/8.3, 1/8.4, 1/8.5, 1/9.1, 1/9.2, 1/9.3, 1/9.4, 1/9.5, 1/10.1, 1/10.2, 1/10.3, 1/10.4, 1/10.5, 5/12.1, 5/13.1, 5/14.1, 5/15.1, 5/15.2, 9/12.1, 9/12.3, 12/8.1
SC 8	1/7.4, 1/7.5, 9/10.1, 9/10.2, 9/10.3, 9/11.2, 9/11.3, 9/12.2, 11/9.1, 11/9.2, 11/9.3, 11/9.4, 11/9.5, 11/10.1, 11/10.2, 11/10.3, 11/10.4, 11/10.5, 17/5.1, 17/5.2, 17/5.3
SC 9	4/1.1, 4/1.2, 4/1.3, 4/1.4, 4/1.5, 4/2.1, 4/2.2, 4/2.3, 4/2.4, 4/2.5

**Table 3.5** Structural attributes of the structural complexes.

Table cells are mean height (m) and cover (%) of strata. Standard errors are indicated in brackets. Sample sizes are indicated (n = ). P-values from analysis of variance comparing structural attribute means between structural complexes are shown. Means were compared by Tukey multiple comparison tests ( $p < 0.05$ ). Means sharing any superscript letter are not significantly different. Means not included in ANOVA calculations are indicated (\*).

Stratum	Attribute	Structural complex									p-value
		SC 1	SC 2	SC 3	SC 4	SC 5	SC 6	SC 7	SC 8	SC 9	
		n = 29	n = 38	n = 31	n = 4	n = 58	n = 37	n = 26	n = 21	n = 10	
Shrub	height	1.68 (0.07) <sup>e</sup>	0.90 (0.05) <sup>c</sup>	1.47 (0.04) <sup>d</sup>	1.60 (0.04) <sup>e</sup>	0.71 (0.03) <sup>b</sup>	0.50 (0.02) <sup>a</sup>	0.48 (0.03) <sup>a</sup>	0.06 (0.03) <sup>*</sup>	0.00 (0.00) <sup>*</sup>	<0.001
	coverage	101 (2) <sup>f</sup>	86 (3) <sup>e</sup>	76 (3) <sup>d</sup>	80 (4) <sup>de</sup>	62 (2) <sup>c</sup>	25 (3) <sup>b</sup>	11 (3) <sup>a</sup>	0 (0)	0 (0)	<0.001
Sub-shrub	height	0.46 (0.06) <sup>d</sup>	0.27 (0.03) <sup>c</sup>	0.49 (0.02) <sup>d</sup>	0.61 (0.07) <sup>e</sup>	0.23 (0.02) <sup>c</sup>	0.14 (0.01) <sup>b</sup>	0.03 (0.02) <sup>a</sup>	0.00 (0.00) <sup>*</sup>	0.00 (0.00) <sup>*</sup>	<0.001
	coverage	5 (1) <sup>b</sup>	5 (1) <sup>b</sup>	11 (1) <sup>d</sup>	16 (11) <sup>bcde</sup>	14 (1) <sup>e</sup>	8 (1) <sup>c</sup>	1 (1) <sup>a</sup>	0 (0)	0 (0)	<0.001
Graminoid	height	0.76 (0.06) <sup>e</sup>	0.47 (0.04) <sup>cd</sup>	0.40 (0.03) <sup>c</sup>	0.60 (0.08) <sup>def</sup>	0.42 (0.02) <sup>c</sup>	0.34 (0.01) <sup>b</sup>	0.51 (0.03) <sup>d</sup>	0.59 (0.04) <sup>e</sup>	0.04 (0.02) <sup>a</sup>	<0.001
	coverage	10 (1) <sup>a</sup>	10 (1) <sup>a</sup>	11 (2) <sup>ab</sup>	20 (6) <sup>bc</sup>	22 (2) <sup>c</sup>	33 (3) <sup>d</sup>	15 (2) <sup>b</sup>	69 (5) <sup>e</sup>	15 (4) <sup>ab</sup>	<0.001
Groundcover	height	0.01 (0.01) <sup>a</sup>	0.04 (0.01) <sup>b</sup>	0.04 (0.00) <sup>b</sup>	0.02 (0.00) <sup>a</sup>	0.10 (0.01) <sup>c</sup>	0.19 (0.01) <sup>d</sup>	0.19 (0.01) <sup>d</sup>	0.11 (0.01) <sup>c</sup>	0.02 (0.01) <sup>ab</sup>	<0.001
	coverage	1 (0) <sup>a</sup>	3 (1) <sup>b</sup>	6 (1) <sup>c</sup>	11 (4) <sup>cd</sup>	9 (1) <sup>c</sup>	20 (2) <sup>e</sup>	48 (3) <sup>f</sup>	41 (5) <sup>f</sup>	20 (8) <sup>cde</sup>	<0.001
	pparex	0.98 (0.00) <sup>f</sup>	0.95 (0.01) <sup>e</sup>	0.94 (0.01) <sup>e</sup>	0.95 (0.01) <sup>e</sup>	0.90 (0.01) <sup>d</sup>	0.84 (0.01) <sup>c</sup>	0.70 (0.02) <sup>a</sup>	0.79 (0.03) <sup>b</sup>	0.00 (0.00) <sup>*</sup>	<0.001

proportionate extinction of photosynthetically active radiation (PPAREX). Reference to quadrat numbers (Table 3.4) and Table 3.1 shows that the former group contains all the platform heaths which have remained unburnt in recent years. The second group of SCs contains non-shrub based vegetation (herbfields, grasslands, sedgelands), burnt heaths on sandstone platform and burnt wet heaths in intermediate areas. Heaths on sand dunes burnt in July 1991 (reconnaissance zones 6 and 14) occur in both major groups, vegetation with better developed shrub strata occurring in the first major group, vegetation with lesser developed shrub strata but better developed graminoid and groundcover strata occurring in the second major group. Heath on the sand dune north of Tabbagai Gap which was burnt in March 1992 occurs exclusively in the second major group, due to less well developed shrub strata.

It is clearly evident from Table 3.5 that individual SCs are differentiated within major groups on the basis of multiple attributes. Within the first major group, SC 1 is differentiated by a tall shrub stratum of high cover. However it is also differentiated by high PPAREX, a suppressed groundcover stratum and tall graminoid stratum. The shrub stratum of SC 2 is significantly lower in both height and cover compared with that of SC 1. Concurrently, it has significantly lower PPAREX, a shorter graminoid stratum and a groundcover stratum of significantly higher height and cover. It also has a significantly shorter sub-shrub stratum. The shrub stratum of SC 3 is intermediate in height between the previous two SCs but has significantly lower cover. Concurrently, coverage of both sub-shrub and groundcover strata is significantly greater. SC 4 is the smallest of the SCs, with only four quadrats included. However, it is distinctive from the previous three SCs in having a significantly taller sub-shrub stratum. SC 5 contains the burnt dune heath quadrats included in this major group as well as some structurally similar platform heath quadrats. This SC is differentiated by having the shortest and lowest cover shrub stratum in this major group. However, it is also clearly demarcated by having the tallest groundcover stratum and markedly lower PPAREX.

In the second major group of SCs the classification has made a clear distinction between SCs 6 and 7, and SCs 8 and 9. As shown in Table 3.5, this is based on the virtual absence of shrub and sub-shrub strata in the last-mentioned SCs. Reference to Table 3.4 shows that SC 6 contains mainly quadrats from burnt dune heath, and SC 7 contains mainly quadrats from burnt platform heath. While the height of shrub and

groundcover strata is similar between these SCs, SC 6 has significantly higher shrub stratum cover whereas SC 7 has significantly greater groundcover stratum cover. SC 8 includes quadrats from swamps and some from burnt platform heaths as well as burnt heaths in intermediate positions. As shown in Table 3.5 this SC has the greatest graminoid stratum cover of all SCs. It also has a groundcover stratum cover similar to that of SC 7. However, this stratum is significantly shorter and PPAREX is significantly greater. The shrub stratum means for this SC (Table 3.5) are not representative, and are attributable to the infrequent occurrence of shrubs in some of the swamp quadrats. SC 9 concords entirely with the *Samolus repens/Zoysia macrantha* community located on frontal platform areas, and is characterised by short graminoid and groundcover strata and zero PPAREX. As shown in Table 3.5, this SC differs significantly from SC 8 with respect to all common attributes.

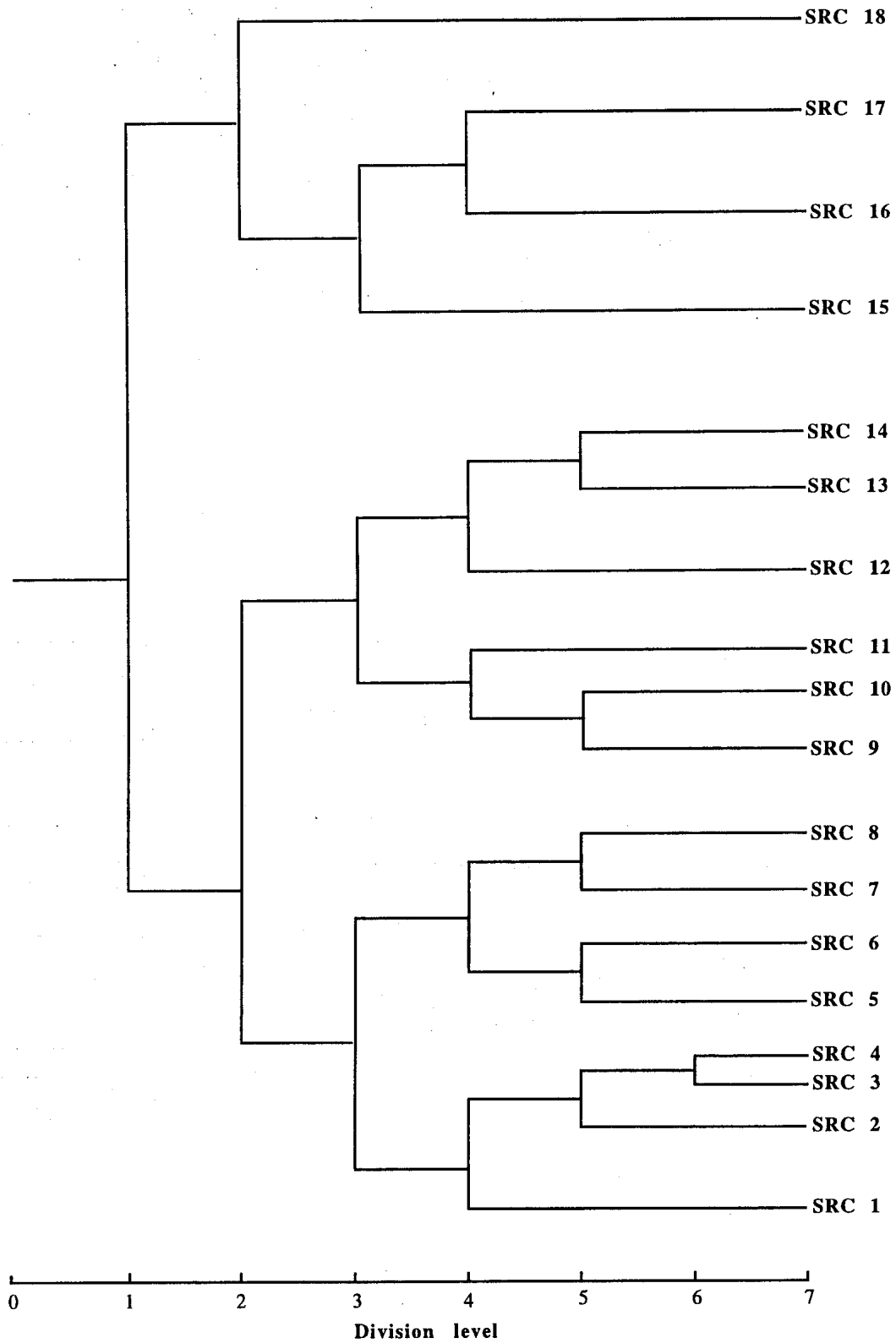
### 3.3.3 Multivariate classification of species richness

The classification dendrogram is shown in Fig. 3.4. As shown in Fig 3.4 18 species richness complexes (SRCs) were recognised. Quadrat membership to SRCs is provided in Table 3.6.

Total and strata species richness of SRCs is shown in Table 3.7. It is clearly evident that all SRCs differ from one another significantly with respect to either total species richness or richness of a particular stratum(a), or both. This provides evidence that a meaningful classification of species richness has been obtained.

The basis for the first classification division separating SRCs 1-14 from SRCs 15-18 (Fig. 3.4) is evident in Table 3.7. Clearly, SRCs 15 to 18 have significantly greater groundcover stratum richness (although see SRC 12). Also, in general, they have greater graminoid stratum richness and lower richness of the sub-shrub strata.

The first grouping of SRCs (SRC 1-14) was divided into two sub-groupings at the second division level, SRCs 1 to 8 and 9 to 14 (Fig. 3.4). General differences are evident between these groupings in Table 3.7, the former grouping having significantly lower total, shrub stratum, graminoid stratum and groundcover stratum species richness. This grouping (SRC 1-8) contains virtually all of the platform heath that has remained



**Fig. 3.4** Indicator species analysis dendrogram showing recognised species richness complexes.

Table 3.6 Quadrat membership of the species richness complexes.

Species richness complex	Quadrats
SRC 1	2/3.1, 2/3.2, 2/3.3, 2/3.5, 2/4.1, 2/4.3, 2/4.4, 2/5.2, 2/5.3, 2/5.4, 2/6.4, 2/6.5, 5/7.2, 5/11.2, 6/14.1, 6/14.2, 6/14.4, 6/14.5, 6/15.4, 6/15.5, 7/11.3, 7/11.4, 7/12.1, 7/12.3, 7/12.4, 7/13.1, 7/13.4, 7/14.2, 7/14.4, 10/7.4, 10/7.5, 13/5.3, 13/6.4, 15/4.2, 15/4.3, 15/4.5, 15/6.2, 15/6.5, 15/7.5, 15/10.2, 15/10.4
SRC 2	2/4.5, 5/5.2, 5/6.1, 5/6.2, 5/7.1, 5/8.1, 5/9.2, 5/10.1, 5/11.1, 5/12.2, 10/7.1 13/6.2
SRC 3	2/5.1, 5/10.2, 13/2.1, 13/6.3
SRC 4	9/10.3, 9/11.1, 9/11.2, 9/12.1, 9/12.2, 9/12.3, 11/9.4, 16/6.1, 16/8.1, 16/9.1, 16/10.1, 17/5.3
SRC 5	2/3.4, 8/6.1, 8/6.2, 8/6.3, 8/6.4, 8/6.5, 8/7.1, 8/7.2, 8/7.3, 8/7.4, 8/7.5, 8/8.1, 8/8.2, 8/8.3, 8/8.4, 8/8.5, 8/9.1, 8/9.2, 8/9.3, 8/9.4, 8/9.5, 13/1.1, 13/1.2, 13/1.4, 13/1.5, 13/3.3, 13/4.1, 13/5.5, 13/6.1, 13/6.5 15/5.1
SRC 6	2/6.2, 6/14.3 10/7.3, 13/1.3, 13/2.3, 13/2.5, 13/3.4, 13/4.3, 13/4.4, 13/4.5, 13/5.1, 13/5.2, 13/5.4, 15/5.5, 15/6.1, 15/8.3
SRC 7	7/12.2, 7/13.2, 7/13.3, 7/14.1, 7/14.3, 7/15.1, 7/15.2, 7/15.3 7/15.4, 10/7.2, 13/3.1, 13/3.5, 15/5.3, 15/6.3, 15/7.1, 15/7.2, 15/7.4, 15/8.1, 15/8.2, 15/10.1
SRC 8	2/4.2, 2/6.3, 7/11.1, 7/11.2, 13/2.2, 13/2.4, 13/3.2, 13/4.2, 15/4.1, 15/4.4, 15/5.2, 15/5.4, 15/6.4, 15/7.3, 15/8.4, 15/8.5, 15/9.1, 15/9.2, 15/9.3, 15/9.4, 15/10.3
SRC 9	14/12.1, 14/12.3, 14/12.5, 14/13.1, 14/13.3, 14/13.4, 14/13.5, 14/14.2, 14/14.3, 14/14.5, 14/15.4, 14/15.5
SRC 10	2/5.5, 2/6.1, 5/4.1, 5/4.2, 5/5.1, 5/8.2, 5/9.1, 5/13.2, 6/15.1, 6/15.2, 6/15.3, 14/12.2, 14/12.4, 14/13.2, 14/14.1 14/15.3
SRC 11	14/14.4, 14/15.1, 14/15.2
SRC 12	1/7.2, 1/8.3, 1/8.4, 1/9.2, 1/9.3, 1/9.5, 1/10.2, 1/10.3, 1/10.5, 5/14.1, 5/14.2, 5/15.1
SRC 13	1/8.5, 1/9.4, 5/12.1, 5/13.1, 5/15.2, 9/10.1, 12/8.1, 12/8.2, 12/8.3, 12/8.4, 12/8.5, 16/7.1
SRC 14	9/10.2, 9/11.3, 11/9.3, 11/10.2, 11/10.3, 11/10.4, 17/5.1, 17/5.2
SRC 15	1/7.1, 1/7.3, 1/8.1, 1/8.2, 3/1.2, 3/1.3, 4/2.4
SRC 16	1/7.4, 1/7.5, 1/9.1, 1/10.1, 1/10.4, 11/9.1, 11/9.2, 11/9.5, 11/10.1, 11/10.5
SRC 17	3/2.1, 4/1.1, 4/1.2, 4/1.3, 4/1.4, 4/1.5, 4/2.1, 4/2.2, 4/2.3, 4/2.5
SRC 18	3/1.1, 3/1.4, 3/1.5, 3/2.2, 3/2.3, 3/2.4, 3/2.5

**Table 3.7** Mean total and stratal species richness of the species richness complexes

Standard errors are indicated in brackets. P-values from one-way ANOVAs comparing means between SRCs are indicated. All ANOVAs conducted on square root transformed data. Significance of differences between means tested by Tukey tests. Means which do not share any superscript letter are significantly different ( $p < 0.05$ ).

Species richness group	Total (m <sup>2</sup> )	Species richness Stratum			
		Shrub (m <sup>2</sup> )	Sub-shrub (m <sup>2</sup> )	Graminoid (m <sup>2</sup> )	Groundcover (m <sup>2</sup> )
SRG 1	0.47 (0.01) <sup>c</sup>	0.19 (0.01) <sup>c</sup>	0.13 (0.01) <sup>c</sup>	0.12 (0.01) <sup>b</sup>	0.14 (0.01) <sup>b</sup>
SRG 2	0.61 (0.03) <sup>cd</sup>	0.14 (0.02) <sup>b</sup>	0.15 (0.01) <sup>c</sup>	0.15 (0.01) <sup>b</sup>	0.21 (0.02) <sup>bc</sup>
SRG 3	0.45 (0.02) <sup>bc</sup>	0.11 (0.02) <sup>ab</sup>	0.07 (0.01) <sup>a</sup>	0.20 (0.02) <sup>bc</sup>	0.15 (0.03) <sup>bc</sup>
SRG 4	0.42 (0.02) <sup>b</sup>	0.09 (0.02) <sup>ab</sup>	0.00 (0.00)	0.15 (0.01) <sup>b</sup>	0.25 (0.01) <sup>cd</sup>
SRG 5	0.17 (0.01) <sup>a</sup>	0.06 (0.00) <sup>a</sup>	0.04 (0.01) <sup>a</sup>	0.06 (0.01) <sup>a</sup>	0.03 (0.01) <sup>a</sup>
SRG 6	0.31 (0.01) <sup>ab</sup>	0.11 (0.01) <sup>ab</sup>	0.08 (0.01) <sup>ab</sup>	0.15 (0.01) <sup>b</sup>	0.04 (0.01) <sup>ab</sup>
SRG 7	0.26 (0.02) <sup>ab</sup>	0.15 (0.01) <sup>bc</sup>	0.08 (0.01) <sup>ab</sup>	0.07 (0.01) <sup>a</sup>	0.00 (0.00)
SRG 8	0.30 (0.02) <sup>ab</sup>	0.13 (0.01) <sup>b</sup>	0.12 (0.01) <sup>bc</sup>	0.07 (0.00) <sup>a</sup>	0.08 (0.01) <sup>ab</sup>
SRG 9	1.10 (0.02) <sup>e</sup>	0.31 (0.03) <sup>e</sup>	0.30 (0.03) <sup>e</sup>	0.31 (0.02) <sup>d</sup>	0.35 (0.03) <sup>de</sup>
SRG 10	0.79 (0.03) <sup>cd</sup>	0.24 (0.02) <sup>d</sup>	0.20 (0.01) <sup>d</sup>	0.24 (0.02) <sup>c</sup>	0.25 (0.02) <sup>cd</sup>
SRG 11	1.44 (0.06) <sup>f</sup>	0.48 (0.04) <sup>e</sup>	0.29 (0.02) <sup>e</sup>	0.33 (0.02) <sup>d</sup>	0.38 (0.00) <sup>de</sup>
SRG 12	0.95 (0.04) <sup>de</sup>	0.17 (0.02) <sup>bc</sup>	0.04 (0.02) <sup>a</sup>	0.17 (0.02) <sup>b</sup>	0.70 (0.05) <sup>f</sup>
SRG 13	0.71 (0.04) <sup>d</sup>	0.22 (0.02) <sup>cd</sup>	0.01 (0.01) <sup>a</sup>	0.23 (0.01) <sup>c</sup>	0.31 (0.04) <sup>de</sup>
SRG 14	0.70 (0.05) <sup>cd</sup>	0.00 (0.00)	0.00 (0.00)	0.31 (0.04) <sup>d</sup>	0.39 (0.03) <sup>de</sup>
SRG 15	1.21 (0.14) <sup>ef</sup>	0.39 (0.16) <sup>ef</sup>	0.00 (0.00)	0.13 (0.06) <sup>b</sup>	0.79 (0.14) <sup>f</sup>
SRG 16	1.14 (0.07) <sup>e</sup>	0.05 (0.03) <sup>a</sup>	0.00 (0.00)	0.35 (0.04) <sup>d</sup>	0.77 (0.03) <sup>f</sup>
SRG 17	3.30 (0.60) <sup>g</sup>	0.10 (0.10) <sup>ab</sup>	0.00 (0.00)	1.20 (0.13) <sup>f</sup>	2.10 (0.57) <sup>g</sup>
SRG 18	4.43 (0.75) <sup>g</sup>	1.57 (0.20) <sup>f</sup>	1.29 (0.36) <sup>f</sup>	0.57 (0.20) <sup>e</sup>	1.86 (0.63) <sup>g</sup>
ANOVA (p-value)	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.001

unaffected directly by fire in recent years. Both SRC sub-groupings (1-8 & 9-14) were further sub-divided at lower division levels (Fig. 3.4). As shown in Table 3.7 multiple differences in species richness are evident at all subsequent divisions of both groupings, particularly with the 9-14 subgrouping in differences are generally more pronounced.

The second grouping of SRCs (SRC 15-18) is distinguished from the first by component SRCs having markedly higher total species richness (although see SRC 11), low species richness of shrub and sub-shrub strata except for SRC 12, and markedly higher species richness of graminoid and groundcover strata. This second SRC grouping contains mainly quadrats from burnt platform heath (reconnaissance zone 1), swamps (reconnaissance zone 11), 'maritime herbfields' (reconnaissance zone 4) and frontal heathland islands (reconnaissance zone 3). This last-mentioned group of quadrats is contained mainly within SRC 18, which is distinctive in having markedly higher richness of shrub and sub-shrub strata as well as having high richness of graminoid and groundcover strata.

SRC 17 contains mainly quadrats of reconnaissance zone 4 as well as a single quadrat of reconnaissance zone 3. Like SRC 18 SRC 17 is not spatially expansive. In terms of the total number of species present this vegetation is species poor. However, in terms of species richness of graminoid and groundcover strata it was found to comprise the most species-rich SRC.

SRCs 15 and 16 contain quadrats mainly from swamps and more graminoid rich burnt platform heaths. Total species richness of these SRCs is approximately one third to one half of that of SRCs 17 and 18. Graminoid stratum species richness of SRC 15 is commensurate with that of SRCs 1 to 8 in the first major grouping, whereas graminoid stratum species richness of SRC 16 is commensurate with that of SRCs 9 to 14. As with total species richness, groundcover stratum species richness of SRCs 15 and 16 is approximately one third to one half that of SRCs 17 and 18. However, it is nevertheless significantly greater than that of SRCs comprising the first major grouping, except for SRC 12.



### 3.3.4 Concordance of property classifications and the site reconnaissance

The concordances between property classifications are shown in Fig. 3.5. The highest concordances between property classifications were recorded between the floristic and structural classifications. Approximately half the information in the structural classification was contained in the floristic classification whereas approximately one third of the information in the floristic classification was carried by the structural classification (Fig. 3.5). Similar amounts of information in both these classifications were contained in the classification of species richness (Fig. 3.5). However, relatively small amounts of information of the species richness classification were contained in either the floristic classification (10%) or the structural classification (11%).

Concordances between the site reconnaissance and property classifications are also shown in Fig. 3.5. Over half the information of the floristic classification was contained in the site reconnaissance (Fig. 3.5). Approximately a third of the information of the structural classification was contained in the site reconnaissance and approximately one fifth of the species richness classification (Fig. 3.5). As shown in Fig. 3.5 the information of the species richness classification contained in the site reconnaissance was approximately double that contained in either the floristic or structural classifications.

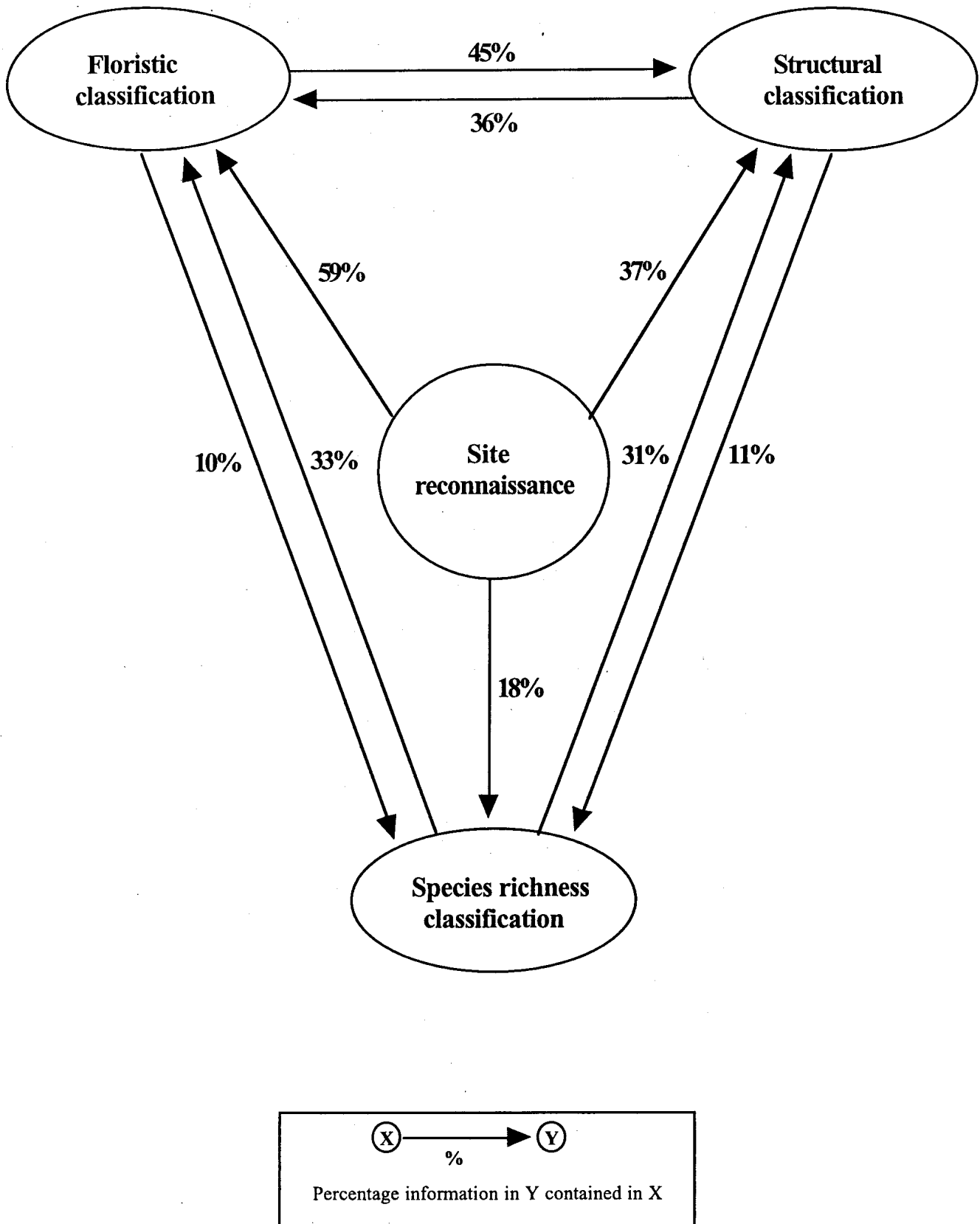


Fig. 3.5 Cross-information contents between property classifications and the site reconnaissance.

### 3.4 DISCUSSION

#### 3.4.1. The floristic component of community structure

This study has shown that the floristic component of cliff-top coastal heathlands in Botany Bay National Park displays marked variation in internal organisation. This indicates that the general diversity of cliff-top coastal heathlands lies not only in their richness of species (see Specht 1981b) but also in the variance displayed in composite floristic composition at local spatial scales.

Despite this detected patterns may simply be a function of stochastic processes and reflect the chance co-occurrence of species. However, the general concordance of complexes with reconnaissance zones, and hence major physiographic features, shows that the detected patterns are at least in part, functionally significant. This is also supported by the occurrence of many species in habitats in which they have previously been recorded (see Siddiqi *et al.* 1972).

Results of this study are consistent with previous studies of cliff-top coastal heathlands in the Sydney area which recognise multiple floristic complexes within localised areas (see Siddiqi *et al.* 1972; Clemens & Franklin 1980). However, in this study use of cover data coupled with polythetic classification has revealed clearly that platform heaths are differentiated by variation in cover of small subsets of structurally dominant species. These include: *Baeckea imbricata*, *Banksia ericifolia*, *Melaleuca armillaris*, *Westringia fruticosa*, and to a lesser degree *Hakea teretifolia*. All of these species are known to predominate in areas of impeded drainage and/or extreme exposure to maritime influences (see Siddiqi *et al.* 1972; Clemens & Franklin 1980; Adam *et al.* 1989a; Benson & Howell 1990).

Despite functional environmental factors, the role of competitive interactions of structurally dominant species cannot be dismissed in differentiation of platform heaths. Although competition itself has not been demonstrated in this study, observations and results of the classification suggest that *Baeckea imbricata* and *Banksia ericifolia* may be the most successful in terms of displacement of other species. In the former case this appears to be due to high numbers of individuals, while in the last-mentioned case it appears to be more the high density of foliage that precludes other species. Mean cover

of *Westringia fruticosa* in complexes was negatively correlated with that of the above two species (Appendix 3.3). The predominance of this species in positions of extreme exposure may reflect competitive displacement from other areas.

Four of the 11 floristic complexes corresponded to recently burnt vegetation. Fire has hence been a proximate influence on the observed complexity of the studied vegetation. Of the burnt complexes the *Rulingia hermaniifolia* complex was the only one with a direct unburnt counterpart, this being the *Banksia ericifolia/Baeckea imbricata/Melaleuca armillaris/Hakea teretifolia* complex. Comparisons between these complexes revealed that a large proportion of species in the latter were also present in the former burnt complex. This is consistent with the occurrence of 'autosuccession' whereby the vegetation is essentially self-replacing (see Groves & Specht 1981; Kruger 1983).

The occurrence of autosuccession is notwithstanding the dominance of the shrub *Rulingia hermaniifolia* at the time of survey. Although locally common this species is considered rare (Briggs & Leigh 1988; Robinson 1991). McRae (1990) noted very small populations in Bouddi National Park north of Sydney and suggested that this species may be fire sensitive. However, he did not make clear what was meant by the term 'fire sensitive'. In my study this species was observed to flower in early summer, just over a year subsequent to fire. This, along with its virtual restriction to recently burnt platform heaths shows that it is a fugitive species (i.e. grows and seeds only for a short time following fire, then is displaced).

The *Baumea juncea/Leptocarpus tenax* complex occurred at swamp sites. These were shown to have a distinctive and species-rich flora in the groundcover stratum. This diversity remains largely hidden by the dense and uniform graminoid stratum. Despite this, these swamp sites are not as diverse as swamp vegetation elsewhere (see Buchanan 1980; Keith & Myerscough 1993). This may be a reflection of their small spatial extent and disjunctive distribution in the landscape. Accounts by other workers suggest that swamps and other wetlands are closely associated with heathlands in the cliff-top coastal environment (see Hamilton 1918; Adam *et al.* 1988; Adam *et al.* 1989a; Johnson 1994). This has been confirmed by this study, swamps appearing as a characteristic element of the studied vegetation. It is of importance to note that swamp sites support high densities of graminoids, many of which are distributed throughout the

platform heaths and burnt platform heaths. It is foreseeable that these swamps may act as important genetic sources for the graminoid component in the landscape generally.

The *Samolus repens/Zoysia macrantha* complex, although species poor, is a distinctive complex. This complex is located exclusively on bare frontal platform areas which are subject to high levels of salt-spray deposition (see Chapter 5). I suggest that this complex may represent a primary successional stage of platform heath complexes. The two dominant species are observed to bind the substrate where they occur, providing stabilisation for the establishment of other species, which at the current time are principally maritime herbs. In this complex, establishment of *Baeckea imbricata* seedlings appears to be an immediate precursor to development of heath vegetation. This is supported by observations made outside the research area of small *Baeckea imbricata* shrublands developed over this complex. Also, the fact that 'heathland islands' distributed in the same area were classified as part of the *Baeckea imbricata* complex suggests that these islands are a result of the succession above rather than being remnants of heath retreating from the cliff-top. It appears that this complex may constitute part of a dynamic system which either builds or maintains cliff-top coastal heathlands in positions of extreme exposure. This, however, requires further investigation.

The classification of the vegetation based on floristic attributes alone shows a small-scale diversity of complexes previously undescribed for cliff-top coastal heathlands in the Sydney area. However, at a general level my recognised complexes correspond to heath ecosystems recognised at other localities. Both the *Aotus ericoides/Banksia serrata* complex and the *Lepidosperma squamatum/Gonocarpus teucrioides* complex correspond to 'sand heath' (Groves & Specht 1965) being located on entirely sandy and well drained dunes.

In the study of Siddiqi *et al.* (1972), the sand heath was divided into 'dry' and 'wet' types based on the presence of *Banksia ericifolia* in the latter type. A similar monothetic division may have been made in my study between the *Aotus ericoides/Banksia serrata* complex and the *Lepidosperma squamatum/Gonocarpus teucrioides* complex. However, use of cover data revealed that *Banksia ericifolia* and other species more typical of wetter situations were only a minor biomass component of the *Lepidosperma squamatum/Gonocarpus teucrioides* complex. Also, there appeared to be a more marked disjunction in the distribution of species between the two dry sand

heaths in my study. Factors other than the depth of the water table are presumably operating in the current study to produce the observed differences. Time since fire is an obvious candidate, as the two complexes have differing most recent burn dates. However, floristic differences between the complexes have been observed to be maintained for a period exceeding the difference between their burn dates. Other factors must hence also be considered.

In addition to sand heaths, 'groundwater heaths' have been identified by both Siddiqi *et al.* (1972) and Clemens & Franklin (1980). These are seasonally waterlogged heaths which occur on substrates where infiltration and/or drainage is impeded. The platform heaths identified in this study correspond to this heath ecosystem. However, differences in floristic structure are indicated between the groundwater heaths identified in this study and those identified in the above studies, in particular with those identified by Siddiqi *et al.* (1972). In their study, communities had significant proportions of exclusive species whereas in my study this is not the case. This may reflect more heterogenous physiography and physical soil properties in their study.

My study shows that the floristic component of cliff-top coastal heathlands displays considerable variance in internal organisation. Overall, this is characterised by spatial disjunctions in the distributions of both structurally dominant and sub-ordinate species. However, it is also characterised by more continuous spatial variation in the distributions of structurally dominant species within complexes and complex groups. In these instances (e.g. in platform heaths) heterogeneity in the abundance of sub-ordinate species is functionally linked to the cover of structurally dominant species (see Appendix 3.4). This supports the notion that detected multivariate patterns of internal organisation are of ecological significance insofar as there is not a large component of species that behave as noise in the data set.

In addition, this study highlights the need for use of cover (or alternative abundance data) and polythetic classification in the analysis of floristic composition of cliff-top coastal heathlands. Had presence/absence data been collected and analysed much of the internal organisation of floristic composition, as previously discussed, would likely have remained unresolved. This may be attributed to the fact that variance in floristic composition of cliff-top coastal heathlands results not only from *what* species co-occur but also from *how* they co-occur. In seeking to summarise variance in floristic

composition of cliff-top coastal heathlands the discarding of information should thus be approached with caution.

### 3.4.2 The structural component of community structure

This study shows that the vegetation displays considerable complexity in terms of both the number and multi-strata structure of the recognised structural complexes (SCs). The spatial diversity in shrub-based structure alone is commensurate with previous studies which have either described or quantified high levels of spatial diversity in shrub-based structure within local areas of cliff-top coastal heathlands in the Sydney area (e.g. McRae 1990; Benson & Howell 1994). This study confirms that shrub-based structure is a significant but variable component of community structure of cliff-top coastal heathland vegetation.

This study also shows that cliff-top coastal heathlands display fine-scale but marked differentiation in multi-strata structure. The patterns of differences in strata attributes between SCs were consistent with prior studies which have examined correlations of strata attributes of heathland vegetation. In general, positive correlations were evident between height and coverage of individual strata. Such correlations have been shown in the past for shrub and herbaceous strata of heathland vegetation (e.g. Keith & Myerscough 1993; Keith 1994). However, these studies did not seek to separate graminoids from other groundcover elements. In my study the graminoid stratum was found to be an exception, due primarily to a 'structurally plastic' height response where shrub stratum height and coverage were maximal (SC 1). This differential response would have remained unresolved had attributes of a composite groundcover stratum been employed in the classification.

Also, attributes of both the graminoid and groundcover strata were important in demarcating SCs across the full range of structural variation as well as within groups of related SCs. This utility parallels that of similar structural demarcations made in ecological studies of grassland and other non-shrub-based vegetation types (*see* Tremont & McIntyre 1994). Clearly, non-shrub-based structure in more complex heathland assemblages has utility for the classification of composite structure of this vegetation.

Although SCs have been demarcated on the basis of multiple attributes the primary functional influence of the shrub stratum attributes should not be overlooked. Keith & Myerscough (1993) provided evidence that light penetration through upland swamp (including heath) communities comprised a major component of a gradient underlying floristic composition and species diversity. They suggested that large species eliminated shorter species through limiting the availability of light, shown as a suppression of herbaceous height and cover with increasing height and cover of the shrub stratum and concurrently increasing light extinction. Similar relationships were shown in my study and it is clear that height and cover of the shrub stratum have functionally suppressive effects on graminoid and groundcover strata in the studied vegetation.

While this suppressive relationship may have a primary influence on multivariate structure as a whole, it is nevertheless obvious that it is mediated substantially by fire in the studied vegetation. Notwithstanding the added complexity and variability in structure brought about by fire, it was shown that the multivariate classification effectively recovered patterns which were related to both spatial and temporal aspects of previous fires. This shows that the multivariate classification has functional utility with respect to fire. This may be considered of particular importance given the relatively high frequency of fire in heathland vegetation (see Specht 1981c; Groves & Specht 1981).

### **3.4.3 The species richness component of community structure**

This study has shown species richness to be a useful attribute for the classification of cliff-top coastal heathlands. Although not directly comparable to other studies total species richness recorded for the studied heathlands would appear to be relatively low, with variance occurring within a relatively narrow range. This suggests that variance in species richness may contribute little to overall variance in community structure and by extension is not worthwhile investigating. However, the current study has shown that the studied vegetation displays considerable differentiation in terms of the multi-strata internal organisation of this property. It has also shown the existence of statistically significant differences in both total species richness and richness of individual



strata within the ranges recorded. Given the fact that species richness is known to be closely related to environment (*see* Terborgh 1973; Peet 1978; Hopkins & Hnatiuk 1981; Lamont *et al.* 1984; Robertson *et al.* 1984a; Day *et al.* 1988; Adam *et al.* 1989b; Van der Moezel & Bell 1989; Bowman *et al.* 1991; Hoover & Parker 1991; Keith & Myerscough 1993) it appears likely that differences in species richness recorded in this study would may be expressive of differences in environment and hence be of ecological importance. This is investigated in Chapter 5.

Differences (or variation) in species richness may be seen as occurring in a multidimensional hyperspace, the dimensionality of which is defined by many biotic and abiotic factors. It follows, particularly for complex communities, that interpretable resolution of differences (variation) in species richness should be enhanced by multidimensional solutions. This has previously been shown to be the case with respect to traditional direct gradient analyses of northern hemisphere forest ecosystems (e.g. Auclair & Goff 1971; Whittaker 1972, 1977). However, the number of environmental factors which can be effectively included in these analyses simultaneously is limited. Also, in these studies species richness has been treated essentially as a univariate property of vegetation with little reference to likely biotic dimensions. A possible exception is the considerable attention that has been paid to species richness of individual strata. However, in these instances patterns in species richness of separate strata have been analysed separately with multidimensional patterns implied indirectly. The fact that these studies have also shown close relationships between structure and strata species richness suggests the suitability of stratal dimensions for analysis of integrated community patterns in species richness. The current study shows that this can be effectually achieved for cliff-top coastal heathlands through multivariate classification. Importantly, application of multivariate classification to stratal dimensions of species richness has enabled resolution of a diversity of species richness complexes which differ in total species richness and/or richness of individual strata. This diversity is belied by univariate consideration of either total species richness or richness of individual strata. I hence suggest that a multivariate approach to enumeration of species richness of cliff-top coastal heathlands is an appropriate methodology, particularly in local areas where variance in total species richness may be limited.

#### 3.4.4 Foundations of a secondary synthesis of community structure

The results of this study show clearly the presence of determinable internal organisation in each of the three community properties. While in this chapter only general environmental reference is made, it is evident that this organisation is at least in part, of functional significance with respect to each property. However, irrespective of this significance, it was clear that patterns in variance in each property existed that could not statistically be attributed to stochasticity. From a purely categorical perspective, it is thus evident that variance in both structure and species richness, as well as in floristic composition, is amenable to ecological analysis and interpretation at local scales.

Quantitative comparisons confirmed that classifications of individual properties did not concord in terms of their information contents. The fact that relatively low concordances were recorded for pairwise comparisons indicates the presence of substantial relative amounts of variance in each property that occur independently. This may thus be seen as supporting the need for independent classifications of multiple properties since hierarchal constraintment of properties (either explicitly or implicitly) within a classification of one property may inappropriately divide the variance in attributes of the other properties. If this approach of pre-emphasis is taken then it is clear that additional major properties which co-define community structure can only be considered in a secondary descriptive sense. My study shows this to be the case for cliff-top coastal heathlands.

The advantage of constructing a secondary synthesis of community structure was also reflected by the information in individual classifications carried by the site reconnaissance. The majority of information of the floristic classification was carried by the site reconnaissance. This indicates that major patterns in floristic composition may in fact be adequately resolved by simple reconnaissance exercises. However, my study shows that this is not the case with respect to either structure, or particularly, species richness. The more general nature of these properties hence dictates that detailed analysis of these components is required if variance in internal organisation is to be adequately resolved.

Despite the above attention is drawn to the limitations of comparing separate multivariate classifications in order to identify concordance, or lack of it. In comparing

classifications the end result is most often a single figure expressing similarity, or distance between classifications (see Gauch 1982; Digby & Kempton 1987; although see Chapter 6). Visual summaries of common and independent components in terms of classified property attributes are difficult, if not impossible. Yet it is this detail which is of interest, not only from the perspective of management, but from the perspective of improving knowledge of potential ecological mechanisms underlying community structure as a whole. I suggest that alternative multivariate methodologies which facilitate resolution of these details are required. This is examined in the next chapter in which foundations for a tertiary synthesis of community structure are developed.

### 3.6 CONCLUSIONS

Classification of floristic composition showed that the studied cliff-top coastal heathland vegetation can be structured into 11 recognisable floristic complexes. Concordance of these complexes with 'dry' and 'wet' heath ecosystems, swamps, and 'maritime herbfields' demonstrates general functional structuring of this component of community structure. I conclude that the studied cliff-top coastal heathlands display differentiation in internal organisation of floristic composition rather than being comprised of a single homogenous floristic complex. This differentiation in internal organisation is the greatest thus far recorded at a local scale for the cliff-top coastal heathlands of the Sydney area.

In addition this study shows that floristic differentiation both within and between floristic complexes is equally a function of continuous variation in cover of structurally dominant species and of spatial distributional disjunctions of both structurally dominant and sub-ordinate species. I conclude that for adequate resolution of the floristic component of community structure that both properties need to be taken into account.

Classification of structure of the cliff-top coastal heathlands has shown the vegetation to be structurally differentiated with respect to height and coverage of five recognisable strata and proportionate extinction of photosynthetically active radiation. This study shows that the vegetation can be structured into nine complexes. These complexes were shown to differ significantly from one another in terms of attribute levels of both shrub and non-shrub strata. I conclude that structure of the studied vegetation displays a diversity in internal organisation rather than being comprised of a single structural complex. I also conclude that multivariate classification is an effective tool for fine-scale and meaningful resolution of structure within cliff-top coastal heathland vegetation.

Despite the differentiating capacity of non-shrub based structure in cliff-top coastal heathlands elevated levels of shrub stratum height and cover were shown to suppress non-shrub-based strata. However, graminoids were shown to display a notable increase in height in these circumstances. This response was not taxonomically constrained insofar as the response was noted for widely occurring species. Also non-graminoid herbs did not display this response. I thus conclude that for structural

classifications of cliff-top coastal heathlands that graminoid structure needs to be separated from that of other herbaceous species.

This study showed that total species richness and species richness of four strata vary significantly across the vegetation. When the species richness hyperspace (defined dimensionally by total and strata species richness) was classified 18 species richness complexes were recognised. These differed significantly from one another with respect to at least one but usually several dimensions. I thus conclude that the studied vegetation displays a diversity in internal organisation of species richness rather than being comprised of a single undifferentiated complex.

In addition, this study shows approximately equivalent ranges of variation in mean species richness between species richness complexes with respect to all strata. I conclude that variances in species richness of separate strata are of equivalent importance for variance in total species richness of cliff-top coastal heathlands. Notwithstanding this differentiation of the vegetation in terms of either total species richness or richness of individual strata was in general, less than that conveyed by total and strata richness considered collectively. Given this and the relatively narrow ranges of variation in total richness and richness of individual strata I conclude that consideration of either total species richness or richness of individual strata will likely be of limited utility within local areas of cliff-top coastal heathlands.

This study has thus shown the existence of determinable variance in the internal organisation of floristic composition, structure and species richness of cliff-top coastal heathlands. While this study is spatially restricted, and the ecological significance of resolved patterns remains to be fully established, I conclude that pre-emphasis on individual properties of community structure is unwarranted. I also conclude that a secondary synthesis of community structure leads to a greater understanding of the community structure of cliff-top coastal heathland communities than that obtainable from a primary synthesis. These conclusions were supported by the quantitative comparisons of the information content of classifications which showed differential spatial variance with respect to all properties.

## CHAPTER 4: CLIFF-TOP COASTAL HEATHLANDS IN BOTANY BAY NATIONAL PARK, SYDNEY: FOUNDATIONS OF A TERTIARY SYNTHESIS OF COMMUNITY STRUCTURE.

### 4.1 INTRODUCTION

In the previous chapter the community structure of the vegetation was elucidated in terms of floristic composition, structure and species richness. This constituted in part what has been termed a secondary synthesis. Communities, however, may be viewed as an integration of these three major properties. If integrated patterns and mechanisms maintaining such patterns are to be identified then, logically, relationships between defining properties need to be identified. As outlined by Drake (1990, 1991) this is necessitated in part by the potentially significant role of connectivity (interactions) between individual properties in producing/maintaining community patterns. Clearly, such interactions are unassessable by investigation of single properties. Importantly, it also follows that patterns which are *uniquely* attributable to individual properties also remain unassessable without identification of these relationships, or at least of common variance between properties. Such contributions may be significant to overall community structure.

The study detailed in this chapter investigates both independent (unique) and common (shared) variance components of community properties and constitutes in part what has been termed a tertiary synthesis of community structure. Emphasis is given to pairwise comparisons of properties. This emphasis is given in order to clearly highlight the nature of relationships and differences in pattern between different properties. For clarity and mathematical simplicity higher order relationships concerning all three properties have not been examined. However, this level of interaction is embodied in the community classification of the vegetation which is presented in chapter 6. A brief background to relationships between pairs of properties is provided below. A rationale for adopting a gradient analysis approach to construction of a tertiary synthesis is also provided along with details of research objectives and hypotheses.

#### 4.1.1 Background

##### 4.1.1.1 Floristic composition and structure: Independent and common variance components considered

Pre-emphasis in vegetation analysis, particularly in biogeography/phytosociology, has in the past been on either floristic composition (e.g. Siddiqi *et al.* 1972; Bridgewater 1976, 1981; Russell & Parsons 1978; Holton & Johnson 1979; Clemens & Franklin 1980; Brown & Hopkins 1983; Adam *et al.* 1989b; Gibson *et al.* 1991; Keith & Myerscough 1993; Pharo & Kirkpatrick 1994; Taggart 1994; Le Brocque & Buckney 1995) or structure (e.g. Dansereau 1951; Webb 1959, 1968, 1978; Webb *et al.* 1970, 1976; Barkman 1979, 1988a,b,c, 1990; Fox 1979; Cowling & Cambell 1980; Benson & Falding 1981; Gillison 1981; Walker & Hopkins 1990; Keith & Benson 1988; McRae 1990; Sato 1994). This polarisation has been justified on grounds of the spatial scale and/or logistics of investigations (see Poore 1962). However, I suggest that such pre-emphasis has detracted from research examining relationships between these properties, as well as independent contributions of separate properties to community structure. Notwithstanding this, a number of studies have been conducted which either compare patterns of floristic composition and structure directly or which document patterns in both properties separately, from which relationships or patterns of independent variation may be inferred.

Webb *et al.* (1970) compared multivariate classifications of both floristic composition and structure of rainforest vegetation in eastern Australia. They found concordance between the classifications at higher hierarchal levels. At lower levels, however, concordance was diminished due in part to the fact that structure was shown to be expressive of different environmental conditions than floristic composition.

Hamilton (1975) investigated changes in physiognomic and floristic attributes of Ugandan forests along an altitudinal gradient (ca. 1000 m to 4000 m). Declining floristic similarity was recorded between adjacent altitudinal zonations with increasing altitude. This gradient was shown to be correlated with variation in the number of species present possessing various physiognomic attributes. A variety of other studies has similarly shown variation in physiognomy/structure along environmental

gradients, and shown concurrent variation/differences in floristic composition (e.g. Parsons & Moldenke 1975; Cowling & Campbell 1980; Kirkpatrick 1984; Wilson & Bowman 1987; Druitt *et al.* 1990; Bowman *et al.* 1991; Nilsson & Wilson 1991).

Bridgewater (1978) compared physiognomic and floristic classifications of coastal vegetation of East Gippsland, Victoria. He found a lack of congruence between the classifications which he ascribed to the ecological and structural amplitude of dominant species. While structural data were collected in this study these were only used to place samples in sub-formations according to the scheme of Specht (1970) with one or two dominant species being used to further sub-divide these sub-formations. The classifications were hence not entirely independent. However, the lack of congruence did not appear overly biased or artefactual.

Del Moral *et al.* (1978) examined suppression of coastal heathland by *Eucalyptus baxteri* at Pillar Point, Wilsons Promontory. Through field survey and some experimental studies they showed differential suppression of a number of heath species by shading and/or allelopathy. This demonstrates a functional relationship between structure and floristics associated with *Eucalyptus baxteri*.

Whittaker *et al.* (1979) investigated floristic composition and structure of a mallee stand in New South Wales. They showed that a major compositional gradient was strongly related to a gradient in vegetation height and coverage. This corresponded to a transition from mallee clumps to open areas. They also demonstrated a clear dispersion of floristic composition with respect to height/lifeform of component species.

Williams & Ashton (1987) demonstrated concordant continua of floristic composition and structure for heathland and grassland of the Bogong High Plains, Victoria. Shrub height and coverage, and grass height and coverage were shown to be inversely related along this continuum. Similar relationships were shown for vegetation in the same area by McDougall (1982). However, in this more spatially extensive study, the distribution of species, and structure, displayed a more discontinuous mosaic pattern.

Burgman (1988) used mantel tests to compare matrices of floristic composition, structure and geographical distances for a variety of vegetation in southern Western Australia as well as to relate these matrices to existing soil and vegetation map units. Floristic and structural matrices were found to be significantly related.



Macnally (1990) investigated the roles of floristics and physiognomy in avian community composition in south-eastern Australia. Mantel tests were used to compare dissimilarity matrices of floristic composition and structure. These matrices were found to be significantly correlated, although floristic data for understorey species were omitted from the analysis. I envisage that the recorded correlation would have been greater if these data had been included.

Keith and Myerscough (1993) investigated relationships between floristic composition, structure, species richness and environment for upland swamp vegetation south of Sydney. They found strong correlations between a number of structural attributes and major vectors of a compositional ordination. They also showed inter-correlations between individual structural attributes which were concordant with these vectors. Structural attributes included height and coverage of shrub and herb strata as well as light penetration. Attributes of individual strata were positively inter-correlated with correlations of separate strata being alternatively significant with respect to compositional vectors. Light penetration was found to be closely associated with height and coverage of the shrub stratum, along with species diversity of the vegetation.

Haering & Fox (1995) briefly noted some relationships between structure and floristic composition for coastal heathland at Myall Lakes, New South Wales. They cite an opening of the 'vegetation profile' and an increase in sedge cover as corresponding to variation in composition towards species adapted to waterlogging. This was noted for swamps of relatively low elevation. In higher vegetation of greater complexity, however, species replacements were noted within vegetation of similar structure. These replacements were related to soil moisture and elevation.

The studies outlined above, and a variety of others (e.g. Grubb *et al.* 1963; Veno 1976; Hopkins & Robinson 1981; Rotenberry 1985; Kirkpatrick & Duncan 1987; Barkman 1988a; Komarkova & McKendrick 1988; Wright & Mueller-Dombois 1988; Enright 1989; Bowman *et al.* 1990; Tonteri *et al.* 1990a,b; Keith 1994, Wahren *et al.* 1994), show that relationships and/or pattern differences between floristic composition and structure are resolvable at a variety of scales as well as within a variety of vegetation types. They also show that the detail is ecologically interpretable. Such interpretation may be idiosyncratic with respect to individual studies. However, there appears to be some generalities which can be drawn regarding relationships between

floristic composition and structure. First, it is evident that available light and space in communities provide primary niche axes along which species differentiation is manifested structurally. In this context, floristic composition and structure must necessarily be related. Second, it is evident from the above studies and others (e.g. Hamilton 1918; Boyce 1954; McColl 1969; Buchanan & Humpheys 1980; Enright 1989; Nilsson & Wilson 1991) that floristic composition and structure might be related differently to environment. In such circumstances, floristic-structural gradients/complexes might arise where each property varies independently of the other to some degree. In these instances it becomes important to be able to identify common and independent variance components of both properties, not only to improve the resolution of community structure but also to provide more informative ecological insights into this community structure.

#### 4.1.1.2 Floristic composition and species richness: Independent and common variance components considered

Patterns of floristic composition and species richness must concord to some degree by the simple logic that a given composition must have a specified species richness. The converse, however, is clearly not the case, i.e. that a given species richness must have a specified floristic composition. Many examples may be found in the literature which show similar species richness for floristically differentiated communities (e.g. Naveh & Whittaker 1979; Whittaker *et al.* 1979; Brown & Hopkins 1983; Gentry & Dobson 1987; Specht & Specht 1989a,b; Lunt 1990; Gibson *et al.* 1991). As a consequence of these characteristics it follows that variance in species richness must concord entirely with variance in floristic composition. Conversely, the proportion of total variance in floristic composition that concords with variance in species richness may vary depending on the portion of total variance in floristic composition that is independent, i.e. the portion that arises from turnover of species (pattern/beta diversity) without variance in species richness. Quantification of both of these variance components would allow for the relative importance of each component to overall diversity of the vegetation to be assessed.

Relationships between floristic composition and species richness involve the variance component which is shared between the properties. These relationships must involve the gain or loss of species and the concomitant change in floristic composition. I suggest that investigation of these relationships is likely to reveal quantitative characteristics of species packing and turnover (see Pielou 1975; Harper 1977; Hubbell & Foster 1986; Kitching 1986; Terborgh & Robinson 1986; Tilman 1986; Pacala & Tilman 1994).

The assertion made previously, that the species richness component must concord entirely with that of floristic composition, is correct with respect to total species richness. However, in my study species richness is defined multivariately by both total species richness and richness of individual strata. A number of recorded shrub species were not restricted to individual strata and occurred simultaneously in two or more strata. As a result, some variance in species richness may in fact be independent of floristic composition. Such variance would encompass addition or loss of species in strata of otherwise floristically identical vegetation. Such variance might have an environmental explanation. However, I envisage that it will reflect fine-scale successional patterns as well as population dynamics of component species. Full exposition of these aspects are beyond the scope of this study. However, quantification of this variance component and examination of its nature are useful starting points.

#### 4.1.1.3 Structure and species richness: Independent and common variance components considered

It is well known that structural diversity of vegetation promotes structural niche diversification with respect to both animals (see Abbott 1976; Holmes *et al.* 1979; Fox & Fox 1978; Fox 1981; Brown & Stillman 1993; Haering & Fox 1995) and plants (see Grubb 1977, 1986; Cody 1986). A link may thus be seen as existing between structure and species richness, with more structurally complex vegetation being likely to support more species (although see Whittaker 1977). It may thus be reasonably expected that total and strata species richness of the studied vegetation are related, and are related to structural attributes. Previous studies of both heathland and non-heathland vegetation have used tree/shrub/herb or overstorey/understorey classifications of species

richness, and have in general shown negative relationships between coverage or related attributes of the tallest stratum and species richness of lower strata (e.g. Collins & Pickett 1987; Specht & Specht 1989b; Keith & Myerscough 1993; Keith & Bradstock 1994). This is consistent with the inhibition model of succession of Connell & Slatyer (1977) whereby species are lost, principally through shading, as ecological dominance is established. However, these studies have used generalised strata classifications of species richness i.e. overstorey/understorey and shrub stratum/groundcover stratum classifications. While such classifications may be sufficient for resolution of general structural/species richness relationships, I suggest that they are limited for resolution of finer scale relationships in heathland vegetation. In the previous chapter it was shown that significant differences in both structure and species richness exist for at least four discernible strata in the studied vegetation. Previously unresolved relationships might thus present themselves through direct quantitative comparison of the defined structural and species richness matrices.

Despite the likely existence of relationships between structure and species richness, of equivalent interest in terms of this thesis is the degree and nature of vegetation pattern which is expressed by each property independently of the other. Species richness is known to vary within strata of this vegetation, as well as within strata of vegetation types elsewhere. Within this context, independent variation in species richness is assessable for vegetation of a given stratal arrangement. However, such assessment ignores any relationship which may be present between species richness and structural attributes (i.e. height and cover of strata). If independent variation in species richness is to be validly assessed then variance dependent on structural attributes needs to be partialled out. Similar reasoning can be applied to characterisation of variance in structure which is independent of species richness. Like comparisons between other properties, quantification of the independent variance components will enable assessment of information loss attributable to pre-emphasis on one property.

#### 4.1.1.4 A rationale for a gradient analysis approach to construction of a tertiary synthesis of community structure.

In order to characterise variance components it is desirable to be able to represent sites/complexes with respect to variance in attributes which characterise the relevant components. In this way the spatial and/or ecological aspects of variance components could be effectively modelled. This can not be readily achieved through classification algorithms. As outlined in the previous chapter, methods of comparing of classifications generally only return relative measures of similarity or distance between classifications. While possible to characterise the nature of similarities/differences between pairs of complexes in terms of attributes this is unwieldy due to the numbers of complexes involved. It also does not allow for diagnosis of variance components with respect to the entire data set. In addition to this comparisons of classifications does not allow for the quantification of the magnitude of variance components, i.e. similarities/differences between classifications are generally in percentage terms. The relative contribution of the different components to overall community structure can thus not be assessed. Alternative multivariate methodologies are required if variance components are to be effectively modelled.

Multivariate gradient analysis techniques (see Jongman *et al.* 1987; ter Braak & Prentice 1988) present themselves as potentially useful methods for constructing a tertiary synthesis of community structure. Of the techniques available which allow simultaneous representation of sites/complexes and attributes, the correspondence analysis family of techniques has arguably been the most widely accepted (see Kent & Coker 1992). These techniques assume unimodal (Gaussian) attribute responses in data sets, which is consonant with contemporary vegetation theory (see Gauch & Whittaker 1972; Gauch & Chase 1974; Whittaker 1975, 1978a; ter Braak 1985, 1986; Austin 1985, 1987; although see Austin *et al.* 1984). These techniques have also been shown to perform well with both simulated and real data sets (see Austin 1976; Fasham 1977; Gauch *et al.* 1977; Hill 1979b; Gauch *et al.* 1981; Oksanen 1983; Rice & Westoby 1983; Greenacre 1984; ter Braak 1985; ter Braak & Looman 1986; Minchin 1987; ter Braak 1987; ter Braak & Prentice 1988; Montana & Grieg-Smith 1990; Allen *et al.* 1991; Hill 1991; Smith & Jones 1991; Bates 1992; Foster 1992; Glaser 1992;

Balfour & Bond 1993; Lavorel *et al.* 1993; Palmer 1993; Okland & Eilertsen 1994) and are considered to be relatively robust to departures from assumptions (see ter Braak & Prentice 1988; Palmer 1993). I thus suggest that these techniques provide an appropriate basis on which to construct a tertiary synthesis of community structure.

Of particular interest are the techniques of correspondence analysis (Hill 1973) and canonical correspondence analysis (ter Braak 1986) as presented in the computer program CANOCO (ter Braak 1987). In this program both techniques allow for variance partitioning whereby the variance of specified factors can be removed from the final solution. The latter technique allows specifically for the constraining of the final solution by factors of interest. Further, these techniques allow for a quantification of entire variance in properties and that remaining subsequent to any partitioning. These characteristics indicate that these techniques would be commensurate with the purpose of constructing a tertiary synthesis of community structure.

Despite this, these techniques have traditionally been used to relate single properties to various sources of environmental variation (e.g. Oksanen 1983; Montana & Grieg-Smith 1990; Allen *et al.* 1991; Hill 1991; Smith & Jones 1991; Bates 1992; Foster 1992; Glaser 1992; Balfour & Bond 1993; Lavorel *et al.* 1993; Okland & Eilertsen 1994; Le Brocque & Buckney 1995) and have not been used for variance partitioning in the context proposed. This remains inexplicable with the possible exception that the assumptions implicit in these techniques may not be valid with respect to all comparisons made. However, in view of the relatively robust nature of the techniques and the fact that alternative techniques have not been developed for such an application I suggest that a CA/CCA based variance partitioning approach to a tertiary synthesis of community structure be developed.

In this chapter I develop a new application of the CA/CCA techniques for constructing a tertiary synthesis of community structure of the vegetation. In this approach the variance between all quadrats is utilised. This hence differs from the classificatory approach in which differences between groups of quadrats (complexes) were emphasised. However, for consistency and ease of interpretation reference to complexes has been maintained in this chapter where appropriate.

#### 4.1.2 Research objectives and hypotheses

This chapter investigates the major hypothesis that;

*community structure of cliff-top coastal heathlands is a function of both common variance between major properties and variance which is uniquely attributable to individual properties.*

Two research objectives were addressed in examining this hypothesis. The first was to determine the existence and magnitude of independent (unique) and common variance components. The second research objective was to identify the specific nature of both common variance between pairs of properties and independent variance of properties. I considered that such identification would provide new insights into *how* properties are related/not related in cliff-top coastal heathland communities.

Address of these objectives has been approached through application of multivariate gradient analysis techniques. Partial correspondence analyses have been used to isolate and elucidate independent variance components. Partial canonical correspondence analyses have been employed to isolate and elucidate common variance components between pairs of properties. Through these applications it will be established that community structure of cliff-top coastal heathlands is a function of both complex relationships between properties as well as their independent variance.

## 4.2 MATERIALS AND METHODS

### 4.2.1 Data sets

Data sets used in analyses detailed in this chapter are those used for classification of individual properties in the preceding chapter. However, in this chapter data for sites 51 to 60 have been omitted. These sites correspond to the *Samolus repens*/*Zoysia macrantha* complex (see Chapter 3). These omissions were necessary due to the relatively few species contained in these sites and their floristic distinctiveness. The multivariate gradient analysis techniques used in this chapter (see below) are particularly sensitive to these characteristics and will usually express this difference along the major axis of variation while suppressing variation between the larger number of samples. This is not artefactual but was considered undesirable in view of the small number of samples involved and the relatively clear differences in community structure between these and the remaining samples.

### 4.2.2 Numerical analyses

Correspondence analysis was performed on each of the property matrices for floristic composition, structure and species richness. This was done to establish the relative distribution of property complexes and attributes. It was also done to derive the 'trace' for each analysis. The trace is the sum of all the axis eigenvalues in a (unconstrained) correspondence analysis and provides a measure of the total dispersion (inertia) of the attribute data (Montana & Grieg-Smith 1990; Bocard *et al.* 1992). These analyses as well as those described below were all performed using the computer program CANOCO Version 2.1 (ter Braak 1987).

Partial correspondence analyses were applied to each pair of properties in order to isolate common (shared) and independent (unshared) variance components. This was done by specifying all attributes of one property as covariates then performing a correspondence analysis on the other property with the effects of these covariates removed. This was done reciprocally (i.e reversing data sets). For each partial



correspondence analysis the revised trace was taken as a measure of the variance in the relevant property which was independent (unique) of the property whose attributes had been specified as covariates. The difference in trace values between the partialled and unpartialled correspondence analyses was taken as a measure of the variance in the partialled property in common with the property whose attributes had been specified as covariates. In order to identify the nature of independent variance components site/attribute plots were prepared for each partial correspondence analysis. In the case of floristic composition only dominant species were plotted. These were inspected visually and compared with similarly prepared plots of the results of corresponding unpartialled correspondence analyses.

To investigate the nature of common variance (i.e. relationships) between properties canonical correspondence analysis (CCA) was used. I considered that major relationships between properties would be resolved sufficiently by performing one CCA with respect to each property pair rather than performing CCA reciprocally. To this end, CCA was performed on floristic composition constrained by structure, floristic composition constrained by species richness and species richness constrained by structure. Axis scores from the corresponding partial correspondence analysis of the constrained property were specified as covariables in each analysis. In this way variance in the constrained property which was independent of the constraining property was removed (partialled) from the analysis. Subsequently, CCA biplots were constructed and interpreted visually.

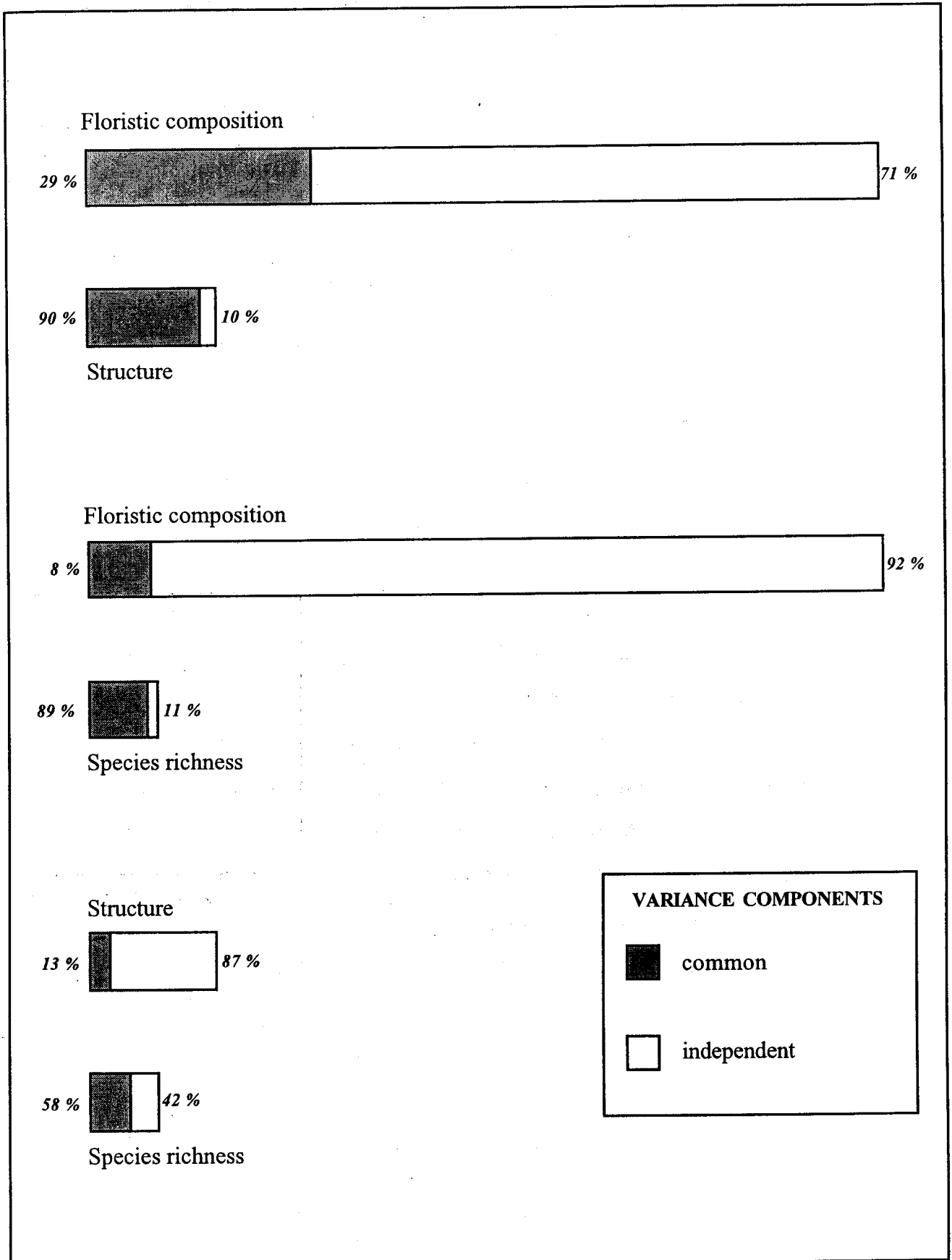
## 4.3 RESULTS

### 4.3.1 The existence and magnitude of independent and common variance components of community properties.

Variance partitioning showed that both common and independent variance components are characteristic of each community property (Fig. 4.1). For each property comparison, common variance components were found to be non-symmetric with respect to both their absolute magnitude and the proportions of total property variance they represented (Fig 4.1).

The majority of variance in structure was found to be common with floristic composition, whereas only 29% of the variance in floristic composition was found to be common with structure. This relatively smaller proportion, however, was found to exceed the total variance in structure in absolute terms (Fig. 4.1). A similar inverse relationship between the proportions and total amounts of common variance was found between floristic composition and species richness. However, in this instance the absolute difference in common variances was marginal. Of the total variance in species richness, 89% was common with floristic composition, a proportion similar to that of structure common with floristic composition. However, only 8% of the variance in floristic composition was common with species richness. In the comparison of structure and species richness, a greater absolute and proportional amount of variance in species richness was common with structure than the variance in structure in common with species richness.

The largest independent variance components found were for floristic composition. It can be seen from Fig. 4.1 that the vast majority of variance in floristic composition is independent of structure and species richness. Proportionally, the variance in structure independent of species richness is equivalent to the independent variance components for floristic composition. That of species richness independent of structure is approximately half this proportion. Relatively small variance components were found for both structure independent of floristic composition and species richness independent of floristic composition (Fig. 4.1).



**Fig. 4.1** Common and independent variance components of community properties based on pairwise comparisons. Lengths of horizontal bars representing property variance are proportional to traces of unpartialled correspondence analyses (see text). Percentages shown are percentages of the trace represented by each of the variance components.

### 4.3.2 The nature of independent variance components of community properties.

#### 4.3.2.1 Floristic composition versus structure

Variance in floristic composition which is independent of structure is shown in Fig. 4.2b. By comparison with the unpartialled analysis of floristic composition (Fig 4.2a) it can be seen that separation of complex centroids has been reduced. With the exception of the *Baumea juncea/Leptocarpus tenax* complex, centroids, in general, lie on a single vector. This is concordant with a floristic gradient involving an approximate sequential replacement of dominant species. In the case of the former complex, displacement of the centroid is due to the fact that *Leptocarpus tenax* dominates in this complex but is a minor component elsewhere. It is also due to a specific sub-ordinate flora (see Chapter 3).

Of interest in Fig. 4.2b is the slight displacement of the *Schoenus brevifolius/Baeckea imbricata(s)* complex centroid to the opposite side of the gradient. This resulted in this centroid and that for the *Baumea juncea/Leptocarpus tenax* complex being located further apart than in the plot for the unpartialled analysis (Fig 4.2a). Removal of floristic variance attributable to structure has accentuated the floristic differentiation of these two structurally similar complexes. Conversely, the *Rulingia hermaniifolia* complex centroid was placed in proximity to those for the unburnt platform heath complexes. The *Rulingia hermaniifolia* complex contains a number of early pyric successional species. While these species distinguish this complex (see Chapter 3) their occurrence is concordant with the gross structural changes brought about by fire. The centroid for this complex has hence been brought closer to the other centroids in Fig 4.2b, the variance due to structure having been removed. It is also worth noting that unburnt platform heath complexes share a substantial proportion of their species with the *Rulingia hermaniifolia* complex, although a number differ in their structural disposition (see Chapter 3). The removal of variance attributable to structure has allowed for greater expression of this similarity in Fig. 4.2b.

Variance in structure which is independent of floristic composition is shown in Fig. 4.3b. The relatively low magnitude of this variance is clearly evident in this plot with the distribution of structural complex centroids and structural attribute optima

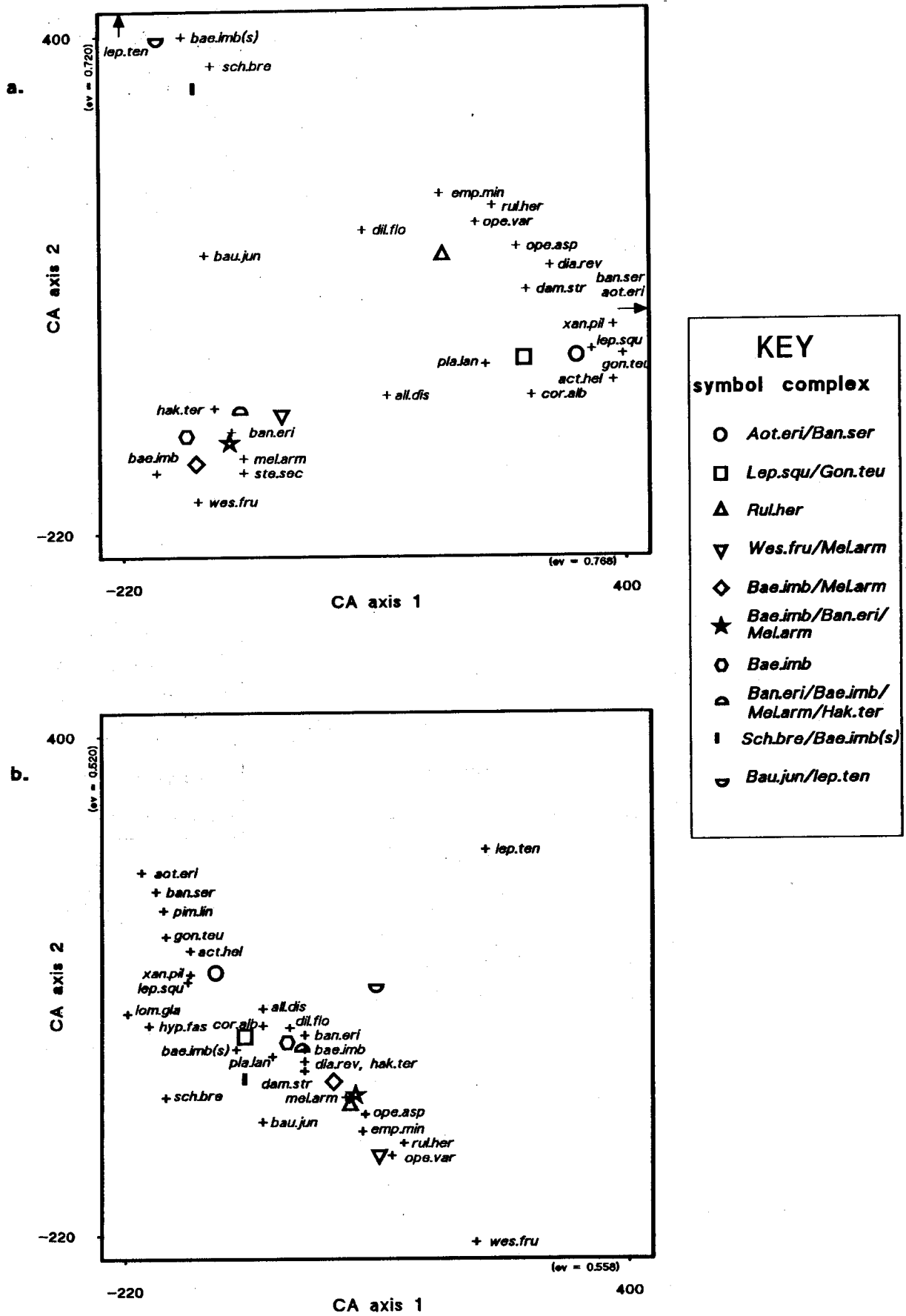
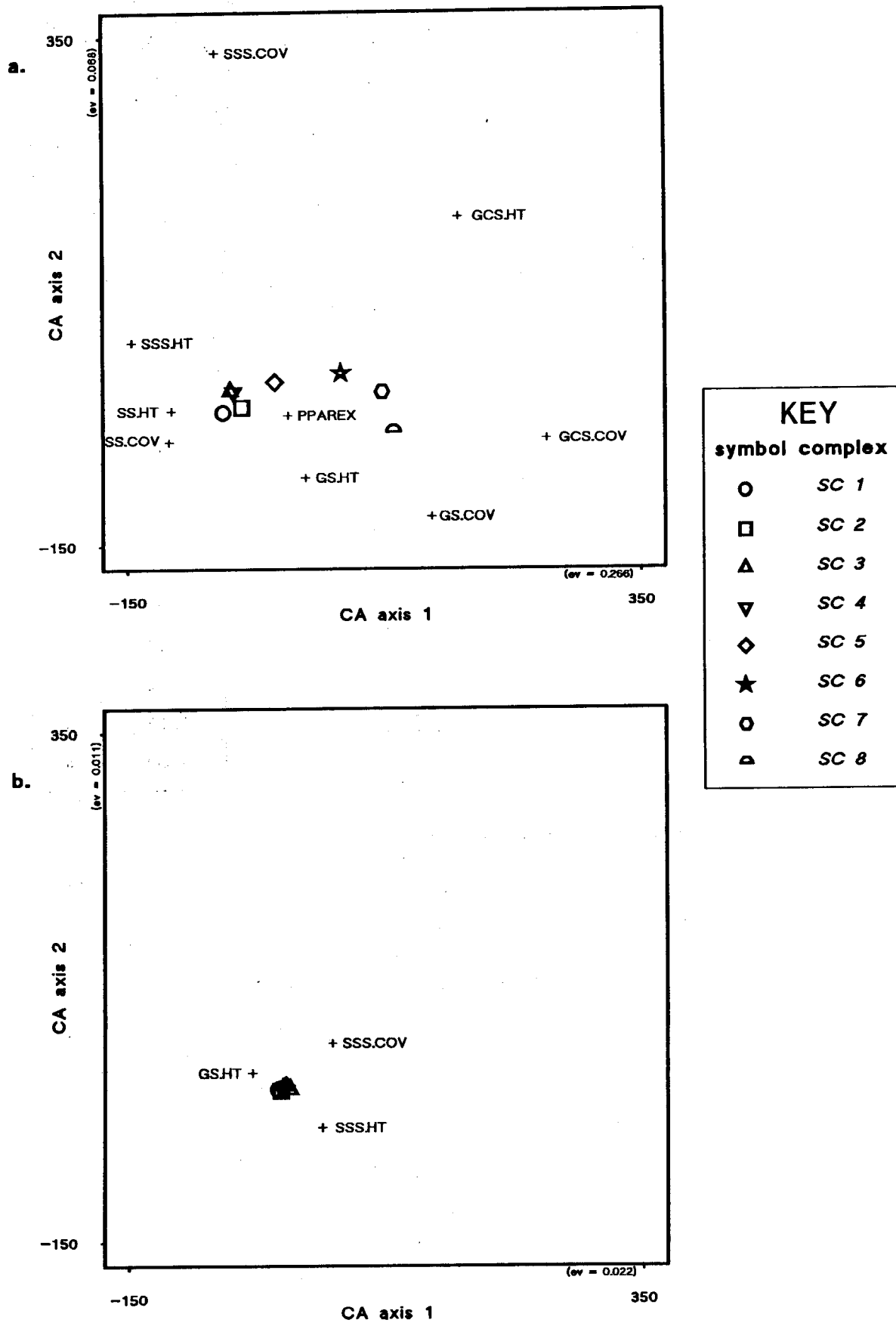


Fig. 4.2 Variance in floristic composition independent of structure. a. Correspondence analysis of floristic composition. b. Partial correspondence analysis of floristic composition with structure partialled out. Only dominant species are shown (see text).



**Fig. 4.3** Variance in structure independent of floristic composition. **a.** Correspondence analysis of structure. **b.** Partial correspondence analysis of structure with floristic composition partialled out. Structural attribute maxima not shown in the partialled analysis are located within the cloud of complex site centroids.

having collapsed towards the origin. Notwithstanding this, independent variance in structure does occur. It is evident in Fig. 4.3b that this is characterised by variance in height and coverage of the sub-shrub stratum, and in height of the graminoid stratum. Variance in height and coverage of the sub-shrub stratum can be attributed to variance in these attributes within a number of areas which would otherwise be considered floristically homogeneous. Independent variance in height of the graminoid stratum can be attributed to substantial plasticity in height of a number of graminoid species but principally *Baumea juncea* and *Schoenus brevifolius*.

#### 4.3.2.2 Floristic composition versus species richness

Variance in floristic composition which is independent of species richness is shown in Fig. 4.4b. It can be seen that the relative distribution of floristic complexes and attributes (species) is similar to the unpartialled analysis of floristic composition (Fig. 4.4a). This reflects the relatively small amount of total variance in floristic composition which is common to species richness. Notwithstanding this, some contraction of complex centroids is evident. This occurs mainly between the dune heath complexes and the *Rulingia hermaniifolia* complex, and shows that the floristic differentiation of these complexes is linked in part to vectors in species richness.

Variance in species richness which is independent of floristic composition is shown in Fig. 4.5b. A similar pattern to that of structure independent of floristic composition (Fig. 4.3b) is evident, with a contraction of centroids and attribute optima towards the origin (compare with Fig. 4.5a). The remaining independent variance in species richness is characterised by variance vectors in species richness of shrub, sub-shrub and graminoid strata. I consider the remaining variance in the latter stratum to be a result of stochasticity. Since graminoid species are restricted to one stratum, variance in species richness of this stratum cannot be independent of variance in floristic composition.

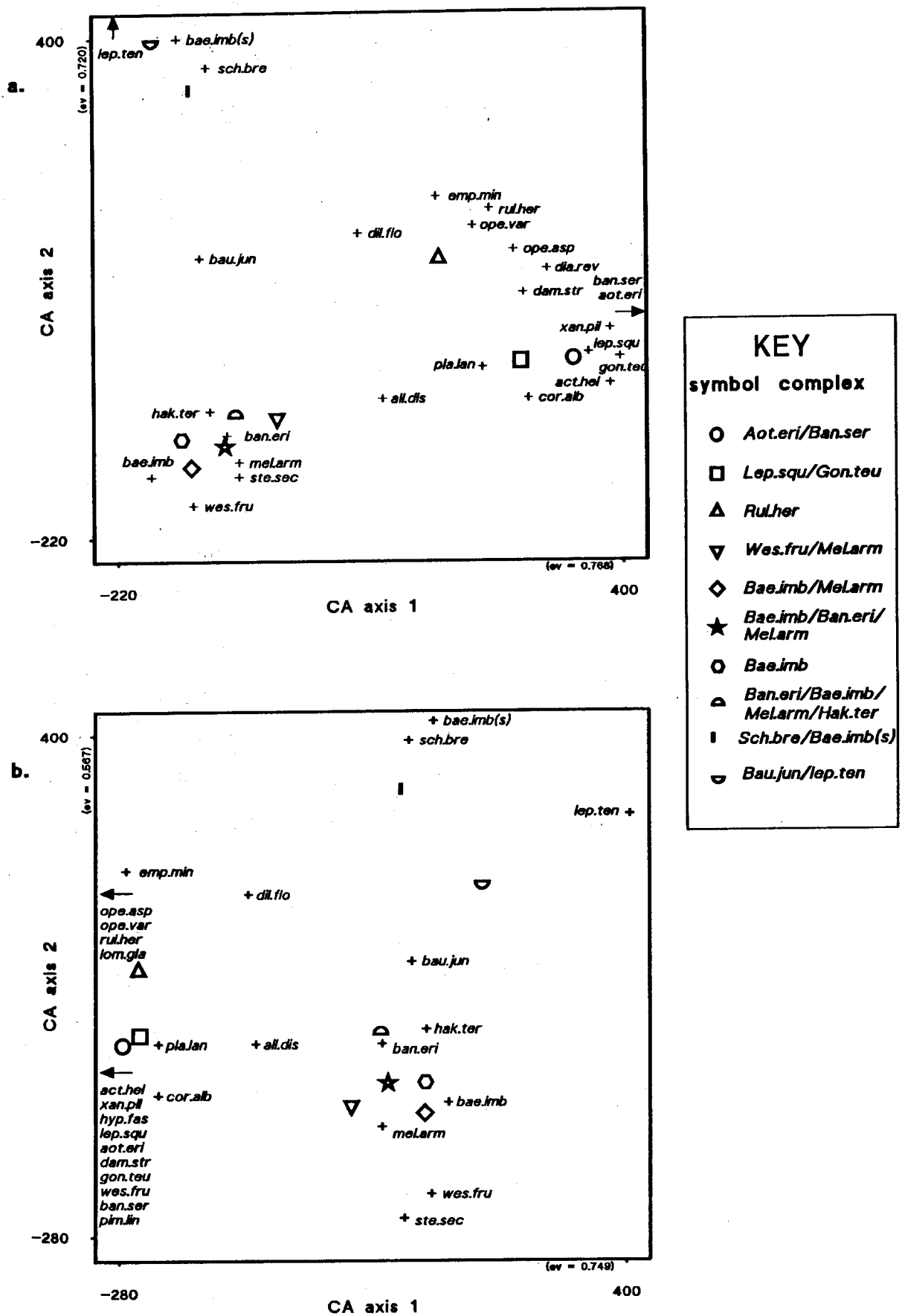
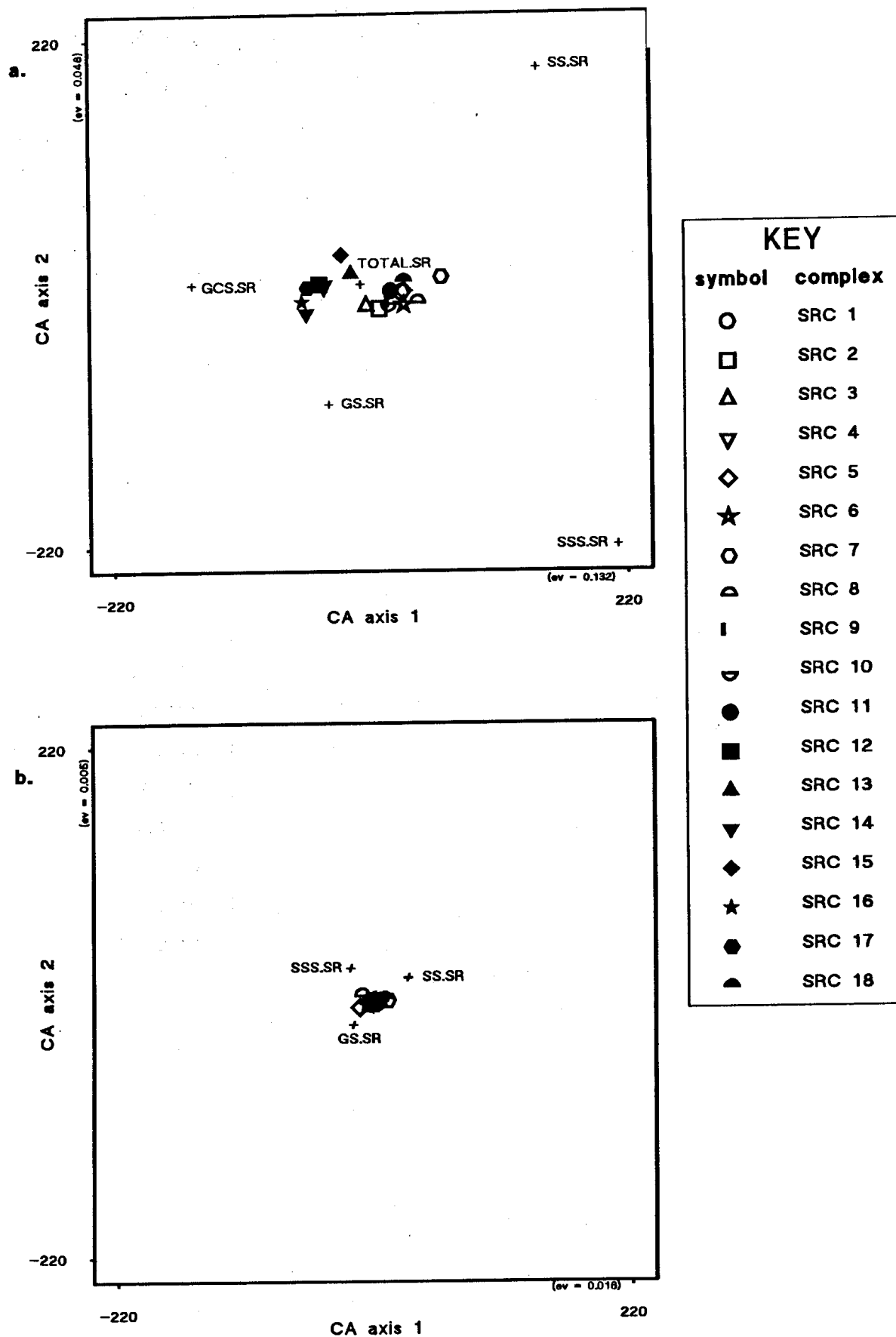


Fig. 4.4 Variance in floristic composition independent of species richness. **a.** Correspondence analysis of floristic composition. **b.** Partial correspondence analysis of floristic composition with species richness partialled out. Axes in **b.** have been rescaled to facilitate location of points.





**Fig. 4.5** Variance in species richness independent of floristic composition. **a.** Correspondence analysis of species richness. **b.** Partial correspondence analysis of species richness with floristic composition partialled out. Species richness attribute maxima not shown in the partialled analysis are located within the cloud of complex site centroids.

#### 4.3.2.3 Structure versus species richness

Variance in structure which is independent of species richness is shown in Fig. 4.6b. By comparison with the unpartialled CA plot (Fig. 4.6a) it can be seen that the relative distribution of centroids and attribute optima has not been altered to any great extent by partialling out species richness, although some convergence of centroids is evident.

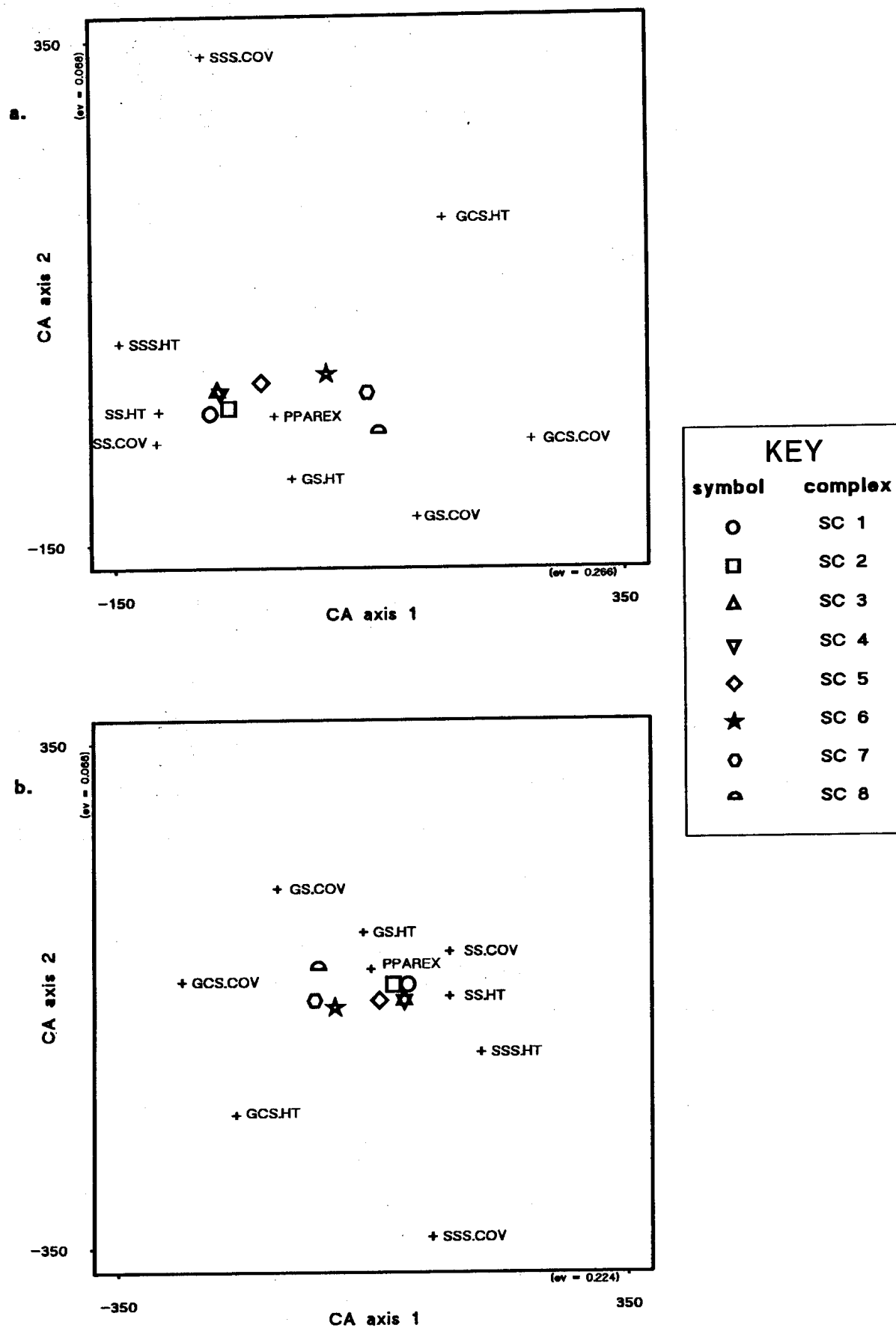
Variance in species richness which is independent of structure is shown in Fig. 4.7b. By comparison with the unpartialled CA plot (Fig. 4.7a) it can be seen that the pattern has again remained essentially unaltered. However, a reduction in separation (convergence) of centroids is clearly evident. It is also evident in Fig 4.7b that independent variance in species richness of the graminoid stratum has been reduced while variance relationships in species richness of the remaining strata have largely been maintained.

### 4.3.3 The nature of common variance components of community properties.

#### 4.3.3.1 Floristic composition versus structure.

Variance in floristic composition in common with structure is shown in Fig. 4.8. The nature of relationships between the two properties is clearly evident. Platform heath complexes are associated with increasing height and coverage of the shrub stratum, increasing height of the sub-shrub stratum and increasing PPAREX. Floristic differentiation of individual platform heath complexes is evident along an axis of increasing height of the graminoid stratum. This culminates with the *Baeckea imbricata* complex, in which PPAREX is also highest.

As shown in Fig 4.8, a major axis of differentiation between floristic complexes, and their dominant species, occurs with respect to height of the groundcover stratum. It is evident that this is associated with fire, with centroids being placed



**Fig. 4.6** Variance in structure independent of species richness. **a.** Correspondence analysis of structure. **b.** Partial correspondence analysis of structure with species richness partialled out. Axes in **b.** have been rescaled to facilitate location of points.

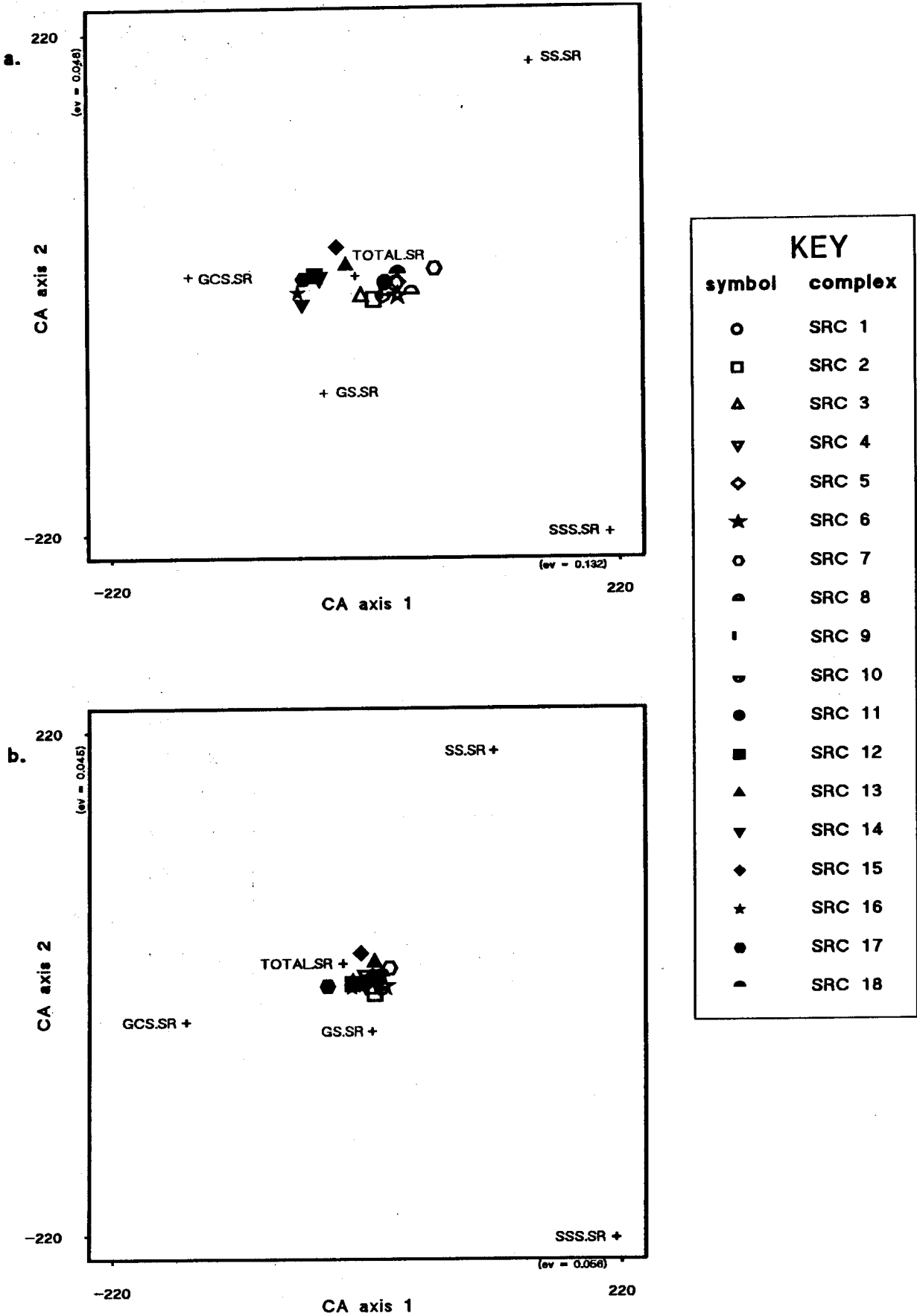


Fig. 4.7 Variance in species richness independent of structure. a. Correspondence analysis of species richness. b. Partial correspondence analysis of species richness with structure partialled out.



in order of decreasing time since fire in the direction of increasing height of the groundcover stratum.

The *Schoenus brevifolius/Baeckeia imbricata*(seedling) and *Baumea juncea/Leptocarpus tenax* complexes and their dominant species were, not surprisingly, found to be associated with increasing coverage of the graminoid stratum (Fig. 4.8). This is notwithstanding the widespread occurrence of *Baumea juncea* in most vegetation, as well as the occurrence of a number of other graminoid species in other complexes. It is evident that it is only in swamps and associated areas where graminoids attain high coverage. It is also evident that this can be attributed to a few graminoid species with an apparent wide ecological amplitude, which have their optima under these conditions. *Leptocarpus tenax* is an exception, however, generally being found only in swamps or bordering areas.

#### 4.3.3.2 Floristic composition versus species richness.

Variance in floristic composition in common with species richness is shown in Fig. 4.9. A prominent feature is the floristic differentiation of the *Baumea juncea/Leptocarpus tenax* complex from other complexes. It is clear in Fig. 4.9 that this is associated with elevated species richness of the graminoid stratum. Also evident in Fig. 4.9 is floristic differentiation along an axis of variation whereby species richness of the sub-shrub and groundcover strata vary in opposite directions. The *Rulingia hermaniifolia* complex centroid is located at a position of maximum groundcover stratum species richness. In other burnt heath complexes, and in unburnt platform heath complexes, sub-shrub stratum species richness increases. This suggests that the groundcover stratum is suppressed by increased shrub development. Also, it is apparent that this occurs relatively early after fire, the groundcover stratum being largely replaced by a shrub/sub-shrub strata arrangement. This was also evident in Fig. 4.8 with regard to structure, which shows that variance in all three properties is associated with this transition.

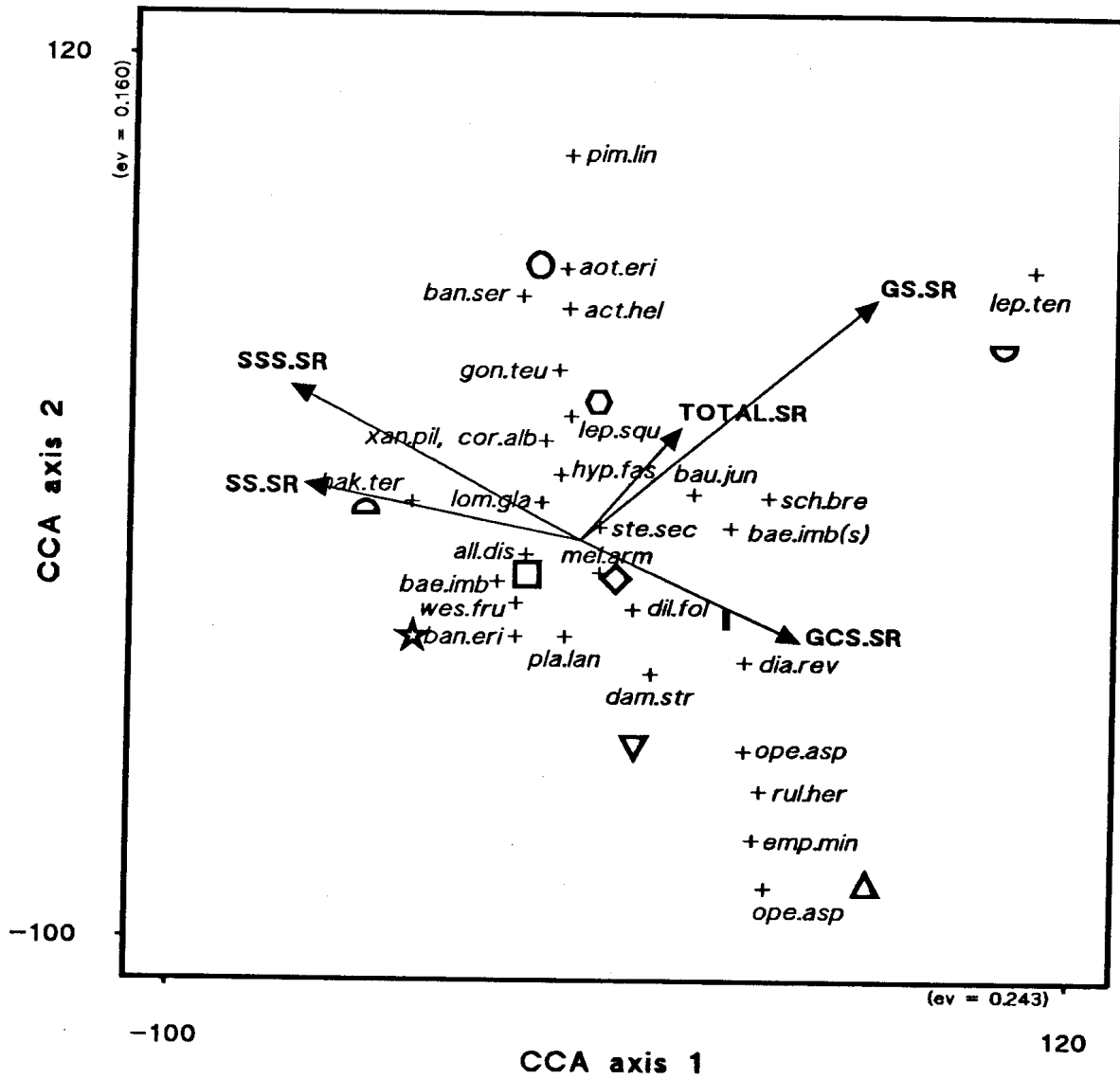


Fig. 4.9 Variance in floristic composition in common with species richness (see text for details of analysis). Nomenclature follows previous figures.

#### 4.3.3.3 Structure versus species richness.

Variance in species richness in common with structure is shown in Fig. 4.10. It can be seen that total species richness is not closely associated with any of the structural attributes. It can also be seen that species richness of particular strata is associated with increasing height and cover of respective strata. Species richness of the groundcover stratum, for example, is associated with increasing height and coverage of that stratum. The same relationship holds for the graminoid stratum. All the abovementioned attributes decline in value from right to left in Fig 4.10. Concurrently, height and coverage of shrub and sub-shrub strata increase, as does their species richness.

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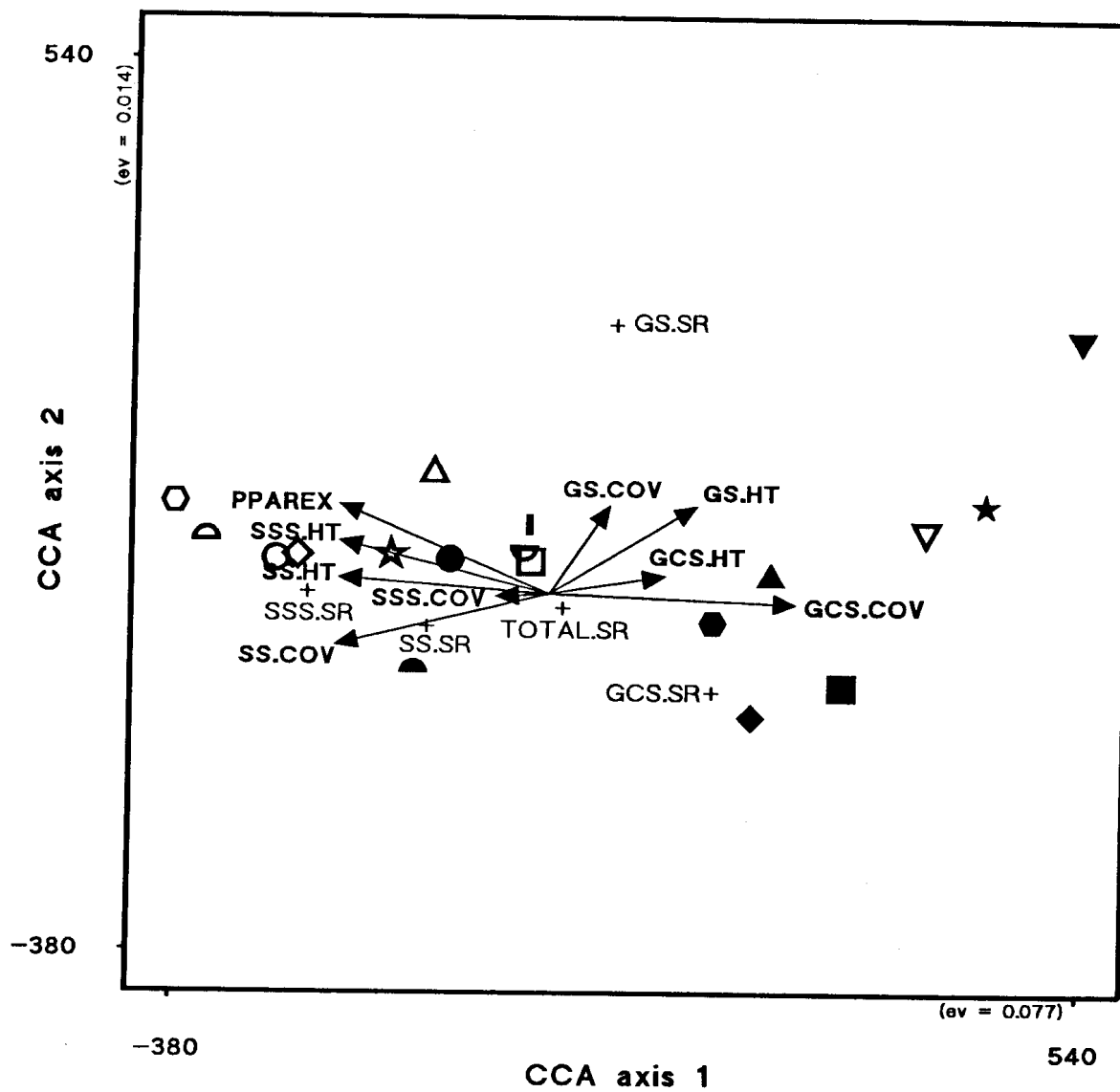


Fig. 4.10 Variance in species richness in common with structure (see text for details of analysis). Nomenclature follows previous figures.

## 4.4 DISCUSSION

### 4.4.1 The existence and magnitude of independent and common variance components of community properties.

The results show that floristic composition, structure and species richness were characterised by both independent and common variance components. This was the case with respect to each property comparison. Variance in one property is thus not conveyed in its entirety by any other individual property. Pre-emphasis on or sole consideration of one property will thus not result in a complete summation of community structure. This may be viewed as trivial. However, the current study has examined comprehensive data sets of three major properties and has shown independent variance in each. Potential for the loss of ecologically relevant structural information must hence exist for cliff-top coastal heathlands if single properties are pre-emphasised.

While variance in individual properties can be partitioned it is readily appreciable that partitioned components may not be ecologically significant and may simply reflect stochasticity. This may arise as a result of the numerical procedures used (see Bocard *et al.* 1992). However, it may also arise due to the fact that the current study was conducted within a relatively small area. It is at these scales that chance events are likely to have the greatest influence on community structure (Grieg-Smith 1986). One way of establishing the ecological significance of variance components would be to establish whether environmental correlates existed for the components. This is addressed in chapter 5.

Variance partitioning showed that all properties were non-symmetric with respect to absolute quantities of common variance, and with respect to the proportion of total property variances that these components represented. Prominent were the relatively small proportions of variance in floristic composition that were common with structure and species richness. Conversely, the majority of variance in both structure and species richness was common with floristic composition. Also, floristic composition exhibited by far the greatest amount of independent variance. In light of these features it may be suggested that floristic composition is the ecologically pre-dominant property of the studied vegetation. However, variance in both structure and species richness does

remain after that attributable to floristic composition is accounted for (independent variances). As emphasised by ter Braak (1987), small amounts of variance can be ecologically significant. The potential importance of independent variance components of structure and species richness can hence not be dismissed. Also, it may be suggested that both structure and species richness are redundant because the majority of their variance can be attributed to floristic composition. This view may be appropriate from a minimalist perspective. However, the fact remains that irrespective of their common variance they represent fundamentally different properties of vegetation (see chapter 3), which may also be underlain by different functional models. This is addressed in the next chapter.

Attention is drawn to the differential nature of variance in floristic composition compared with structure and species richness. Variance in floristic composition occurs as a function of variance in cover of 155 species whereas variances in structure and species richness are functions of variance in fewer than ten attributes. These attributes, also, are more general than species. I hence suggest that the smaller amounts of independent variance in these properties may be of equivalent or greater ecological significance than that of floristic composition. This, however, remains to be assessed. I also suggest that floristic composition, by virtue of being defined by more attributes than the other properties, is likely to be influenced to a greater extent by noise. Although beyond the scope of the current study I envisage that the variance partitioning approach could be extended to account for such influences.

Notwithstanding the considerations above, the independent variance component of floristic composition and the common variance components of structure and species richness with floristic composition, appear sufficiently great to be considered major components of community structure of the studied cliff-top coastal heathlands. Examination of environmental correlates of these, and other components in the subsequent chapter will establish their ecological significance.

4.4.2 The nature of independent variance in and common variance between community properties.

4.4.2.1 Floristic composition and structure considered.

The most prominent feature of community structure was the magnitude of variance in floristic composition that was independent of structure. The results showed this variance to be characterised as a gradient of floristic differentiation along which floristic complexes occurred. The fact that this differentiation can be made subsequent to removing variance attributable to structure implies convergence of different species combinations to a similar structure. However, the recorded differentiation would have remained if species were equivalently variable in their structural disposition.

Both of the situations above apply to the studied vegetation. Low/prostrate growth habits are known characteristics of many species in windswept environments (see Boyce 1954; Parsons & Gill 1968; Parsons 1981; Auld & Morrison 1992), and are community attributes which typify cliff-top coastal heathlands. The results showed the studied heathlands not to be an exception to this. Although data for cover of individual species in individual strata are not presented, it is the case in most floristic complexes that species, mainly dominant shrub species, vary substantially in their structural disposition. In platform heaths, for example, shrubs such as *Baeckea imbricata* occur in both shrub and sub-shrub strata. In recently burnt heaths differences in timing of regeneration and differences in mode of regeneration within species (e.g. resprouting and seedlings in *Platysace lanceolata*) lead to similar variances in structural disposition of species. It is foreseeable that this diversification in structural niche utilisation by dominant species may act to preclude other species, hence reinforcing the differentiation of floristic complexes.

Variance in structure which was independent of floristic composition represented only a small proportion of the total variance in structure. The results showed this variance to be associated with height and coverage of the sub-shrub stratum and with height of the graminoid stratum. In the case of the sub-shrub stratum this variance reflects common structural responses of species which occur as sub-shrubs. This

highlights the need to consider the sub-shrub stratum as a typical structural feature of cliff-top coastal heathlands rather than labelling particular species as sub-shrubs.

Independent variance in height of the graminoid stratum arose due to a number of widespread species, principally *Baumea juncea* and *Schoenus brevifolius*, displaying considerable plasticity in height. These species were particularly tall where the shrub stratum was tall and/or of high coverage, often protruding through the canopy. The widespread occurrence of graminoids in vegetation of oceanic cliff-tops has been previously noted (see Adam *et al.* 1989a). The results of the current study suggest a possible mechanism for this widespread occurrence. It is known that many graminoids are wind pollinated (Whittet 1969; Fairley & Moore 1989). Selection of graminoids growing in conjunction with shrubs may then be for those able to locate inflorescences near or above the shrub canopy so as to be able to utilise the typically strong winds of this environment as pollination vectors. As a consequence of high windspeeds it is foreseeable that outcrossing may then occur over relatively large areas covering a range of environmental conditions. This may favour relatively rapid adaptation of tall graminoids to the range of environmental conditions present, thus allowing for their widespread occurrence in cliff-top coastal heathlands. Although beyond the scope of my study it appears to be worthwhile to investigate this further, given the substantial contribution of graminoids to community structure of cliff-top coastal heathlands.

In addition to revealing the nature of independent variance components, the results showed clearly the nature of common variance between floristic composition and structure. Major groupings of floristic complexes were shown to be clearly differentiated on a structural basis. Although addressed in detail in the next chapter, it was clearly evident that time since fire was a proximate factor influencing the resolved relationships. The breakdown of ecological dominance of shrub species associated with the occurrence of fire was clearly a factor underlying the relationships between the properties, with the number of dominants and number of non-shrub dominants increasing with decreasing time since fire. The results showed this to be associated with increasing height and coverage of the groundcover stratum and decreasing height and coverage of shrub and sub-shrub strata. The fact that both floristic composition and structure change markedly along this axis suggests that factors underlying this variance are important for maintenance of overall habitat diversity of the vegetation. While time since fire is a

relatively obvious candidate, the importance of other factors cannot be dismissed, particularly in view of the fact that most complexes are not represented at all previous burn dates.

#### 4.4.2.2 Floristic composition and species richness considered.

Similar to consideration of structure, the results showed that a large amount of variance in floristic composition existed which was independent of species richness. In general, differentiation of floristic complexes remained unchanged by removal of variance attributable to species richness. This shows that overall floristic diversity of the vegetation is primarily a function of pattern diversity (i.e. species turnover) rather than strong vectors in species richness. Studies of heathlands elsewhere which have been conducted at similar scales have also revealed high pattern diversities (e.g. Westman 1975; Keith & Myerscough 1993). However, these studies have also shown that floristic patterns in the heathlands were also a product of relatively strong differences/gradients in species richness. Differences/gradients in species richness can occur for a wide variety of reasons, including differences in inter-specific competition and resource partitioning (see Chapter 3). Given the environmental diversity of the study site (see chapter 5), it appears unlikely that such processes are uniform with respect to the whole vegetation. I thus suggest the presence of a strong environmental limiting factor which acts to prevent rather than cause strong differences/gradients in species richness and thus causes pattern diversity to contribute more significantly to patterns in floristic composition.

Intuitively, it is logical that information on variance in species richness should be carried in its entirety by variance in floristic composition. The results show this to be mainly correct. However, variance in species richness independent of variance in floristic composition was recorded (Fig. 4.5). This variance was shown to be attributable to species richness of shrub and sub-shrub strata and can be attributed to the way in which species richness was defined. Namely, species richness was defined in terms of total and strata species richness. As was outlined previously, shrub species can exist in both shrub and sub-shrub strata. Species richness of shrub and sub-shrub strata can hence

vary while floristic composition remains unchanged. The independent variance in species richness of shrub and sub-shrub strata is hence reflecting the alternate presence of individual species in these strata. In general this involves dominant shrub species. For example, in platform heaths, with increasing cover *Baeckea imbricata* disappears as a sub-shrub. In recently burnt heaths this variance largely reflects whether a particular species has developed to a sub-shrub or shrub stage at a particular locality.

While a large proportion of the variance in floristic composition was independent of variance in species richness, relationships were nevertheless evident between the properties. The results showed floristic differentiation with increasing species richness of shrub and sub-shrub strata on one hand and with increasing species richness of the groundcover stratum on the other hand. This relationship is consistent with pyric succession in heathlands and general hypotheses of suppression. These were discussed in Chapter 3. Of additional interest was the association of elevated graminoid stratum species richness with the *Baumea juncea/Leptocarpus tenax* complex. This association is not surprising in light of the fact that this complex represents swamps, from which shrubs are largely absent.

#### 4.4.2.3 Structure and species richness considered.

The results showed that variance in structure was largely independent of variance in species richness. In other words, variance in height and coverage of strata was largely independent of the number of species occurring in them. Conversely, approximately half the variance in species richness was independent of structure. This variance was shown to occur with respect to all strata, although less so for the graminoid strata. Of note is that variances in species richness of separate strata appeared to be independent, with approximately equidistant spacing of optima in the ordination diagram (Fig. 4.7). This may reflect different environmental gradients underlying the species richness of separate strata. This, however, remains to be assessed.

Examination of the common variance between structure and species richness revealed the nature of relationships between these properties. The results showed a negative relationship between height and coverage of shrub-based strata and

species richness of graminoid and groundcover strata. This is equivocal with the inhibition model of Connell & Slatyer (1977). However, increases in species richness of separate strata were shown to be associated with increasing height and coverage of respective strata (Fig. 4.10). While increasing height and coverage do not necessarily imply increasing productivity this, would appear to be the case. The resolved relationships hence support productivity hypotheses of species richness (e.g. Connell & Orias 1964). However, this applies only to consideration of strata separately. Results showed that total species richness declines with increasing height and coverage of shrub and sub-shrub strata, as well as with increasing height and coverage of graminoid and groundcover strata (Fig. 4.10). Productivity hypotheses of species richness thus appear to be of limited validity in this vegetation, insofar as total species richness is concerned.

#### 4.4.3 The CA/CCA variance partitioning approach: some comments.

The results provide quantitative information on variance components of floristic composition, structure and species richness. This was achieved by comparison of property pairs using partial correspondence analysis. Most previous variance partitioning approaches which have used a CCA approach have centred on comparing the association of attributes of one or more properties with a target property. Commonly, attributes are of environmental and/or spatial properties and the target property is floristic composition (e.g. Bates 1992; Bocard *et al.* 1992; Brown *et al.* 1993; McIntyre & Lavorel 1994; Okland & Eilersten 1994; Le Brocque & Buckney 1995). Previous studies, however, appear not to have used this approach for comparison of vegetative community properties. Nor has CA alone has been used for purposes of variance partitioning of such properties. The current study shows that partial CA and CCA can be effectively used for isolation, quantification and characterisation of variance components of major community properties.

Although comparative tests are beyond the scope of this study, I suggest that the CA/CCA approach provides a useful and potentially more informative alternative to the already established mantel procedures for comparing data sets (see Burgman 1987a,b; Burgman 1988; Legendre & Fortin 1989; MacNally 1990; Leduc *et al.* 1992).



As outlined by Bocard *et al.* (1992) and Okland & Eilersten (1994) the CA/CCA approach is computationally and conceptually more straightforward and is based on a more precise statistical model. I hence consider it of greater utility for intensive investigation of the variance relationships of individual components of biological systems (see Okland & Eilersten 1994). In view of this I envisage that the CA/CCA variance partitioning approach could be effectively and easily extended to examination of multiple community properties of cliff-top coastal heathlands elsewhere. Equivalent syntheses of community structure as made in the current study could then be made elsewhere. This would provide a substantial framework within which generalisations regarding community structure of this distinctive vegetation type could then be made.

#### 4.4.4 Foundations of a tertiary synthesis of community structure

This study has shown the existence, magnitude and nature of both independent and common variance components of community properties. This shows that tertiary syntheses of community structure, as previously described, are feasible propositions within localised areas of cliff-top coastal heathlands. It also shows that pre-emphasis on attributes of individual community properties involves the loss of information of variance in the other properties. These features indicate a level of complexity in the community structure of cliff-top coastal heathlands that can only be enumerated effectively by a variance partitioning, or tertiary, approach to community synthesis.

The results of this study showed that variance in floristic composition exceeded that of structure and species richness and that the majority of this variance was independent of these properties. This may be seen as suggesting that pre-emphasis on floristic attributes (species) in local community studies is warranted. However, it must be remembered that the variance components examined are necessarily mathematical constructs. Both structure and species richness are more general properties than floristic composition and as such were defined by fewer attributes. This difference in itself may be expected to have contributed to the elevated level of variance in floristic composition.

Despite the fact that floristic composition displayed the greatest amount of variance, pre-emphasis on this property may be seen as implying that floristic composition is of greater functional importance. This may not be the case and is examined in the subsequent chapter.

## 4.6 CONCLUSIONS

Independent comparisons of floristic composition, structure and species richness showed that their respective variances can be partitioned into components independent of and in common with each other. It is concluded that investigation of the community structure of cliff-top coastal heathlands in terms of single major properties involves the loss of information of variance in other major properties. This is irrespective of any ecological significance which may accrue to individual properties or their variance components.

Of the community properties floristic composition displayed the greatest absolute variance as well as the greatest absolute variance which was independent of other properties. It is concluded that floristic composition contributes most variance to overall community structure of the studied cliff-top coastal heathlands. This conclusion, however, is made in a mathematical context only and must be qualified ecologically by the fact that the properties are of different natures and are not equivalent with respect to their variance structures.

Examination of the nature of both independent and common variance components of properties revealed discernible patterns in most cases. In the case of floristic composition and structure examination of variance in floristic composition in common with structure revealed a separation of major floristic complex groups. This differentiation was spatially correlated with respect to physiographic features and time since fire. I thus conclude that structurally related variance in floristic composition is a significant component of community structure of cliff-top coastal heathlands.

While major aspects of floristic differentiation concord with structural differentiation the majority of variance in floristic composition was actually shown to occur independently of structure. I thus conclude that species turnover within similar structures is also a major component of cliff-top coastal heathland communities.

Examination of the variance in structure independent of floristic composition indicated common responses of species which occur as sub-shrubs. In view of this and the fact that many species which occurred as sub-shrubs also occurred as dominants I conclude that the use of the term 'sub-shrub' for particular species is likely to be misleading for cliff-top coastal heathlands.

In addition this study shows that variance in height of the graminoid stratum is largely independent of floristic composition. This can be attributed to height variation in a number of graminoid species which is associated with height and cover of the shrub stratum. This relationship was not found for the groundcover stratum and appears specific to graminoids. I thus conclude that for patterns in herbaceous structure of cliff-top coastal heathlands to be effectively resolved that characteristics of graminoids need to be enumerated independently of other herbaceous forms.

Examination of the variances in floristic composition and species richness revealed that variance in floristic composition was mostly independent of species richness. I thus conclude that floristic differentiation of cliff-top coastal heathlands is primarily a function of species turnover rather than strong gradients/differences in species richness.

Examination of variances in structure and species richness showed reduced levels of groundcover and graminoid strata richness with increased levels of height and cover of shrub-based strata. This is consonant with inhibition models of community structure. However, increased levels of richness in individual strata were indicated for increased levels of height and cover of respective strata. This is consonant, alternatively, with productivity models of species richness. I thus conclude that species richness of cliff-top coastal heathland communities displays a level of ecological complexity that can only be effectively summarised by taking structural dimensions into account.

These patterns are inescapably products of the mathematical techniques used. However, as outlined above, and in discussion, they are interpretable in terms of the proposed operation of general ecological mechanisms. It is concluded that the application of the CA/CCA variance partitioning approach developed in this study is useful for the isolation, quantification and characterisation of ecologically relevant variance components of cliff-top coastal heathland communities.

## **CHAPTER 5: ENVIRONMENTAL RELATIONSHIPS OF COMMUNITY PROPERTIES OF CLIFF-TOP COASTAL HEATHLANDS IN BOTANY BAY NATIONAL PARK, SYDNEY.**

### **5.1 INTRODUCTION**

Examination of the relationships between community patterns and environmental factors has long been a mainstay of plant community ecology research. This can be attributed to the fact that environment provides the abiotic substrate on which, and with which, plants interact and persist according to their physiological tolerances (see Major 1951; Billings 1952, 1974; Whittaker 1975; Begon *et al.* 1986). Countless studies have shown by examination of relationships between environmental factors and community patterns that valuable insights into the ecological nature of community structure can be obtained.

In this chapter environmental relationships of community properties of the cliff-top coastal heathlands in Botany Bay National Park are investigated. This is done in order to assess the ecological significance of the community syntheses described in previous chapters. A brief background to this research is provided below along with details of research objectives and hypotheses.

#### **5.1.1 Background**

**5.1.1.1 Environmental factors of likely importance to community structure of cliff-top coastal heathlands.**

Previous studies of heathlands and related vegetation have indicated that four areas of environmental variability are likely to be of primary ecological importance for community patterns of cliff-top coastal heathlands. These groups may for convenience be classified as being: maritime factors, soil physical factors, soil nutritive factors, and fire factors.

A characteristic feature of the cliff-top coastal heathland environment is its maritime nature. Specifically, vegetation of sea-cliffs is subject to elevated levels of windspeed and salt-spray deposition (Malloch 1971; Adam *et al.* 1989a; Benson & Howell 1990). Evidence shows that salt-spray deposition has effects on both the growth form and distribution of coastal vegetation. The principal effect on growth form is the inducement of asymmetric growth. As outlined by Boyce (1954) and Parsons (1981), this is due to differential deposition of salt-spray on the seaward side of vegetation. Consequently, chloride toxicity causes necrosis and limits growth on the seaward side of vegetation. Boyce (1954) reviews alternative hypotheses for asymmetric growth which, like salt-spray deposition, are wind related. These are desiccation, mechanical damage and sandblasting, the latter predisposing vegetation to entry of chloride. Parsons and Gill (1968) and Parsons (1981) suggest that these factors are of secondary importance to that of salt-spray deposition. However, the relative effects of wind and salt-spray deposition are difficult to separate, and both are possible causative agents for asymmetric growth (Malloch 1972).

The effect of salt-spray deposition on the distribution of coastal vegetation can be attributed to a number of factors, including salt tolerance/avoidance adaptations, differential competitive abilities in highly saline environments, and, possibly, the nutrient effect of salt-spray. It is well known that abundance of succulent maritime species adapted to high internal salt levels decreases with distance away from exposed coastal sites (e.g. Boyce 1954; Parsons & Gill 1968; Malloch 1971, 1972; Goldsmith 1973a, 1973b; Parsons 1981). Succulence in non-maritime species has also been shown to decrease in the same direction (Parsons & Gill 1968; Parsons 1981). Parsons and Gill (1968) provide evidence which suggests that this gradient is likely to be due to salt-spray deposition rather than to salinity of the rooting medium.

Malloch (1971) found a strong correlation between the percentage of succulent maritime species in vegetation nodes and the sodium/organic ratio for corresponding soils. However, Malloch (1972) suggested that both soil salinity and direct salt-spray effects could have contributed to these patterns.

Boyce (1954), Parsons & Gill (1968) and Parsons (1981) cite features of coastal vegetation such as low prostrate growth, low even canopies, pubescence and thick hydrophobic cuticles as responses to salt-spray deposition, and suggest a selective

advantage for these features. This appears likely given previous recognition of ecotypes with such features from exposed coastal environments (e.g. Boyce 1954, Auld & Morrison 1992). Gradients in coastal vegetation communities might exist that reflect mixes of ecotypes and phenotypic responses of individual species to salt-spray deposition. However, this has yet to be investigated.

Variation in relative competitive ability of species in highly saline environments has been cited in the past as a possible cause of gradients in coastal vegetation. Goldsmith (1973a, 1973b) showed a competitive advantage of maritime species over inland species in sea-cliff vegetation due to their adaptations. However, Goldsmith (1973b) demonstrated that increased abundance of maritime species close to sea-cliffs is also due to a reduction in competitive intensity from inland species due to effects of salt-spray deposition.

Holton & Johnson (1979) investigated environmental correlates with floristic variation in dune scrub communities at Point Reyes National Seashore, California. From indirect gradient analysis they found that distance inland was correlated with a major axis of compositional variation. Through field measurements they found salt-spray deposition to be negatively correlated with distance inland. They suggested that differential avoidance/tolerance of species to salt-spray was the principal cause of the observed floristic gradient.

Salt-spray deposition might also be of significance in influencing distribution of coastal vegetation through nutrient inputs. Ingham (1950) provided experimental evidence for atmospheric inputs of plant nutrients maintaining soil fertility over extended periods. He cited salt-spray as an important atmospheric source of plant nutrients. Ranwell (1972) attributed replacement of heathlands by grasslands on coastal cliffs in Sicily to the nutritional effects of salt-spray. Maze & Whalley (1992) showed that co-application of salt-spray, phosphorus and nitrogen to seedlings of *Spinifex sericeus* led to significantly higher growth compared with co-applications of phosphorus and nitrogen alone. Salt-spray may be of importance nutritionally, but as Parsons (1981) points out "comprehensive data are badly needed".

Salt-spray deposition may thus be expected to have important effects on community structure of cliff-top coastal heathland communities. However, direct evidence for the existence of gradients in salt-spray deposition in cliff-top environments

is still mostly lacking in Australia. This is notwithstanding the existence of a number of overseas studies which have demonstrated the existence of strong gradients in salt-spray deposition within close proximity to seashores (e.g. Boyce 1954; Edwards & Claxton 1964; Malloch 1971; Clayton 1972; Goldsmith 1973b; Holton & Johnson 1979).

It is of importance to note that few studies have examined the relative importance of maritime factors for community structure compared with other major sources of environmental variation. It has been suggested that in the immediate proximity of sea-cliffs, other environmental influences are overridden by maritime factors (Adam *et al.* 1989a,b). Whether this is the case or not with respect to cliff-top coastal heathlands is not clear. However, it is clear that attempts to clarify environmental relationships of cliff-top coastal heathlands must account for maritime factors.

Most salt-spray deposition in cliff-top coastal heathland communities may reasonably be expected to be intercepted by upper canopy layers. However, some direct salt-spray deposition might penetrate the upper canopy. It is foreseeable that gradients in below canopy salt-spray deposition might exist that are related to canopy cover and intensity of above canopy salt-spray deposition, and which are of functional importance for community structure. To my knowledge, no studies thus far have examined gradients in below canopy salt-spray deposition. It thus appeared worthwhile in the current study that account be taken of patterns of below canopy salt-spray deposition.

The second area of environmental variation considered to be of ecological relevance to cliff-top coastal heathlands is variance in the physical attributes of the soil, in particular in soil moisture status, organic content, soil texture and, bulk density and related attributes.

Soil moisture status in the field is a known correlate of variance in community structure of cliff-top coastal heathlands and related vegetation. Endpoints of such correlates are generally controlled by local or micro-topographic features, and are often characterised by impedance or (near) total occlusion of drainage on one hand (e.g. perched swamps on sandstone) and free drainage on the other (e.g. high sand dunes). Both endpoints are commonly present within local areas (see Hamilton 1918; Benson 1986; Myerscough & Carolin 1986; Benson & Howell 1990; McRae 1990), allowing for considerable influences on vegetation at these scales. Previous studies have indicated that changes in community structure associated with increasing soil moisture include trends in



floristic composition as well as generally increasing height and coverage of shrub strata (e.g. Siddiqi *et al.* 1972; Noy-Meir 1974; Burrough *et al.* 1977; Buchanan 1980; Kirkpatrick 1984; Bowman *et al.* 1991; Fensham 1993). However, where drainage is persistently impeded peat formation may occur (e.g. swamps). In these instances, previous studies have indicated that the representation of shrubs is reduced and that of graminoids and other herbs increased (e.g. Myerscough & Carolin 1986; Buchanan 1980). These changes are concordant with changes to soil chemistry and soil physical structure typically associated with swamps (see Keith & Myerscough 1993; Johnson 1994). While it is apparent that soil moisture status is of physiological importance by itself, most of the studies cited above have shown inter-correlations between measures of soil moisture status and a range of other environment factors. It is readily appreciable that measures of soil moisture status may thus provide useful scalars for associated complex gradients.

Similar to variation in soil moisture status, variation in organic content of soils has been shown to be a significant correlate of variation in community properties (e.g. Bowman *et al.* 1986; Ellis & Graley 1987; Wilson & Keddy 1988; Tongway & Ludwig 1990; Taggart 1994). It is also known to be correlated with a variety of other soil factors (see Langkemp *et al.* 1981; Collins & Klahr 1991; Pharo & Kirkpatrick 1994; Le Brocque & Buckney 1995) as well as being of likely functional importance to cycling of major plant nutrients (see Chapman 1967; Raison 1979; Keith & Myerscough 1993; Adams *et al.* 1994). It was hence considered instructive to take organic content of the soil into account in my study.

Soil texture has been put forward in the past as a primary differentiating factor in the occurrence of a number of *Banksia* species typical of particular heathland communities (Siddiqi *et al.* 1972; 1976a; Siddiqi & Carolin 1976). The ecological basis is apparently through alteration of competitive ability in response to interactions between soil aeration and soil moisture regimes typical of soils of a particular texture. While soils of cliff-top coastal heathlands in Botany Bay National Park may be generally sandy, initial observations do suggest that significant variation in texture does occur. Accounting for variance in soil texture hence appeared worthwhile.

Bulk density and related soil factors such as pore space ratio and air filled porosity perhaps provide the most fundamental quantification of the physical structure of

soil. Despite this, relatively few studies which have investigated environmental correlates of community properties appear to have quantified these factors. It thus appeared worthwhile to include these factors in this study.

The third area of environmental variation considered to be of importance for community structure of cliff-top coastal heathlands is soil nutrient status. It has long been recognised that soils derived from Hawkesbury sandstone in the Sydney area are impoverished in plant nutrients, particularly in phosphorus (Beadle 1953,1954,1962,1966) and nitrogen (Hannon 1956,1961). It is also accepted that heathlands have evolved on and are ecologically restricted to soils of low nutrient status (Specht & Rayson 1957; Siddiqi *et al.* 1972; Specht 1979a,b; Groves 1981b; Adam *et al.* 1989b; although see Adams *et al.* 1994). Previous fertiliser studies have indicated that heathland soils may be limiting to plant growth (e.g. Specht 1963, 1975, 1976; Specht & Groves 1966; Heddle & Specht 1975; Specht *et al.* 1977; Groves 1981b). However, this remains to be fully substantiated (see Adams *et al.* 1994). I suggest that, since heathland communities have evolved on impoverished soils, they may be sensitive to small fluctuations in soil nutrition within ranges which would otherwise be seen as limiting. Prior studies have indicated that this is likely to be the case with respect to a range of nutrients, as well as with respect to factors which influence their availability (e.g. Specht & Rayson 1957; Grundon 1972; Siddiqi *et al.* 1972; Enright 1989; Keith & Myerscough 1993; Le Brocque & Buckney 1995). It hence appeared worthwhile to investigate the significance of soil nutrients to patterns in community structure of the studied heathlands.

The fourth area of environmental variation considered to be of importance for the community structure of cliff-top coastal heathlands is that concerning fire history. Pyric factors (e.g. time since fire and fire frequency) are known to be of overriding importance for most aspects of community structure of heathlands (see Siddiqi *et al.* 1976a; Gill & Groves 1981; Groves & Specht 1981; Specht 1981c; Kruger 1983; Keith & Bradstock 1994). Effects are wide ranging, as are interactions between fire and other environmental factors. Readers are referred to Gill & Groves (1981) and Kruger (1983) for reviews of these effects. Given the wide ranging effects of fire on community structure of heathlands I suggest that failure to account in some way for fire effects promotes the likelihood that interpretation of environmental correlates of community structure will be confounded. I also suggest that this may be a particularly

important consideration for cliff-top coastal heathlands due to characteristic spatial burning patterns. Patterns of burning in cliff-top coastal heathlands are outlined by Adam *et al.* (1989a). These are characterised by relatively high frequency, but also by spatial patchiness due to a number of factors including the action of onshore winds, microtopographic variation and certain characteristics of the heathland canopy. Fire may hence be of particular importance at small (local) scales for community structure of cliff-top coastal heathlands.

#### 5.1.1.2 Differential environmental relationships of community properties and their variance components.

It is reasonable to assume that different properties have different environmental relationships. As outlined previously, exposure to maritime influences has generic effects on structure of cliff-top coastal heathlands in promoting low even growth of the shrub stratum. Although floristic composition and species richness may also be influenced by maritime factors (see Malloch 1971, 1972; Goldsmith 1973a,b; Holton & Johnson 1979; Adam *et al.* 1989a) it appears implicit in most descriptive accounts of sea-cliff vegetation that the primary effect of exposure to maritime influences is on structure (see Hamilton 1918; Pidgeon 1938; Benson & Howell 1990). This necessarily implies differential environmental relationships of this property.

In addition to exposure to maritime influences, structure may also be influenced differentially by soil moisture status. It has previously been noted that shrub height and coverage increase with increasing persistent dampness of the soil (see Specht 1979a; Specht & Morgan 1981). Again, variance in floristic composition and species richness may occur, but it would appear that this environmental factor has a different weight with respect to different properties.

In the previous chapter it was shown that a large amount of variance in overall community structure could be attributed to a substantial degree of species turnover. I suggest that this implies that floristic composition may have different environmental relationships compared to the other two properties. This may involve different/additional factors. However, the greater variance in floristic composition may

also reflect a response of relatively greater magnitude to the same factors influencing the other properties. I thus suggest a need to account for both qualitative and quantitative aspects of vegetation responses in examining the differential nature of environmental relationships.

In addition to the possibility of properties having different environmental relationships, variance components of properties may also have different environmental relationships. Studies of such relationships appear to be absent from the literature. It appears, however, that such studies would add substantial knowledge as to the ecological nature of community structure. For example, it could be established whether common variance components of different properties are ecologically co-incident. It may reasonably be expected that common variance components of compared properties will display similar environmental relationships. However, this may not be the case. Environmental relationships of different properties may differ markedly, with common variances simply reflecting co-incident patterns. It could also be established whether independent and common components of particular properties have differing environmental relationships. As outlined earlier, the non-concordance of properties in heathlands may have an environmental basis. This implies that common and independent variance components differ in their environmental relationships. It would be instructive to determine the existence and nature of such differences.

#### 5.1.1.3 A rationale for a correlative approach to assessing the ecological significance of vegetation patterns

As mentioned earlier, the study of plant-environment relationships is central to the study of community ecology since environment provides the abiotic substrate on which vegetation is structured according to physiological tolerances, and according to competition conditioned by environment (see Major 1951; Billings 1952, 1974; Whittaker 1975; Begon *et al.* 1986). Identification of environmental correlates of vegetation patterns is hence fundamental to establishing the ecological significance of these patterns in indicating what the potential functional relationships of vegetation are.

In considering sources of environmental variation of likely it is important to recognise that correlative studies, such as that described in this chapter, cannot by themselves answer questions regarding causality of plant/environment relationships (see Ludwig & Reynolds 1988; Partridge & Wilson 1989; Tongway & Ludwig 1990). Measured environmental factors may only be related to resolved patterns by virtue of correlation to an unmeasured factor. Such correlations may also apply between measured factors. It follows that if ecological causality is to be revealed in detail then further controlled experimentation is required. However, where multiple factors and properties are considered in a field context such experimentation generally becomes logistically unfeasible. Correlative studies may hence be seen as providing detailed information of vegetation/environment relationships from which experimental research can then be effectively formulated. It is this 'hypothesis generation function' context in which correlative studies have traditionally been viewed (see Underwood 1986; Myerscough 1990).

It is worthwhile pointing out that even where *a priori* hypotheses concerning functional relationships of vegetation with a single factor are tested in natural communities, that largely, the same limitations apply as to multi-factor correlative studies. In this instance there is still no guarantee that the factor of interest is of functional importance in an ecological sense since other factors, whether correlated or not, may be influential in producing the observed patterns.

The true functional nature of environmental factors to multivariate community patterns largely remains to be established for most natural communities. It is important to note, however, that it is becoming increasingly obvious, that vegetation patterns are related to multiple rather than single environmental factors (see Margules *et al.* 1987; Fensham & Kirkpatrick 1992; Le Brocque & Buckney 1995). Correlative studies which incorporate multiple factors and are able to demonstrate complex relationships of vegetation with these factors, I suggest, are most likely to provide the appropriate foundations for more intensive experimental study. They should thus allow for greater insights to be developed regarding the ecological foundations of community structure and its variance components.

### 5.1.2 Research objectives and hypotheses

The first research objective was to investigate associations amongst environmental factors. This was considered a useful prelude to linking vegetation data with environment. I envisaged that major axes of environmental variation would be identified prior to such analyses, thus aiding in their interpretation.

The second research objective was to determine the environmental characteristics of recognised property complexes and to establish the existence of significant differences in environmental factors between complexes. The ecological separation of the complexes recognised through multivariate classification would thus be established, hence completing the secondary synthesis of community structure.

The third research objective was to determine the differential nature of environmental relationships of properties and their variance components. This is done through direct multivariate gradient analysis and constitutes completion of the tertiary synthesis of community structure.

In incorporating environmental factors into both secondary and tertiary syntheses the main hypothesis developed in Chapter 1 is examined, this being that;

*major properties of cliff-top coastal heathlands and their common and independent variance components are underlain by different environmental gradients.*

In examining this hypothesis the need to address community structure at a level above that of a primary synthesis will foreseeably be established.

In examining the hypothesis above emphasis is provided, first, to differences between common variance components between pairs of properties. This will establish the value of constructing tertiary syntheses in highlighting whether common variance components are ecologically coincidental with respect to environment. This is only assessable within the framework of a tertiary synthesis. Secondly, emphasis is given to differences between properties considered as wholes and their independent variance components. The existence of differences will establish the value of constructing tertiary syntheses in highlighting the potential distortions involved in analysing properties without due regard to variance which is unique to these properties.

## 5.2 MATERIALS AND METHODS

### 5.2.1 Environmental survey

#### 5.2.1.1 Environmental factors: summary of included factors

In this survey, groups of factors are included which quantify four areas of environmental variation. These areas cover the maritime nature of the environment, variation in physical soil structure, variation in soil nutrients and the pyric successional state of the vegetation. In this study groups of factors which quantify these areas are referred to as the maritime factor group, the soil physical factor group, the soil nutrition factor group and the fire factor group respectively. Factors included in all groups are summarised in Table 5.1.

**Table 5.1** Summary of factors included in the environmental survey

Included environmental factors are summarised by environmental factor group. Abbreviations used for factor groups and individual factors are indicated in parentheses.

<u><i>Maritime factor group (MFG)</i></u>	<u><i>Soil nutrition factor group (SNFG)</i></u>
Distance from cliff-top (DFCT)	pH (pH)
Electrical conductivity (EC)	Total phosphorus (P)
Chloride content (Cl)	Total nitrogen (N)
Exchangable sodium (Na)	Exchangable magnesium (Mg)
Above canopy salt-spray deposition (ACSD)	Exchangable calcium (Ca)
Below canopy salt-spray deposition (BCSD)	Exchangable potassium (K)
<u><i>Soil physical factor group (SPFG)</i></u>	<u><i>Fire factor group (FFG)</i></u>
Field soil moisture (FSM)	Years since last fire (YSLF)
Bulk density (BD)	
Pore space ratio (PSR)	
Air filled porosity (AFP)	
Organic content (org)	
Fine particle fraction (fine)	
Coarse particle fraction (coarse)	

### 5.2.1.2 Sampling strategy

Mean levels of environmental factors have been ascribed as the factor levels for the respective quadrats. Replication has thus been conducted on an intra-quadrat basis for most environmental factors. This approach was considered desirable as it negates the statistical problems associated with sample 'pooling' (see: Mead & Curnow 1986) and allows for different levels of variability to be examined if required (e.g. between individual quadrats).

### 5.2.1.3 Soil sampling

Levels of most environmental factors (see below) have been determined on replicate soil samples. Except where otherwise stated, three soil cores of known volume ( $196 \text{ cm}^3$ ) were taken from each quadrat using a stainless steel corer (with handle). Core positions within each quadrat were determined by random co-ordinate selection. All cores were extracted in a three day period, starting two days subsequent to one substantial rainfall episode in March, 1994. This was done in order to maximise the likelihood that field soil moisture status was maximal (see below). Cores were of 10 cm depth. Where soils were less than 10 cm in depth oblique cores were taken except in quadrats in reconnaissance zone 4 (frontal deposition areas). Cores were not taken here as it was deemed that this would have been overly destructive. Small surface samples were taken here using a stainless steel trowel.

Cores were then placed in individual plastic sample bags and the bags wrapped around the core so as to maintain as great an air-tight seal as possible. Sample bags were secured with elastic bands. Prior to analyses, these fresh samples were stored in a cool dark place. Individual sample bags were stored in plastic garbage bags. Plastic garbage bags were stored in hessian sacks. The hessian sacks were moistened so that evaporation would aid in keeping the contents cool. Storage was not extended. Immediately prior to analyses, sample bags were removed from storage and the contents were thoroughly kneaded and mixed.



#### 5.2.1.4 Environmental factors: methods of determination

##### *Maritime factor group*

##### Factor 1 - Distance from cliff-top (DFCT)

As previously outlined, sampling grids were stratified with respect to distance from the cliff-top. Quadrats in strata were simply assigned the median distance from the cliff-top for that stratum e.g. quadrats in strata ranging from 50 m to 60 m from the cliff-top were assigned a distance of 55 m.

##### Factor 2 - Electrical conductivity (EC)

Electrical conductivity was measured in 1:5 soil:water (reagent grade) extracts. For each replicate sample, 12 g of fresh soil was placed in a plastic screw-top jar. To this 60 ml of reagent grade water was added. Jars were then shaken vigorously by hand for 30 seconds every half hour for two hours (Rhoades 1982). Samples were then allowed to stand for one hour. Electrical conductivity of the supernatant (extract) of samples was then measured using a YSI Salinity-Conductivity-Temperature meter (model no. 33) at a temperature setting of 25°C. Measurements were read as  $\mu\text{mhos.cm}^{-1}$ , but subsequently converted to the SI unit  $\text{dS.m}^{-1}$ . For each group of samples, duplicate blanks (reagent grade water only) were analysed. The average reading for blanks (where obtained) was deducted from those of group samples.

##### Factor 3 - Chloride content (Cl)

Chloride ion concentration was determined in the same extracts used to determine electrical conductivity. Extracts were titrated using a Radiometer chloride titrator (model CMT-10). Extracts were titrated in 100  $\mu\text{l}$  units until a chloride ion concentration reading was obtained ( $\text{meq.l}^{-1}$ ). If a reading was not obtained after having titrated 1 ml of extract a value of zero was ascribed. For each group of samples, duplicate blanks (reagent grade water only) were analysed.

Values were adjusted first for calibrations of the instrument. Values were then adjusted for extract volume, and converted to  $\mu\text{g.g}^{-1}$  fwt of soil sample. Values were then converted to an oven dry weight basis (see factor 6). These values were multiplied by bulk density (factor 7) to convert to a volumetric basis, then divided by 1,000. Results were recorded as  $\text{kg.m}^{-3}$ .

#### Factor 4 - Extractable sodium (Na)

Extractable sodium was determined on the same extract as used for extractable magnesium using Atomic absorption spectrophotometry (see factor 17). Flame type used was air-acetylene, slit-width used was 0.5 mm, wavelength used was 589.0 nm and the burner was rotated 90°.

The same sampling protocol and data transformations as used for extractable magnesium were used. Standard concentrations used in construction of the calibration curve were 10  $\text{mg.l}^{-1}$ , 20  $\text{mg.l}^{-1}$  and 40  $\text{mg.l}^{-1}$ .

#### Factor 5 - Above canopy salt deposition (ACSD)

For each quadrat, above canopy salt deposition was predicted using a model developed in a subsidiary study to this thesis which examined spatial patterns of salt-spray deposition over the research site. Above canopy salt-spray deposition was predicted from distance from cliff-tops using the following model:

$$\ln(\text{salt-spray deposition}) = 1.36 - 0.425 * (\ln(\text{distance from cliff-tops})).$$

Results were recorded as  $\text{t.ha}^{-1} \cdot \text{annum}^{-1}$ . Further details are supplied in Appendix 5.1.

#### Factor 6 - Below canopy salt deposition (BCSD)

For each quadrat, below canopy salt deposition was predicted using models developed in a subsidiary study to this thesis which examined spatial patterns of salt-spray deposition over the research site. Below canopy salt-spray deposition was predicted from distance from cliff-tops using the following models:

For shrub stratum coverage of 0% to 80%:

$$\ln(\text{salt-spray deposition}) = -0.020 - 0.302 * (\ln(\text{distance from cliff-tops})).$$

For shrub stratum coverage of 81% to 100%:

$$\ln(\text{salt-spray deposition}) = -0.659 - 0.163 * (\ln(\text{distance from cliff-tops})).$$

Results were recorded as  $\text{t} \cdot \text{ha}^{-1} \cdot \text{annum}^{-1}$ . Further details are supplied in Appendix 5.1.

### *Soil physical factor group*

#### Factor 7 - Field soil moisture (FSM)

As previously outlined, samples were collected two days after a substantial rainfall episode. The two day interval was to allow for drainage. I envisaged that sites would either dry or become wetter due to drainage, and that soil moisture under such conditions may be an appropriate reflection of general soil moisture status.

Approximately 80 g of fresh soil from each of the samples was placed in individual foil pie dishes, which were then accurately weighed. Twenty empty foil dishes were weighed and the mean weight deducted from all fresh weight measurements, to estimate the fresh weight of soil. Samples were then dried for 24 hours at 105°C, allowed to cool for one hour under ambient laboratory conditions, then reweighed. Due to the large number of samples and the dish dimensions, samples were not cooled in desiccators. Initial weighing and reweighing, however, was conducted at approximately the same time in the morning, and at the same location using the same balance. The same twenty empty foil dishes used to initially estimate dish weight were heated and cooled under the same conditions. These were also reweighed and the mean weight deducted from the reweighings to estimate oven-dry weights of samples. Field soil moisture was subsequently calculated as  $((\text{g fwt.} - \text{g dwt.})/\text{g dwt.})$ . Results were recorded as  $\text{g water} \cdot \text{g}^{-1} \text{dwt soil}$ .

### Factor 8 - Bulk density (BD)

Since soil cores of known volume were collected calculation of bulk density and related physical parameters was possible. In order to calculate bulk density samples in sample bags were first accurately weighed prior to any soil being taken for other analyses. Twenty empty sample bags were also weighed and the mean weight deducted from all sample plus bag weights to estimate weight of soil cores. A multiplication factor was then calculated for each sample, this being the core fresh weight divided by the weight of fresh soil taken subsequently for determination of factor 6. The oven dry weight of each sample from determination of Factor 6 above was then multiplied by this factor to give the oven dry weight of the soil core. This weight was then divided by the core volume ( $196 \text{ cm}^3$ ) and taken as an estimate of bulk density. Results were recorded as  $\text{g.cm}^{-3}$ .

### Factor 9 - Pore space ratio (PSR)

Pore space ratio was estimated for each sample by the formula  $(1 - (\text{bulk density}/\text{particle density}))$ . As an approximation, the value for particle density was taken as an average of soil inorganic particle density ( $2.65 \text{ g.cm}^{-3}$ ) in each case. Although this factor is linearly related to factor 8 it has been retained in analyses.

### Factor 10 - Air filled porosity (AFP)

Air filled porosity was estimated for each sample by the formula (pore space ratio - (water content/soil volume)). Water content was ml of water in each soil core.

### Factor 11 - Organic content (org)

Organic content of each sample was estimated using the loss on ignition procedure described by Grimshaw (1989). Results were recorded as % weight loss.

### Factor 12 - fine particle fraction ( fine)

Due to the number of samples and the fact that only one particle size division was sought, soil samples used in particle size fractionation were not predispersed, dry-sieving rather than wet-sieving was used. Although less consistent than wet sieving for particle size divisions below that used in my study dry sieving gives better particle size discrimination within the range in which the division in my study was made (see Robertson *et al.* 1984b).

The percentage coarse particle fraction for each soil sample was estimated by first accurately weighing approximately 20 g of oven-dry, 2 mm sieved soil into a pre-weighed 106  $\mu\text{m}$  sieve. The sample was then dry-sieved using a Fritsche 'Analysette 3' vibration sieve shaker (15 minutes, medium intensity). The soil fraction remaining in the sieve was then weighed along with the sieve. The sieve weight was then deducted and the resultant weight deducted from the original sample weight. This amount was expressed as a percentage of the original sample weight, and taken as an estimate of the percentage weight of the fine particle fraction.

### Factor 13 - coarse particle fraction (coarse)

The percentage coarse particle fraction for each soil sample was estimated by expressing the weight of sample left in the sieve (above) as a percentage of the original sample weight.

## ***Soil nutrition factor group***

### Factor 14 - pH (pH)

pH (soil reaction) was determined in the extracts used immediately prior for electrical conductivity and chloride content. Prior to measuring pH, however, 600  $\mu\text{l}$  of 1M  $\text{CaCl}_2$  solution was added to each 60 ml extract. The addition of  $\text{CaCl}_2$  is recommended for saline extracts to counter effects of high salt concentrations on the

activity of some pH electrodes (Grimshaw 1989). pH was measured using a Radiometer pH meter (model no. 28).

#### Factor 15 - Total phosphorus (P)

All glassware and plasticware used in phosphorus (and nitrogen) determinations was acid washed (2%  $\text{H}_2\text{SO}_4$ ) for at least 24 hours, rinsed four times with R.O. (reverse osmosis) water, then rinsed with reagent grade water. All glassware and plasticware that was reused was first washed with phosphate free detergent, rinsed once with R.O. water, acid washed (2%  $\text{H}_2\text{SO}_4$ ) for twenty four hours, rerinsed four times with R.O. water, then rinsed with reagent grade water.

Total phosphorus was determined in acid digests. For each sample, approximately 0.2 g of 2 mm sieved oven-dry soil was accurately weighed into a 100 ml digestion tube. Samples were then digested following a modified form of the sulphuric acid-hydrogen peroxide digestion procedure described by Grimshaw (1989). Due to high organic content in a number of samples, digests were allowed to stand for one hour subsequent to addition of hydrogen peroxide and prior to heating. The digest solutions were then thoroughly mixed. Additional hydrogen peroxide was added where necessary to ensure that all the added sample was in the digest solution, and to ensure adequate breakdown of organic material.

Digest solutions were heated in groups of 30 in digest blocks. Temperature was raised  $50^\circ\text{C}$  every half hour with mixing every half hour until a temperature of  $300^\circ\text{C}$  was reached. Digest solutions were maintained at this temperature for approximately three hours. If digestion was incomplete, the temperature was raised to  $350^\circ\text{C}$  and digestion continued until completion (indicated by a clear supernatant and white powdery appearance of the digested sample).

Solutions were then allowed to cool for approximately three hours, after which time digest tubes were covered and allowed to stand for a further 8 hours. Digest tubes were then uncovered, and 10 ml of reagent grade water added. Digest solutions were then vigorously mixed on a vortex mixer, diluted to 100 ml, stoppered, then re-mixed. Digest solutions were then allowed to stand for approximately a further 6 hours.

Supernatants were then decanted into 120 ml plastic screw-top jars, and stored until analysis. Digest reagent blanks were included with each group of samples digested.

A 5 ml aliquot of digest solution was taken from each sample to be analysed. Solutions were prepared for analysis using the manual molybdenum blue (ascorbic acid reduction) method described by Clesceri *et al.* (1989). Prior to analysis, calibration curves were constructed. Standards were prepared from a working standard solution of  $2 \mu\text{g P.ml}^{-1}$ , which was prepared from a stock standard solution of  $100 \mu\text{g P.ml}^{-1}$ . This was prepared from  $\text{KH}_2\text{PO}_4$ . Volumes of 1 ml, 2 ml, 3 ml, 4 ml and 5 ml of working standard solution were transferred to digest tubes for each lot of standards to be prepared. These were digested as above except that the final dilution was not made. Instead, the solutions were transferred to 50 ml volumetric flasks for analysis. Absorbances of all sample and standard solutions were then measured at 880 nm using a LKB Biochrom Ultrospec II spectrophotometer.

Subsequent to analysis, mg P present in sample aliquots was determined from calibration curves. Values were then multiplied by 20 to attain mg P in the 100 ml digest solution (5ml aliquot \* 20). These values were then divided by the sample weight (g) and multiplied by 1,000 to obtain ppm ( $\mu\text{g.g}^{-1}$ ). These figures were converted to a volumetric basis by multiplying by the respective bulk densities. These figures were divided by 1,000 and recorded as  $\text{kg.m}^{-3}$ .

Values obtained from the above manual method were confirmed by segmented flow analysis. Fifty sample digest solutions considered representative were selected from the whole sample set. These were analysed by a Segmented Flow ('auto') Analyser (Skalar Sanplus System) using colorimetry based on the ascorbic acid reduction method (Clesceri *et al.* 1989). Method and instrument settings are given by Skalar (1993).

In addition to the above, two international standard reference materials were analysed. The reference materials were Standard Reference Material 1646 Estuarine Sediment (U.S. Dept. of Commerce, National Bureau of Standards) and PACS-1 Marine Sediment (National Research Council of Canada). Total phosphorus levels in these materials are 540 ppm +/- 5 ppm and 1017 ppm +/- 8 ppm respectively. Five samples of each material were digested as described previously. Five replicate solutions for each digest were prepared by the manual method. Analyses showed

recoveries of 90.7% +/- 0.5% (s.e.m) and 84.0% +/- 0.4% (s.e.m) for the two reference materials respectively.

#### Factor 16 - Total nitrogen (N)

Total nitrogen was determined in the same digest solutions as used for total phosphorus. Colorimetry was performed using the indophenol-blue method described by Allen *et al.* (1974). However, 20 ml test tubes were used rather than 50 ml volumetric flasks. Reagent quantities were adjusted accordingly, and 1 ml of sample digest solutions prepared. Absorbances were read at 625 nm using a LKB Biochrom Ultrospec II spectrophotometer. Calibration curves were constructed from digested standard solutions. These solutions were digested as outlined for phosphorus, but by digesting  $\text{NH}_4\text{Cl}$  instead of soil. Standard digest solutions contained  $0.8 \mu\text{g N.ml}^{-1}$ ,  $2 \mu\text{g N.ml}^{-1}$ ,  $4 \mu\text{g N.ml}^{-1}$ ,  $8 \mu\text{g N.ml}^{-1}$  and  $20 \mu\text{g N.ml}^{-1}$ .

Nitrogen present in sample digest solutions was read from calibration curves. These values were multiplied by 100, then divided by digested sample weight (g) to obtain ppm. These figures were then converted to a volumetric basis by multiplying by the respective bulk densities and then dividing by 1,000, to obtain  $\text{kg.m}^{-3}$ .

#### Factor 17 - Extractable magnesium (Mg)

All glassware and plasticware used in determination of extractable cations was subject to the same cleaning regime as specified for phosphorus and nitrogen determinations. All glassware that was reused, however, was acid washed using nitric acid rather than sulphuric acid. Also, the washing with phosphate free detergent step was omitted.

Extractable magnesium was determined from extracts of air-dry soil. For each sample, approximately 50 g of fresh soil sample was dried in a fan-forced oven at  $30^\circ\text{C}$  for approximately 48 hours. The number of samples precluded air-drying under ambient laboratory conditions. Soil samples were dried in foil pie dishes identical to those used for oven-drying (see factor 7). After drying, samples were sieved using a 2 mm brass sieve, then stored in air-tight screw-top plastic jars until extraction.



For each sample, approximately 2 g of air-dry soil was accurately weighed into a separate plastic screw-top jar. This soil was then extracted using 50 ml of ammonium acetate. The extraction procedure used was a modified form of that used by Bower *et al.* (1952). Rather than repeated washings with ammonium acetate, the jars containing soil and ammonium acetate were shaken vigorously for 24 hours on a rotary shaker. The supernatant was then separated by quantitative filtration using Whatman No. 43 filter paper. This step was employed in place of the centrifugation specified in the original method. This was done due to high organic matter in a number of samples. Also, since an automated analysis procedure was employed (see below), it was of prime importance to ensure supernatants were as free from particulate matter as possible. Samples were extracted in batches of 30. For each batch extracted a sample blank was prepared and shaken using the same ammonium acetate preparation as contained in the samples.

Extracts were analysed for extractable magnesium using a Varian SpectrAA 800 atomic absorption spectrometer fitted with an automated robotic sampling device. Flame type was air-acetylene, slit-width used was 1.0 mm, wavelength used was 202.6  $\mu\text{m}$  and the burner was rotated 30°.

Three solution replicates were analysed for each sample. The instrument was calibrated using three standards and a standard blank. Standard concentrations of magnesium were 10  $\text{mg.l}^{-1}$ , 20  $\text{mg.l}^{-1}$  and 50  $\text{mg.l}^{-1}$ . Samples and sample blanks were analysed in batches of 50. The instrument was recalibrated after every 40 samples. The calibration (standard) curve was resloped every 10 samples using the standard blank and 20  $\text{mg.l}^{-1}$  standard.

Readings were recorded as  $\text{mg.l}^{-1}$ . These readings were first corrected for solution volume (50 ml) then divided by the air-dry weight of the sample extracted to give  $\text{mg.g}^{-1}$  air dry soil. These figures were multiplied by 1000 to give parts per million.

#### Factor 18 - Extractable calcium (Ca)

Extractable calcium was determined in the same extract as used for magnesium and using AAS. Flame type was air-acetylene, slit-width used was 0.5 mm, wavelength used was 422.7  $\mu\text{m}$  and the burner was rotated 30°.

The sampling protocol, standard concentrations and data transformations were as used for magnesium.

#### Factor 19 - Extractable potassium (K)

Extractable potassium was determined in the same extract as used for calcium and using AAS. Flame type was air-acetylene, slit-width used was 1.0 mm, wavelength used was 769.9  $\mu\text{m}$  and the burner was rotated 30°.

The sampling protocol and data transformations were as used for calcium. Standard concentrations used in construction of the calibration curve were 5  $\text{mg.l}^{-1}$ , 10  $\text{mg.l}^{-1}$  and 20  $\text{mg.l}^{-1}$ .

#### *Fire factor group*

#### Factor 20 - Years since last fire (YSLF)

Quadrats were assigned a value of years since the most recent fire. This was determined from the date at which vegetation sampling began and was ascertained from fire records held at the Botany Bay sub-district office of the National Parks and Wildlife Service of New South Wales. Records only extended back for approximately three years. Information from unsubstantiated sources suggested that vegetation in the site which did not appear to have been burnt in recent years had remained unburnt for approximately 20 years. Quadrats located in these areas were assigned a value of 20.

### 5.2.2 Numerical analyses

Associations between environmental factors were investigated using correspondence analysis. Correspondence analysis was performed on a site by environmental factor matrix with environmental data range standardised. Associations

were assessed according to the relative positions of the environmental factor maxima in the ordination diagram.

To examine environmental differentiation of property complexes, mean levels of environmental factors were compiled for all complexes. Complex means were then compared within properties using one-way analyses of variance. Assumptions of analyses were assessed by inspection of standard deviations, by normal probability plots, by residual plots and by application of the Shapiro-Wilk statistic. Data transformations were made where necessary.

Environmental relationships of properties and their variance components were investigated through the use of canonical correspondence analysis (CCA) using the computer program CANOCO (ter Braak 1987). Data sets used for properties were the respective site by attribute matrices. In the case of independent variance components, property matrices were analysed with attributes of the compared property specified as co-variates. In the case of common variance components, property matrices were analysed with the axis scores of the CA analysis defining the relevant independent variance specified as covariates. Data for sites 51 to 60 were omitted from all analyses (see Chapter 4).

Properties and their variance components were constrained using all environmental factors together, all factors individually, and using only factors of individual factor groups. The percentage variance accounted for by environmental factors/factor groupings was calculated for all analyses. This was calculated as the ratio of the sum of eigenvalues of the constrained axes to the sum of eigenvalues of the relevant unconstrained analysis (see Chapter 4). This measure is also known as the multiple correlation ratio (see McIntyre & Lavorel 1994; Okland & Eilersten 1994).

The differential nature of environmental relationships of properties was assessed by interpretation of CCA biplots. This analysis, however, was not extended to variance components of properties. Rather, differential environmental relationships of variance components were assessed by comparison of the importance and ranks of individual factors and factor groups between the relevant variance components. Percentage variance accounted for was taken as the measure of importance, and comparisons made on a subjective basis.

## 5.3 RESULTS

### 5.3.1 Associations between environmental factors

The correspondence analysis of environmental factors is presented in Fig. 5.1. Two features of association are clearly evident in this figure. The first is the strong negative association between distance from cliff-tops and the "non-soil based" maritime factors of above canopy salt-spray deposition and below canopy salt-spray deposition. This was not entirely unexpected given that the factors are not mathematically independent. Also of note was the strong negative association between years since last fire and distance from the cliff-top which reflects the unburnt state of much of the platform heath close to the cliff-top.

The second prominent feature of association between environmental factors is the complex gradient of soil physical and soil nutrition factors. As shown in Fig 5.1, optima for pH, bulk density and coarse particle fraction are closely associated at one end of the 'gradient'. At the other end, optima for extractable cations, electrical conductivity, fine particle fraction, field soil moisture and organic content are associated. Optima for total phosphorus, total nitrogen, air filled porosity, pore space ratio and chloride content are medial in position and near the origin of the ordination (Fig. 5.1). While these may be true optima it is worth keeping in mind that correspondence analysis may place species/attributes which have no clear relationship with others near the centre of the ordination (ter Braak & Prentice 1988). These factors may hence be largely independent of the other factors forming the major pattern.

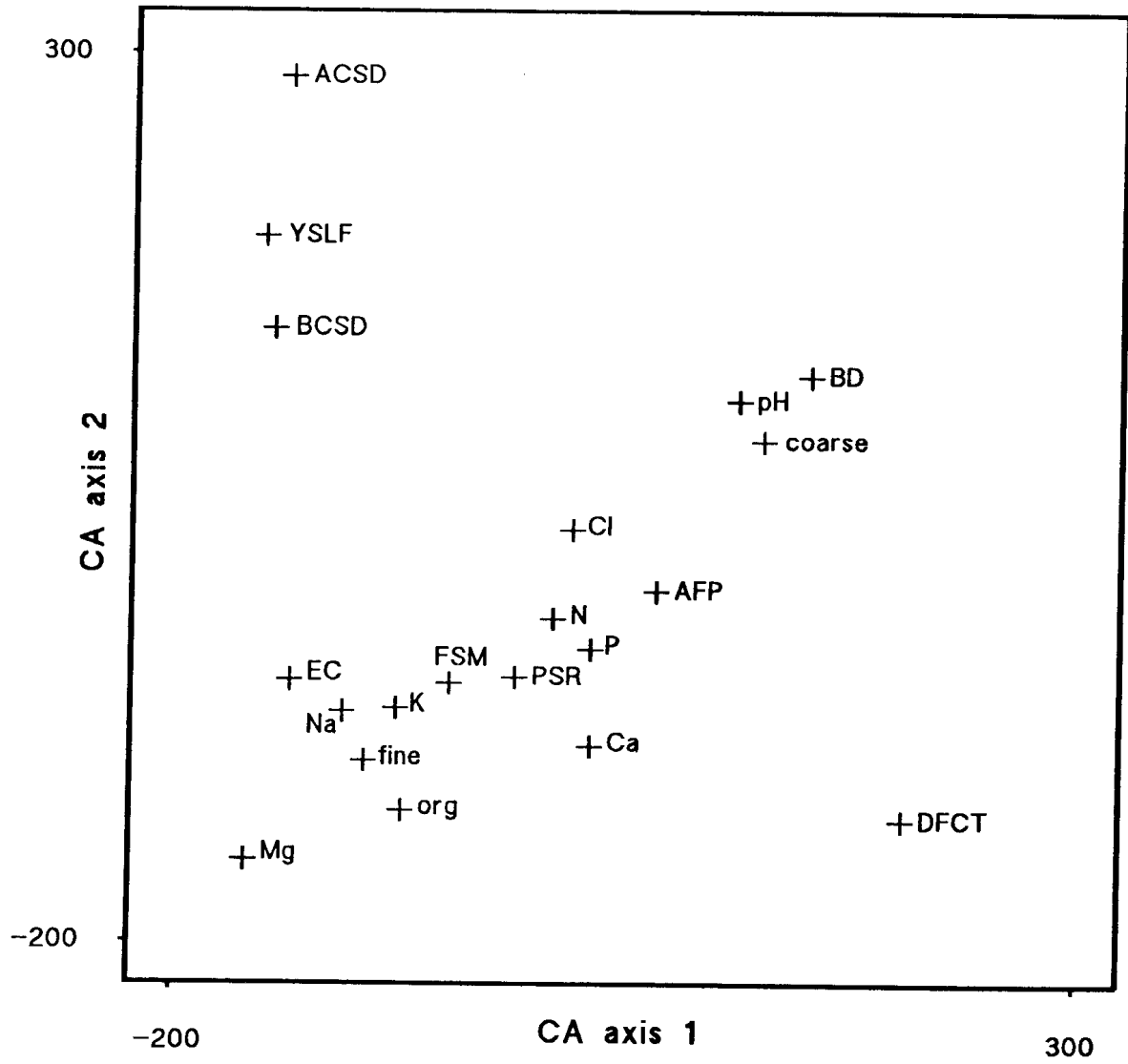


Fig. 5.1 Correspondence analysis of environmental factors. Maxima for environmental factors are identified by abbreviation (see text).

### 5.3.2 Environmental characteristics of property complexes

#### 5.3.2.1 Environmental characteristics of floristic complexes

Environmental characteristics of floristic complexes are summarised in Table 5.2. FC 1 and FC 2 are environmentally similar, both being located on deep and well drained sand dunes. However, FC 1 is located significantly further inland, and accordingly has a significantly lower predicted mean above canopy salt-spray deposition. As shown in Table 5.2, soil physical factors and soil nutrition factors remain statistically inseparable between these complexes. With respect to other complexes, however, they are characterised by low field soil moisture, high bulk densities, low pore space ratios, low organic contents and high coarse particle fractions. They also have the lowest nutrient status of all the complexes, principally with respect to extractable potassium.

Like FC 2, FC 3 contains quadrats burnt 1.4 years before survey. However, this complex is located on sandstone platform. In terms of maritime factors, FC 3 is characterised by significantly greater extractable sodium levels than FCs 1 and 2. With respect to soil physical factors, it has markedly higher field soil moisture, lower bulk density, higher pore space ratio and a significantly greater fine particle fraction. With respect to soil nutrition factors, pH is significantly lower in this complex compared with the previous two, as is extractable calcium. Extractable potassium, however, is significantly greater.

FC 4 is the first of a group of platform heath complexes (see Chapter 3). It is located significantly closer to the cliff-edge than the previous complexes, and accordingly has a significantly greater predicted above canopy salt-spray deposition. As shown in Table 5.2, field soil moisture of this complex is intermediate between that of FCs 1 and 2 on one hand and FC 3 on the other. Both bulk density and pore space ratio resemble that of FCs 1 and 2 rather than FC 3. Values for the remaining soil physical factors are intermediate between FCs 1 and 2 and FC 3. With respect to soil nutrition levels, pH of FC 4 resembles that of FCs 1 and 2 in being greater than that of FC 3. However, with some exceptions, soil nutrient levels of FC 4 resemble those of FC 3 rather than that of FCs 1 and 2. Also, it is evident in Table 5.2 that variability in all factors is generally greater in FC 4 than FCs 1 to 3. As was outlined in Chapter 3, this complex was heterogeneous with respect to location, general substrate conditions

**Table 5.2 Environmental characteristics of floristic complexes**

Environmental factors are listed by factor group. Factor units are indicated. Values for environmental factors are means. Standard errors are shown in parentheses. Values not determined for complexes are indicated as (nd). P - values for ANOVAs comparing environmental factor means between complexes are provided. Transformations (T) made for the purpose of analysis are indicated as 0 - no transformation, 1 -  $\log_{10}(x)$ , 2 -  $\sqrt{x}$ . Significantly different means are indicated by superscripts with no letters in common. Multiple comparisons were made using Tukey tests with significance of differences assessed at  $p < 0.05$  using the studentised range. Floristic complexes are identified by complex code (see text). Numbers of quadrats included in complexes is indicated.

Environmental factors	Units	T	Floristic complexes											P
			FC 1	FC 2	FC 3	FC 4	FC 5	FC 6	FC 7	FC 8	FC 9	FC 10	FC 11	
<i>Quadrats</i>			33	20	27	22	34	9	18	54	14	13	10	
<i>Maritime factor group</i>														
Distance from cliff-tops	m	0	127(4) <sup>d</sup>	73(5) <sup>c</sup>	93(5) <sup>c</sup>	45(5) <sup>b</sup>	37(4) <sup>b</sup>	87(6) <sup>c</sup>	50(5) <sup>b</sup>	77(6) <sup>c</sup>	94(5) <sup>c</sup>	80(6) <sup>c</sup>	10(2) <sup>a</sup>	< 0.001
Electrical conductivity	dS.m <sup>-1</sup>	1	0.085(0.009) <sup>a</sup>	0.092(0.010) <sup>ab</sup>	0.164(0.019) <sup>bc</sup>	0.211(0.054) <sup>bc</sup>	0.421(0.044) <sup>de</sup>	0.245(0.024) <sup>cd</sup>	0.580(0.065) <sup>e</sup>	0.372(0.030) <sup>d</sup>	0.565(0.086) <sup>e</sup>	0.346(0.017) <sup>d</sup>	0.610(0.125) <sup>e</sup>	< 0.001
Chloride content	kg.m <sup>-3</sup>	1	0.134(0.027) <sup>a</sup>	0.152(0.026) <sup>a</sup>	0.235(0.027) <sup>ab</sup>	0.483(0.173) <sup>abc</sup>	0.837(0.081) <sup>d</sup>	0.559(0.099) <sup>bc</sup>	1.084(0.124) <sup>d</sup>	0.701(0.063) <sup>cd</sup>	0.713(0.087) <sup>cd</sup>	0.548(0.104) <sup>bc</sup>	nd	< 0.001
Extractable Na	ug.g <sup>-1</sup>	1	73(5) <sup>a</sup>	73(14) <sup>a</sup>	239(28) <sup>b</sup>	382(132) <sup>bc</sup>	852(122) <sup>d</sup>	427(55) <sup>c</sup>	1191(176) <sup>d</sup>	465(43) <sup>c</sup>	1042(170) <sup>d</sup>	519(37) <sup>c</sup>	676(146) <sup>cd</sup>	< 0.001
Above canopy salt-spray dep.	t.ha <sup>-1</sup> .a <sup>-1</sup>	1	0.507(0.011) <sup>a</sup>	0.652(0.023) <sup>bc</sup>	0.579(0.012) <sup>ab</sup>	0.943(0.096) <sup>d</sup>	1.036(0.077) <sup>d</sup>	0.589(0.016) <sup>ab</sup>	0.812(0.072) <sup>cd</sup>	0.695(0.034) <sup>bc</sup>	0.572(0.015) <sup>ab</sup>	0.622(0.024) <sup>abc</sup>	1.599(0.122) <sup>e</sup>	< 0.001
Below canopy salt-spray dep.	t ha <sup>-1</sup> .a <sup>-1</sup>	1	0.229(0.003) <sup>a</sup>	0.275(0.007) <sup>ab</sup>	0.293(0.024) <sup>b</sup>	0.345(0.024) <sup>bc</sup>	0.337(0.015) <sup>bc</sup>	0.256(0.004) <sup>ab</sup>	0.294(0.009) <sup>bc</sup>	0.277(0.008) <sup>b</sup>	0.335(0.037) <sup>bc</sup>	0.596(0.037) <sup>d</sup>	1.599(0.122) <sup>e</sup>	< 0.001
<i>Soil physical factor group</i>														
Field soil moisture	g.g <sup>-1</sup>	1	0.040(0.003) <sup>a</sup>	0.074(0.010) <sup>a</sup>	0.181(0.018) <sup>c</sup>	0.124(0.031) <sup>b</sup>	0.262(0.029) <sup>c</sup>	0.231(0.035) <sup>c</sup>	0.440(0.066) <sup>d</sup>	0.222(0.031) <sup>c</sup>	0.457(0.053) <sup>d</sup>	1.603(0.217) <sup>e</sup>	0.168(0.017) <sup>bc</sup>	< 0.001
Bulk density	g.cm <sup>-3</sup>	0	1.616(0.034) <sup>d</sup>	1.565(0.036) <sup>d</sup>	1.181(0.047) <sup>c</sup>	1.542(0.075) <sup>d</sup>	1.165(0.055) <sup>bc</sup>	1.298(0.073) <sup>cd</sup>	0.923(0.080) <sup>ab</sup>	1.173(0.040) <sup>c</sup>	0.776(0.073) <sup>a</sup>	0.610(0.108) <sup>a</sup>	nd	< 0.001
Pore space ratio	-	0	0.391(0.013) <sup>a</sup>	0.411(0.014) <sup>a</sup>	0.555(0.018) <sup>b</sup>	0.418(0.028) <sup>a</sup>	0.561(0.021) <sup>bc</sup>	0.511(0.027) <sup>ab</sup>	0.652(0.030) <sup>cd</sup>	0.558(0.015) <sup>b</sup>	0.707(0.027) <sup>d</sup>	0.769(0.040) <sup>d</sup>	nd	< 0.001
Air filled porosity	-	0	0.327(0.014) <sup>b</sup>	0.298(0.016) <sup>b</sup>	0.354(0.024) <sup>b</sup>	0.269(0.022) <sup>b</sup>	0.294(0.009) <sup>b</sup>	0.217(0.056) <sup>ab</sup>	0.318(0.048) <sup>b</sup>	0.345(0.022) <sup>b</sup>	0.400(0.035) <sup>b</sup>	0.052(0.042) <sup>a</sup>	nd	< 0.001
Organic content	%	2	5.9(0.4) <sup>ab</sup>	4.6(0.5) <sup>ab</sup>	11.9(1.0) <sup>bc</sup>	7.9(1.7) <sup>b</sup>	15.9(1.7) <sup>c</sup>	12.3(1.9) <sup>bc</sup>	29.2(3.7) <sup>d</sup>	14.4(1.4) <sup>c</sup>	32.0(4.9) <sup>d</sup>	37.3(3.9) <sup>d</sup>	3.0(0.4) <sup>a</sup>	< 0.001
Fine particle fraction	%	2	1.4(0.1) <sup>a</sup>	1.7(0.2) <sup>ab</sup>	5.0(0.3) <sup>cd</sup>	3.7(0.8) <sup>bc</sup>	6.5(0.4) <sup>d</sup>	5.9(0.8) <sup>cd</sup>	8.1(1.0) <sup>de</sup>	6.2(0.4) <sup>d</sup>	12.4(1.4) <sup>e</sup>	10.5(0.6) <sup>e</sup>	12.4(2.5) <sup>e</sup>	< 0.001
Coarse particle fraction	%	2	98.6(0.1) <sup>e</sup>	98.3(0.2) <sup>e</sup>	95.0(0.3) <sup>cd</sup>	96.3(0.8) <sup>cde</sup>	93.5(0.4) <sup>c</sup>	94.1(0.8) <sup>c</sup>	91.9(1.0) <sup>bc</sup>	93.8(0.4) <sup>c</sup>	87.6(1.4) <sup>a</sup>	89.5(0.6) <sup>ab</sup>	87.6(2.5) <sup>a</sup>	< 0.001
<i>Soil nutrition factor group</i>														
pH	-	0	4.63(0.06) <sup>b</sup>	4.66(0.06) <sup>b</sup>	4.24(0.04) <sup>a</sup>	4.72(0.05) <sup>b</sup>	4.67(0.06) <sup>b</sup>	4.41(0.08) <sup>ab</sup>	4.36(0.08) <sup>a</sup>	4.22(0.05) <sup>a</sup>	4.49(0.08) <sup>ab</sup>	4.39(0.04) <sup>ab</sup>	5.60(0.15) <sup>c</sup>	< 0.001
Total P	kg.m <sup>-3</sup>	1	0.147(0.017) <sup>ab</sup>	0.090(0.014) <sup>a</sup>	0.221(0.023) <sup>b</sup>	0.267(0.052) <sup>bc</sup>	0.275(0.027) <sup>bc</sup>	0.375(0.046) <sup>c</sup>	0.259(0.025) <sup>bc</sup>	0.198(0.014) <sup>b</sup>	0.195(0.021) <sup>ab</sup>	0.184(0.018) <sup>ab</sup>	nd	< 0.001
Total N	kg.m <sup>-3</sup>	1	2.530(0.201) <sup>a</sup>	2.585(0.231) <sup>a</sup>	3.264(0.252) <sup>a</sup>	3.110(0.384) <sup>a</sup>	5.156(0.333) <sup>b</sup>	4.805(0.711) <sup>b</sup>	5.563(0.419) <sup>b</sup>	3.358(0.166) <sup>a</sup>	3.177(0.237) <sup>ab</sup>	4.893(0.380) <sup>b</sup>	nd	< 0.001

(cont/d.)

Table 5.2 (cont/d.)

Environmental factors	Units	T	Floristic complexes											P
			FC 1	FC 2	FC 3	FC 4	FC 5	FC 6	FC 7	FC 8	FC 9	FC 10	FC 11	
Extractable Mg	ug.g <sup>-1</sup>	0	163(12) <sup>a</sup>	148(18) <sup>a</sup>	287(18) <sup>ab</sup>	291(70) <sup>ab</sup>	580(65) <sup>c</sup>	462(85) <sup>bc</sup>	573(54) <sup>c</sup>	351(24) <sup>b</sup>	642(91) <sup>c</sup>	355(36) <sup>b</sup>	284(59) <sup>ab</sup>	< 0.001
Extractable Ca	ug.g <sup>-1</sup>	2	346(28) <sup>b</sup>	332(57) <sup>b</sup>	180(24) <sup>a</sup>	259(35) <sup>ab</sup>	407(47) <sup>bc</sup>	368(67) <sup>b</sup>	434(43) <sup>bc</sup>	274(20) <sup>ab</sup>	552(64) <sup>c</sup>	367(31) <sup>b</sup>	102(20) <sup>a</sup>	< 0.001
Extractable K	ug.g <sup>-1</sup>	1	46(3) <sup>a</sup>	45(5) <sup>a</sup>	298(30) <sup>d</sup>	107(27) <sup>b</sup>	213(18) <sup>cd</sup>	183(21) <sup>c</sup>	219(16) <sup>cd</sup>	194(25) <sup>cd</sup>	179(22) <sup>c</sup>	96(11) <sup>b</sup>	104(18) <sup>b</sup>	< 0.001
<i>Fire factor group</i>														
Years since last fire <sup>1</sup>	years	0	2.3	1.4	1.4	20	20	20	20	20	2.3	20	20	

<sup>1</sup> - most frequent value in complex



and years since last fire. The added variability in environmental factors in this complex can be attributed to this.

The remaining platform heaths (FCs 5 to 8) display similar environmental characteristics to FC 4. However, marked differences do occur both within this group and between these FCs and the first four described. As with FC 4, but unlike the first three FCs, the majority of quadrats in FCS 5 to 8 have remained unburnt in recent years. In general the level of maritime factors is greater in this group of FCs than in the first four with the most marked differences occurring with respect to electrical conductivity and chloride content (Table 5.2). Interestingly, these factors were highest in FCs 5 and 7, where *Baeckea imbricata* is particularly dominant (see Chapter 3). With respect to soil physical factors, field soil moisture in FCs 5 to 8 is greater than in FCs 1 to 4, with the exception of FC 7 which is not significantly different from FC 3. FCs 5 to 8 also had greater fine particle fractions than FCs 1 to 4, with the exception of FC 6. Also, FC 7 stands out from the other FCs already mentioned in having a significantly greater pore space ratio and organic content. With respect to soil nutrition factors, levels of soil nutrients in FCs 5 to 8 were greater than those for FCs 1 to 4. These differences were more marked for extractable cations than for total phosphorus or total nitrogen.

FC 9 represented a burnt area of impeded drainage intermediate in location between dunes and platform (see Chapter 3). With respect to maritime factors, this complex was distinguished from those already described, except for FCs 5 and 7, by significantly greater electrical conductivity and extractable sodium. With respect to soil physical factors, this complex was distinguished by high field soil moisture, organic content and fine particle fraction as well as by low bulk density. Soil nutrient factors were similar to those of FCs 5 to 8.

FC 10 represented unburnt swamp (see Chapter 3). Of note with respect to maritime factors was the high level of predicted below canopy salt- spray deposition. This can be attributed to the absence of shrub cover. Electrical conductivity and chloride content of this complex may have been expected to be concordantly high. However, levels of soil physical factors which may mediate this include high field soil moisture and low bulk density. This complex also displayed high organic content and a high fine particle fraction. Soil nutrient levels were generally commensurate with or lower than those for other complexes.

FC 11 was distinct from other complexes in terms of maritime factors. This complex was located significantly closer to the cliff-edge than the other complexes. Concordantly, it also had significantly higher levels of other maritime factors. Of note with respect to soil physical factors were low field soil moisture, low organic content and a high fine particle fraction. Soil nutrients were also generally low, with pH in this complex being significantly greater than that for other complexes.

### 5.3.2.2 Environmental characteristics of structural complexes

Environmental characteristics of structural complexes are shown in Table 5.3. Structural complexes were in general more similar environmentally than floristic complexes. However, significant differences existed between most complexes in levels of one or more factors. Reference to the structural classification (see Chapter 3) shows these differences to be located primarily towards lower division levels of the classification. SC 2 was separated from SC 1 by being located significantly closer to the cliff-top, and accordingly by having a significantly greater predicted above canopy salt-spray deposition. Extractable sodium was also significantly higher than in SC 1. SC 3 was separated from SC 2 by a significantly lower predicted above canopy salt-spray deposition similar to SC 1. However, a significant difference in distance from cliff-tops could not be established between these complexes. SC 3 was also characterised by a significantly lower pH and significantly lower extractable sodium than SC 2.

SC 4 could not be separated environmentally from SC 3. SCs 5 and 6 were similar environmentally to SC 4. However, a number of significant differences existed between SC 4 and SC 6. Notable with respect to SC 6 were significantly lower field soil moisture, pore space ratio, organic content and fine particle fraction, as well as significantly higher bulk density. pH was significantly higher, while nutrient levels were generally lower.

SC 7 was similar to SC 6 in having generally low levels of maritime factors. Both complexes were amongst the furthest from the cliff-top. Both complexes, unlike the other complexes, also had the majority of their quadrats burnt 1.4 years before

**Table 5.3** Environmental characteristics of structural complexes

Environmental factors are listed by factor group. Factor units are indicated. Values for environmental factors are means. Standard errors are shown in parentheses. Values not determined for complexes are indicated as (nd). P - values for ANOVAs comparing environmental factor means between complexes are provided. Transformations (T) made for the purpose of analysis are indicated as 0 - no transformation, 1 -  $\log_{10}(x)$ , 2 -  $\sqrt{x}$ . Significantly different means are indicated by superscripts with no letters in common. Multiple comparisons were made using Tukey tests with significance of differences assessed at  $p < 0.05$  using the studentised range. Structural complexes are identified by complex code. Numbers of quadrats included in complexes is indicated.

Environmental factors	Units	T	Structural complexes									P
			SC 1	SC 2	SC 3	SC 4	SC 5	SC 6	SC 7	SC 8	SC 9	
Quadrats			29	38	31	4	58	37	26	21	10	
<b>Chemical factor group</b>												
Distance from cliff-tops	m	0	93(7) <sup>c</sup>	46(4) <sup>b</sup>	69(5) <sup>bc</sup>	58(20) <sup>abc</sup>	73(6) <sup>c</sup>	90(6) <sup>c</sup>	94(5) <sup>c</sup>	85(4) <sup>c</sup>	10(2) <sup>a</sup>	< 0.001
Electrical conductivity	dS.m <sup>-1</sup>	1	0.405(0.048) <sup>c</sup>	0.412(0.051) <sup>c</sup>	0.314(0.025) <sup>bc</sup>	0.356(0.060) <sup>bc</sup>	0.254(0.033) <sup>ab</sup>	0.206(0.047) <sup>a</sup>	0.182(0.036) <sup>a</sup>	0.357(0.021) <sup>c</sup>	0.610(0.125) <sup>c</sup>	< 0.001
Chloride content	kg.m <sup>-3</sup>	1	0.739(0.101) <sup>b</sup>	0.747(0.080) <sup>b</sup>	0.671(0.073) <sup>b</sup>	0.696(0.085) <sup>b</sup>	0.485(0.068) <sup>ab</sup>	0.369(0.111) <sup>a</sup>	0.242(0.033) <sup>a</sup>	0.522(0.067) <sup>ab</sup>	nd	< 0.001
Extractable Na	ug.g <sup>-1</sup>	1	555(90) <sup>bc</sup>	832(133) <sup>d</sup>	448(40) <sup>b</sup>	560(98) <sup>bc</sup>	433(78) <sup>ab</sup>	304(90) <sup>ab</sup>	277(61) <sup>a</sup>	574(50) <sup>c</sup>	676(146) <sup>cd</sup>	< 0.001
Low canopy salt-spray dep.	t.ha <sup>-1</sup> .a <sup>-1</sup>	1	0.610(0.027) <sup>a</sup>	0.938(0.072) <sup>b</sup>	0.682(0.025) <sup>a</sup>	0.764(0.097) <sup>ab</sup>	0.779(0.048) <sup>ab</sup>	0.664(0.055) <sup>a</sup>	0.575(0.011) <sup>a</sup>	0.604(0.017) <sup>a</sup>	1.599(0.122) <sup>c</sup>	< 0.001
High canopy salt-spray dep.	t.ha <sup>-1</sup> .a <sup>-1</sup>	1	0.255(0.006) <sup>a</sup>	0.308(0.011) <sup>a</sup>	0.276(0.006) <sup>a</sup>	0.292(0.018) <sup>a</sup>	0.301(0.012) <sup>a</sup>	0.274(0.014) <sup>a</sup>	0.264(0.014) <sup>a</sup>	0.559(0.033) <sup>b</sup>	1.559(0.122) <sup>c</sup>	< 0.001
<b>Physical factor group</b>												
Field soil moisture	g.g <sup>-1</sup>	1	0.184(0.033) <sup>abc</sup>	0.272(0.034) <sup>bc</sup>	0.273(0.042) <sup>bc</sup>	0.458(0.186) <sup>bcd</sup>	0.152(0.028) <sup>a</sup>	0.130(0.027) <sup>a</sup>	0.202(0.026) <sup>b</sup>	1.131(0.190) <sup>d</sup>	0.168(0.017) <sup>ab</sup>	< 0.001
Soil bulk density	g.cm <sup>-3</sup>	0	1.157(0.055) <sup>b</sup>	1.172(0.065) <sup>b</sup>	1.188(0.054) <sup>bc</sup>	1.018(0.101) <sup>ab</sup>	1.408(0.048) <sup>c</sup>	1.475(0.058) <sup>c</sup>	1.180(0.053) <sup>b</sup>	0.692(0.075) <sup>a</sup>	nd	< 0.001
Open space ratio	-	0	0.563(0.021) <sup>b</sup>	0.558(0.024) <sup>b</sup>	0.552(0.020) <sup>b</sup>	0.616(0.038) <sup>bc</sup>	0.469(0.018) <sup>ab</sup>	0.444(0.022) <sup>a</sup>	0.555(0.020) <sup>b</sup>	0.739(0.028) <sup>c</sup>	nd	< 0.001
Open filled porosity	-	0	0.387(0.022) <sup>c</sup>	0.308(0.024) <sup>bc</sup>	0.272(0.034) <sup>abc</sup>	0.230(0.137) <sup>abc</sup>	0.320(0.014) <sup>c</sup>	0.300(0.017) <sup>bc</sup>	0.343(0.025) <sup>c</sup>	0.186(0.050) <sup>a</sup>	nd	< 0.001
Organic content	%	2	14.8(1.7) <sup>bc</sup>	18.4(2.5) <sup>cd</sup>	15.3(1.9) <sup>c</sup>	20.0(3.4) <sup>cde</sup>	10.7(1.4) <sup>bc</sup>	9.3(1.9) <sup>ab</sup>	14.0(2.4) <sup>bc</sup>	31.6(3.1) <sup>e</sup>	2.9(0.4) <sup>a</sup>	< 0.001
Fine particle fraction	%	2	6.8(0.6) <sup>b</sup>	6.2(0.7) <sup>b</sup>	6.0(0.6) <sup>b</sup>	7.5(1.5) <sup>bc</sup>	3.5(0.4) <sup>a</sup>	3.2(0.6) <sup>a</sup>	5.6(0.6) <sup>b</sup>	11.6(0.8) <sup>c</sup>	12.4(2.5) <sup>c</sup>	< 0.001
Coarse particle fraction	%	2	93.2(0.6) <sup>b</sup>	93.8(0.7) <sup>b</sup>	94.0(0.6) <sup>bc</sup>	92.5(1.5) <sup>ab</sup>	96.5(0.4) <sup>c</sup>	96.8(0.6) <sup>c</sup>	94.4(0.6) <sup>bc</sup>	88.4(0.8) <sup>a</sup>	87.6(2.5) <sup>a</sup>	< 0.001
<b>Nutrition factor group</b>												
Available P	kg.m <sup>-3</sup>	1	4.33(0.06) <sup>ab</sup>	4.55(0.06) <sup>bc</sup>	4.22(0.07) <sup>a</sup>	4.13(0.25) <sup>a</sup>	4.60(0.05) <sup>c</sup>	4.65(0.08) <sup>c</sup>	4.28(0.04) <sup>a</sup>	4.46(0.05) <sup>ab</sup>	5.60(0.15) <sup>d</sup>	< 0.001
Available N	kg.m <sup>-3</sup>	1	0.225(0.017) <sup>b</sup>	0.238(0.024) <sup>bc</sup>	0.244(0.023) <sup>bc</sup>	0.335(0.079) <sup>c</sup>	0.204(0.020) <sup>b</sup>	0.143(0.028) <sup>a</sup>	0.228(0.024) <sup>bc</sup>	0.199(0.014) <sup>b</sup>	nd	< 0.001
			3.614(0.326) <sup>a</sup>	4.495(0.373) <sup>b</sup>	4.111(0.270) <sup>b</sup>	4.858(0.331) <sup>b</sup>	3.508(0.240) <sup>a</sup>	2.607(0.168) <sup>a</sup>	3.448(0.272) <sup>a</sup>	4.182(0.329) <sup>b</sup>	nd	0.001

nt/d.)



survey. However, both complexes displayed significant differences in both soil physical factors and soil nutrition factors which are summarised in Table 5.3.

SC 8 was characterised by high levels of predicted below canopy salt-spray deposition. This complex was also strongly differentiated from the others by having significantly greater field soil moisture, organic content and fine particle fraction as well as by a low air filled porosity. pH and soil nutrient levels were commensurate with the other complexes. SC 9 concords entirely with FC 11, the environmental characteristics of which were described in the previous section.

### 5.3.2.3 Environmental characteristics of species richness complexes

Environmental characteristics of species richness complexes are summarised in Table 5.4. Again, it is evident that most SRCs can be differentiated in terms of one or more environmental factors. As shown in Table 5.4, these differences encompass all environmental factor groups. In terms of maritime factors SRCs significantly further from the cliff-top in general had significantly lower levels of other maritime factors, e.g. compare SRCs 9 and 10 with SRCs 17 and 18.

In terms of soil physical factors, many significant differences were evident between SRCs (Table 5.4). Field soil moisture and organic content are the primary differentiating factors. Low levels of the former factor were recorded for SRCs 9 to 11 while levels approximately 30 times higher were recorded for SRCs 14 and 16. As shown in Table 5.4, differences in other soil physical factors are correlated with field soil moisture. Differences in soil nutrition factors between SRCs were generally less marked than for maritime and soil physical factors. Significant differences nevertheless existed. Of note were relatively fine scale differences in pH within a highly acidic range. This was also the case for structural complexes, but far less so than for floristic complexes. Also of note was that SRCs 4 to 7 in general displayed higher levels of soil nutrients than the other complexes.

**Table 5.4 Environmental characteristics of species richness complexes**

Environmental factors are listed by factor group. Factor units are indicated. Values for environmental factors are means. Standard errors are shown in parentheses. Values not determined for complexes are indicated as (nd). P - values (P) for ANOVAs comparing environmental factor means between complexes are provided. Transformations (T) made for the purpose of analysis are indicated as 0 - no transformation, 1 -  $\log_{10}(x)$ , 2 -  $\sqrt{x}$ . Significantly different means are indicated by superscripts with no letters in common. Multiple comparisons were made using Tukey tests with significance of differences assessed at  $p < 0.05$  using the studentised range. Species richness complexes are identified by complex code. Numbers of quadrats included in complexes is indicated.

Environmental factors	Units	T	Species richness complexes									
			SRC 1	SRC 2	SRC 3	SRC 4	SRC 5	SRC 6	SRC 7	SRC 8	SRC 9	SRC 10
<i>Quadrats</i>			41	12	4	12	31	16	20	21	12	16
<i>Maritime factor group</i>												
Distance from cliff-tops	m	0	79(7) <sup>cd</sup>	71(7) <sup>cd</sup>	53(17) <sup>bc</sup>	91(7) <sup>e</sup>	55(5) <sup>bc</sup>	46(8) <sup>b</sup>	94(9) <sup>e</sup>	60(6) <sup>bc</sup>	128(3) <sup>f</sup>	98(11) <sup>e</sup>
Electrical conductivity	dS.m <sup>-1</sup>	1	0.288(0.036) <sup>b</sup>	0.154(0.050) <sup>ab</sup>	0.495(0.175) <sup>c</sup>	0.612(0.092) <sup>cd</sup>	0.428(0.054) <sup>c</sup>	0.413(0.065) <sup>c</sup>	0.384(0.061) <sup>bc</sup>	0.291(0.050) <sup>b</sup>	0.076(0.003) <sup>a</sup>	0.125(0.028) <sup>ab</sup>
Extractable Na	ug.g <sup>-1</sup>	1	406(65) <sup>c</sup>	217(113) <sup>b</sup>	1087(412) <sup>e</sup>	1137(182) <sup>e</sup>	872(133) <sup>e</sup>	819(163) <sup>e</sup>	498(119) <sup>cd</sup>	531(142) <sup>cd</sup>	64(7) <sup>a</sup>	147(49) <sup>b</sup>
Chloride content	kg.m <sup>-3</sup>	1	0.570(0.083) <sup>c</sup>	0.208(0.054) <sup>a</sup>	0.750(0.286) <sup>cd</sup>	0.775(0.086) <sup>d</sup>	0.912(0.128) <sup>d</sup>	0.843(0.158) <sup>d</sup>	0.625(0.102) <sup>cd</sup>	0.456(0.100) <sup>bc</sup>	0.126(0.007) <sup>a</sup>	0.205(0.058) <sup>a</sup>
Above canopy salt-spray dep.	t.ha <sup>-1</sup> .a <sup>-1</sup>	1	0.672(0.027) <sup>c</sup>	0.660(0.029) <sup>bc</sup>	0.819(0.145) <sup>cd</sup>	0.587(0.023) <sup>ab</sup>	0.858(0.080) <sup>d</sup>	0.893(0.087) <sup>d</sup>	0.614(0.036) <sup>b</sup>	0.751(0.045) <sup>cd</sup>	0.496(0.005) <sup>a</sup>	0.599(0.037) <sup>b</sup>
Below canopy salt-spray dep.	t.ha <sup>-1</sup> .a <sup>-1</sup>	1	0.276(0.007) <sup>b</sup>	0.276(0.009) <sup>b</sup>	0.290(0.019) <sup>bc</sup>	0.369(0.054) <sup>c</sup>	0.303(0.016) <sup>c</sup>	0.338(0.023) <sup>c</sup>	0.258(0.008) <sup>ab</sup>	0.286(0.010) <sup>b</sup>	0.227(0.002) <sup>a</sup>	0.256(0.011) <sup>ab</sup>
<i>Soil physical factor group</i>												
Field soil moisture	g.g <sup>-1</sup>	1	0.217(0.042) <sup>cd</sup>	0.178(0.086) <sup>c</sup>	0.413(0.133) <sup>ef</sup>	0.549(0.084) <sup>f</sup>	0.298(0.027) <sup>e</sup>	0.228(0.047) <sup>cd</sup>	0.157(0.035) <sup>c</sup>	0.197(0.049) <sup>cd</sup>	0.040(0.010) <sup>a</sup>	0.094(0.022) <sup>b</sup>
Bulk density	g.cm <sup>-3</sup>	0	1.325(0.057) <sup>c</sup>	1.401(0.114) <sup>cd</sup>	0.877(0.201) <sup>ab</sup>	0.732(0.081) <sup>a</sup>	1.141(0.058) <sup>b</sup>	1.176(0.080) <sup>b</sup>	1.171(0.073) <sup>b</sup>	1.314(0.078) <sup>c</sup>	1.676(0.062) <sup>e</sup>	1.458(0.061) <sup>d</sup>
Pore space ratio	-	0	0.500(0.021) <sup>b</sup>	0.471(0.043) <sup>ab</sup>	0.669(0.076) <sup>cd</sup>	0.724(0.031) <sup>d</sup>	0.569(0.022) <sup>c</sup>	0.556(0.030) <sup>c</sup>	0.558(0.027) <sup>c</sup>	0.504(0.030) <sup>bc</sup>	0.367(0.023) <sup>ab</sup>	0.450(0.023) <sup>ab</sup>
Air filled porosity	-	0	0.291(0.023) <sup>b</sup>	0.326(0.017) <sup>bc</sup>	0.394(0.032) <sup>cd</sup>	0.377(0.051) <sup>cd</sup>	0.260(0.034) <sup>b</sup>	0.335(0.029) <sup>bc</sup>	0.410(0.022) <sup>d</sup>	0.305(0.033) <sup>bc</sup>	0.301(0.024) <sup>bc</sup>	0.326(0.020) <sup>bc</sup>
Organic content	%	2	12.8(1.9) <sup>cd</sup>	10.2(3.9) <sup>bc</sup>	28.2(10.6) <sup>ef</sup>	34.7(5.3) <sup>f</sup>	18.8(2.2) <sup>e</sup>	16.9(2.0) <sup>de</sup>	13.5(1.9) <sup>d</sup>	12.0(2.1) <sup>cd</sup>	5.7(0.7) <sup>ab</sup>	7.5(1.3) <sup>b</sup>
Fine particle fraction	%	2	4.7(0.5) <sup>c</sup>	3.0(0.9) <sup>b</sup>	9.9(2.9) <sup>de</sup>	12.4(1.7) <sup>e</sup>	7.5(0.5) <sup>cd</sup>	5.3(0.8) <sup>cd</sup>	5.0(0.7) <sup>c</sup>	5.0(0.9) <sup>c</sup>	1.3(0.1) <sup>a</sup>	3.0(1.0) <sup>b</sup>
Coarse particle fraction	%	2	95.3(0.5) <sup>c</sup>	97.0(0.9) <sup>cd</sup>	90.1(2.9) <sup>ab</sup>	87.6(1.7) <sup>a</sup>	92.5(0.5) <sup>b</sup>	94.7(0.8) <sup>c</sup>	95.0(0.7) <sup>c</sup>	95.0(0.9) <sup>c</sup>	98.7(0.1) <sup>d</sup>	97.0(1.0) <sup>cd</sup>
<i>Soil nutrition factor group</i>												
pH	-	0	4.27(0.05) <sup>a</sup>	4.53(0.10) <sup>bc</sup>	4.35(0.16) <sup>ab</sup>	4.42(0.08) <sup>ab</sup>	4.52(0.04) <sup>bc</sup>	4.36(0.09) <sup>ab</sup>	4.44(0.07) <sup>b</sup>	4.47(0.07) <sup>b</sup>	4.80(0.13) <sup>c</sup>	4.54(0.11) <sup>bc</sup>
Total P	kg.m <sup>-3</sup>	1	0.217(0.020) <sup>c</sup>	0.116(0.023) <sup>b</sup>	0.224(0.096) <sup>c</sup>	0.179(0.020) <sup>b</sup>	0.362(0.027) <sup>d</sup>	0.293(0.040) <sup>cd</sup>	0.201(0.022) <sup>bc</sup>	0.191(0.029) <sup>bc</sup>	0.146(0.032) <sup>b</sup>	0.155(0.024) <sup>b</sup>
Total N	kg.m <sup>-3</sup>	1	3.512(0.283) <sup>b</sup>	3.138(0.527) <sup>ab</sup>	4.560(0.342) <sup>c</sup>	3.625(0.332) <sup>b</sup>	5.020(0.288) <sup>cd</sup>	5.381(0.426) <sup>d</sup>	3.405(0.427) <sup>b</sup>	3.117(0.363) <sup>b</sup>	2.142(0.346) <sup>a</sup>	3.048(0.324) <sup>ab</sup>

(cont/d.)

Table 5.4 (cont/d.)

Environmental factors	Units	T	Species richness complexes								P
			SRC 11	SRC 12	SRC 13	SRC 14	SRC 15	SRC 16	SRC 17	SRC 18	
<i>Quadrats</i>			3	12	12	8	7	10	10	7	
<i>Maritime factor group</i>											
Distance from cliff-tops	m	0	142(3) <sup>f</sup>	98(8) <sup>e</sup>	90(7) <sup>e</sup>	83(8) <sup>de</sup>	44(13) <sup>b</sup>	85(4) <sup>de</sup>	10(2) <sup>a</sup>	11(2) <sup>a</sup>	<0.001
Electrical conductivity	dS.m <sup>-1</sup>	1	0.076(0.007) <sup>a</sup>	0.130(0.018) <sup>ab</sup>	0.162(0.031) <sup>ab</sup>	0.341(0.031) <sup>bc</sup>	0.340(0.140) <sup>bc</sup>	0.288(0.039) <sup>b</sup>	0.523(0.113) <sup>cd</sup>	0.394(0.087) <sup>bc</sup>	<0.001
Chloride content	kg.m <sup>-3</sup>	1	0.138(0.038) <sup>a</sup>	0.208(0.046) <sup>a</sup>	0.251(0.056) <sup>ab</sup>	0.590(0.167) <sup>c</sup>	0.329(0.084) <sup>b</sup>	0.346(0.040) <sup>b</sup>	nd	0.798(0.180) <sup>cd</sup>	0.010
Extractable Na	ug.g <sup>-1</sup>	1	45(5) <sup>a</sup>	187(26) <sup>b</sup>	247(74) <sup>b</sup>	481(67) <sup>c</sup>	469(209) <sup>bcd</sup>	415(16) <sup>c</sup>	529(99) <sup>d</sup>	378(81) <sup>c</sup>	<0.001
Above canopy salt-spray dep.	t.ha <sup>-1</sup> .a <sup>-1</sup>	1	0.475(0.005) <sup>a</sup>	0.567(0.017) <sup>a</sup>	0.586(0.017) <sup>ab</sup>	0.616(0.035) <sup>b</sup>	1.104(0.237) <sup>d</sup>	0.593(0.012) <sup>ab</sup>	1.599(0.122) <sup>e</sup>	1.547(0.148) <sup>e</sup>	<0.001
Below canopy salt-spray dep.	t.ha <sup>-1</sup> .a <sup>-1</sup>	1	0.220(0.002) <sup>a</sup>	0.249(0.005) <sup>ab</sup>	0.255(0.005) <sup>ab</sup>	0.616(0.035) <sup>e</sup>	0.445(0.133) <sup>cd</sup>	0.497(0.055) <sup>d</sup>	1.519(0.167) <sup>f</sup>	0.449(0.055) <sup>cd</sup>	<0.001
<i>Soil physical factor group</i>											
Field soil moisture	g.g <sup>-1</sup>	1	0.043(0.010) <sup>a</sup>	0.158(0.011) <sup>c</sup>	0.170(0.038) <sup>c</sup>	1.243(0.286) <sup>e</sup>	0.139(0.019) <sup>c</sup>	1.135(0.334) <sup>e</sup>	0.160(0.020) <sup>c</sup>	0.129(0.025) <sup>bc</sup>	<0.001
Bulk density	g.cm <sup>-3</sup>	0	1.810(0.079) <sup>e</sup>	1.277(0.046) <sup>bc</sup>	1.337(0.087) <sup>c</sup>	0.747(0.155) <sup>a</sup>	1.232(0.171) <sup>b</sup>	0.719(0.126) <sup>a</sup>	nd	1.376(0.113) <sup>c</sup>	<0.001
Pore space ratio	-	0	0.317(0.030) <sup>a</sup>	0.518(0.017) <sup>bc</sup>	0.496(0.033) <sup>b</sup>	0.718(0.059) <sup>d</sup>	0.535(0.065) <sup>bc</sup>	0.729(0.048) <sup>d</sup>	nd	0.481(0.043) <sup>b</sup>	<0.001
Air filled porosity	-	0	0.244(0.020) <sup>b</sup>	0.321(0.022) <sup>bc</sup>	0.307(0.021) <sup>bc</sup>	0.061(0.075) <sup>a</sup>	0.366(0.092) <sup>bc</sup>	0.239(0.068) <sup>b</sup>	nd	0.308(0.057) <sup>bc</sup>	<0.001
Organic content	%	2	3.9(0.5) <sup>a</sup>	10.4(1.1) <sup>c</sup>	11.6(1.9) <sup>c</sup>	32.6(5.7) <sup>f</sup>	9.3(2.5) <sup>bc</sup>	28.9(5.4) <sup>c</sup>	2.7(0.3) <sup>a</sup>	6.5(1.1) <sup>b</sup>	<0.001
Fine particle fraction	%	2	1.2(0.2) <sup>a</sup>	4.7(0.3) <sup>c</sup>	3.9(0.6) <sup>bc</sup>	12.1(0.8) <sup>e</sup>	7.4(2.4) <sup>cd</sup>	8.5(0.6) <sup>d</sup>	10.6(2.4) <sup>cde</sup>	4.3(0.8) <sup>bc</sup>	<0.001
Coarse particle fraction	%	2	98.8(0.2) <sup>d</sup>	95.3(0.3) <sup>c</sup>	96.1(0.6) <sup>cd</sup>	87.9(0.8) <sup>a</sup>	92.6(2.4) <sup>b</sup>	91.5(0.6) <sup>ab</sup>	89.4(2.4) <sup>ab</sup>	95.7(0.8) <sup>c</sup>	<0.001
<i>Soil nutrition factor group</i>											
pH	-	0	5.03(0.08) <sup>cd</sup>	4.26(0.05) <sup>a</sup>	4.55(0.10) <sup>bc</sup>	4.46(0.09) <sup>b</sup>	4.84(0.27) <sup>c</sup>	4.25(0.06) <sup>a</sup>	5.55(0.15) <sup>e</sup>	4.92(0.16) <sup>cd</sup>	<0.001
Total P	kg.m <sup>-3</sup>	1	0.042(0.033) <sup>a</sup>	0.228(0.015) <sup>c</sup>	0.196(0.025) <sup>bc</sup>	0.210(0.026) <sup>bc</sup>	0.143(0.046) <sup>b</sup>	0.238(0.059) <sup>c</sup>	nd	0.014(0.002) <sup>a</sup>	<0.001
Total N	kg.m <sup>-3</sup>	1	1.855(0.451) <sup>a</sup>	3.319(0.383) <sup>b</sup>	3.884(0.451) <sup>bc</sup>	4.525(0.514) <sup>c</sup>	2.085(0.262) <sup>a</sup>	4.058(0.511) <sup>bc</sup>	nd	2.752(0.243) <sup>ab</sup>	<0.001

(cont/d.)

Table 5.4 (cont/d.)

Environmental factors	Units	T	Species richness complexes									
			SRC 1	SRC 2	SRC 3	SRC 4	SRC 5	SRC 6	SRC 7	SRC 8	SRC 9	SRC 10
Extractable Mg	ug.g <sup>-1</sup>	0	297(33) <sup>bc</sup>	215(38) <sup>b</sup>	615(197) <sup>cd</sup>	677(99) <sup>d</sup>	606(57) <sup>d</sup>	492(71) <sup>c</sup>	406(64) <sup>c</sup>	359(71) <sup>bc</sup>	166(19) <sup>b</sup>	202(27) <sup>b</sup>
Extractable Ca	ug.g <sup>-1</sup>	2	256(20) <sup>b</sup>	296(34) <sup>b</sup>	428(125) <sup>bc</sup>	588(67) <sup>d</sup>	444(44) <sup>c</sup>	387(40) <sup>c</sup>	401(41) <sup>c</sup>	319(38) <sup>bc</sup>	342(41) <sup>bc</sup>	405(83) <sup>bc</sup>
Extractable K	ug.g <sup>-1</sup>	1	166(32) <sup>c</sup>	96(40) <sup>b</sup>	298(103) <sup>cd</sup>	182(25) <sup>c</sup>	226(17) <sup>c</sup>	167(22) <sup>c</sup>	137(19) <sup>c</sup>	128(21) <sup>bc</sup>	44(5) <sup>ab</sup>	74(16) <sup>ab</sup>
<i>Fire factor group</i>												
Years since last fire <sup>1</sup>	years	0	20	1.4	20	2.3	20	20	20	20	2.3	2.3

<sup>1</sup> - most frequent value in complex

Environmental factors	Units	T	Species richness complexes								P
			SRC 11	SRC 12	SRC 13	SRC 14	SRC 15	SRC 16	SRC 17	SRC 18	
Extractable Mg	ug.g <sup>-1</sup>	0	95(10) <sup>a</sup>	276(18) <sup>bc</sup>	283(52) <sup>bc</sup>	340(43) <sup>bc</sup>	330(75) <sup>bc</sup>	307(40) <sup>bc</sup>	230(36) <sup>b</sup>	256(35) <sup>b</sup>	<0.001
Extractable Ca	ug.g <sup>-1</sup>	2	278(2) <sup>b</sup>	146(22) <sup>a</sup>	309(49) <sup>bc</sup>	351(36) <sup>bc</sup>	135(30) <sup>a</sup>	227(41) <sup>b</sup>	84(11) <sup>a</sup>	94(11) <sup>a</sup>	<0.001
Extractable K	ug.g <sup>-1</sup>	1	38(2) <sup>a</sup>	313(44) <sup>d</sup>	143(37) <sup>c</sup>	100(15) <sup>bc</sup>	288(59) <sup>cd</sup>	192(52) <sup>c</sup>	93(10) <sup>b</sup>	218(40) <sup>c</sup>	<0.001
<i>Fire factor group</i>											
Years since last fire <sup>1</sup>	years	0	2.3	1.4	2.3	20	1.4	1.4	20	20	

<sup>1</sup> - most frequent value in complex



### 5.3.3 Differential environmental relationships of community properties

Environmental relationships of the floristic component of community structure are shown in Fig. 5.2. In general, these reflect the pattern of differences between floristic complexes as described in the previous section. They also reflect the major patterns of environmental associations described in the first section. As shown in Fig 5.2, a major differentiation occurs between FCs 1 to 3 (burnt dune heaths and a burnt platform heath) and FCs 4 to 8 (unburnt platform heaths), which corresponds most strongly with the influence of increasing distance from cliff-tops on one hand and decreasing years since last fire and above canopy salt-spray deposition on the other. Separation between individual floristic complexes can also be seen along this environmental axis. This is also true with respect to soil based maritime factors, extractable magnesium, extractable potassium, below canopy salt-spray deposition and to lesser extents, total phosphorus and total nitrogen. Increases in bulk density, coarse particle fraction and to lesser extents, pH and air filled porosity, serve to separate FCs 1 and 2 (dune heaths) from both unburnt platform heaths (FCs 4 to 8) and the burnt platform heath (FC 3). They also serve to separate all these complexes from FCs 9 and 10. However, as shown in Fig 5.2, these factors form only part of a complex gradient separating these last two complexes. FCs 9 and 10 are also closely associated with increases in field soil moisture, organic content and fine particle fraction. Increases in these factors are also associated with the prominent factors, as noted previously, which separate the unburnt platform heaths from the burnt heaths, although not being as well correlated with this axis of floristic differentiation.

These characteristics show that major environmental gradients underlying variance in floristic composition are non-orthogonal, i.e. are correlated. They also show that individual factors display multi-collinearity with respect to floristic variance, i.e. individual factors are inter-correlated.

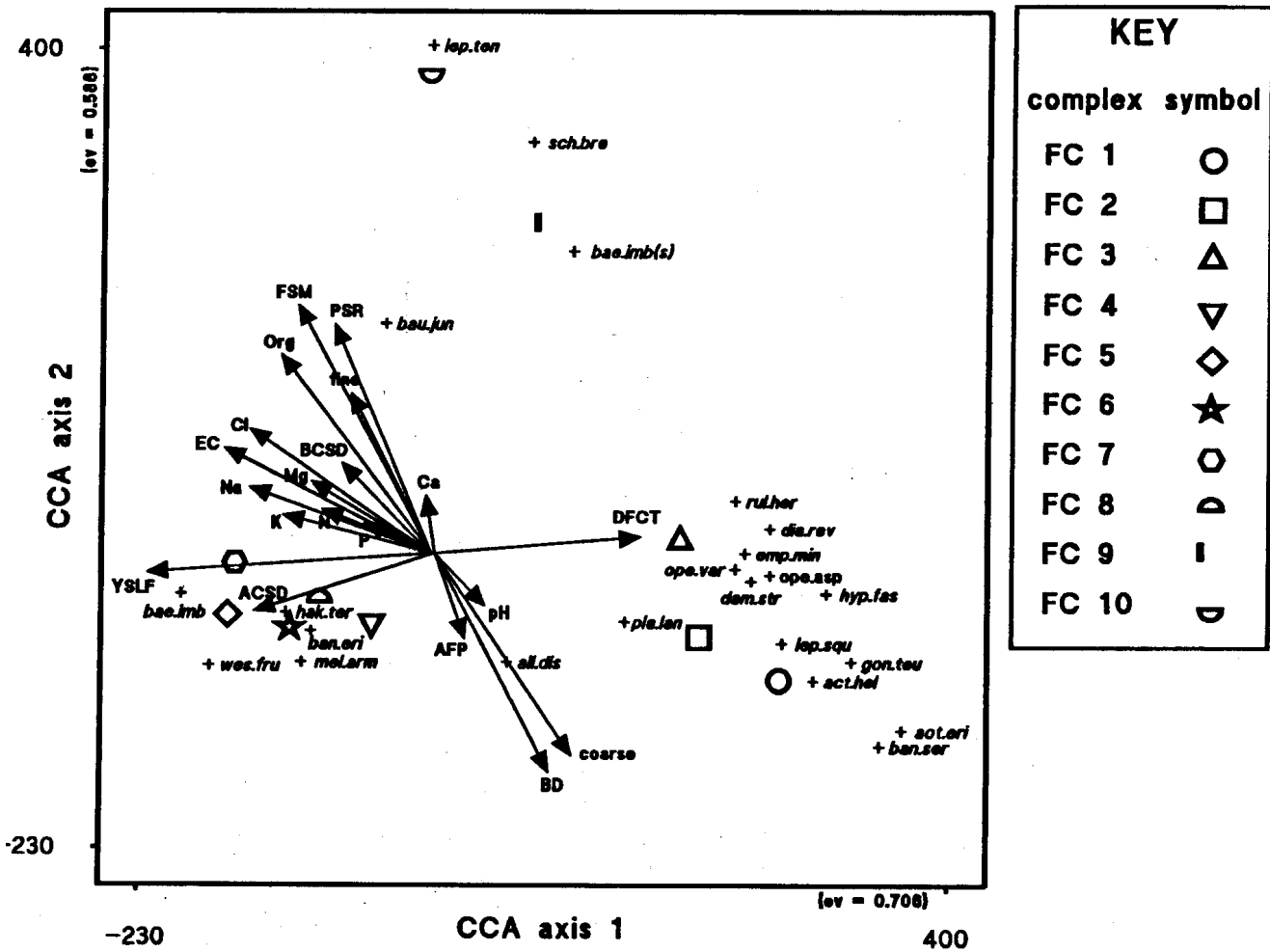


Fig. 5.2 Canonical correspondence analysis of the floristic component of community structure. Site centroids for floristic complexes and species maxima for dominant species are shown. Arrows corresponding to environmental factors are indicated by abbreviation.

In addition to the above, it is of importance to note that the major patterns of floristic differentiation do not differ markedly from the unconstrained analysis of floristic composition (see Chapter 4). This shows that there is no significant influence on variance in floristic composition that has not been either directly or indirectly accounted for by the supplied environmental factors.

The percentages of variance in floristic composition accounted for by different environmental factor groups and environmental factors are shown in Table 5.5. Variance in floristic composition accounted for by all factors is also shown. As shown in Table 5.5, 75 % of variance in floristic composition was accounted for by the supplied factors collectively. Of the factor groups, the maritime factor group was of the highest importance, explaining 53 % of the variance in floristic composition. The fire factor group explained the least amount of variance (24 %). However, this group is comprised of a single factor (YSLF), which was clearly the most important single factor. Maritime and soil physical factors were individually of approximately equivalent importance (Table 5.5). Soil nutrition factors were generally of lowest importance, with variance in total phosphorus being of least importance (4 %).

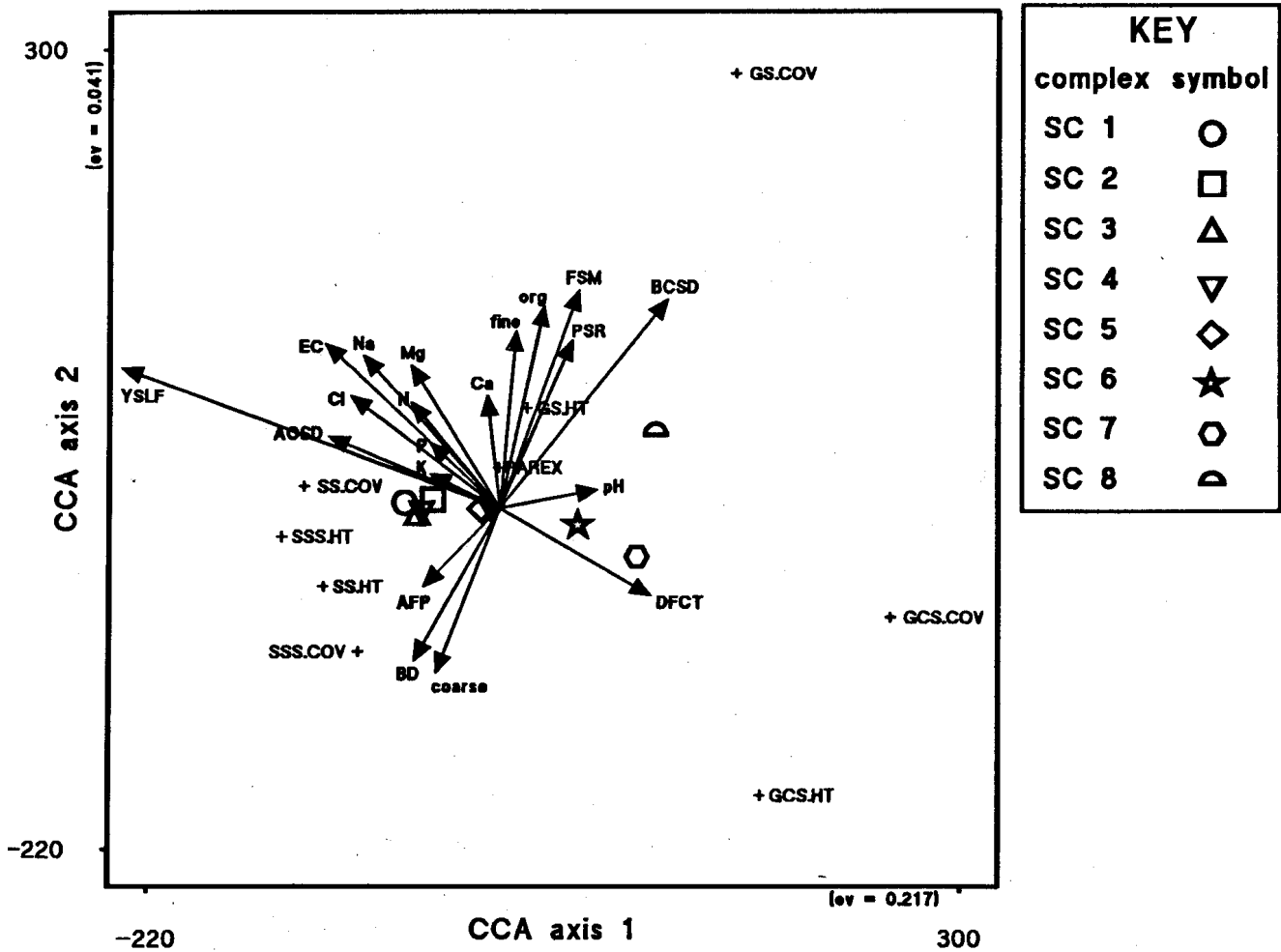
The canonical correspondence analysis of structure is shown in Fig. 5.3. Years since fire, above canopy salt-spray deposition and distance from cliff-tops appear most closely associated with the first axis differentiation between SCs 1 to 5 and SCs 6 to 8. However, as shown in Table 5.5, years since last fire is clearly the most important factor, and of substantially greater importance to the overall pattern than the other two factors mentioned.

As with floristic composition, Fig 5.3 shows the existence of multicollinearity with respect to the relationships of structure with individual environmental factors. Soil nutrients and soil based maritime factors are closely associated with the main axis of differentiation in structure which resembles the situation with floristic composition. However, clear differences from floristic composition are evident in Fig 5.3 with respect to both major gradients and individual factors. First, the gradient including variance in fine particle fraction, organic content, field soil moisture and pore space ratio is more clearly separated from that including soil nutrients and soil based maritime factors than was the case with floristic composition. If the variances in extractable calcium and pH are ignored (Fig. 5.3), it can be seen that these two gradients are

**Table 5.5** Percentage variance of community properties and their variance components accounted for by environmental factors.

Table cells are percentages of variance accounted for by environmental factors and factor groups. Percentage variance accounted for is the sum of the eigenvalues of canonical axes of a canonical correspondence analysis constrained by the relevant factors expressed as a percentage of the trace of the unconstrained correspondence analysis corresponding to the indicated property or variance component (see text for further details). Columns correspond to properties and variance components which are identified by abbreviation; FC - floristic composition, STR - structure, SR - species richness, X c. Y - variance in X common with Y, X i. Y - variance in X independent of Y. Values have been rounded to the nearest percentage. Values less than one have been set at one. Ranks within the group of factor groups and within the group of individual factors are shown in brackets. Ranks are given in order of decreasing percentage variance accounted for. Mean ranks are assigned to ties.

Factor group/Factor	Variance component															
	FC	STR	SR	FC c. STR	FC i. STR	FC c. SR	FC i. SR	STR c. FC	STR i. FC	STR c. SR	STR i. SR	SR c. FC	SR i. FC	SR c. STR	SR i. STR	
<b>All factors</b>	75	69	49	78	58	57	75	72	37	37	65	55	56	7	30	
<b>Maritime factor group</b>	53 (1)	32 (2)	21 (1)	54 (1)	39 (1)	44 (1)	55 (1)	34 (2)	13 (3)	17 (1)	29 (2)	23 (1)	26 (2)	3 (1)	12 (3)	
<b>Soil physical factor group</b>	45 (2)	17 (3)	17 (2)	42 (2)	35 (2)	40 (2)	44 (2)	17 (3)	16 (1)	8 (3)	15 (3)	19 (2)	15 (3)	2 (2.5)	15 (2)	
<b>Soil nutrient factor group</b>	37 (3)	12 (4)	15 (3)	33 (3)	30 (3)	31 (3)	37 (3)	12 (4)	15 (2)	12 (2)	11 (4)	16 (3)	28 (1)	1 (4)	16 (1)	
<b>Fire factor group</b>	24 (4)	33 (1)	4 (4)	25 (4)	18 (4)	13 (4)	25 (4)	35 (1)	4 (4)	4 (4)	32 (1)	5 (4)	1 (4)	2 (2.5)	3 (4)	
<b>Individual factors</b>																
<i>Distance from cliff-tops</i>	15 (9)	4 (13)	2 (15)	12 (12.5)	13 (3)	10 (5)	15 (11)	4 (13)	2 (10.5)	3 (6.5)	4 (12.5)	2 (15)	3 (14.5)	1 (11)	2 (15)	
<i>Electrical conductivity</i>	17 (5)	7 (3.5)	1 (18.5)	18 (5)	10 (9)	5 (17.5)	18 (4.5)	8 (2.5)	1 (16.5)	1 (17)	9 (2)	1 (18.5)	3 (14.5)	1 (11)	6 (2.5)	
<i>Chloride content</i>	13 (14)	4 (13)	1 (18.5)	12 (12.5)	10 (9)	5 (17.5)	14 (14)	4 (13)	2 (10.5)	1 (17)	4 (12.5)	1 (18.5)	5 (12)	1 (11)	1 (18.5)	
<i>Extractable sodium</i>	18 (3.5)	6 (6)	2 (15)	19 (3.5)	12 (5.5)	9 (7.5)	19 (2.5)	6 (6)	1 (16.5)	1 (17)	4 (12.5)	2 (15)	9 (4)	1 (11)	4 (8)	
<i>Above can. salt-spray dep.</i>	14 (12.5)	5 (9.5)	4 (10.5)	11 (14.5)	13 (3)	11 (3)	16 (7)	5 (9.5)	4 (6)	5 (1)	5 (8.5)	5 (9.5)	1 (19)	1 (11)	3 (12)	
<i>Below can. salt-spray dep.</i>	14 (12.5)	8 (2)	4 (10.5)	14 (10)	11 (7)	15 (1)	15 (11)	8 (2.5)	5 (3)	3 (6.5)	8 (3)	5 (9.5)	2 (16.5)	1 (11)	4 (8)	
<i>Field soil moisture</i>	19 (2)	7 (3.5)	8 (3.5)	20 (2)	12 (5.5)	10 (5)	19 (2.5)	7 (4)	1 (16.5)	3 (6.5)	6 (5)	9 (3)	4 (13)	1 (11)	3 (12)	
<i>Bulk density</i>	15 (9)	5 (9.5)	9 (1.5)	16 (8.5)	9 (11.5)	7 (11.5)	15 (11)	5 (9.5)	7 (1.5)	3 (6.5)	5 (8.5)	9 (3)	6 (10)	1 (11)	4 (8)	
<i>Pore space ratio</i>	15 (9)	5 (9.5)	9 (1.5)	16 (8.5)	9 (11.5)	7 (11.5)	15 (11)	5 (9.5)	7 (1.5)	3 (6.5)	5 (8.5)	10 (1)	6 (10)	1 (11)	4 (8)	
<i>Air filled porosity</i>	5 (19)	2 (18.5)	1 (18.5)	6 (18.5)	4 (18.5)	6 (14.5)	5 (20)	2 (18.5)	4 (6)	1 (17)	2 (19)	1 (18.5)	1 (19)	1 (11)	1 (18.5)	
<i>Organic content</i>	15 (9)	5 (9.5)	6 (6.5)	17 (6.5)	8 (14)	8 (9)	16 (7)	5 (9.5)	4 (6)	2 (11.5)	5 (8.5)	6 (6.5)	10 (3)	1 (11)	1 (18.5)	
<i>Fine particle fraction</i>	18 (3.5)	6 (6)	8 (3.5)	19 (3.5)	10 (9)	7 (11.5)	18 (4.5)	6 (6)	1 (16.5)	2 (11.5)	6 (5)	9 (3)	8 (6)	1 (11)	8 (1)	
<i>Coarse particle fraction</i>	16 (6)	6 (6)	7 (5)	17 (6.5)	8 (14)	7 (11.5)	16 (7)	6 (6)	1 (16.5)	2 (11.5)	6 (5)	8 (5)	6 (10)	1 (11)	5 (4.5)	
<i>pH</i>	6 (17.5)	4 (13)	2 (15)	6 (18.5)	4 (18.5)	4 (20)	6 (18)	4 (13)	4 (6)	4 (2.5)	3 (16)	1 (18.5)	7 (8)	1 (11)	4 (8)	
<i>Total phosphorus</i>	4 (20)	2 (18.5)	4 (10.5)	4 (20)	6 (16.5)	5 (17.5)	6 (18)	2 (18.5)	2 (10.5)	3 (6.5)	2 (19)	4 (12)	17 (1.5)	1 (11)	2 (15)	
<i>Total nitrogen</i>	8 (16)	3 (16)	3 (13)	8 (16)	6 (16.5)	6 (14.5)	9 (16)	3 (15.5)	1 (16.5)	1 (17)	4 (12.5)	3 (13)	17 (1.5)	1 (11)	2 (15)	
<i>Extractable magnesium</i>	11 (15)	3 (16)	1 (18.5)	11 (14.5)	8 (14)	9 (7.5)	12 (15)	2 (18.5)	1 (16.5)	2 (11.5)	3 (16)	6 (6.5)	8 (6)	1 (11)	1 (18.5)	
<i>Extractable calcium</i>	6 (17.5)	1 (20)	6 (6.5)	7 (17)	3 (20)	5 (17.5)	6 (18)	2 (18.5)	2 (10.5)	1 (17)	2 (19)	5 (9.5)	8 (6)	1 (11)	6 (2.5)	
<i>Extractable potassium</i>	15 (9)	3 (16)	5 (8)	13 (11)	13 (3)	10 (5)	15 (11)	3 (15.5)	1 (16.5)	1 (17)	3 (16)	2 (15)	2 (16.5)	1 (11)	5 (4.5)	
<i>Years since last fire</i>	24 (1)	33 (1)	4 (10.5)	25 (1)	18 (1)	13 (2)	25 (1)	35 (1)	4 (6)	4 (2.5)	32 (1)	5 (9.5)	1 (19)	2 (1)	3 (12)	



**Fig. 5.3** Canonical correspondence analysis of the structural component of community structure. Site centroids for structural complexes and maxima for structural attributes are shown. Arrows corresponding to environmental factors are indicated by abbreviation.

approximately orthogonal, the former gradient separating SC 8 (swamps) from the remaining complexes. Secondly, it can be seen in Fig. 5.3 that below canopy salt-spray deposition is more strongly associated with this gradient than was the case for floristic composition. It also appears of greater importance. This reflects the predicted elevated levels of salt-spray penetration in swamps in the virtual absence of shrub based strata.

In addition to the above, it is of importance to note that the major patterns of structural differentiation do not differ markedly from the unconstrained analysis of structure (see Chapter 4). This shows, similarly to floristic composition, that there is no significant influence on variance in structure that has not been either directly or indirectly accounted for by the supplied environmental factors.

The importance of individual environmental factors and factor groups to variance in structure is shown in Table 5.5. As for floristic composition, the majority of variance in structure was explained by all environmental factors considered together. As a group, maritime factors were of lesser importance compared with floristic composition, and accounted for a similar amount of variance as the fire factor group (years since last fire). Soil physical and soil nutrition factor groups were of equivalent and lesser importance compared with the other two factor groups. They were also of lower importance to variance in structure compared with floristic composition. Individual factors were in general of lower importance to variance in structure than to variance in floristic composition. The exception to this was years since last fire (Table 5.5), which was of greater importance to variance in structure than variance in floristic composition. Examination of the rank importance of environmental factors (Table 5.5) reveals a similarity between structure and floristic composition. However, notable exceptions include below canopy salt-spray deposition, which is of higher rank importance to structure and extractable potassium, which is of lower rank importance (note the reciprocal expression of ranks in Table 5.5).

Of additional interest in Table 5.5 are the relative importances of individual factors to structure and floristic composition compared with the respective importances of all factors considered collectively. In the case of floristic composition, it can be seen that the sum of importances of factors considered individually greatly exceeds the collective importance. This was not the case for structure, and implies the existence of redundancies between factors in the case of floristic composition.

Environmental relationships of species richness are shown in Fig. 5.4. In this case, years since the last fire and distance from cliff-tops do not solely provide the major axis of differentiation in species richness. Years since the last fire does correspond with this axis, however, fine particle fraction, pore space ratio, field soil moisture and organic content are also components of this major axis, along with bulk density and coarse particle fraction which increase in the opposite direction. The latter factors correspond to increasing shrub and sub-shrub strata richness, while the former factors correspond to increasing graminoid and groundcover strata richness (Fig 5.4).

Reference to the unconstrained variance in species richness (see Chapter 4) again shows that the predominant pattern of variance has been preserved in the CCA. Notwithstanding the fact that variance in multivariate species richness is comparatively low, this shows again that there is no significant influence on variance in species richness that has not been either directly or indirectly accounted for by the supplied environmental factors.

Importances of environmental factors and factor groups to variance in species richness are shown in Table 5.5. Variance accounted for by all factors is 49%, which is lower than that for either floristic composition or structure. The same applies to environmental factor groups, with the exception that both soil physical and soil nutrition factor groups are of equivalent importance to structure. Examination of the rank importances of individual factors to species richness (Table 5.5) supports the relatively greater importance of soil physical factors to species richness than structure. This is also the case in comparison with floristic composition if only ranks are considered. It can also be seen in Table 5.5 that maritime factors are of lower importance for species richness than structure in both rank and absolute terms. It is also of importance to note that time since the last fire is of substantially lower importance for species richness than the other two properties.

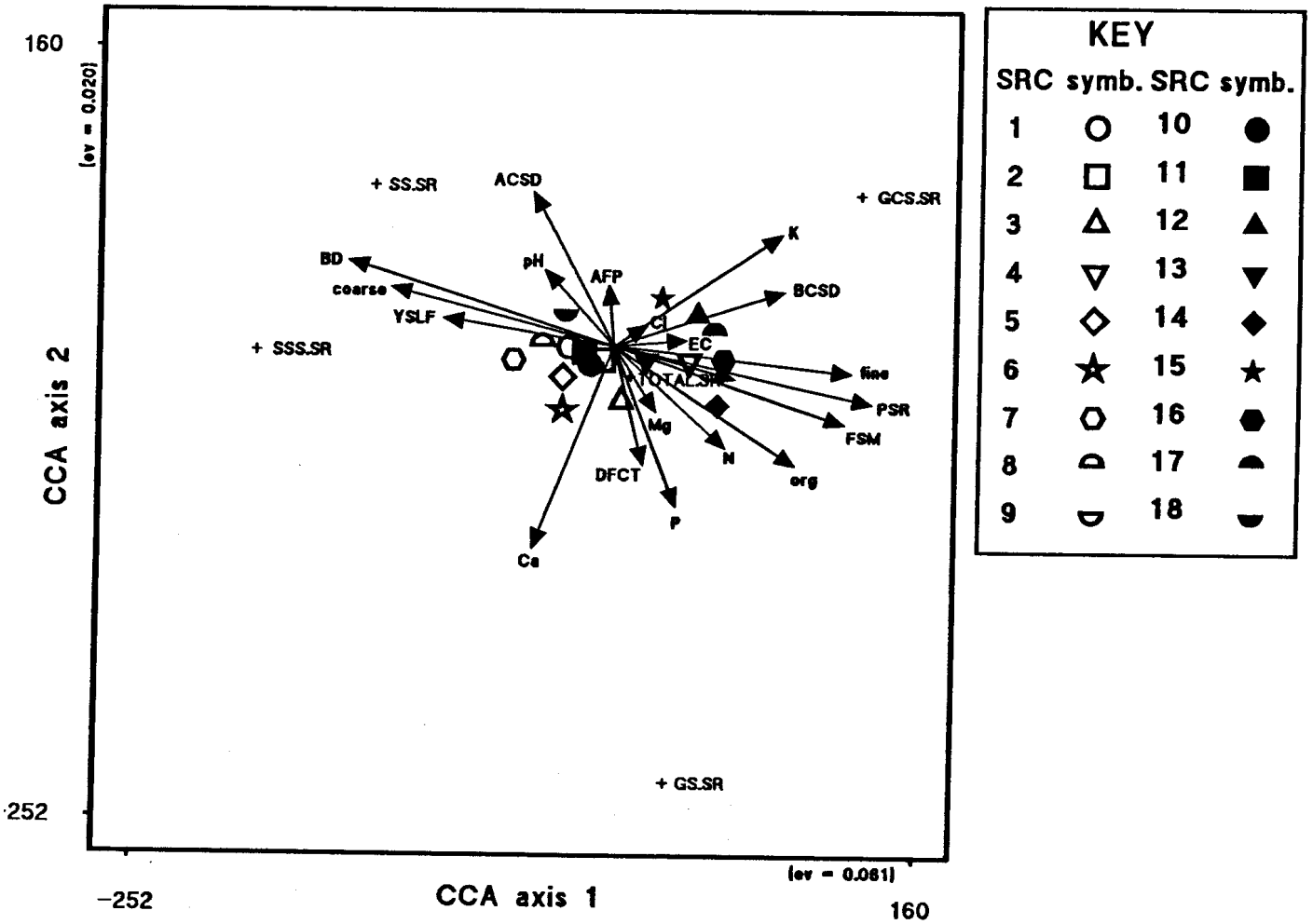


Fig. 5.4 Canonical correspondence analysis of the species richness component of community structure. Site centroids for species richness complexes and maxima for species richness attributes are shown. Arrows corresponding to environmental factors are indicated by abbreviation.



### 5.3.4 Differential environmental relationships of common variance components of community properties

Similar percentages of common variance components between floristic composition and structure were explained by environmental factors collectively (Table 5.5). However, there were marked differences in the relative importances of individual environmental factors and factor groups. All environmental factor groups except the fire factor group were of lower importance for structure than floristic composition. The fire factor group (years since last fire) was of greater importance for the common component of structure (Table 5.5) and was of highest importance for the common component of structure, whereas the maritime factor group was of greatest importance for the common component of floristic composition. Importances of individual environmental factors largely reflected the relative importances of corresponding environmental factor groups. As for the comparison of the parent properties, quantitative differences were again evident in the general level of relative importances of factors between the two components. Except for years since last fire, importances of all factors were greater for the common component of floristic composition.

Similarly, approximately equivalent percentages of common variance components between floristic composition and species richness were explained by environmental factors collectively (Table 5.5). In this case, the importance of all environmental factor groups for the common component of species richness was approximately half that of factors for the common floristic composition component. However, the rank order of importances of environmental factor groups was identical with respect to these components. This was also generally reflected by the importances of individual factors (Table 5.5).

Common variance components between structure and species richness displayed marked differences in the importances of environmental factors and factor groups. In the former case, all factors explained 37% of the variance, and in the latter case only 7% (Table 5.5). In the former case the maritime factor group was clearly of greatest importance and the fire factor group of least importance. However, as an individual factor years since last fire was amongst the most important. In the case of maritime factors, distance from cliff-tops and salt-spray deposition factors were of

greatest importance whereas soil based maritime factors were of least importance. In the case of the common species richness component, all individual factors displayed equivalently low importances and could not be differentiated.

### 5.3.5 Differential environmental relationships of community properties and their independent variance components

Variance in floristic composition independent of structure displayed similar environmental relationships to that of floristic composition as a whole (Table 5.5). However, the importance of factors and factor groups for this component were generally lower than for floristic composition as a whole. This was particularly true with respect to years since last fire.

Variance in structure independent of floristic composition differed from that of structure as a whole. As shown in Table 5.5, a substantially lower amount of variance in this component was explained by environmental factors collectively. Of particular note was the lower importance of both the maritime and fire factor groups for this component.

It is of interest to note that importances for the variance in floristic composition independent of species richness were almost identical to those for floristic composition as a whole. This reflects the majority of floristic variance being independent of variance in species richness.

The component of species richness independent of floristic composition was explained to a greater extent than species richness as a whole by environmental factors collectively. It is also of particular interest to note the elevated importance of the soil nutrition factor group with respect to the independent component of species richness. As shown in Table 5.5, this can be attributed to elevated importances of total phosphorus and total nitrogen. It is only with this component that these factors attain a high rank of importance (Table 5.5).

Variance in structure independent of species richness resembled structural variance as a whole, in terms of the importance of environmental factors and factor

groups. This pattern resembled that between floristic composition as a whole and that portion independent of species richness, as noted earlier.

The importances of all environmental factors and factor groups for variance in species richness as a whole were higher than those pertaining to the variance independent of structure. Of particular note, however, was the markedly lower importance of the maritime factor group for variance in species richness independent of structure.

## 5.4 DISCUSSION

### 5.4.1 Associations between environmental factors

Results showed that direct exposure to maritime influences (DFCT, ACSD, BCSD) provides a major axis of environmental variation in the studied cliff-top coastal heathlands. However, results also showed the association of years since the last fire with these factors. This association has been alluded to in the past in consideration of fire patterns in cliff-top environments generally (see Adam *et al.* 1989a). It thus appears that effects of maritime exposure cannot be effectively considered with respect to cliff-top coastal heathlands unless fire effects are addressed concurrently. This association may be of particular consequence for environments such as that under study where previous fires have occurred relatively recently and where replicate stands are not available at appropriate distances from the cliff-top.

Results show that a second major axis of environmental variation can be distinguished comprised by variance in soil physical, soil nutrition and soil based maritime factors. This was shown to be correlated with the axis discussed above. There is hence evidence to suggest the presence of strong spatially autocorrelated environmental patterns in the site. I envisage that this may contribute to maintenance of diversities of community structures within local areas of cliff-top coastal heathlands. This has either been shown or implied in local studies of heathlands elsewhere (see Chapter 1), and appears likely in the current case in view of substantial variance in most environmental factors recorded in this study.

An important consequence of these autocorrelations is that unburnt heaths located near the cliff-edge, which may otherwise be considered as wet heaths, have high levels of soil maritime factors (EC, Cl, Na). Wet heaths have generally been shown to be more nutrient enriched and physiologically favourable for plant growth than dry dune heaths (see Siddiqi *et al.* 1972, 1976b; Specht 1979a,b; Myerscough & Carolin 1986). However, with high levels of salt in the substrate I envisage that species adapted to take advantage of such conditions would also need to be adapted to highly saline conditions. A more ecologically relevant distinction between wet and dry heaths in maritime cliff-top environments may thus be between heaths which are physically dry

(viz. heaths on deep freely drained dunes) and physiologically dry heaths where soil water potentials would be low due to salinity.

#### 5.4.2 Environmental differentiation of property complexes

With few exceptions, all floristic, structural and species richness complexes could be environmentally differentiated within their respective classification systems. This demonstrates the ecological significance of each of the three classifications. In general, environmental differences between complexes involved different subsets of factors encompassing all the included factor groups. This was evident with respect to each classification. This, along with the fact that significant differences were recorded for all individual factors, shows that differences within properties are not functions of single overriding environmental factors. The possibility still exists, however, that a single environmental control with multiple correlated factors exists. However, in view of the multiple and differential nature of environmental differences revealed, I suggest that this would be unlikely.

The results showed clear differentiation of floristic complexes with distance from cliff-tops. This can largely be attributed to major geological/topographical site features as described in Chapter 2. However, the results showed differentiation with respect to this factor between the platform heaths. With the exception of FC 4 the results showed that floristic complexes dominated by *Baeckea imbricata* (FCs 5 & 7) were located closest to the cliff-tops. This is consistent with observations of previous workers who have noted dense stands of *Baeckea imbricata* in frontal platform positions (e.g. Johnson & Briggs 1965; Adam *et al.* 1989a). This, along with the fact that other maritime factors displayed elevated levels in these complexes, shows that *Baeckea imbricata* has a substantial ecological advantage under exacerbated maritime conditions.

The results showed that soil based maritime factors (EC, Cl, Na) were generally correlated with distance from cliff-tops. However, these factors were more strongly correlated with the physical soil factors of organic content, fine particle fraction and pore space ratio. Similar correlations have been shown in vegetation elsewhere (e.g. Bowman *et al.* 1986; Tongway & Ludwig 1990; Johnson 1994; Le Brocque & Buckney

1995) and can be attributed to additional cation exchange capacity provided by organic matter (see Keith & Myerscough 1993). It thus appears likely that physical soil factors are functional in integrating soil based maritime influences. This is consistent with observations made in maritime cliff-top environments elsewhere (see Malloch 1971, 1972).

Results showed that field soil moisture was a major differentiating factor between floristic complexes. They also showed this factor to be positively correlated with the soil maritime and physical factors. It was evident from the results that elevated field soil moisture was a function more of occlusion of drainage rather than sites being wetter as a consequence of through drainage. This appears functional not only in maintaining wetter sites but also in promoting accumulation of organic matter, and thus also in promoting concomitant changes in soil maritime factors as referred to above.

Differentiation of floristic complexes with respect to the soil nutrient factor group was generally less marked than with respect to other factor groups. There were, however, exceptions, which corresponded to floristic differentiation of dune and platform heaths. The deeper more freely drained substrates of the dune heaths were in general of markedly lower nutrition. This was generally consistent with observations elsewhere (e.g. Siddiqi *et al.* 1972; Myerscough & Carolin 1986; Adam *et al.* 1989b), and it appears likely that leaching of nutrients and generally lower quantities of organic matter caused this difference. The vegetation of dune heaths, however, had been burnt in recent years, whereas the majority of platform heaths had remained unburnt. It is known that fire regimes can drastically alter nutrient budgets in vegetation in both short and long terms (see Raison 1979; Groves & Specht 1981; Grove *et al.* 1986; Adams *et al.* 1994). It thus appears likely that fire has also been functional in producing nutritional differences between these major heath types.

Notwithstanding differences in maritime, soil physical and other soil nutrition factors, complexes were remarkably similar in terms of pH. Irrespective of the causation of this uniformity, it is evident that vegetation can not be separated by pH within the range sampled. This uniformity and high acidity of substrates may nevertheless be of indirect importance in that it may allow for other aspects of soil chemistry to assume relatively greater importance.

An exception to the relatively uniform pH values recorded for complexes was that recorded for FC 11. The pH of this complex was markedly higher than all others. This complex represents frontal maritime herbfields. Being located at the cliff-top, they are continually flushed by drainage of rainfall from the platform. This may be responsible for alleviating otherwise highly acidic conditions.

The results showed that major floristic differences between complex groups were effectively resolved by considering years since the last fire alone. This factor is a gross simplification of fire effects, but nevertheless shows that fire is of primary importance for creating differences in floristic composition of cliff-top coastal heathlands. However, the spatial pattern of previous fires in the vegetation largely corresponds to the spatial patterns of other major environmental factors (e.g. a fire burning down a dune to a drainage line at the base separating dune from platform heath). The presence of differences in multiple factors thus confounds to some degree interpretation of differences in pattern between complexes differing in their previous burn date. This is particularly true with respect to direct maritime influences since years since last fire was found to be negatively correlated with distance from cliff-tops. Adam *et al.* (1989a) outline the dynamics of fire behaviour in cliff-top environments which act to prevent vegetation in the immediate vicinity of cliff-tops from being burnt as frequently or as intensely as other vegetation. This appears to be the case in the studied vegetation, and presents itself as a potential causative agent of environmental autocorrelation.

In view of the gross changes in community structure brought about by fire, and the strength of maritime factors in the studied vegetation, it would appear likely that interactions between time since the last fire and maritime factors would be ecologically significant. Despite this, the results showed that years since last fire was an important factor at high division levels in the floristic classification. I thus envisage that on a spatial basis these interactions would be important for relatively fine-scale differences in floristic composition. On a temporal scale, however, such interactions could be more substantial.

The results showed structural complexes to display complex patterns of environmental differentiation. Significant environmental differences occurred more between individual complexes than between groups of complexes. In other words differences were more evident where individual complexes were defined more so than at

higher classificatory levels. This in part may reflect the relatively few and general nature of the structural variables used in the classification. In such instances the presence of multiple structural attributes responding in the same way may be required in order to resolve a statistically significant difference in environment. This means that establishment of such differences would be weighted towards lower divisions of the classification. Alternatively, independent environmental expression of different structural attributes may be masked to some degree by inter-correlations amongst structural attributes which are independent of environment. The extent to which this is the case is not known. However, it is known that structural attributes do display high levels of inter-correlation (see Chapter 3).

In addition to the above, it should also be noted that radiation extinction (PPAREX) was considered as a structural attribute rather than as an environmental factor. Previous studies of vegetation which have included radiation attenuation measures as environmental factors have generally found that significant differences exist between both different structural types (e.g. Le Brocq & Buckney 1995) and between related structural types which display relatively finer-scale structural differences (e.g. Turton & Duff 1992; Keith & Myerscough 1993). I thus envisage that PPAREX would have been an important factor at a high level in the classification if included in the current study as an environmental factor. However, because of the intimate relationship between light attenuation and structure in general I suggest it is better considered as a structural attribute.

As for floristic composition, an ordering of complexes with respect to distance from cliff-tops was evident with the same considerations of autocorrelation made for floristic composition evidently also applicable to structure. However, differentiation between structural complexes displayed a distinct polarisation in terms of years since fire. The most recently burnt vegetation, located relatively far from the cliff-tops (the majority of SC 6-dune heath and SC 7-platform heath), was separated from the remainder. This polarisation was evidently strengthened by the fact that vegetation of intermediate burn date tended to merge structurally with the unburnt heaths (SC 5). The results showed that this polarisation with respect to fire was also associated with maritime factors increasing towards unburnt complexes, which were in general located closer to the cliff-top. Because of the merging of various dune heaths of intermediate



burn dates with platform heaths, the corresponding differences in soil physical factors appeared, in general, of secondary importance in such differentiation.

The results showed swamp vegetation (SC 8) to be environmentally as well as structurally distinct. Primary environmental differences from other complexes were in factors associated with occluded drainage. It is of interest to note the general lack of shrubs in this complex. It is well known that wet heaths generally have a shrub stratum of greater height and coverage than open heaths (see Specht 1989b). However, further increases in field soil moisture beyond that reasonably expected for wet heaths (e.g. to swamps) evidently leads again to a decline in height and coverage of the shrub stratum. This is generally supported by observations in similar vegetation elsewhere (e.g. Hamilton 1918; Siddiqi *et al* 1972; Buchanan 1980; Benson & Howell 1990). However, this is the first study in which this response has been quantified. Importantly, this shows that primary structural characteristics of cliff-top coastal heathlands can display unimodal responses to environment. Structural attributes of vegetation have traditionally been considered as linear variates and analysed as such (e.g. MacArthur & MacArthur 1961; Rotenberry & Wiens 1980; Chan 1990). However, my study shows that this general consideration requires some revision, at least with respect to cliff-top coastal heathlands.

The results showed environmental differences between species richness complexes to be many and varied. Accordingly, I do not intend to discuss the potential ecological significance of all these differences. However, it is of interest to note that, in general, the range of variation encompassed by differences in most factors was in excess of that of either floristic or structural classifications. The fact that this applied to most factors suggests an equivalent participation of all factors in differentiation of species richness complexes. The quantitative differences from floristic and structural classifications imply a more extensive environmental separation of species richness complexes. However, the fact that more species richness complexes were defined than either floristic or structural complexes suggests that these environmental separations are likely to be of a more specific (i.e. between individual pairs of complexes) than general (between distinct groups of complexes) nature.

In addition to the above, it is of importance to note that significant differences in individual environmental factors were insufficient to recover the multivariate classification. This, along with the fact that pairs of complexes tended to be

separated by significant differences in different environmental factors suggests that the differentiation of complexes is a product of attribute responses to multiple rather than single factors. This shows the necessity of considering multiple environmental factors in explaining complex patterns of community structure. Similarities of the species richness classification with those of floristic composition and structure suggest this to be the case irrespective of which property is being considered.

Notwithstanding the above, investigation of complex responses of cliff-top coastal heathlands to multiple environmental factors has received relatively little attention in the Sydney area. Previous studies were reviewed in Chapter 1 and show that such considerations have been largely dependent on implementation of multivariate analysis procedures. These studies have generally taken the form of multivariate classifications coupled with indirect environmental analysis. This type of analysis enables effective summary of complex vegetation patterns, particularly with 'multi-scale' classifications which classify increasing finer-scale patterns. They also allow for general environmental relationships to be uncovered through comparisons, as shown in this study. However, they do not allow direct multivariate comparisons of vegetation patterns with multiple environmental factors. While internal structure of properties and their general environmental relationships can be unravelled through the classificatory approach, the results of this study indicate that interpretation of complex vegetation-environment relationships may be better served through direct multivariate gradient analysis which enables direct linkage between multivariately defined vegetation and environment. These techniques were employed in examining differential environmental relationships of the different properties and of their variance components, and are considered in subsequent sections.

#### 5.4.3 Differential environmental relationships of community properties

The results showed substantial amounts of variance in each of the three community properties could be explained by supplied environmental factors. This, along with the resemblances of constrained and unconstrained analyses of each property, show the absence of significant environmental influences which were not accounted for by the

included factors: Given that included factors were designed to encompass major areas of local environmental variation, this shows the likelihood of strong local environmental control of cliff-top coastal heathlands. Previous studies of cliff-top and other heathlands (see Chapter 1) have shown this to be the case with respect to floristic composition. My study, however, also shows this to also be the case with respect to structure and species richness. These properties thus contribute to the overall ecological structure and diversity of cliff-top coastal heathland communities.

Comparisons of the percentages of variance explained by environmental factors individually and that explained by all factors considered together revealed a quantitative difference in the environmental relationships of floristic composition on one hand and structure and species richness on the other. In the former case, the sum of values for individual factors greatly exceeded that of all factors considered together whereas in the other two properties the total value approximately reflected the sum of individual factors. This suggests a greater degree of redundancy among environmental factors underlying variance in floristic composition. It may thus be said that survey of subsets of species might have been sufficient to recover environmental relationships of floristic composition. However, it may not apply to subsets of related complexes within which different environmental relationships may apply. This, however, must await further investigation.

The results showed that the redundancy of environmental factors with respect to floristic composition could be attributed in part to the high correlation of factors as well as the inter-correlation of major gradients. This was also the case with structure. However, in this case results showed soil physical factors formed a near orthogonal gradient to that formed by fire/maritime factors, and showed this to be largely associated with swamp vegetation (Fig. 5.3). It is thus evident that the typical environmental characteristics of this vegetation have been better identified by the structural rather than the floristic response of vegetation. This difference can be attributed to the fact that many of the swamp species are also found throughout the remaining vegetation, principally in platform heaths.

The results showed species richness to differ markedly from both floristic composition and structure in its environmental relationships. Of particular note were the lower importances of maritime and fire factor groups. In the case of maritime factors, it

is reasonable to expect that these factors had a strong effect over an extended period on the evolution and general structure of the communities present. In a contemporary sense, maritime factors may also provide strong limitations to processes such as competition and establishment. It may thus be that, while of importance, these factors may not appear as such within local maritime areas, at least with respect to properties as general as species richness. In the case of years since the last fire, it may have been expected that a greater proportion of variance would have been explained, since decreases in species richness with time since fire is a known characteristic of heathland vegetation (see Groves & Specht 1981; Kruger 1983). However, the observed lack of importance of this factor may in part be attributed to the fact that quadrat sizes appropriate to the spatial structuring of the vegetation present were used. Burnt heaths recognised on a floristic basis may well contain more species overall (see Chapter 3). However, they generally display smaller scale spatial structuring than unburnt heaths. As a consequence, when this is taken into account the species richness of unburnt heaths can actually be equivalent or greater than that of burnt heaths. While representing a break from convention, this approach appears appropriate given the probable differences in the spatial scale of ecological processes.

Overall, the results of this study show that variance in each of the major community properties is a function of multiple environmental factors and that attributes of each property are related differentially to these factors. While similarities existed between properties in terms of the composition of major environmental gradients, the importance and inter-relationship of these gradients was shown to differ between properties. This was also shown to be the case at the level of individual factors. These characteristics support the hypothesis that floristic composition, structure and species richness display different environmental relationships.

The fact that differential environmental relationships can be demonstrated indicates a previously unresolved ecological complexity for cliff-top coastal heathlands of the Sydney area. Included factors may encompass those which are truly causative. Causation, however, requires experimental research in order to isolate the effects of particular factors and their interactions. The multiplicity of environmental relationships of the different properties shown in this study indicate that effective experimentation may be beyond practical limits, unless field based. Even then, experimentation would be

logistically extensive. Also, such research would likely need to be spatially constrained, given the distribution of cliff-top coastal heathlands in the Sydney area. In view of this, and the infancy of community research in this vegetation type, I suggest that, in the short term, correlative studies are likely to provide the most effective means whereby insights into the general ecological dynamics of this vegetation with respect to environment can be developed.

#### 5.4.4 Differential environmental relationships of common variance components of community properties

Examination of the importance of environmental factors and factor groups for common variance components between floristic composition and structure revealed a number of differences. The magnitude of importances for the common component of floristic composition were generally greater than those for the common component of structure. This shows that environmental relationships of species better explained the common variance between the properties than environmental relationships of structural attributes. It must be kept in mind, however, that far more floristic attributes (species) were included than structural attributes. This possibly allowed for this increased sensitivity of floristic composition. The results also showed differences in the relative importance of factors and factor groups between each component. In particular, the maritime factor group was of relatively greater importance for the common component of floristic composition, while years since last fire was of relatively greater importance for the common component of structure. This observation, and others, suggests that common variance between these properties is not completely integrated with respect to environment. This in turn suggests that these components are in part, ecologically coincidental.

It has long been purported that plant communities are assemblages of species populations which behave largely independently with respect to environmental gradients, i.e the continuum concept (see McIntosh 1967; Austin 1985, 1987; Anderson & Kikkawa 1986; although see Goodall 1963, Daubenmire 1966). The results discussed above suggest that this concept could possibly be extended to a more integrated level by

inclusion of structural attributes. They have been shown in the current case to be related to environment, and in part to be ecologically co-incidental with common variance in floristic composition. Inclusion of structure in community models would thus be likely to add ecological information not carried by the distribution of species populations, at least with respect to cliff-top coastal heathlands.

Comparisons of the common variance components between floristic composition and species richness revealed that similar proportions of variance in these components were explained by all environmental factors considered together. The results also showed that rank importance of factors and factor groups was similar between the components. This suggests that environmental relationships of these components are essentially the same, and are hence not ecologically co-incidental. This is not surprising, since the substantial variance encompassing species turnover does not form part of the compared variances, the compared variances in both properties encompassing species addition and deletion.

The results showed common variance components between structure and species richness to bear little relationship with one another in terms of their environmental relationships. However, this was shown to be largely a function of the fact that relationships of the common species richness component were too small to be determined by included factors.

#### 5.4.5 Differential environmental relationships of community properties and their independent variance components

Years since the last fire was found to be an important component of the environmental relationships of both floristic composition and structure. However, a marked diminution of importance of this factor was noted for the respective independent variance components. This suggests that, beyond the short term structural and floristic changes, time since last fire may be of relatively limited influence. This interpretation, however, is necessarily limited in the current study by the lack of fire frequency and intensity data, by the relative polarisation of previous burn dates and by the lack of an extensive fire history for the site.

It was of particular interest to note the reduction in the importance of maritime factors in relation to variance in structure independent of floristic composition. As outlined in the introduction, there was reason to suspect that exposure to maritime factors would be a primary cause of such variance. However, the above characteristic shows that there is little evidence for this within the immediate proximity of cliff-tops. Rather, both soil physical and soil nutrition factors present themselves as more probable causes of this variation. It is known that wetter soils in general carry heath of greater height and coverage (see Specht 1979b; Specht 1983). In my study, this may be of primary influence. However, while maritime factors as a group may be of relatively lower importance for independent variance in structure, the presence of interactions with other factors cannot be dismissed. High salt contents in the substrate, for example, may affect the influence of elevated soil moisture through promoting associated physiological dryness (see Malloch 1971, 1972). In the current study it appears likely that such interactions would occur and may be as equally functional in producing independent patterns in structure. Account of this, however, awaits further investigation.

As noted in the previous chapter, variance in species richness independent of floristic composition can only arise within the current data set by the alternate presence/absence of individual species in shrub and sub-shrub strata. The results showed that the importance of total phosphorus and nitrogen was of greatest importance for this variance component. Given the nature of this variance component, and the fact that species capable of occupying one or the other strata are generally dominants, it appears reasonable that the establishment/diminution of ecological dominance is associated with nutrient levels in the soil.

Similar to the independent variance components discussed above, those of structure and species richness which were independent of one another were shown to have ecological foundation, in that substantial amounts of their respective variances could be explained by included environmental factors. They thus represent ecologically relevant community patterns which, like those independent components discussed above, go unaddressed by contemporary approaches to community ecology. This study shows, however, that such ignorance may be inconsequential ecologically if most variance in a property is independent of others. In this case, environmental relationships of independent variance components resemble those of properties considered as wholes.

However, where this is not the case, differences of both a qualitative and quantitative nature occur. Studies which do not seek to partition variance in community structure of cliff-top coastal heathlands are thus likely to involve distortions as to the environmental relationships which are uniquely attributable to particular properties.



## 5.6 CONCLUSIONS

Analyses of association between environmental factors independent of vegetation data showed the presence of two major inter-related axes of environmental variation. The first was related to distance from cliff-tops, and hence to direct exposure to maritime influences. This axis, however, was strongly correlated with years since last fire. I conclude that while exposure to maritime influences comprises a primary environmental gradient in cliff-top coastal environments, such a gradient may not be considered *a priori* as overriding other factors.

The second primary axis of environmental variation was shown to consist primarily of variance in soil physical and nutrition factors, ranging from dry environments of low organic matter and soil nutrients to wet environments of high organic matter and soil nutrients. Association of soil based maritime factors was shown with the latter environment. I conclude that physiologically favourable conditions for plant growth are subjugated by the extent of substrate salinity.

Complexes recognised from classifications of floristic composition, structure and species richness were shown to be separated by at least one environmental factor within their respective classification systems. Environmental separations were also shown to commonly involve multiple and different factors between different complexes of the same properties. I conclude each classification is thus of ecological significance. I also conclude that internal structure of each property is related to environment by multiple factors which are of differential importance within each property classification.

Variance in each property which was constrained by all environmental factors resembled respective unconstrained variances. I conclude that the major patterns in each property are structured functionally, and that the effects of causal factors are encompassed by the factors included in this survey.

The results showed floristic composition, structure and species richness to be related differentially to environment. I conclude that greater definition of community structure, i.e. in terms of multiple properties, allows for resolution of environmental responses of community structure which would remain unresolved in terms of single property classifications.

Common variance components between properties were shown to differ quantitatively in their environmental relationships with respect to importances of environmental factors and factor groups. I conclude that common variance components do not represent an entirely integrated response to environment. I thus also conclude that common variance components are ecologically co-incidental to varying degrees.

Except in the case of independent variance components comprising most of a property's variance (e.g. as with floristic composition), independent variance components were shown to display differential environmental relationships compared with properties taken as wholes. I hence conclude that variance uniquely attributable to a particular property is functionally distinct from composite variance in that property. This conclusion necessarily implies that tertiary syntheses of community structure are required for cliff-top coastal heathlands if functional responses of particular properties are to be accurately resolved.

Overall, this study shows that complex patterns of community structure of cliff-top coastal heathlands display equally complex patterns of environmental relationships at small local scales. I conclude that the studied cliff-top coastal heathlands represent an ecologically complex system in which principal processes regulating community structure occur at the local scale. In view of the localised and restricted distribution of cliff-top coastal heathlands in the Sydney area, this indicates that the loss of even small areas of cliff-top coastal heathlands in the area will involve a concomitant significant loss in the ecological diversity of the coastline.

## CHAPTER 6: COMMUNITY STRUCTURE OF CLIFF-TOP COASTAL HEATHLANDS IN BOTANY BAY NATIONAL PARK, SYDNEY: A COMPREHENSIVE COMMUNITY CLASSIFICATION AND COMPARISONS WITH CLASSIFICATIONS OF INDIVIDUAL PROPERTIES.

### 6.1 INTRODUCTION

#### 6.1.1 Background

Classifications of community structure have traditionally been conducted using attributes of single major community properties, usually either floristic composition (e.g. Siddiqi *et al.* 1972; Clemens & Franklin 1980; Adam *et al.* 1989a; Keith & Myerscough 1993; Le Broque & Buckney 1995), or structure (e.g. Richards *et al.* 1940; Dansereau 1951; Webb *et al.* 1970, 1976; Cowling & Campbell 1980; Gillison 1981; Fox & Fox 1981; Haering & Fox 1995). In being based on attributes of single properties such classifications ignore the fact that community structure is an expression of variance in multiple community properties. These properties may vary independently or be of differing ecological amplitude. Single property classifications may thus be considered 'ecologically restrictive' in that, if the conditions above hold, single property classifications may return an ecologically poor summary of the vegetation being classified.

While classifications of single properties are in fact desirable in some circumstances, I suggest that more ecologically informative and cohesive classifications are attainable by considering attributes of multiple properties within a single classificatory framework. By considering more attributes, the influence of stochasticity in any single attribute on clustering would be reduced unless all attributes varied randomly, which is unlikely. This consideration may also be extended to properties. One property may display a higher level of stochasticity than another in response to certain factors. While this stochasticity may remain in a multi-property classification, it would nevertheless be placed at the appropriate position in the data set due to the presence of the less stochastic property(ies) in the classification.

In addition, inclusion of attributes of multiple properties should allow for a more comprehensive classification of community structure, unless all properties coincide. By virtue of utilising a broader spectrum of variance, finer scale differences in community structure should be resolvable. By virtue of being able to detect finer-scale differences in community structure I suggest that multi-property classifications will likely detect finer-scale differences of ecological relevance than single-property counterparts.

If the characteristics of multi-property classifications as outlined above hold, then, by inference, recognised complexes should be more ecologically cohesive. In that differences in vegetation reflect direct or indirect (e.g. modified by competition) responses to environment, this cohesiveness should, I suggest, be evidenced by greater environmental homogeneity of recognised complexes.

Despite this, few classifications of vegetation data have been conducted using attributes of multiple properties. A number of classification schemes have been produced which incorporate floristic and structural attributes at different levels of classification hierarchies (e.g. Beadle & Costin 1952; Johnson & Lacey 1984). However, these necessarily pre-emphasise the importance of one or the other property, hence negating any independent contribution of the other properties to the classification. I thus suggest attributes of different properties need to be considered concurrently in multi-property classifications.

Numerical multivariate classification methods present an obvious choice of method for comprehensive classifications of community structure. Many attributes can be considered concurrently and participate independently. However, such methods have yet to gain acceptance for multi-property applications in community studies. This is notwithstanding the fact that numerical classification techniques have been applied in classifying diverse attribute sets, such as those of varied physiognomic/structural attributes (e.g. Webb *et al.* 1970, 1976; Kikkawa 1982; Komarkova & McKendrick 1988; Haering & Fox 1995). In these attribute sets, differences between individual attributes may be seen as no greater than differences between attributes of different properties.

The fact that 'mixed' attribute matrices have not been the focus of numerical classification in community studies may reflect difficulties in considering attributes of different properties as equivalent in a single analysis. However, there

appears to be no inherent mathematical difficulty in classifying such matrices if variance structures of the different properties can be equated. I envisage that use of numerical classification for the purpose of producing comprehensive classifications of vegetation would enable more ecologically coherent units to be recognised than is possible using classifications of single properties.

In considering a multi-property classification it is important to note that a 'combined classification' is not the only approach available. In the field of systematics there has been considerable debate over whether phylogenetic data should be analysed using a combined classification, or whether 'consensus classifications' are to be preferred (see Donoghue *et al.* 1989; Barrett *et al.* 1991; Baum 1992; de Quiroz *et al.* 1995). In the latter type of analysis trees are constructed that reflect the common component between trees constructed separately for different properties. Arguments for favouring consensus techniques have included that consensus techniques provide a quick method of detecting agreements/disagreements between data sets (de Quiroz *et al.* 1995), that by avoiding combining data sets directly they do not allow for obscuring of significant patterns of congruence or conflict among attributes (see Swofford 1991; Bull *et al.* 1993; de Quiroz 1993, de Quiroz *et al.* 1995), and that by keeping data sets separate they provide the best acknowledgment of the independence of sources of evidence for phylogenetic relationships (see Penny & Hendy 1986; Hillis 1987; de Quiroz 1993; de Quiroz *et al.* 1995; although see Barrett *et al.* 1991). In view of these arguments consensus techniques have been viewed as more conservative techniques for constructing phylogenetic relationships (see de Quiroz *et al.* 1995).

Notwithstanding this, arguments similarly exist for favouring a classification of combined data sets. These include, that combined classifications provide a more highly resolved tree by virtue of including all data and that this provides for greater global parsimony (see Barrett *et al.* 1991), that use of all information is commensurate with the philosophical principal of total evidence (see Carnap 1950; Good 1983; Jones *et al.* 1993; de Quiroz *et al.* 1995), and that by using more attributes combined analyses are more likely to express true phylogenetic signals, and thus have superior explanatory power (see Hillis 1987; Baum 1992; de Quiroz *et al.* 1995).

I envisage that arguments for either consensus or combined analyses could equally be applied to multi-property classifications of plant community data.

The first research objective addressed in examining this hypothesis was to determine whether recognised community complexes displayed greater environmental homogeneity than complexes of individual properties. I envisaged that such determination would establish the relative 'ecological cohesiveness' of complexes recognised through all classifications.

The second research objective addressed in examining the above hypothesis was to determine whether comprehensive classification groupings displayed greater environmental homogeneity with respect to all division levels than groupings of individual property classifications. This was done in order to provide a more general comparison than that between complexes, which were in part recognised subjectively.

I envisaged that address of the hypothesis at both levels above would establish the relative performance of the classifications in producing ecologically cohesive groupings.

## 6.2 MATERIALS AND METHODS

### 6.2.1 Classification of combined variance in community structure and description of community complexes

Site by attribute matrices for floristic composition, structure and species richness attributes were first combined into a single matrix. Matrices combined were as described for individual properties in Chapter 3. The single matrix was then classified by indicator species analysis using TWINSpan. Minimum group size for division was set to 5. Cut levels used to define pseudospecies were 0%, 10%, 20%, 30%, 40%, 50% and 60%. Community complexes were defined at the lowest division levels where clear disjunctions in the distribution of one or more pseudospecies was evident. Divisions considered minor were not considered as a basis for complex recognition. Attribute and environmental characteristics of community complexes were described through application of canonical correspondence analysis to the matrix above. The combined variance matrix was constrained in this analysis by the matrix of environmental factors as used in the previous chapter. However, chloride content, bulk density, pore space ratio, air filled porosity, total phosphorus and total nitrogen were omitted, due to the fact that these factors were not determined for quadrats of reconnaissance zone 4 (see Chapter 5).

The comparative information contents of the community classification and site reconnaissance were quantified using a measure of similarity between the respective classifications based on the similarity of clusters according to quadrat grouping. This measure and the methodology for its derivation were outlined in Chapter 3.

### 6.2.2 Comparisons of the environmental homogeneity of the community classification with those of individual properties

For investigations of environmental homogeneity a site by environmental factor matrix was first obtained. This was as described in the previous chapter. All factors in the matrix were range standardised (0 to 100). Site by environmental factor matrices were

then prepared for all property and community complexes. They were also compiled for all division groupings in each classification. Bray-Curtis dissimilarity values were then calculated for each site by site comparison in each complex and division grouping i.e. each grouping at each division level of each classification. This was done using the PATN pattern analysis package (Belbin 1989). All dissimilarity values were then deducted from 1 to obtain a measure of association. These values were averaged for all complexes and division groupings and the respective means assigned as measures of environmental homogeneity.

Environmental homogeneity measures of community and property complexes were compared using one-way analysis of variance. Assumptions of the analysis were checked by inspection of residual and normal probability plots, application of the Shapiro-Wilks statistic and inspection of standard deviations. Data transformations were made where necessary.

To compare classification systems, environmental homogeneity measures for division groupings were compared using two-way analysis of variance, using division level and property classification system as factors. Assumptions of the analysis were assessed as above.



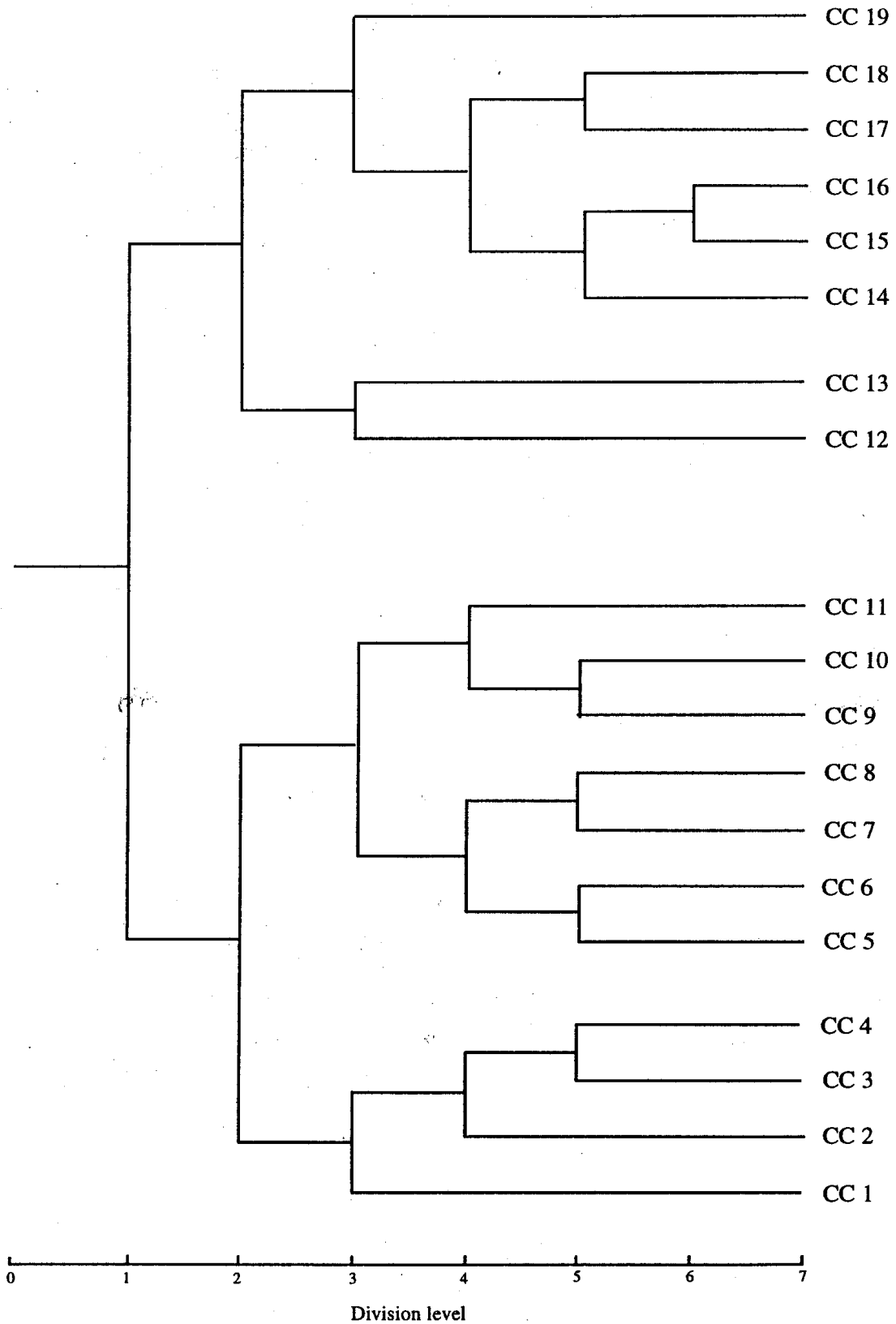
## 6.3 RESULTS

### 6.3.1 The community classification and description of community complexes

A total of nineteen community complexes were identified through classification of the combined data matrix. The classification dendrogram showing the relationship between community complexes is provided in Fig. 6.1. Quadrat membership to community complexes is shown in Table 6.1. Although some exceptions exist, it can be seen in Table 6.1 that quadrats from individual reconnaissance zones have in general been grouped together. Quadrats from similar reconnaissance zones have also been grouped together in community complexes (e.g. RZs 6 and 14 in CC 12). These characteristics were also evident with respect to classifications of individual properties (see Chapter 3). However, the concordance between the site reconnaissance and community classification was found to be the greatest of any classification comparison with 65.4% of the information in the community classification contained in the site reconnaissance.

Community complexes and attributes are shown in relation to environmental variance in Fig. 6.2. CC 19 is distinctive floristically and environmentally, and concurs entirely with the frontal maritime herbfields which have been described in previous chapters. The remaining complexes fall generally into two main groupings. The first consists of CC 1 and CC 3 to CC 11. These complexes correspond predominantly to the unburnt platform heaths. As shown in Fig. 6.2 these complexes are associated to varying degrees with relatively high levels of field soil moisture, soil nutrition and soil based maritime factors. This is particularly the case with CC 1, which represents islands of platform heath in frontal platform areas.

In addition to the above the first grouping of complexes displays marked internal differentiation with respect to attributes of all three properties. Of note is the elevated affinity of CC 1 and total species richness. Also of note is the floristic differentiation of complexes in terms of the most abundant dominants (i.e. *Baeckea imbricata* and *Banksia ericifolia*) versus less abundant dominants (i.e. *Hakea teretifolia*, *Melaleuca armillaris* and *Westringia fruticosa*). As shown in Fig 6.2, complexes more



**Fig. 6.1** Indicator species analysis dendrogram showing the recognised community complexes. Community complexes are identified by code (see text).

**Table 6.1** Quadrat membership in community complexes.

Community complex	Quadrats
1	3/1.1, 3/1.2, 3/1.3, 3/1.4, 3/1.5, 3/2.1, 3/2.2, 3/2.3, 3/2.4, 3/2.5, 13/1.5
2	12/8.2, 12/8.3, 12/8.4, 12/8.5
3	8/7.1, 8/7.5, 10/7.4, 10/7.5, 13/1.4
4	13/1.1, 13/1.2, 13/1.3, 13/2.1, 13/2.2, 13/2.3, 13/2.5
5	2/3.1, 2/3.2, 2/3.3, 2/3.5, 2/4.1, 2/4.2, 2/4.3, 2/4.4, 2/5.1, 2/5.2, 2/5.3, 2/5.4, 2/6.1, 2/6.2, 2/6.3, 2/6.4, 2/6.5, 7/11.1, 7/14.2, 8/8.4, 15/8.3, 15/10.3, 15/10.4
6	2/4.5, 2/5.5, 7/11.3, 7/12.3, 7/13.4, 7/14.4, 8/8.2, 8/8.5, 15/4.1, 15/8.4, 15/9.1, 15/9.3
7	2/3.4, 7/11.2, 7/12.1, 7/12.2, 7/13.1, 7/13.2, 7/13.3, 7/14.1, 7/14.3, 7/15.1, 7/15.2, 7/15.3, 7/15.4, 8/8.1, 8/8.3, 15/5.1, 15/6.1, 15/7.1, 15/7.2, 15/8.1, 15/8.2, 15/9.2, 15/10.1
8	10/7.1, 15/6.3, 15/7.3, 15/9.4, 15/10.2
9	8/6.1, 8/6.5, 8/7.3, 8/7.4, 13/2.4, 13/3.1, 13/3.2, 13/3.3, 13/3.4, 13/3.5, 13/4.1, 13/4.2, 13/4.3, 13/4.4, 13/4.5, 13/5.1, 13/5.2, 13/5.3, 13/5.4, 13/5.5, 13/6.1, 13/6.2, 13/6.3, 13/6.4, 13/6.5
10	7/11.4, 7/12.4, 8/6.2, 8/6.3, 8/6.4, 8/7.2, 8/9.1, 8/9.2, 8/9.3, 8/9.4, 8/9.5, 10/7.2, 10/7.3, 15/5.4
11	6/14.2, 15/4.2, 15/4.3, 15/4.4, 15/4.5, 15/5.2, 15/5.3, 15/5.5, 15/6.2, 15/6.4, 15/6.5, 15/7.4, 15/7.5, 15/8.5
12	6/14.1, 6/14.3, 6/14.4, 6/14.5, 6/15.1, 6/15.2, 6/15.3, 6/15.4, 6/15.5, 14/12.1, 14/12.2, 14/12.3, 14/12.4, 14/12.5, 14/13.1, 14/13.2, 14/13.3, 14/13.4, 14/13.5, 14/14.1, 14/14.2, 14/14.3, 14/14.4, 14/14.5, 14/15.1, 14/15.2, 14/15.3, 14/15.4, 14/15.5
13	5/4.1, 5/4.2, 5/5.1, 5/5.2, 5/6.1, 5/6.2, 5/7.1, 5/7.2, 5/8.1, 5/8.2, 5/9.1, 5/9.2, 5/10.1, 5/10.2, 5/11.1, 5/11.2, 5/12.1, 5/12.2, 5/13.2
14	5/13.1, 5/14.1, 5/14.2, 5/15.1, 12/8.1
15	1/7.1, 1/7.2, 1/8.1, 1/8.2, 1/8.3, 1/8.4, 1/8.5, 1/9.1, 1/9.2, 1/9.3, 1/9.4, 1/9.5, 1/10.1, 1/10.2, 1/10.3, 1/10.4, 1/10.5, 5/15.2
16	1/7.3, 1/7.4, 1/7.5
17	9/10.1, 9/10.2, 9/10.3, 9/11.1, 9/11.2, 9/11.3, 9/12.1, 9/12.2, 9/12.3, 16/6.1, 16/7.1, 16/8.1, 16/9.1, 16/10.1
18	11/9.1, 11/9.2, 11/9.3, 11/9.4, 11/9.5, 11/10.1, 11/10.2, 11/10.3, 11/10.4, 11/10.5, 17/5.1, 17/5.2, 17/5.3
19	4/1.1, 4/1.2, 4/1.3, 4/1.4, 4/1.5, 4/2.1, 4/2.2, 4/2.3, 4/2.4, 4/2.5



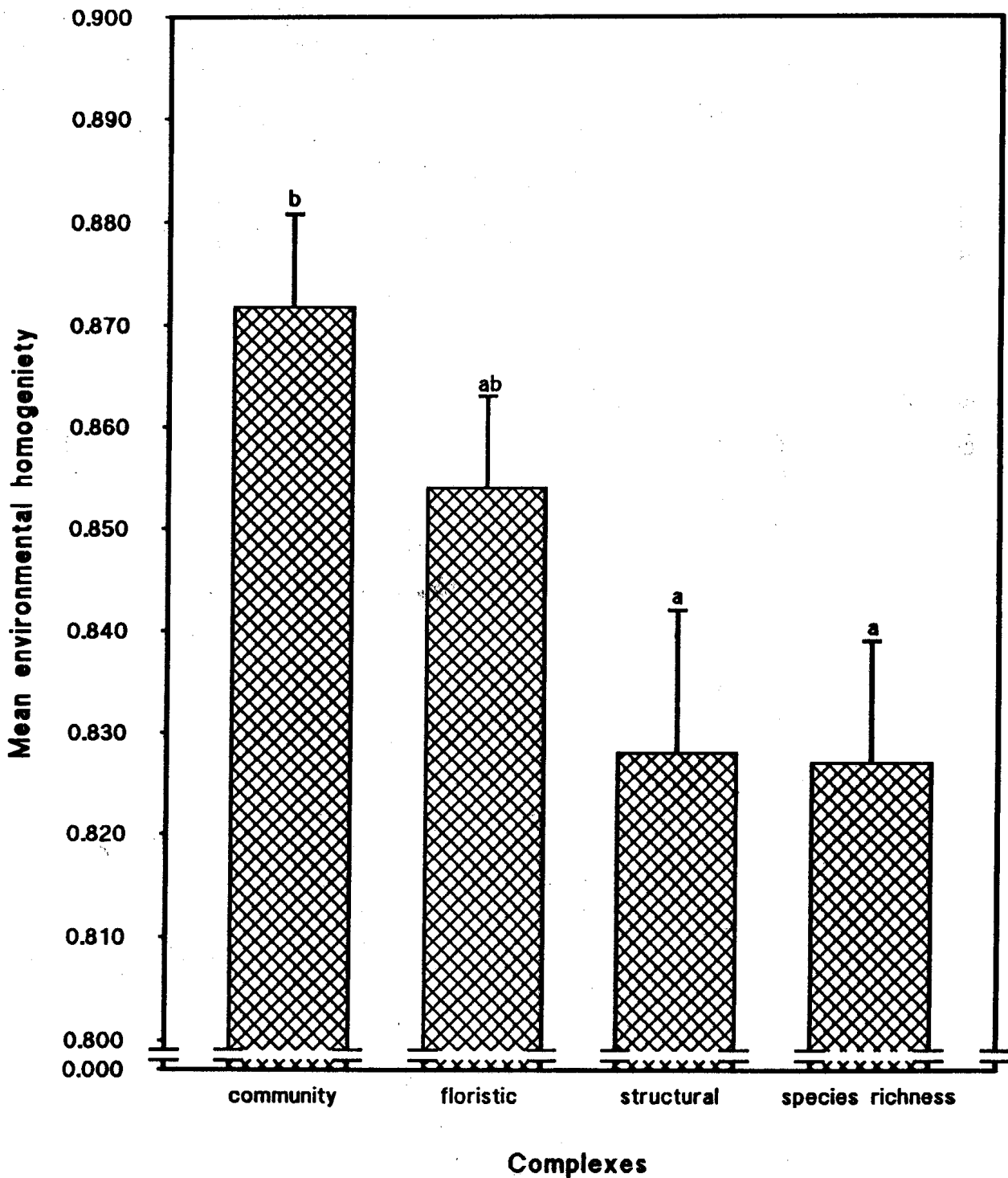
closely associated with the first-tier dominants also tend to be associated with optima for shrub-based structural attributes.

The second major grouping of community complexes comprises CC 12 to CC 18. This grouping corresponded mainly to all recently burnt vegetation and swamps. As shown in Fig. 6.2, these complexes are in general characterised by relatively lower levels of soil nutrients and soil-based maritime factors as well as by being located further from cliff-tops.

Like the first major grouping internal differentiation of the second grouping is evident. This occurs in two major directions. The first concords approximately with the first CCA axis (Fig. 6.2). This is associated with the change from relatively higher graminoid and groundcover representation in the most recently burnt vegetation to greater shrub representation in the dune heaths of intermediate burn date. The second major direction of variation in this group concords approximately with the second CCA axis. As shown in Fig. 6.2, this is associated with increasing representation of graminoids in wetter complexes. It is also associated with increasing species richness of both groundcover and graminoid strata.

### 6.3.2 Comparative environmental homogeneity of community and property complexes

Mean environmental homogeneities of community and property complexes are shown in Fig. 6.3. As shown, all values recorded were high, lying between 0.8 and 0.9. The greatest mean value was recorded with respect to community complexes. As shown in Fig 6.3, this value was significantly higher than those pertaining to structural and species richness complexes. Values for community and floristic complexes were statistically inseparable. Values for individual properties were also statistically inseparable from one another (Fig. 6.3).



**Fig. 6.3** Mean environmental homogeneity of community and property complexes. Standard errors of means are indicated. Significantly different means (Tukey tests) are indicated by lettering. Means with no letters in common are significantly different ( $p < 0.05$ ). See text for determination of environmental homogeneity values.

### 6.3.3 Comparative environmental homogeneity of community and property classification systems

Variance in mean environmental homogeneity of the different classification systems across division levels is shown in Fig 6.4. All classification systems had approximately the same form of increase in mean environmental homogeneity across division levels. This observation was confirmed by the corresponding two-way analysis of variance (Table 6.2) in which a non-significant interaction between classification and division level was recorded. This analysis also showed that statistically significant differences in environmental homogeneity existed with respect to both classification and division level. As shown in Fig. 6.4, the mean environmental homogeneities for the floristic classification were statistically inseparable from those of the community classification at all division levels. It is of interest to note, however, that differences between recorded mean environmental homogeneities of these classifications became less at the lower division levels. It is apparent from Fig. 6.4 that this is due to a declining rate of increase in mean environmental homogeneity of floristic groupings, whereas the rate of increase in mean environmental homogeneity of the community classification groupings was approximately constant.

Differences in mean environmental homogeneity between the structural and species richness classifications on one hand and the community and floristic classifications on the other were most evident below the fourth division level (Fig. 6.4). It is clearly evident in Fig. 6.4 that mean environmental homogeneity of both structural and species richness groupings levels off below this division level. However, environmental homogeneity of community and floristic groupings continues to rise. At higher division levels differences between these pairs of classifications are not as evident. The general pattern was of close similarity between structural and species richness classifications, the floristic classification displaying the greatest values and the community classification being intermediate (Fig. 6.4).

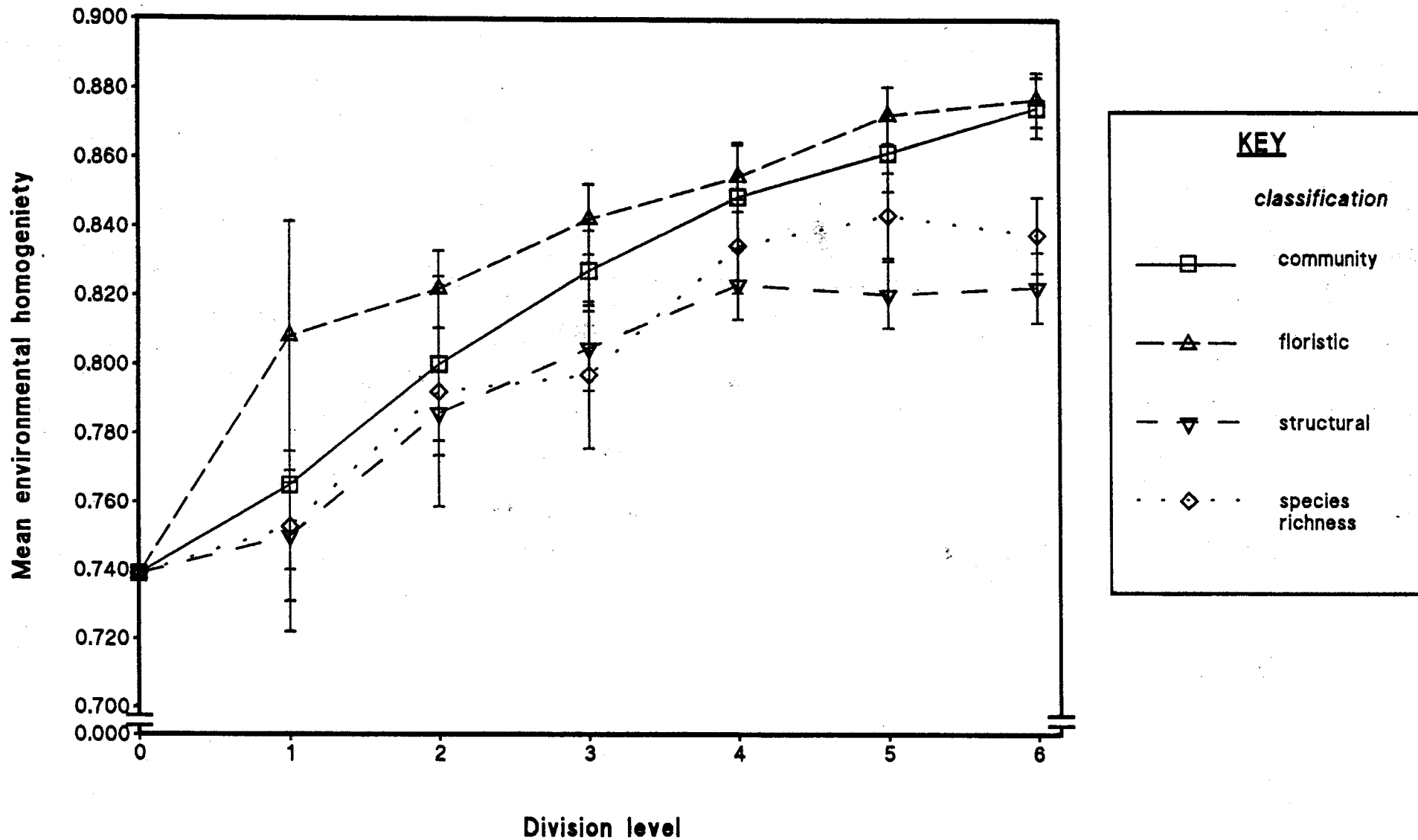


Fig. 6.4 Mean environmental homogeneity characteristics of community and property classifications. Standard errors of means are indicated. See text for determination of environmental homogeneity values.



**Table 6.2** Two-way analysis of variance of environmental homogeneity of classification groupings.

Factors are classification (community and individual property classifications) and classification division level (six division levels).

<b>Source</b>	<b>DF</b>	<b>Sum Sq.</b>	<b>Mean Sq.</b>	<b>F</b>	<b>P</b>
Classification	3	0.042	0.013	4.90	0.002
Division level	5	0.111	0.022	7.77	0.000
Class. * Div. level	15	0.013	0.001	0.30	0.996
Error	321	0.910	0.003		
Total	344				

## 6.4 DISCUSSION

### 6.4.1 Definition and description of communities through classification of variance in multiple community properties

The results showed the community classification to recover most of the subjective site. This shows that the initial reconnaissance and stratification of vegetation provided an adequate summation of the complexity of community structure present as resolved through the community classification. This result suggests that there may be little need to proceed to a community classification since the majority of information it embodies is contained in the site reconnaissance. However, there is no way this can be assessed prior to actually doing the additional sampling and classification. Also, I consider it desirable to provide some objective measure of the efficacy of a site reconnaissance. Comparison of information contents between the site reconnaissance and community classification provides this to the greatest extent possible.

Results of this study show that not only is community definition/description possible through classification of multi-property attributes but that subsequent ecological interpretations are enhanced by inclusion of attributes of multiple properties. In the current study this was demonstrated through application of canonical correspondence analysis to the combined attribute matrix. This analysis showed three principal groupings of community complexes which were clearly differentiated in terms of all three properties and environment. The results show this major differentiation is related predominantly to different pyric successional stages of the vegetation. Notwithstanding this major difference, results also showed individual complexes to be differentiated within the two major groupings (Fig. 6.2). Again, these differences were ecologically explicable, i.e. in terms of environment. However, the results showed that these finer scale differences, like the major differences, involved variance in attributes of all three properties. It may thus be said that inclusion of attributes of all properties in the analysis allows for superior resolution of fine-scale composite variance in community structure. Application of "community classifications" may hence be of particular utility for application to other locally distributed complex systems

Despite the apparent advantages of adopting more extensive classifications of community structure, I have found no prior studies which have applied multivariate classification to attributes of multiple community properties. This lack of application, and thus acceptance, appears inexplicable. However, I suggest that in the quest for development of generalities in vegetation science that complex aspects of community structure may have received relatively little attention. The current study shows that complex aspects of community structure can be effectively summarised in a way in which the ecological interpretability of detail is enhanced. I thus suggest that ignorance of complex aspects of community structure in the name of parsimony is ecologically untenable. In view of the local distribution of cliff-top coastal heathlands in the Sydney area it would appear appropriate that generalisations regarding this vegetation should be sought from further local intensive studies. New insights into general but complex aspects of the ecology of this vegetation may thus be developed.

#### 6.4.2 The comparative ecological cohesiveness of community and property classifications

The results showed mean environmental homogeneity of community complexes is significantly greater than that of structural and species richness complexes. The hypothesis that community complexes possess greater environmental homogeneity is thus accepted with respect to these properties. The results also showed, however, that mean environmental homogeneity of floristic complexes was statistically inseparable from that of community complexes. The respective means must hence be considered as statistically equivalent. This shows that the floristic classification was of equivalent ecological cohesion compared with the community classification. This may suggest that there is little reason to include additional attributes quantifying structure and species richness. However, it must be kept in mind that both classifications summarise environmental details differently, and it will be the response of interest in community structure that dictates which classification would be appropriate. Notwithstanding this, I suggest that for applications such as environmental calibration the community classification would be preferable.

However, in my study I have sought a classification which is as fully resolved as possible, uses all available information, and allows for expression of independent and common variance components of properties. I have thus considered that a combined approach is more commensurate with these objectives than a consensus approach. A consensus approach has thus not been used in constructing the classification described in this chapter.

### 6.1.2 Research objectives and hypotheses

The first research objective was to classify the studied vegetation on the collective basis of floristic composition, structure and species richness. This was done in order to identify what I term 'community complexes'. It is known from classifications of individual properties that property complexes can be differentiated in terms of attributes of these properties individually. It appeared likely therefore that this would also apply with respect to a comprehensive classification. A hypothesis of vegetation differentiation is hence not assessed with respect to the comprehensive classification.

The second research objective was to quantify the comparative information contents of the community classification and site reconnaissance. This was considered instructive as a complementary comparison to those made in chapter 3. I also considered it instructive from the point of view of appraising sampling methodologies required to attain an effective classification of vegetation patterns, i.e. a comparison between the classification requiring the least effort (site reconnaissance) and that requiring the most effort (the community classification).

The remaining objectives address the main hypothesis developed in chapter 1 that;

*more ecologically robust community classifications are possible by consideration of attributes of multiple properties in the one framework as opposed to classifications based on attributes of single properties.*

The equivalent mean homogeneity of community and floristic complexes may be seen as a consequence of the use of many attributes in the classifications. Such use may enable relatively finer-scale environmental differences to be summarised than otherwise possible, thus leading to greater environmental homogeneity. The approximately equivalent number of attributes included in the community and floristic classifications thus appears a reasonable explanation for the statistical inseparability of their respective complexes. This also appears to be a feasible explanation for the difference between community and floristic complexes on one hand and structural and species richness complexes on the other. However, mean environmental homogeneity of floristic complexes could not be separated statistically from that of either structural or species richness complexes. This was despite the differences in numbers of attributes between the classifications. This shows that the difference in mean environmental homogeneity between community complexes on one hand and structural and species richness complexes on the other is likely to be a function not only of increased numbers of attributes but also of the combination of attributes of different properties in the one classification.

Comparisons of mean environmental homogeneities between classification systems revealed that community classification groupings were not of consistently higher value than those of other classifications. However, the results showed that below the fourth division the community classification provided a more ecologically cohesive classification than either the structural or species richness classification. This may reflect the more general nature of the latter properties and the fact that stochastic variance in these properties is likely to represent a comparatively greater component of the total variance in their respective systems compared with the composite matrix. It may also reflect the influence of extraneous environmental factors or ecological processes which do not have environmental correlates. It is foreseeable that differences in ecological models between individual properties may have also contributed to the inseparability of classifications at the higher division levels. Whatever the cause, however, this study establishes the increased ecological cohesiveness of the community classification over those of structure and species richness at lower classification division levels. The ecological significance of these differences hence lies with comparatively fine-

scale variance in community structure. As suggested above, this likely reflects the greater sensitivity of the community classification in reflecting environmental differences.

## 6.6 CONCLUSIONS

Canonical correspondence analysis of the combined attribute matrix showed community complexes to be separated in terms of multiple environmental factors. Organisation of community complexes was also shown with respect to major axes of environmental variation as identified in the previous chapter. I conclude that the community classification is of ecological significance.

Inclusion of attributes of multiple properties in the classification and canonical correspondence analysis showed that separation of community complexes could be interpreted not only with respect to environment but also with respect to the variance in multi-property attributes. This served to clarify complex vegetation/environment relationships, particularly with respect to pyric succession and internal structuring of platform heaths. This shows that interpretability of 'single-scale' direct gradient analyses can be enhanced by inclusion of multi-property attributes. In view of this, and limits to the interpretability of conventional statistical comparisons in a multi-attribute/complex situation, I conclude that direct multivariate gradient analyses provide useful if not necessary adjuncts to community classifications of vegetation.

Mean environmental homogeneity of community complexes was shown to be significantly greater than that pertaining to either structural or species richness complexes. I conclude that classifications of composite variance in community structure are more ecologically cohesive than those of either structure or species richness.

Notwithstanding the above, mean environmental homogeneity of community complexes remained statistically inseparable from that pertaining to floristic complexes. In light of this, I conclude that the classification of floristic composition is of equivalent ecological cohesiveness as the community classification. However, attention is drawn to the fact that mean environmental homogeneity of floristic complexes was shown to be statistically inseparable from that of the other single properties. In view of this, I conclude that the community classification is to be preferred over that of floristic composition for provision of an ecologically cohesive classification of the community structure of the studied cliff-top coastal heathlands.

Environmental homogeneity of classification groupings at different division levels reflected the pattern of differences between complexes of the different

classifications. However, these differences were only evident at lower division levels. The results again showed the inseparability of the community and floristic classifications. However, the floristic classification groupings were also shown to have significantly greater homogeneity than structural or species richness groupings at these lower levels. I conclude that the equivalently high numbers of attributes of both community and floristic classifications, most of which are shared, make them relatively more sensitive to detection of environmental differences than structural or species richness classifications. Despite this, the results suggest that the increased sensitivity of these classifications was in part due to the greater number of attributes included in these classifications. I thus also conclude that, for the full potential of a community classification to be realised, attributes quantifying variance in different properties should be approximately equivalent in number.



## CHAPTER 7: GENERAL DISCUSSION AND CONCLUSIONS

### 7.1 A SECONDARY SYNTHESIS OF CLIFF-TOP COASTAL HEATHLAND COMMUNITIES: PRE-EMPHASIS ON INDIVIDUAL PROPERTIES CONSIDERED

Cliff-top coastal heathlands in Botany Bay National Park, Sydney, display a remarkable diversity in community structure at the local spatial scale. The classification of floristic composition revealed clear patterns of internal organisation. This pattern was characterised by both quantitative variation, principally in cover of structurally dominant species within groups of related complexes, and by qualitative differences (spatial distributional disjunctions) in cover of both structurally dominant, and sub-ordinate species. I conclude, that at local scales, both sources of variation in floristic composition need to be accounted for, for effective resolution of internal organisation of floristic composition.

Through consideration of the floristic classification and an ancillary quantitative study it was shown that cover of structurally sub-ordinate species is related negatively to cover of structurally dominant species. This was the case for all but the most recently burnt vegetation. I conclude that in cliff-top coastal heathlands structural dominance equates with ecological dominance (*sensu* Anderson 1965b, Greig-Smith 1983). In that the majority of species occur as structural sub-ordinates, this shows that overall diversity in floristic composition is likely a function of factors which effect resource utilisation by structural dominants. The equivalence of structural and ecological dominance in cliff-top coastal heathlands serves to distinguish this vegetation type from other floristically rich vegetation types such as rainforest (see Webb *et al.* 1970) where structural sub-ordinates behave as noise in the system.

Examination of environmental differences between floristic complexes showed the statistical separation of all complexes in terms of at least one, but more commonly, multiple environmental factors. I conclude that internal organisation of floristic composition of cliff-top coastal heathlands is of functional significance. The spatial concordance of major groups of complexes with site physiographic features and vegetation differing in years since the last fire shows that the functional significance of the

classification is likely to equate to ecological significance since factors which were considered *a priori* to be of ecological significance were correlated with these differences.

Previous broad-scale studies have alluded to the presence of spatial auto-correlation in cliff-top coastal heathlands between distance from cliff-tops and the frequency, and intensity of fires (see Adam *et al.* 1989a). My study shows the existence of this autocorrelation in small local areas of cliff-top coastal heathlands. My study, however, also shows that maritime factors, soil physical factors and soil nutrients also comprise part of this auto-correlation. This auto-correlation is thus more extensive than previously recorded. Insofar as this is typical of cliff-top coastal heathlands generally, then correlative environmental studies of this vegetation may need to include areas away from cliff-tops, or alternatively, be more spatially expansive, if field conditions are to be adequately replicated.

Notwithstanding the above, previous studies (see Adam *et al.* 1989a) have cited two major environmental axes underlying organisation of floristic composition of cliff-top coastal heathlands. The first is that of maritime exposure and the second is variation in soil nutrients. My study confirms the first axis at small local scales. Consideration of variance within recently unburnt platform heath complexes showed distinct organisation with respect to distance from cliff-tops and other non-soil based maritime factors. This was mostly comprised of variance in several dominant species. Soil-based maritime factors were also correlated with this differentiation. However, these were also shown to be positively correlated with physical soil factors, in particular field soil moisture and organic content. This shows that physical conditions favourable for plant growth are subjugated by elevated levels of maritime factors. This variance in physical soil factors along with the fact that soil nutrient factors varied relatively less also shows, importantly, that soil physical factors must also be considered as a major environmental axis of importance to floristic composition of cliff-top coastal heathlands at the local scale. Further, this study shows that these factors are of equivalent, if not greater importance to soil nutrient factors at this scale. Acceptance of soil nutrition as a second major environmental axis relevant to floristic differentiation is thus unfounded at local scales.

Because of the pre-emphasis on floristic attributes at local scales previous studies have not considered classifications of other emergent properties. In this thesis independent classifications of both structure and species richness showed clear internal organisation in both these community properties.

In the case of structure, my study showed high levels of spatial diversity in shrub-based structure. This is commensurate with previous studies which have described such diversity within local areas of cliff-top coastal heathlands (e.g. McRae 1990; Benson & Howell 1994). However, this has not been previously quantified to the level achieved in my study. More importantly, however, my study has shown significant differences in both height and cover of dominant strata which do not correspond to the divisions used in the generalised scheme of Specht (1970). I thus conclude that multivariate classification of the structure of vegetation provides a classification of appropriate sensitivity for application at local spatial scales. I also conclude that such a classification is to be preferred over generalised classifications such as that of Specht (1970) at local scales.

Importantly, the results showed that the structural complexes differed significantly in terms of attributes of multiple strata. Attributes of strata other than the shrub stratum were shown to display approximately equivalent variation across complexes as those of the shrub stratum. I thus conclude that non-shrub-based structure has utility for classification of complex multivariate patterns within cliff-top coastal heathlands.

Despite the variance in attributes of multiple strata my study shows the suppressive effects of the shrub stratum on groundcover and graminoid strata. This is consistent with existing theory. However, division of graminoid forms from other groundcovers revealed a differential response in height of graminoids. Namely, where height and cover of the shrub-stratum were maximal the height of graminoids increased, and was observed in many instances to exceed that of the shrub stratum. This response was not noted for the groundcover stratum. I suggest that this height response is functional for the persistence of graminoid populations in cliff-top coastal heathlands and may also be of adaptive significance in allowing for reproduction of graminoids with characteristics which allow for effective integration into shrub-based heathland structure.

Examination of environmental differences between structural complexes revealed similar environmental relationships to floristic composition. However, several

notable differences were revealed. First, differences between complexes were manifest mainly between individual complexes rather than groups of complexes. This can be attributed to the more general nature of structure and points to the need to adequately define multivariate structure in order to effectively resolve environmental relationships of this property.

Secondly, swamp vegetation was shown to be associated with elevated levels of physical soil factors associated with occluded drainage. This distinction was shown to be more clearly recognised in terms of structure rather than floristic composition. In that swamp vegetation is an integral component of cliff-top coastal heathlands I conclude that floristic studies should be complemented by determinations of structure where this vegetation is present.

Thirdly, the results showed that structure is polarised with respect to years since the last fire. While temporal and spatial aspects of this factor were effectively recovered by structure some loss of resolution occurred with respect to the vegetation of intermediate burn date. This occurred principally due to rapid establishment of structural dominance so that the structure of some of this vegetation resembled that of the unburnt platform heaths. I thus conclude, conversely to the above, that determinations of structure of vegetation which differs with respect to previous burn date should be complemented by determinations of floristic composition.

Multivariate classification of species richness showed internal organisation of this property varied within relatively narrow ranges. This is commensurate with what may be expected within localised areas. However, statistically significant differences were demonstrated within the ranges of variation recorded. Also, differences were shown to encompass all strata. Consideration of differences in all strata, and total species richness were shown to be necessary in order to effectively summarise this property. I conclude that multidimensional solutions to analysis of species richness patterns are required for cliff-top coastal heathlands at local scales.

Examination of the environmental relationships of species richness showed the presence of statistically significant differences in mean levels of factors between complexes. As with floristic composition and structure these were shown to encompass all major areas of environmental variation. However, I have shown that environmental relationships of species richness of cliff-top coastal heathlands differ

substantially from those of either floristic composition or structure. Of note was the reduced significance of the previously described environmental auto-correlation. Also, major soil nutrients and soil physical factors were of relatively greater importance for species richness compared with the other areas of environmental variation. Collectively, these characteristics showed an equivalence of all factors for the functional significance of species richness.

Overall, my study shows that ecologically meaningful patterns within each of the studied properties exist in local areas of cliff-top coastal heathlands. Each of these properties was shown to differ with respect to their environmental relationships. This shows that pre-emphasis on individual properties at local scales necessarily involves an incomplete synthesis of community structure. However, this pre-emphasis is simply a matter of convention and ignorance. From an alternative perspective it is more pertinent to ask whether pre-emphasis is justified on the grounds that variance in individual properties is concordant with patterns in the alternate properties. My study has also addressed this. Comparisons showed a significant lack of concordance between the classifications. There are hence major patterns present, irrespective of cause, that are not effectively summarised by classification of individual properties. In view of these characteristics I conclude that pre-emphasis on individual properties in local community studies of cliff-top coastal heathlands is unwarranted.

## **7.2 A TERTIARY SYNTHESIS OF CLIFF-TOP COASTAL HEATHLAND COMMUNITIES: COMMUNITY STRUCTURE AS A FUNCTION OF COMMON AND INDEPENDENT VARIANCE COMPONENTS CONSIDERED**

While greater detail of community structure can be obtained through classifications of separate properties a true synthesis is only attainable if these different properties can be related. To this end a new application of correspondence analysis techniques has been introduced in this thesis for the specific purpose of enumerating and visualising variance in both common and independent components of community properties. As was shown in Chapter 4 this application enables representation of sites and attributes with respect to the relevant variance structures. Other contemporary multivariate approaches to comparing data sets such as mantel tests (see Leduc *et al.* 1992) or procrustes rotation (see Digby & Kempton 1987) in general do not allow for interpretation in terms of this level of detail. Nor do they allow for isolation of separate variance components. I thus suggest that the application developed in this thesis has substantial potential for more general use in cliff-top coastal heathlands and other vegetation types.

Results of this investigation supported the hypothesis that community structure of cliff-top coastal heathlands is a function of both common variance between properties and variance in individual properties which is independent of others properties. Quantification of these components showed that the absolute variance displayed by floristic composition was far greater than that displayed by the other properties and that the majority of this variance was independent of the other properties. In addition to this the majority of variance in both structure and species richness was shown to be common with floristic composition. These characteristics admittedly suggest that pre-emphasis on floristic composition at local scales may be justified. However, it must be remembered that the different properties have different variance structures which may also be of differing functional significance. There is thus an additional requirement that variance components be summarised visually in terms of analysed attributes and that such patterns be made amenable to linkage with environmental data. In this way ecological interpretation of variance components can proceed.

Examination of the nature of variance components, and their relationships with environment, revealed a number of facets of community structure of cliff-top coastal heathlands which have not previously come to light. First, examination of the relatively large component of floristic composition independent of the other properties showed that floristic differentiation of the heathlands to be mainly a function of species turnover within structural constraints rather than being a function of strong gradients in species richness. Notwithstanding this general characteristic examination of the common components between floristic composition and structure revealed that floristic differentiation is nevertheless partially linked with increasing height and cover of shrub-based strata on one hand, and increasing height and cover of the groundcover stratum on the other hand. This was also shown to be associated with establishment of ecological dominance and mediated by primary factors influencing such establishment *viz.* time since the last fire. These relationships accounted for 29% of the variance in floristic composition whereas the independent component accounted for the remaining 71%. I thus conclude that both components contribute significantly to variance in community structure although species turnover is the predominant source of floristic differentiation.

It was of interest to note that the majority of variance in structure was common with the second component of floristic composition mentioned above. Examination of environmental relationships of this component showed the elevated importance of years since the last fire compared with the corresponding common component of floristic composition. This shows that fire is a more proximate influence on structure considered collectively than on floristic composition considered collectively.

In addition it is important to note the differences in environmental relationships of properties and their components.. Where independent components comprised the majority of variance in a property then the environmental relationships of the property considered by itself resembled these relationships. Conversely, where an independent component represented a relatively small amount of the total variance in a property the environmental relationships of that component differed from that of the property considered as a whole. In the absence of variance partitioning this scale dependency necessarily goes unrecognised. I thus conclude that for cliff-top coastal heathlands, the consideration of environmental relationships of entire properties distorts

interpretation of environmental relationships which are uniquely attributable to particular properties.

As was outlined in a previous chapter there was reason to believe that variance in structure independent of floristic composition would primarily be a function of maritime exposure. However, results of my study show that this is not the case. This component was shown to comprise variation in height of a number of graminoid species and common structural responses of species which occur as sub-shrubs. Both maritime and fire factors were shown to be of secondary importance to this variation compared with soil physical and nutrition factors. This highlights the need to consider structure multivariately since this independent variation is a function of 'secondary' structural attributes and would have remained undetected if a more general definition of structure had been used. The independent variation in height of graminoids has been discussed previously. The common structural response of sub-shrubs is of interest as many 'sub-shrubs' also occur as dominant shrubs. It would appear that the succession of sub-shrubs to structural dominance is associated with soil nutrients. In view of the fact that this is one of the few components where soil nutrients assume elevated importance this appears worthwhile pursuing in the future. This association is also supported by the fact that variance in species richness independent of floristic composition was found to be associated with elevated levels of soil nutrients. As outlined in a previous chapter this variance must be comprised by the alternate presence of species as shrubs and sub-shrubs, and it would appear that major soil nutrients are associated with this transition.

Examination of the common variance components between properties revealed these components to be non-symmetric with respect to both their absolute and proportional magnitudes. That is, common components of respective compared properties differed in magnitude and differed in the proportion of total property variance they represented. I thus conclude that variance in particular properties can not be treated as an effective scalar for an equivalent amount of variance in alternate properties. This characteristic serves to highlight the different variance structures, and thus, the differing nature of the community properties.

Examination of the nature of the common variance components revealed discernible relationships between all pairs of properties. In the case of floristic composition and structure floristic complexes were shown to be differentiated



structurally. This was characterised by elevated height and cover of groundcover and graminoid strata on one hand and elevated height and cover of shrub and sub-shrub strata on the other. Years since last fire was shown to be a principal factor correlated with this differentiation. In the case of floristic composition and species richness relationships reflected the floristic differentiation associated with variance in species richness. This was shown to encompass all strata. Again, the negative relationship between shrub-based and non-shrub-based strata was evident. This was also evident with respect to the common variance components between structure and species richness, this being consistent with existing models of inhibition (see Connell & Slatyer 1977). However, species richness of individual strata was associated with increasing height and cover of respective strata, which is consistent with productivity hypotheses of species richness (e.g. Connell & Orias 1964). I thus conclude that consideration of general hypotheses of species richness to cliff-top coastal heathlands at local scales requires specification of the component of species richness being considered. Otherwise, conflicting evidence could be obtained. Also, total species was shown to bear little relationship with structure. This belies the demonstrated structural relationships of the stratal components of species richness. I conclude that for effective enumeration of the species richness component of community structure that multi-dimensional structural solutions need to be sought.

Examination of the environmental relationships of common variance components showed differences between compared components, in the relative importance of individual environmental factor groups. I thus conclude that common variance components between properties are not functionally concordant. This necessarily implies that common variance components, are to varying degrees, ecologically coincidental, and again shows the need for caution in considering common variance in one property as a scalar for common variance in another.

In considering the importance of environmental factors and factor groups to composite variance in community structure it was shown that both factors, and factor groups, were of approximately equivalent importance. Consonant with the notion of parsimony, prior correlative studies have sought to reduce environmental explanations of community structure to correlates of few environmental factors (e.g. Adam et al. 1989b, Keith & Myerscough 1993). In the case of maritime cliff-top vegetation this has also been done but based on a reasonable preconception that the environmental axis of primary

importance comprises maritime factors (see Malloch 1971, 1972, Goldsmith 1973a,b; Adam et al. 1989a,b). Such studies, however, as well as seeking a reductionist explanation of community structure in terms of environmental factors also generally only model single properties of communities, usually floristic composition. In this case reductionism for the sake of parsimony may be warranted. However, this study has shown with respect to cliff-top coastal heathlands that multiple sources of environmental variation can individually explain substantial amounts of variance in individual properties. It has also shown the differential importance of different sources of environmental variation to different community properties and their variance components. This shows a greater order of functional complexity of cliff-top coastal heathland communities than has previously been demonstrated at similar scales. It also shows that this complexity can not be encompassed by enumeration of any single property. Studies which pre-emphasise single properties and which do not seek to partition variance in these properties thus remain incomplete as ecological syntheses of community structure. I have shown that complex local patterns of community structure in cliff-top coastal heathlands are a function of equally complex patterns in environment. Analyses also showed the absence of significant extraneous factors influencing detected patterns. In view of the demonstrated local complexity in community structure and the local control of these patterns I suggest that generalisations regarding the ecological relationships of cliff-top coastal heathlands will be most likely to be borne from further localised, and intensive studies of this vegetation type.

### **7.3 COMBINED MULTI-PROPERTY CLASSIFICATIONS: A NEW APPROACH TO CLASSIFICATION OF CLIFF-TOP COASTAL HEATHLAND COMMUNITIES**

Consideration of cliff-top coastal heathland communities in terms of floristic composition, structure and species richness led to the hypothesis, examined in this thesis, that more ecologically cohesive classifications than those of individual properties were attainable by inclusion of attributes of all properties in a comprehensive 'community' classification. Results showed this to be the case with respect to structure and species richness as judged by the comparative mean environmental homogeneity of respective complexes and classification division level quadrat groupings. Classification of floristic composition, however, provided a classification of equivalent ecological cohesiveness to the community classification. This equivalence was interpreted primarily as being a function of the large number of shared attributes between the classifications. However, the statistical inseparability of the floristic classification from those of structure and species richness indicated that the equivalence was also a function of the type of attribute combination.

Notwithstanding this, comparison of the classification systems with respect to division level revealed characteristics which suggest a more ecologically cohesive performance of the community classification at lower division levels, and hence with respect to fine-scale detail in community structure. I thus envisage that further developments as regards numbers and types of included attributes will in the future enable further improved community classifications to be developed which are ecologically robust and more so than classifications of single community properties. I also envisage that such classifications will, as shown in this study, have advantages for interpretability of patterns in complex systems at local scales where differential environmental responses of multiple properties is evident.

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**APPENDICES**

## Appendix 3.1: Quadrat cross-references

Quadrat numbers are provided for quadrats placed in each reconnaissance zone.

Quadrats are numbered by quadrat number and analysis number. Quadrat numbers are in the form x/y.z where, x = reconnaissance zone, y = distance stratum with respect to distance from cliff-tops (e.g. 1 = 0 m to 10 m from cliff-tops) and z = the quadrat number within strata. Within strata, quadrats are numbered from the northern most sampling grid border. Analysis numbers are integers from 1 to 254 and parallel the order of quadrat numbers.

### Reconnaissance zone 1

Quadrat number	Analysis number	Quadrat number	Analysis number
1/7.1	1	1/9.1	11
1/7.2	2	1/9.2	12
1/7.3	3	1/9.3	13
1/7.4	4	1/9.4	14
1/7.5	5	1/9.5	15
1/8.1	6	1/10.1	16
1/8.2	7	1/10.2	17
1/8.3	8	1/10.3	18
1/8.4	9	1/10.4	19
1/8.5	10	1/10.5	20

### Reconnaissance zone 2

Quadrat number	Analysis number	Quadrat number	Analysis number
2/3.1	21	2/5.1	31
2/3.2	22	2/5.2	32
2/3.3	23	2/5.3	33
2/3.4	24	2/5.4	34
2/3.5	25	2/5.5	35
2/4.1	26	2/6.1	36
2/4.2	27	2/6.2	37
2/4.3	28	2/6.3	38
2/4.4	29	2/6.4	39
2/4.5	30	2/6.5	40

### Reconnaissance zone 3

Quadrat number	Analysis number	Quadrat number	Analysis number
3/1.1	41	3/2.1	46
3/1.2	42	3/2.2	47
3/1.3	43	3/2.3	48
3/1.4	44	3/2.4	49
3/1.5	45	3/2.5	50

### Reconnaissance zone 4

Quadrat number	Analysis number	Quadrat number	Analysis number
4/1.1	51	4/2.1	56
4/1.2	52	4/2.2	57
4/1.3	53	4/2.3	58
4/1.4	54	4/2.4	59
4/1.5	55	4/2.5	60

### Reconnaissance zone 5

Quadrat number	Analysis number	Quadrat number	Analysis number
5/4.1	61	5/10.1	73
5/4.2	62	5/10.2	74
5/5.1	63	5/11.1	75
5/5.2	64	5/11.2	76
5/6.1	65	5/12.1	77
5/6.2	66	5/12.2	78
5/7.1	67	5/13.1	79
5/7.2	68	5/13.2	80
5/8.1	69	5/14.1	81
5/8.2	70	5/14.2	82
5/9.1	71	5/15.1	83
5/9.2	72	5/15.2	84



**Reconnaissance zone 6**

Quadrat number	Analysis number	Quadrat number	Analysis number
6/14.1	85	6/15.1	90
6/14.2	86	6/15.2	91
6/14.3	87	6/15.3	92
6/14.4	88	6/15.4	93
6/14.5	89	6/15.5	94

**Reconnaissance zone 7**

Quadrat number	Analysis number	Quadrat number	Analysis number
7/11.1	95	7/13.3	105
7/11.2	96	7/13.4	106
7/11.3	97	7/14.1	107
7/11.4	98	7/14.2	108
7/12.1	99	7/14.3	109
7/12.2	100	7/14.4	110
7/12.3	101	7/15.1	111
7/12.4	102	7/15.2	112
7/13.1	103	7/15.3	113
7/13.2	104	7/15.4	114

**Reconnaissance zone 8**

Quadrat number	Analysis number	Quadrat number	Analysis number
8/6.1	115	8/8.1	125
8/6.2	116	8/8.2	126
8/6.3	117	8/8.3	127
8/6.4	118	8/8.4	128
8/6.5	119	8/8.5	129
8/7.1	120	8/9.1	130
8/7.2	121	8/9.2	131
8/7.3	122	8/9.3	132
8/7.4	123	8/9.4	133
8/7.5	124	8/9.5	134

**Reconnaissance zone 9**

Quadrat number	Analysis number	Quadrat number	Analysis number
9/10.1	135	9/11.3	140
9/10.2	136	9/12.1	141
9/10.3	137	9/12.2	142
9/11.1	138	9/12.3	143
9/11.2	139		

**Reconnaissance zone 10**

Quadrat number	Analysis number
10/7.1	144
10/7.2	145
10/7.3	146
10/7.4	147
10/7.5	148

**Reconnaissance zone 11**

Quadrat number	Analysis number	Quadrat number	Analysis number
11/9.1	149	11/10.1	154
11/9.2	150	11/10.2	155
11/9.3	151	11/10.3	156
11/9.4	152	11/10.4	157
11/9.5	153	11/10.5	158

**Reconnaissance zone 12**

Quadrat number	Analysis number
12/8.1	159
12/8.2	160
12/8.3	161
12/8.4	162
12/8.5	163

**Reconnaissance zone 13**

Quadrat number	Analysis number	Quadrat number	Analysis number
13/1.1	164	13/4.1	179
13/1.2	165	13/4.2	180
13/1.3	166	13/4.3	181
13/1.4	167	13/4.4	182
13/1.5	168	13/4.5	183
13/2.1	169	13/5.1	184
13/2.2	170	13/5.2	185
13/2.3	171	13/5.3	186
13/2.4	172	13/5.4	187
13/2.5	173	13/5.5	188
13/3.1	174	13/6.1	189
13/3.2	175	13/6.2	190
13/3.3	176	13/6.3	191
13/3.4	177	13/6.4	192
13/3.5	178	13/6.5	193

**Reconnaissance zone 14**

Quadrat number	Analysis number	Quadrat number	Analysis number
14/12.1	194	14/14.1	204
14/12.2	195	14/14.2	205
14/12.3	196	14/14.3	206
14/12.4	197	14/14.4	207
14/12.5	198	14/14.5	208
14/13.1	199	14/15.1	209
14/13.2	200	14/15.2	210
14/13.3	201	14/15.3	211
14/13.4	202	14/15.4	212
14/13.5	203	14/15.5	213

**Reconnaissance zone 15**

Quadrat number	Analysis number	Quadrat number	Analysis number
15/4.1	214	15/7.1	229
15/4.2	215	15/7.2	230
15/4.3	216	15/7.3	231
15/4.4	217	15/7.4	232
15/4.5	218	15/7.5	233
15/5.1	219	15/8.1	234
15/5.2	220	15/8.2	235
15/5.3	221	15/8.3	236
15/5.4	222	15/8.4	237
15/5.5	223	15/8.5	238
15/6.1	224	15/9.1	239
15/6.2	225	15/9.2	240
15/6.3	226	15/9.3	241
15/6.4	227	15/9.4	242
15/6.5	228	15/10.1	243
		15/10.2	244
		15/10.3	245
		15/10.4	246

**Reconnaissance zone 16**

Quadrat number	Analysis number
16/6.1	247
16/7.1	248
16/8.1	249
16/9.1	250
16/10.1	251

**Reconnaissance zone 17**

Quadrat number	Analysis number
17/5.1	252
17/5.2	253
17/5.3	254

## Appendix 3.2: Research site floristic list

Species are arranged alphabetically by family then genus then species.

Species abbreviations and analysis numbers used in text are provided.

Nomenclature follows Harden (1990, 1991, 1992, 1993).

Seedlings are included as species and are indicated by a (S) following both species name and corresponding abbreviation.

Unidentifiable species are included as unknowns.

Species identifiable to genus level only are indicated by three digit number following genus abbreviation.

Additional species appear in the list without abbreviations or analysis numbers. These species were observed to be present within one or several of the sampling grids used in this study but were not intercepted by quadrat placement and are hence not included in the study.

A taxonomic summary is provided which is inclusive of additional species. This is adjusted for seedling duplication. Unidentified bryophytes and fungi are not included in this summary.

<u>SPECIES</u>	<u>ABBREVIATION</u>	<u>NUMBER</u>
<b>AIZOACEAE</b>		
<i>Carpobrotus glaucescens</i>	car.gla	1
<b>APIACEAE</b>		
<i>Actinotus helianthi</i>	act.hel	2
<i>Centella asiatica</i>	cen.asi	3
<i>Hydrocotyle bonariensis</i>	hyd.bon	4
<i>Platysace lanceolata</i>	pla.lan	5
<i>Platysace lanceolata</i> (S)	pla.lan(S)	6
<i>Xanthosia pilosa</i>	xan.pil	7
<i>Xanthosia tridentata</i>	xan.tri	8
<b>ASTERACEAE</b>		
<i>Aster subulatus</i>	ast.sub	9
<i>Chrysanthemoides monilifera</i> ssp. <i>rotundata</i>	chr.mon	10
<i>Chrysanthemoides monilifera</i> ssp. <i>rotundata</i> (S)	chr.mon(S)	11
<i>Epaltes australis</i>	epa.aus	12
<i>Ozothamnus diosmifolius</i>	ozo.dio	13
<i>Senecio lautus</i> (complex)	sen.lac	14
<i>Senecio lautus</i> ssp. <i>maritimus</i>	sen.lau	15
<i>Senecio madagascarensis</i>	sen.mad	16
<i>Taraxacum officinale</i>	tar.off	17
<b>CASSYTHACEAE</b>		
<i>Cassytha paniculata</i>	cas.pan	18
<i>Cassytha pubescens</i>	cas.pub	19
<b>CASUARINACEAE</b>		
<i>Allocasuarina distyla</i>	all.dis	20
<i>Allocasuarina distyla</i> (S)	all.dis(S)	21
<i>Allocasuarina</i> spp.	all.001	22
<b>CENTROLEPIDACEAE</b>		
<i>Centrolepis strigosa</i> ssp. <i>strigosa</i>	cen.str	23
<b>CHENOPODIACEAE</b>		
<i>Rhagodia candolleana</i> ssp. <i>candolleana</i>		

**CYPERACEAE**

<i>Baumea acuta</i>	bau.acu	24
<i>Baumea juncea</i>	bau.jun	25
<i>Baumea rubiginosa</i>	bau.rub	26
<i>Hypolaena fastigiata</i>	hyp.fas	27
<i>Isolepis cernua</i>	iso.cer	28
<i>Isolepis nodosa</i>	iso.nod	29
<i>Lepidosperma quadrangulatum</i>	lep.qua	30
<i>Lepidosperma squamatum</i>	lep.squ	31
<i>Schoenus apogon</i>	sch.apo	32
<i>Schoenus brevifolius</i>	sch.bre	33

**DENNSTAEDITACEAE**

<i>Pteridium esculentum</i>	pte.esc	34
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**DILLENIACEAE**

<i>Hibbertia fasciculata</i>	hib.fas	35
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**DROSERACEAE**

<i>Drosera spathulata</i>	dro.spa	36
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**EPACRIDACEAE**

<i>Astroloma pinifolium</i>	ast.pin	37
<i>Epacris longiflora</i> (S)	epa.lon(S)	38
<i>Epacris microphylla</i>	epa.mic	39
<i>Epacris microphylla</i> (S)	epa.mic(S)	40
<i>Epacris obtusifolia</i>	epa.obt	41
<i>Epacris obtusifolia</i> (S)	epa.obt(S)	42
<i>Leucopogon esquamatus</i> (S)	leu.esc	43
<i>Monotoca elliptica</i>	mon.ell	44
<i>Monotoca scoparia</i>	mon.sco	45
<i>Sprengelia incarnata</i>	spr.inc	46
<i>Styphelia triflora</i>		
<i>Woolisia pungens</i>	wol.pun	47

**EUPHORBIACEAE**

<i>Amperea xiphoclada</i>	amp.xip	48
<i>Ricinocarpos pinifolius</i>	ric.pin	49
<i>Poranthera corymbosa</i>	por.cor	50
<i>Poranthera microphylla</i>		

**FABACEAE**

<i>Aotus ericoides</i>	aot.eri	51
<i>Bossiaea ensata</i>	bos.ens	52
<i>Bossiaea ensata</i> (S)	bos.ens(S)	53
<i>Dillwynia floribunda</i>	dil.flo	54
<i>Dillwynia floribunda</i> (S)	dil.flo(S)	55
<i>Dillwynia retorta</i>	dil.ret	56
<i>Dillwynia retorta</i> (S)	dil.ret(S)	57
<i>Gompholobium grandiflorum</i>		
<i>Mirbelia rubiifolia</i>	mir.rub	58
<i>Oxylobium cordifolium</i>		
<i>Pultenaea dentata</i>	pul.den	59
<i>Pultenaea linophylla</i>		
<i>Viminaria juncea</i>		

**GENTIANACEAE**

<i>Centaurium tenuiflorum</i>	cen.ten	60
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<b>GERANIACEAE</b>		
<i>Pelargonium capitatum</i>	pel.cap	61
<b>GLEICHENIACEAE</b>		
<i>Gleichenia microphylla</i>	gle.mic	62
<b>GOODENIACEAE</b>		
<i>Dampiera stricta</i>	dam.str	63
<i>Goodenia dimorpha</i>	goo.dim	64
var. <i>angustifolia</i>		
<i>Goodenia paniculata</i>	goo.pan	65
<i>Scaevola ramosissima</i>	sca.ram	66
<b>HALORAGACEAE</b>		
<i>Gonocarpus micranthes</i>	gon.mic	67
<i>Gonocarpus tetragynus</i>	gon.tet	68
<i>Gonocarpus teuroides</i>	gon.teu	69
<i>Gonocarpus teuroides</i> (S)	gon.teu(S)	70
<i>Myriophyllum gracile</i>	myr.gra	71
<i>Myriophyllum criopatum</i>	myr.cri	72
<b>JUNCACEAE</b>		
<i>Juncus kraussii</i>	jun.kra	73
<i>Juncus microcephalus</i>		
<b>LAMIACEAE</b>		
<i>Westringia fruticosa</i>	wes.fru	74
<i>Westringia fruticosa</i> (S)	wes.fru(S)	75
<b>LILIACEAE</b>		
<i>Thelionema umbellata</i>	the.umb	76
<i>Thysanotus juncifolius</i>	thy.jun	77
<i>Dianella revoluta</i> var. <i>revoluta</i>	dia.rev	78
<b>LINDSAEACEAE</b>		
<i>Lindsaea linearis</i>	lin.lin	79
<b>LOBELIACEAE</b>		
<i>Lobelia alata</i>	lob.ala	80
<b>LOGANIACEAE</b>		
<i>Mitrasacme paludosa</i>	mit.pal	81
<b>MENYANTHACEAE</b>		
<i>Villarsia exaltata</i>	vil.exa	82
<b>MIMOSACEAE</b>		
<i>Acacia sophorae</i>	aca.sop	83
<i>Acacia sophorae</i> (S)	aca.sop(S)	84
<i>Acacia myrtifolia</i>	aca.myr	85
<i>Acacia myrtifolia</i> (S)	aca.myr(S)	86
<i>Acacia suaveolens</i>	aca.sua	87
<i>Acacia suaveolens</i> (S)	aca.sua(S)	88

<b>MYRTACEAE</b>		
<i>Baeckea imbricata</i>	bae.imb	89
<i>Baeckea imbricata</i> (S)	bae.imb(S)	90
<i>Callistemon citrinus</i>	cal.cit	91
<i>Callistemon linearis</i>	cal.lin	92
<i>Kunzea ambigua</i>		
<i>Leptospermum laevigatum</i>		
<i>Leptospermum squarrosum</i>	lep.squ	93
<i>Melaleuca armillaris</i>	mel.arm	94
<i>Melaleuca armillaris</i> (S)	mel.arm(S)	95
<i>Melaleuca nodosa</i>	mel.nod	96
<i>Melaleuca nodosa</i> (S)	mel.nod(S)	97
<i>Micromyrtus ciliata</i>		
<b>OXALIDACEAE</b>		
<i>Oxalis corniculatum</i>	oxa.cor	98
<b>PHILYDRACEAE</b>		
<i>Phylidrum lanuginosum</i>	phy.lan	99
<b>PLANTAGINACEAE</b>		
<i>Plantago coronopus</i> ssp. <i>coronopus</i>	pla.cor	100
<b>POACEAE</b>		
<i>Cynodon dactylon</i>	cyn.dac	101
<i>Deyeuxia quadriseta</i>	dey.qua	102
<i>Entolasia stricta</i>	ent.str	103
<i>Imperata cylindrica</i> var. <i>major</i>	imp.cyl	104
<i>Paspalidium distans</i>	pas.dis	105
<i>Phragmites australis</i>		
<i>Stenotaphrum secundatum</i>	ste.sec	106
<i>Stipa mollis</i>	sti.mol	107
<i>Themeda australis</i>	the.aus	108
<i>Zoysia macrantha</i>	zoy.mac	109
<b>PRIMULACEAE</b>		
<i>Samolus repens</i>	sam.rep	110
<b>PROTEACEAE</b>		
<i>Banksia ericifolia</i>	ban.eri	111
<i>Banksia ericifolia</i> (S)	ban.eri(S)	112
<i>Banksia integrifolia</i>	ban.int	113
<i>Banksia serrata</i>	ban.ser	114
<i>Banksia serrata</i> (S)	ban.ser(S)	115
<i>Conospermum ellipticum</i>	con.ell	116
<i>Conospermum ellipticum</i> (S)	con.ell(S)	117
<i>Darwinia fascicularis</i> ssp. <i>fascicularis</i>	dar.fas	118
<i>Darwinia fascicularis</i> ssp. <i>fascicularis</i> (S)	dar.fas(S)	119
<i>Grevillea mucronulata</i>	gre.muc	120
<i>Hakea dactyloides</i>		
<i>Hakea teretifolia</i>	hak.ter	121
<i>Hakea teretifolia</i> (S)	hak.ter(S)	122
<i>Isopogon anethifolius</i> (S)	iso.ane(S)	123
<i>Persoonia lanceolata</i>	per.lan	124
<i>Persoonia lanceolata</i> (S)	per.lan(S)	125
<i>Persoonia levis</i>		
<i>Xylomelum pyriforme</i>		

<b>RESTONIACEAE</b>		
<i>Empodisma minus</i>	emp.min	126
<i>Leptocarpus tenax</i>	lep.ten	127
<i>Lepyrodia muelleri</i>	lep.mue	128
<i>Restio complanatus</i>	res.com	129
<i>Restio fastigatus</i>	res.fas	130
<b>RHAMNACEAE</b>		
<i>Cryptandra ericoides</i> (S)	cry.eri(S)	131
<b>RUBIACEAE</b>		
<i>Opercularia aspera</i>	ope.asp	132
<i>Opercularia varia</i>	ope.var	133
<b>RUTACEAE</b>		
<i>Boronia parviflora</i>	bor.par	134
<i>Correa alba</i>	cor.alb	135
<i>Correa alba</i> (S)	cor.alb(S)	136
<i>Eriostemon buxifolius</i> ssp. <i>buxifolius</i>	eri.bux	137
<i>Eriostemon buxifolius</i> ssp. <i>buxifolius</i> (S)	eri.bux(S)	138
<i>Eriostemon buxifolius</i> ssp. <i>obovatus</i> (S)	eri.obo(S)	139
<i>Philotheca salsolifolia</i>	phi.sal	140
<i>Ziera laevigata</i>	zie.lae	141
<i>Ziera laevigata</i> (S)	zie.lae(S)	142
<b>SELAGINELLACEAE</b>		
<i>Selaginella uliginosa</i>	sel.uli	143
<b>SOLANACEAE</b>		
<i>Solanum nigrum</i>	sol.nig	144
<b>STERCULIACEAE</b>		
<i>Rulingia hermanniifolia</i>	rul.her	145
<i>Lasiopetalum ferrugineum</i> var. <i>ferrugineum</i>		
<b>THYMELAEACEAE</b>		
<i>Pimelia linifolia</i>	pim.lin	146
<i>Pimelia linifolia</i> (S)	pim.lin(S)	147
<b>VERBENACEAE</b>		
<i>Lantana camara</i>		
<b>XANTHORRHOEACEAE</b>		
<i>Lomandra longifolia</i>	lom.lon	148
<i>Lomandra glauca</i> ssp. <i>glauca</i>	lom.gla	149
<i>Xanthorrhoea resinosa</i>	xan.res	150
<b>UNKNOWN</b>		
Bryophyte (type 1)	bry.001	151
Bryophyte (type 2)	bry.002	152
Bryophyte (type 3)	bry.003	153
Bryophyte ( <i>Sphagnum</i> sp.)	bry.004	154
Fungi (type 1)	fun.001	155

**SUMMARY**

<b><u>taxon</u></b>	<b><u>number recorded</u></b>
Families:	45
Genera:	105
Species:	139

**ADDITIONAL SPECIES**

*Crytomium falcatum*



### Appendix 3.3: Mean foliage projective coverages of species in floristic complexes

Data is provided for communities as recognised by two-way indicator species analysis (see text); A- *Aotus ericoides/Banksia serrata* complex, B- *Gonocarpus teucrioides/Lepidosperma squamatum* complex, C- *Rulingia hermanniifolia* complex, D- *Westringia fruticosa/Melaleuca armillaris* complex, E- *Baeckea imbricata/Melaleuca armillaris* complex, F- *Baeckea imbricata/Banksia ericifolia/Melaleuca armillaris* complex, G- *Baeckea imbricata* complex, H- *Banksia ericifolia/Baeckea imbricata/Melaleuca armillaris/Hakea teretifolia* complex, I- *Schoenus brevifolius/Baeckea imbricata*(seedling) complex, J- *Baumea juncea/Leptocarpus tenax* complex, K- *Samolus repens/Zoysia macrantha* complex.

Values have been rounded to nearest integer. Values below 1 have been set to 1.

Species order in both tables is identical and follows order suggested by two-way indicator species analysis on cover data (see text).

Species cross-reference number is provided (CR).

	CR	A	B	C	D	E	F	G	H	I	J	K
<i>Carpobrotus glaucescens</i>	1	0	1	0	1	0	0	0	0	0	0	1
<i>Actinotus helianthi</i>	2	6	3	1	1	0	0	0	1	1	0	0
<i>Xanthosia pilosa</i>	7	2	3	1	1	0	0	0	1	0	0	0
<i>Pteridium esculentum</i>	34	1	0	0	0	0	0	0	0	0	0	0
<i>Astroloma pinifolium</i>	37	1	0	0	0	0	0	0	0	0	0	0
<i>Woolisia pungens</i>	47	1	1	0	0	0	0	0	0	0	0	0
<i>Amperea xiphoclada</i>	48	1	1	1	0	0	0	0	0	0	0	0
<i>Ricinocarpus pinifolius</i>	49	1	0	0	0	0	0	0	0	0	0	0
<i>Aotus ericoides</i>	51	16	0	0	1	0	0	0	0	0	0	0
<i>Bossiaea ensata</i>	52	3	1	0	1	0	0	0	1	0	0	0
<i>Bossiaea ensata</i> (S)	53	1	1	0	0	0	0	0	0	0	0	0
<i>Scaevola ramosissima</i>	66	1	0	0	0	0	0	0	0	0	0	0
<i>Gonocarpus tetragynus</i>	68	1	1	1	0	0	0	0	1	0	0	0
<i>Gonocarpus teucrioides</i>	69	7	6	1	2	0	0	0	1	0	0	0
<i>Gonocarpus teucrioides</i> (S)	70	1	1	0	0	0	0	0	0	0	0	0
<i>Acacia myrtifolia</i>	85	1	0	0	0	0	0	0	0	1	0	0
<i>Deyeuxia quadriseta</i>	102	1	0	0	1	0	0	1	0	0	0	0
<i>Entolasia stricta</i>	103	4	1	1	0	0	0	0	1	1	0	0
<i>Stipa mollis</i>	107	1	1	0	0	0	0	0	0	0	0	0
<i>Banksia serrata</i>	114	14	1	0	1	0	0	0	1	0	0	0
<i>Banksia serrata</i> (S)	115	1	0	0	0	0	0	0	0	0	0	0
<i>Conospermum ellipticum</i> (S)	117	1	0	0	0	0	0	0	0	0	0	0
<i>Philotheca salsolifolia</i>	140	1	0	0	0	0	0	0	0	0	0	0
<i>Ziera laevigata</i>	141	1	1	1	0	0	0	0	1	0	0	0
<i>Ziera laevigata</i> (S)	142	1	0	0	0	0	0	0	0	0	0	0
<i>Solanum nigrum</i>	144	1	0	0	0	0	0	0	0	0	0	0
<i>Pimelia linifolia</i>	146	5	1	0	1	0	0	0	0	0	0	0
<i>Pimelia linifolia</i> (S)	147	1	0	0	0	0	0	0	1	0	0	0
<i>Platysace lanceolata</i>	5	1	5	1	1	0	3	0	1	0	1	0
<i>Hypolaena fastigiata</i>	27	1	4	1	0	0	0	0	1	0	0	0
<i>Hibbertia fasciculata</i>	35	1	1	1	0	0	0	0	0	0	0	0
<i>Acacia suaveolens</i>	87	1	2	0	1	0	0	0	0	0	0	0
<i>Eriostemon buxifolius</i> ssp. <i>buxifolius</i>	137	1	2	1	1	0	0	0	1	0	0	0
<i>Eriostemon buxifolius</i> ssp. <i>buxifolius</i> (S)	138	0	1	1	1	0	0	0	1	0	0	0
<i>Lomandra glauca</i> ssp. <i>glauca</i>	149	0	3	0	0	0	0	0	0	0	0	0
<i>Cassytha pubescens</i>	19	0	1	0	1	0	0	0	1	0	0	0
<i>Lepidosperma squamatum</i>	31	11	12	3	1	0	0	0	2	0	0	0
<i>Monotoca scoparia</i>	45	1	1	0	1	0	0	0	1	0	0	0
<i>Lomandra longifolia</i>	148	4	2	0	1	1	1	1	1	0	0	0
<i>Pelargonium capitatum</i>	61	1	0	0	1	0	0	0	0	0	0	0
<i>Correa alba</i>	135	5	1	0	4	0	0	0	0	0	0	0
<i>Correa alba</i> (S)	136	1	1	0	1	0	0	0	0	0	0	0
<i>Poranthera corymbosa</i>	50	1	1	1	0	0	0	0	0	0	0	0
<i>Dampiera stricta</i>	63	1	2	3	1	0	0	0	1	0	0	0
<i>Dianella revoluta</i> var. <i>revoluta</i>	78	1	1	2	0	0	0	0	1	0	0	0
<i>Opercularia aspera</i>	32	1	1	5	0	0	0	0	1	0	0	0
<i>Platysace lanceolata</i> (S)	6	1	1	1	0	0	0	0	0	0	0	0
<i>Xanthosia tridentata</i>	8	0	0	1	1	0	0	0	0	0	0	0



	CR	A	B	C	D	E	F	G	H	I	J	K
<i>Acacia sophorae</i>	83	1	1	1	2	1	1	0	1	0	0	0
<i>Acacia suaveolens</i> (S)	88	1	0	0	1	0	0	0	0	0	0	0
<i>Cynodon dactylon</i>	101	1	0	0	1	1	0	0	0	0	0	0
<i>Stenotaphrum secundatum</i>	106	1	1	1	10	1	1	1	1	1	1	0
<i>Themeda australis</i>	108	1	0	0	1	3	9	1	0	0	0	0
<i>Conospermum ellipticum</i>	116	1	1	0	1	0	0	0	1	0	0	0
<i>Chrysanthemoides monilifera</i> ssp. <i>rotundata</i>	10	1	0	0	1	1	3	0	1	0	0	0
<i>Chrysanthemoides monilifera</i> ssp. <i>rotundata</i> (S)	11	0	1	0	1	1	1	0	1	1	0	0
<i>Senecio laetus</i> (complex)	14	0	0	0	1	0	0	0	0	0	0	0
<i>Senecio laetus</i> ssp. <i>maritimus</i>	15	0	0	0	0	1	0	1	0	0	0	0
<i>Senecio madagascariensis</i>	16	0	0	0	0	1	0	0	0	0	0	0
<i>Taraxacum officinale</i>	17	0	0	0	1	1	1	1	0	0	0	0
<i>Cassytha paniculata</i>	18	0	0	0	0	0	1	0	0	0	0	0
<i>Allocauarina</i> spp	22	0	0	0	2	1	7	1	1	1	1	0
<i>Schoenus apogon</i>	32	0	0	0	0	1	0	3	0	1	1	0
<i>Pultenea dentata</i>	59	0	0	0	1	0	0	1	0	0	0	0
<i>Centaurium tenuiflorum</i>	60	0	0	0	0	1	0	0	0	0	0	0
<i>Juncus kraussii</i>	73	0	0	0	0	1	0	1	0	1	0	0
<i>Westringia fruticosa</i>	74	1	1	0	18	13	10	4	3	1	0	0
<i>Lobelia alata</i>	80	0	0	0	1	0	0	1	0	0	0	0
<i>Baeckea imbricata</i>	89	0	0	0	2	53	18	66	23	3	1	0
<i>Melaleuca armillaris</i>	94	3	6	1	11	17	11	8	13	1	0	0
<i>Oxalis corniculata</i>	98	0	0	0	1	0	0	1	0	0	0	0
<i>Imperata cylindrica</i> var. <i>major</i>	104	1	0	0	2	1	2	1	1	0	1	0
<i>Banksia integrifolia</i>	113	0	0	0	3	0	1	0	0	0	0	0
Bryophyte (type1)	151	0	1	0	1	1	2	2	1	0	2	0
Bryophyte (type2)	152	0	0	1	0	1	2	2	1	1	0	0
Fungi (type1)	155	0	0	0	1	0	0	0	0	0	0	0
<i>Hydrocotyle bonariensis</i>	4	0	0	0	2	1	1	1	0	1	2	1
<i>Isolepis cernua</i>	28	0	0	0	0	0	0	1	0	1	1	1
<i>Baeckea imbricata</i> (S)	90	0	0	1	2	1	1	1	1	26	1	1
<i>Epaltes australis</i>	12	0	0	0	0	1	0	1	1	1	1	1
<i>Isolepis nodosa</i>	29	0	0	1	2	1	0	1	1	0	0	4
<i>Zoysia macrantha</i>	109	0	0	0	1	1	0	0	0	0	0	10
<i>Plantago coronopus</i> ssp. <i>coronopus</i>	100	0	0	0	0	0	0	0	0	0	0	2
<i>Samolus repens</i>	110	0	0	0	0	1	0	0	0	0	0	16

### Appendix 3.4 Relationship between total cover of sub-ordinate species and total cover of dominant species within floristic complexes

Dominant species within each complex are defined as those highest ranking species in terms of cover which account for 40% (or as close to but above 40%) of total cover. Total cover of a complex is defined as the sum of mean covers for all species within a complex. Relationships between total cover of sub-ordinate species and total cover of dominant species are described by least squares regression. Total covers for sub-ordinate species and for dominant species have been calculated for each quadrat. Values for quadrats were then used in a regression for each complex, total quadrat cover of sub-ordinate species being regressed on total quadrat cover of dominant species. Dominant species, fitted models and statistical parameters of models are provided. Dominant species are identified by analysis number (Appendix 3.1). Floristic complexes are identified by code.

Complex	Dominant species	Fitted model <sup>1</sup>	R <sup>2</sup> (%)	p - value
FC 1	2, 31, 51, 69, 114, 146	TSC = 63.8 - 0.372*TDC	12.5	0.044
FC 2	2, 5, 7, 20, 27, 31, 69, 94, 149	TSC = 30.6 - 0.104*TDC	0.7	0.724
FC 3	20, 25, 31, 54, 63, 78, 111, 126, 132, 133, 145	TSC = 25.2 - 0.079*TDC	1.6	0.527
FC 4	25, 74, 94, 106, 135	TSC = 68.2 - 0.475*TDC	43.2	0.001
FC 5	89	TSC = 91.2 - 0.771*TDC	78.1	0.000
FC 6	89, 94, 111	TSC = 113 - 1.220*TDC	66.2	0.008
FC 7	89	TSC = 71.3 - 0.477*TDC	38.0	0.006
FC 8	89, 94, 111, 121	TSC = 75.8 - 0.511*TDC	53.0	0.000
FC 9	25, 33, 90	TSC = 116.0 - 0.914*TDC	39.4	0.016
FC 10	25, 33, 127	TSC = 66.7 - 0.440*TDC	31.5	0.046
FC 11	109, 110	TSC = 24.8 - 0.333*TDC	28.0	0.116

<sup>1</sup> TSC = total sub-ordinate cover, TDC = total dominant cover

## **Appendix 5.1: Determination of salt-spray deposition in cliff-top coastal heathlands in Botany Bay National Park, Sydney**

### **Objective**

To develop predictive models for above and below canopy salt-spray deposition based on distance from cliff-tops.

### **Detailed methods**

#### ***Field survey design***

The field survey design consisted of sample points for estimation of salt-spray inputs both above and beneath the shrub stratum canopy. Sample points were located for seven distances from the cliff-top, 0 m, 1 m, 10 m, 20 m, 40 m, 80 m and 150 m. Sample points were also located for six canopy cover classes defined on the basis of foliage projective cover of the shrub stratum (see Chapter 3). Classes were: 0% FPC (above canopy salt-spray deposition), 1-20% FPC, 21-40% FPC, 41-60% FPC, 61-80% FPC and 81-100% FPC. Three replicate sample points were located for each distance/canopy cover class combination, i.e. 7 distances \* 6 canopy cover classes \* 3 replicates = 126 sample points.

In locating sample points the entire research site was first divided into four segments, segment divisions running approximately east-west. For the purpose of this study the research site was extended to the southern border of the National Park. Segment divisions corresponded to the north and south research site boundaries, and to each of the three gaps present (Tabbagai, Blue Hole, un-named). A two-way table was then formed consisting of distances by canopy cover class. Numbers between one and four from a random number list were then ascribed to each cell of the table. This determined in which segment a particular distance/canopy cover class deposition estimate was to be made.

For each distance/canopy cover class estimate (not including 0 m or 1 m estimates) to be made, a distance from the northern most point of the relevant segment, running south, was selected from a random number list. This distance mark was located by tape measure. A point was then located by measuring the relevant distance from the cliff-top from the distance mark above. From this point, a transect running parallel to the cliff-line was defined, running the full length of the relevant segment. Consultation of a random number list determined whether this transect would be surveyed in a northerly or southerly direction from the point above. The transect was then moved along until a 4 m by 10 m quadrat, centred on the transect, could be defined as being structurally homogeneous and as having a shrub layer cover falling in the relevant cover division. Cover was estimated visually. Further conditions were imposed, these being that shrub layer height be between 0.5 m and 1.0 m, and that below shrub-stratum structure (see Chapter 3) have minimal cover (*viz.* lower than 10 %). Three sampling points were then located within the quadrat by means of random co-ordinates (1 m gridlines).

For distance/canopy cover class estimates 0 m, distance marks were located as above, but by taping at a safe distance from the cliff-top. The same selection as above as to survey in a northerly or southerly direction was then made. An approximately 4 m wide transect was then followed along the cliff-top until a 4 m by 10 m quadrat could be defined as being structurally homogeneous (as above). Three sampling points were then located at the cliff-edge by random selection of metre marks (1 m divisions) along the landward side of the transect. The same procedure was used to locate sample points for distance/canopy class estimates to be made at 1 m. In this instance sample points were located by measuring 3 m seaward from the landward side of the transect.

Sampling points for the 0% canopy cover class (above canopy salt-spray deposition estimate) were not in fact located above canopies as this would have been logistically impractical. These points were located at ground level as part of the location process described above. These points were located in unvegetated quadrats with the extra condition that the quadrats not apparently be afforded protection from surrounding vegetation. Further, no quadrats were located within 30 m of gaps which defined segment divisions. This restriction was enacted to avoid potential confounding influences from possible disturbance effects of gaps on air-flow.

### *Determination of salt-spray deposition*

The salt-spray collection device was simply a small plastic box with the lid replaced with a sheet of aluminium foil. The area of foil exposed to the atmosphere was 204 cm<sup>2</sup>. Sand was placed inside the box as a weight.

Collection devices were placed in the field at sample points for a period of exactly 48 hours in February 1994. Because of the inherent danger of working in dense vegetation next to unfenced cliff-tops, collection devices were not placed at sample points for below canopy estimations at 0 m. These points were omitted from the study altogether. Also, three devices were placed in exposed locations in the field with foil sheets attached but covered by the box lids. These were used as controls.

No rain was recorded over the sampling period. Prevailing wind conditions were fresh onshore (ca. 9 m.s<sup>-1</sup>) and steady during the sampling period.

At the conclusion of the sampling period foil sheets were removed from the plastic boxes and folded in such a way that the area exposed was now protected i.e. folded in on itself. Foil sheets (including controls) were then placed in individual plastic sample bags and returned to the laboratory.

Individual foil sheets were unfolded and placed in 120 ml plastic screw-top jars so that the entire area exposed during the sampling period was exposed inside the jar; 100ml of reagent grade water was then added to each jar. Jars were then shaken vigorously for one hour on a SRE rotary shaker, and the sheets removed from jars. Electrical conductivity of the water was then measured using a YSI salinity-conductivity-temperature meter (model no. 33). Measurements were recorded as  $\mu\text{mohs.cm}^{-1}$ .

Ten unexposed aluminium foil sheets were analysed as above so as to determine whether the foil itself contributed to conductivity readings. No conductivity was recorded for any of the replicates.

### *Numerical analyses*

Numerical analyses have been based on salt-spray deposition rates ( $\text{t.ha}^{-1}.\text{annum}^{-1}$ ) derived from electrical conductivity readings. This transformation of data has

been made for convenience and matters of reference only. The transformation is not intended to imply that accurate estimates of yearly salt-spray deposition have been obtained for the site under study.

Conversions were achieved by first dividing electrical conductivity readings by 1,000. This converted readings to the SI unit  $\text{dS}\cdot\text{m}^{-1}$ . Next, values were multiplied by 640 to obtain approximate salt concentration ( $\text{mg}\cdot\text{l}^{-1}$ ) for the 100ml solutions for which electrical conductivity was measured (Rhoades 1982). These figures were then divided by 10 to obtain mg of salt present. These figures were then multiplied by 182.5 (365 days/2 days) to obtain mg of salt deposited on the collecting surface in one year. These figures were then multiplied by  $10^8 \text{ cm}^2/204 \text{ cm}^2$  to obtain mg of salt deposited on one hectare in one year. Finally, figures were divided by  $10^9$  to obtain  $\text{t}\cdot\text{ha}^{-1}\cdot\text{annum}^{-1}$ .

All replicate salt-spray deposition determinations for the 0% canopy cover class were plotted against distance from cliff-tops. Replicate determinations of salt-spray deposition for 150 m were unavailable, salt-spray collection devices being buried by a local hermit during the sampling period.

As a preliminary investigation a line was constructed joining distance replicate means. This line was interpreted visually. Subsequently, distance replicates for 0 m were excluded from further analysis. The remaining data was analysed by least squares regression. Models fitted included linear and curvi-linear regression models. Curvi-linear models fitted included above canopy salt-spray deposition regressed on the natural logarithm of distance from cliff-tops, above canopy salt-spray deposition regressed on polynomial functions of distance from cliff-tops (all orders up to order 7), and a power function model (the natural logarithm of above canopy salt-spray deposition regressed on the natural logarithm of distance from cliff-tops).

Only the best fitting model was retained. Goodness of fit of models was assessed by visual inspection, by the maximum  $R^2$  value, by the smallest regression p-value, by normal probability plots of residuals, and by residual plots against both above canopy salt-spray deposition and against distance from cliff-tops.

For each canopy cover class, all replicate below canopy salt-spray deposition determinations were plotted against distance from cliff-tops. Visual inspection



suggested a model of the form used for above canopy salt-spray deposition would be appropriate. Five regression models were fitted, one for each canopy cover class.

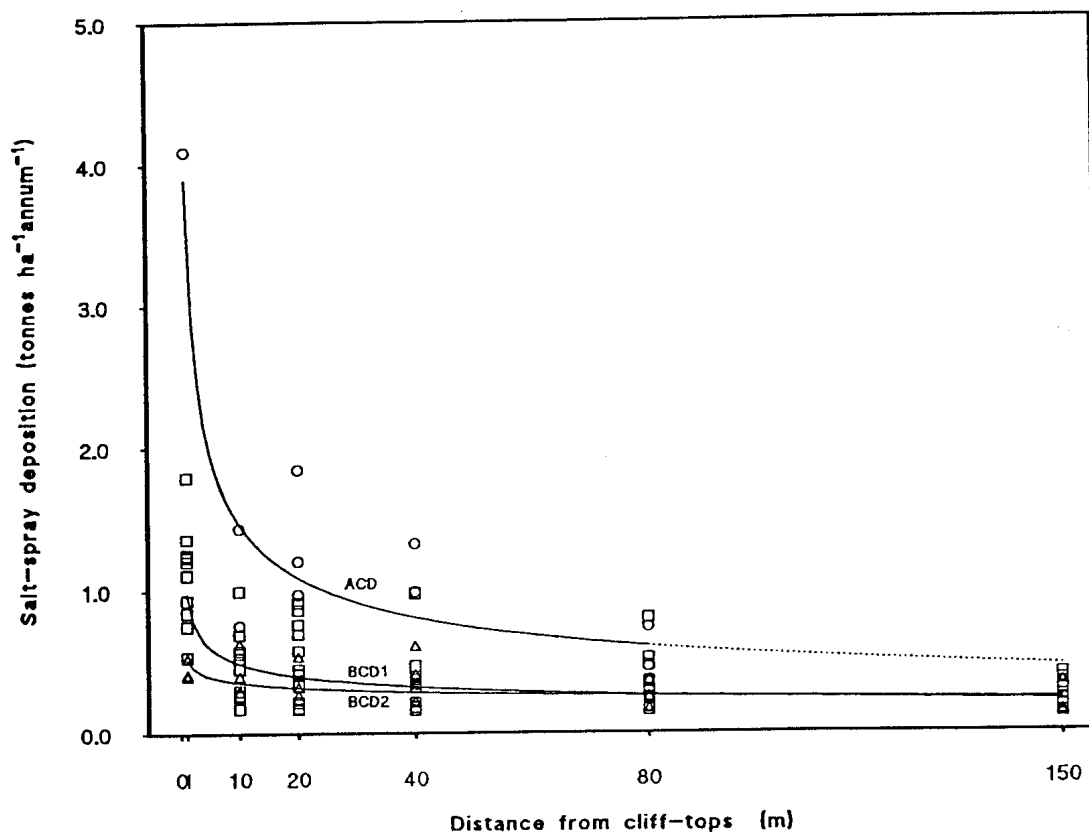
Effects of canopy cover and distance from cliff-tops were investigated by comparing the separate models for canopy cover classes using a single classification analysis of covariance layout (see Sokal & Rohlf 1981). Distance from cliff-tops was treated as the co-variate. F-tests were performed to compare means between classes adjusted for distance (y-intercepts), and to compare model slopes.

The model selected for above canopy salt-spray deposition was retained as a predictive model. This was considered to be the best model attainable from the data.

For beneath canopy salt-spray deposition, models for canopy cover classes that could not be separated statistically were combined into single models using data pooled from the relevant classes. Resulting models were retained as predictive models.

## Results

Retained models for the prediction of above and below canopy salt-spray deposition are shown below with respect to individual determinations of salt-spray deposition. Statistical parameters of fitted models are also provided. These models have been used to attach estimates of above and below canopy salt-spray deposition to all quadrats included in community structure studies. This has been done using the median distance of quadrats in distance strata from the cliff-tops, e.g. a quadrat in the 0 m to 10 m distance strata is assigned a value of 5 m on which values of salt-spray deposition are modelled. In the case of below-canopy salt-spray deposition shrub stratum cover (see Chapter 3) has been used to determine the appropriate model.



<u>KEY</u>				
Class	Symbol	Fitted model	R <sup>2</sup>	p-value
ACD — above canopy deposition	○	$\ln(\text{dep.}) = 1.360 - 0.425 \cdot \ln(\text{dist.})$	68.4%	0.002
BCD1 — below canopy deposition (0-80% cov.)	□	$\ln(\text{dep.}) = -0.020 - 0.302 \cdot \ln(\text{dist.})$	51.9%	0.000
BCD2 — below canopy deposition (80-100% cov.)	△	$\ln(\text{dep.}) = -0.659 - 0.163 \cdot \ln(\text{dist.})$	31.6%	0.015
		———— fitted model	..... model extrapolation (ACD 80m to 150m)	