Long-term changes in grassland, woodland and forest vegetation of south-eastern Australia: Impacts of land-use change

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Cover photographs:

Top left	*Remnant native grassland, Melbourne–Lancefield Road Railway Reserve, Clarkefield, Victoria.*
Top middle	*Unlogged native wet sclerophyll forest gully, Monga National Park, New South Wales.*
Top right	*Remnant native grassland, Elaine–Blue Bridge Road Railway Reserve, Elaine, Victoria.*
Bottom left	*Logged native wet sclerophyll forest, Tallaganda State Forest, New South Wales.*
Bottom middle	*Remnant native grassland, Bolac Plains Road via Woorndoo, Victoria.*
Bottom right	*Logged native wet sclerophyll forest, Tallaganda State Forest, New South Wales.*

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I certify that this thesis is my own work and to the best of my knowledge contains no materials previously published or written by another person, or substantial portions of material which have been accepted for the award of any other degree or diploma at any university, except where acknowledgement is made in the thesis. Any contribution made to the research by others is explicitly acknowledged in the thesis. I also certify that the intellectual content of this thesis is the product of my own work, except to the extent that assistance from others in the project's design and conception or in style, presentation and linguistic expression is acknowledged.

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Table of Contents

List of Figures

List of Tables

Abstract

Since European settlement of south-eastern Australia in 1788, native vegetation assemblages have been dramatically changed by Europeans with activities such as land clearing associated with forestry, agriculture and urban development. These have either destroyed or fragmented a large proportion of the original native vegetation. The plant species composition of vegetation assemblages has been modified by native species extinctions and exotic species colonizations. Acting in concert, the alteration of native vegetation by human activities, the decline and extinction of native species and the successful colonization by exotic species have the potential to lead to the homogenization and/or differentiation of the plant species composition of native vegetation associations.

In this thesis, I address the broad question: Have native species extinctions and exotic species colonizations resulted in the plant species composition of vegetation assemblages becoming more similar (i.e. homogenized) or less similar (i.e. differentiated) in south-eastern Australia? I compared historical species assemblages with contemporary species assemblages in three vegetation associations, at three separate spatial scales, to determine change in species composition over time. Specifically, I examined forest vegetation at the catchment spatial scale over a period of four decades, grassland vegetation at a regional scale over two decades and both woodland and forest vegetation at a continental scale over a period of c. 220 years.

At the catchment spatial scale, I used historical (1968–69) and contemporary (2007) vegetation surveys to determine change in species composition of vegetation assemblages. I investigated the effects of logging as well as both native species extinctions and exotic species colonizations on changes in species composition of 30 native wet sclerophyll forest stands, 10 unlogged and 20 logged, in the upper Shoalhaven River catchment over a period of four decades. Changes in the similarity of species composition of the unlogged and logged stands over time were compared, the findings indicating the species composition of wet sclerophyll forest in the catchment has become homogenized since the historical survey. It is likely that homogenization in unlogged stands is due to successional changes in the vegetation resulting

from long inter-fire intervals. However, logging has been the key driver of homogenization across the logged stands.

Historical surveys are generally not available at large spatial and long temporal scales because accurate surveys were not conducted in the long-term past at large spatial scales or records of such surveys no longer exist. To circumvent the problem of a lack of historical survey data, ecologists have devised a method to reconstruct the species composition of historical vegetation assemblages. Historical species assemblages are reconstructed by both removing exotic species from the species inventory of the contemporary assemblage and adding currently extinct native species. Exotic species are removed because these species are assumed to not have been present in the historical assemblage. Added extinct native species account for species lost due to extinction.

I used the above method to reconstruct the historical species composition of woodland and forest vegetation in 20 conservation reserves, first comparing changes in the similarity of species composition at a continental scale cross a broad region of south-eastern Australia since European settlement (c. 220 years ago). Then, observed patterns of homogenization and differentiation were related to the geographic and human-related attributes of each conservation reserve. Both native species extinctions and exotic species colonizations differentiated the species composition for all species, native species only and exotic species only in woodland vegetation. In forest vegetation, however, only native species extinctions differentiated the species composition of all species and native species only. For woodland, patterns of differentiation in woodland for native species were associated with both latitudinal and longitudinal separation of reserves. Furthermore, the differentiating effect of exotic species was also associated with longitudinal separation of reserves. In forest vegetation, the differentiating effect of native species extinctions could not be associated with any of the geographic or human-related factors.

The reconstruction technique above is problematic if data sources are of a different spatial scale. To address the lack of historical data and the shortcomings of the existing method, I employed two novel stochastic models to reconstruct the species composition of historical assemblages at large spatial and temporal scales. I used contemporary survey data on the species composition of 87 woodland and 51 forest locations at a continental scale over a period of c. 220 years (i.e. since European settlement).

Both models consistently indicated that native species extinctions promote homogenization of woodland vegetation. In contrast, exotic species colonizations promote differentiation in woodland vegetation. Similarly, in forest vegetation, both stochastic models suggested that native species extinctions promote homogenization. Furthermore, my observations suggested that exotic species colonizations promoted differentiation.

At a regional scale, I investigated change in the species composition of 30 native remnant grassland sites located along a 280 km urban–rural gradient in western Victoria. Their species composition was first sampled in 1984, re-sampled in 2001 (14 sites) and 2007 (the other 16 sites). The contemporary surveys oversampled the species composition across all 30 sites. I used a variant of the earlier stochastic modelling technique to correct for oversampling. For all 30 sites as well as urban, peri-urban and rural subsets of these sites I determined patterns of homogenization and differentiation resulting from native species extinctions and exotic species extinctions and colonizations.

For all 30 sites across the region, native species extinctions promote differentiation in the native species composition of grassland vegetation. In contrast, exotic species extinctions and colonizations promote homogenization of the exotic species composition of grassland sites. However, the composition of all species remains in stasis. For urban sites, native species extinctions promote differentiation in native species composition. Exotic species extinctions and colonizations promote homogenization in exotic species composition, but these patterns of change are not statistically significant. However, changes in exotic species composition were large enough to buffer the opposite (i.e. differentiating) effect of native species extinctions. As a result, the species composition for all species has become homogenized in urban sites. In peri-urban sites, exotic species extinctions and colonizations homogenize the exotic species composition, but do not have an overall effect on the composition of all species. Native species extinctions promote differentiation in native species, and exotic species extinctions and colonizations homogenize the exotic species composition of rural sites. However, the differentiating effect of extinctions in the native flora is greater

than the homogenizing effect of exotic species extinctions and colonizations. Consequently, the composition for all species in rural sites has become differentiated.

The patterns of homogenization and differentiation above were examined to see how human-related and environmental site attributes might be associated with patterns of vegetation change for the same 30 remnant grassland sites and their subsets – how change in human population density, maximum fire interval, solar radiation, temperature and precipitation are associated with patterns of homogenization and differentiation.

At a regional scale, differentiation in native species composition is associated with change in human population density. However, for urban, peri-urban and rural subsets of these sites no statistically significant association emerged. The only environmental site attribute that was associated with patterns of homogenization and differentiation was maximum temperature, which was associated with homogenization resulting from exotic species extinctions and colonizations in all 30 sites and peri-urban sites as well as change in the composition of all species for urban sites.

Overall my results revealed complex patterns of homogenization and differentiation in forest, woodland and grassland vegetation at a range of spatial and temporal scales. Moreover, I was able to relate change in individual vegetation associations to a range of human-related and environmental factors.

Terminology

In the context of this thesis the following terms are used:

Biotic homogenization – The process by which a species, functional trait and/or genetic trait assemblage becomes more similar in both space and time as a result of species colonizations, species extinctions and habitat modifications. **Biotic differentiation** is the opposite process.

Colonization – The process by which both native and non-native plant species are introduced and established.

Exotic plant species – All non-native and non-indigenous native plant species found growing in areas outside their native geographic range.

Grain size – The level of resolution of an investigation determined by the spatial area of the sampling unit (also **granularity**).

Occupancy - The total number of locations in which a species is found to be present

Revisitation method/technique – A technique that employs vegetation survey data collected from the same location(s) in two time periods.

Reconstruction method/technique – Any technique that uses contemporary lists of extant and extinct species to reconstruct the historical species composition of plant species assemblages.

Standard reconstruction technique – A method that reconstructs the historical species composition of plant species assemblages by both removing exotic species and adding extinct native species. Exotic species are removed from the contemporary list because it is assumed that these species would not have been present in the historical species assemblage. Extinct species are added to account for historically present species lost due to extinction.

1 Introduction

1.1 *Introduction*

1.1.1 Biological colonizations

The movement of species beyond their points of origin to other areas of the globe is a natural biogeographical process. Movements that shift the distributions of species are commonplace at geological and evolutionary time scales, having resulted from changes in physical geography and climate (McKinney 2004c; a; Sax *et al.* 2005; Kühn & Klotz 2006; McKinney 2006; Qian & Ricklefs 2006; Schwartz *et al.* 2006; Castro *et al.* 2007; McKinney & La Sorte 2007; Castro & Jaksic 2008b). At the same time, the oceanic realms and geological activity that has created mountain ranges have, in the past, acted as biogeographic barriers preventing the movement of many species (Rahel 2002). These barriers have created geographical areas of ecological distinctiveness, which, until fairly recently, were relatively isolated from each other. Only recently have humans been able to circumvent these natural barriers to increase the movement of species around the globe.

Humans, like many other animal species, have journeyed to areas beyond their point of evolutionary origin. However, technological advances in the last 1000 years have allowed more humans to make more journeys, over greater distances around the planet, than ever before. These journeys have often led to the accidental and intentional movement of other species around the planet and the breakdown of once isolated geographical areas of ecological distinctiveness (Elton 1958; Lodge 1993).

One consequence of the movement of species to areas outside of their natural range has been the biological colonization of regions previously inaccessible. Species that have colonized areas beyond their native range come from a broad set of taxonomic groups, including mammals, birds, reptiles, amphibians, arthropods, molluscs, plants and microbes (Pimentel *et al.* 2000). Although such colonizations can have positive effects (Zavaleta *et al.* 2001), there is general agreement among scientists and environmental managers that, on the whole, human-assisted biological colonizations have created social, economic, and environmental harm.

Although there are no worldwide estimates of the social, economic, and environmental costs of such colonizations, one estimate (for Australia, Brazil, India, South Africa, United Kingdom and the United States) of damage caused by exotic species is more than US$314 billion per year (Pimentel *et al.* 2001). In Australia alone, colonizations by exotic species that have become invasive cost the economy up to AUD$8.0 billion per year (Agtrans Research & Dawson 2005). Although public and media attention generally focuses on the visible negative effects of colonizations by exotic animal and human diseases, arguably the greatest negative consequences are associated with exotic plant colonizations.

1.1.2 Exotic plant colonization

Notwithstanding the social consequences of exotic plant colonizations, the economic and environmental consequences are significant. The combined economic cost of exotic plant colonizations in crops, pastures and forests in Australia, Brazil, India, South Africa, United Kingdom and the United States amounts to almost US$95 billion per year (Pimentel *et al.* 2001). The cost of exotic plant invasion in Australia is estimated to be up to AUD$4.5 billion per year (Sinden *et al.* 2004). These estimates, however, do not account for the negative impacts that exotic plant colonizations have on the environment and thus are gross underestimates of the full economic and environmental cost.

Furthermore, full accounting of the environmental cost requires an understanding of the impact that plant colonizations have on the goods and services provided by the natural environment. These goods and services (termed ecosystem services) on which humans depend, are provided by the biodiversity of natural ecosystems (Chapin III *et al.* 2000; Murray *et al.* 2006). Many ecosystem services are provided, directly or indirectly, by native plant assemblages. Exotic plant colonizations can affect ecosystem services negatively by altering natural habitat and thereby disrupting a range of ecosystem functions and processes. These include atmospheric composition, hydrology, litter accumulation and decomposition, soil chemistry, nutrient cycling and nutrient availability (Kizlinski *et al.* 2002; Ehrenfeld 2003; Dukes & Mooney 2004; Standish *et al.* 2004; D'Antonio & Hobbie 2005; Hawkes *et al.* 2005; Vilà *et al.* 2006).

1.1.3 Habitat alteration

Not only have exotic plant colonizations, facilitated by human activity, altered the environment and disrupted ecosystem services, human activity – in and of itself – alters habitat. This process of habitat alteration results from activities associated with human land-use and can occur in many ways. For example, many Australian ecosystems have been modified since the arrival of the indigenous Australians >40,000 BP. Principally, the use of fire over thousands of years by indigenous Australians has fundamentally shaped the continent's ecology (Flannery 1994).

However, since the arrival of Europeans further significant changes have taken place. Three common ways human activity alters natural habitat are land clearing, habitat fragmentation and disturbance. Land clearing for agriculture and urban development alters natural habitat by partially or fully destroying native vegetation. In particular, habitat loss due to land clearing has been responsible for the extinction of species and the current conservation status of many other rare plant species (Burgman *et al.* 2007). The process of clearing native vegetation also contributes to creating smaller patches of fragmented habitat. Habitat fragmentation can alter the composition of native plant species assemblages by changing the microclimate at fragment edges (Collinge 1996) or interrupting natural landscape-scale disturbances (Leach & Givnish 1996). Disturbance caused by human activity associated with land-use can lead to changes in natural fire and grazing regimes, which can also change the composition of native vegetation. Working alone or in unison, these three habitat alteration processes can lead to the decline and extinction of plants in native assemblages leading to a loss of biodiversity.

1.1.4 Native plant extinction

Both habitat alteration and exotic plant colonizations are implicated in the decline in abundance and extinction of native plant species. A range of empirical investigations indicate that habitat loss from land clearing negatively affects biodiversity (reviewed in Fahrig 2003). Long-term vegetation research suggests that habitat fragmentation is largely or partly responsible for native plant declines and extinctions (Leach & Givnish 1996; Fischer & Stöcklin 1997; Bennie *et al.* 2006). Similarly, other long-term research indicates that changes to natural disturbance regimes (e.g. fire and grazing) are at least partly responsible for the local extinction of native species (Kwiatkowska 1994; Wahren *et al.* 1994; Rooney & Dress 1997; Rooney *et al.* 2004; Taverna *et al.* 2005; Williams 2005; Williams *et al.* 2005b; Williams *et al.* 2006).

Evidence from a range of ecosystems and regions around the world suggests that exotic plant colonizations are responsible for the extinction of native plant species. Plant colonizations can affect natural disturbance regimes and/or displace native plants through competitive pressure. For instance, exotic plants have been found to alter natural fire and erosion regimes in Hawaii, South Africa, North America, and Australia (reviewed in Mack & D'Antonio 1998). In Australia, exotic plant species have been found to displace natives (Groves & Willis 1999) and 47 species have been identified as having a medium to high potential to form monocultures that competitively displace native species (Thorp & Lynch 2000).

Rare plant species, listed as threatened or endangered, have been found to be at particular risk of decline due to competitive pressure from exotic species colonizations (Wilcove *et al.* 1998; Burgman *et al.* 2007). Long-term vegetation studies suggest plant species and populations found to be rare or in low abundance in historical surveys were more likely to have become extinct in contemporary surveys (Robinson *et al.* 1994; Fischer & Stöcklin 1997; Rooney & Dress 1997; Duncan & Young 2000). Clearly, plant extinctions, and the extinction of rare plant species in particular, are a central element in the conservation of native plant biodiversity.

1.2 Review of theoretical and empirical findings on biotic homogenization

1.2.1 Biodiversity and the biotic homogenization framework

Species richness is widely regarded as a common currency for assessing biodiversity (Gaston & Spicer 2004). Also known as 'α-diversity' (Whittaker 1972), species richness is calculated by counting the total number of plant species occurring in a given area. Clearly, changes to plant species richness result from the interaction of colonizations and extinctions. It is also plain that plant invasions and extinctions are mediated by habitat alteration.

Surprisingly, it has only been within the last fifteen years that a unified framework linking the three factors responsible for biodiversity change (the biotic homogenization framework) has evolved. Alterations of natural habitats by human activities and human-assisted transport of species around the globe have been recognized as key factors in the successful colonization by exotic species, the decline and extinction of many native species, and homogenization of the earth's biota (Lodge 1993; Brown 1995; Myers 1997; Vitousek *et al.* 1997; McKinney & Lockwood 1999).

As a relatively new component of biodiversity research, the development of theory and empirical methodologies are still in their early stages. To date, only a relatively small number of empirical studies have investigated biotic homogenization in plant assemblages (Appendix 1). In this section, I review the growing body of work in the field of biotic homogenization within plant species assemblages. I provide essential background information and then describe in detail the significant issues to be considered when conducting studies of biotic homogenization of plant assemblages.

1.2.2 Definition of biotic homogenization

First coined by McKinney and Lockwood (1999), the term biotic homogenization was initially loosely defined as a process involving the replacement of unique indigenous species in native assemblages with widely-distributed exotic species. The definition of the term was later tightened with the inclusion of a temporal component, and is represented as an increase in similarity of ecological communities over time as a result of the replacement of native species with exotic species, usually resulting from human activity (Rahel 2002). Biotic homogenization was proposed to arise from three interacting processes: (i) species colonizations, (ii) species extinctions, and (iii) environmental alterations that facilitate these two processes (Rahel 2002). Both of the above definitions (McKinney & Lockwood 1999; Rahel 2002) imply that homogenization is limited to changes in the taxonomic composition (i.e. species composition) of species assemblages, and thus use biotic homogenization and taxonomic homogenization interchangeably.

Recently, a more comprehensive definition of biotic homogenization has emerged. This defines biotic homogenization as a process that incorporates species colonizations, species extinctions and habitat modifications, and centres on how the taxonomic identity of species, as well as their functional or genetic characteristics, change both in space and time (Olden & Rooney 2006). Importantly, this definition explicitly reflects that the process of biotic homogenization has not only a taxonomic component, but functional and genetic elements as well (Olden *et al.* 2004; Olden & Rooney 2006). Importantly, this definition recognizes homogenization as a process that occurs across space and time. In this thesis I adopt this definition of biotic homogenization and here the term 'biotic homogenization' refers to all levels of biological organization, including taxonomic, functional and genetic levels.

1.2.3 Calculation of biotic homogenization

Homogenization of plant species assemblages is measured by assessing changes in the turnover of species composition across space and through time. Also known as 'β-diversity' (Whittaker 1972), this metric is another common measure for assessing biodiversity. Species turnover across space is determined by calculating the compositional similarity of plant species assemblages. Increased compositional similarity both across space and through time (i.e. homogenization) equates to decreased β-diversity.

Indices that have commonly been used to calculate compositional similarity in floral homogenization studies include Sorensen's Index (as used in Schwartz *et al.* 2006), Simpson's Index (as used in Kühn & Klotz 2006) and Jaccard's Index (as used in Rejmánek 2000; McKinney 2002; 2004c; a; 2005; McKinney & Lockwood 2005; Kühn & Klotz 2006; Olden & Rooney 2006; Qian & Ricklefs 2006; Schwartz *et al.* 2006; Castro *et al.* 2007; Qian *et al.* 2008). Such indices employ species occupancy data to estimate compositional similarity and do not account for species abundance. Calculations are based on pairwise comparisons of the number of shared species and unshared species between the two assemblages under consideration. Shared species are those species present in both assemblages, while unshared species are unique to each assemblage. Traditionally, comparisons of compositional similarity among assemblages using such indices can only be made either across space or through time in a single pairwise comparison; it is not possible to compare changes in space and time simultaneously, and thus, such comparisons can tell us about vegetation change in one dimension (i.e. across space or through time). The calculation of compositional changes across space or through time is governed by gain of new species through colonization and the loss of species through extinction.

1.2.4 Differential patterns of colonization and extinction can lead to both biotic homogenization and differentiation

Early theoretical discussion only considered the possibility that biodiversity changes precipitated by colonizations, extinctions and habitat alteration would inevitably lead to homogenization (Lodge 1993; Brown 1995; Myers 1997; Vitousek *et al.* 1997; McKinney & Lockwood 1999). However, it was demonstrated both theoretically and empirically that colonizations and extinctions could lead to homogenization, differentiation (i.e. assemblages becoming less alike in their species compositions) or indeed stasis in plant species composition (Rahel 2000; Rahel 2002; Olden & Poff 2003; Castro & Jaksic 2008a).

When making a pairwise comparison between assemblages, the addition of new species (by colonization) or loss of existing species (by extinction) can lead to either increasing or decreasing compositional similarity (Rahel 2002). Colonizations lead to homogenization when the same species or traits are gained by assemblages that have historically different compositions. Extinctions generate homogenization when different species or traits are lost from assemblages that are historically different, thereby creating two similar contemporary assemblages. Conversely, colonizations lead to differentiation when different species or traits are gained by assemblages with the same historical composition. Extinctions can also lead to differentiation when the same species or traits found in two historical assemblages are lost from contemporary assemblages. Further, if colonization and/or extinction events occur differentially (i.e. in one assemblage and not the other), depending on the historical composition of the assemblage, such events could also lead to either homogenization or differentiation (Olden & Poff 2003).

1.2.5 Conceptual framework of issues critical to the study of biotic homogenization and differentiation in plant species assemblages

1.2.5.1 Importance of temporal and spatial replication

Evidence for biotic homogenization can only be acquired by assessing changes in the compositional similarity of species assemblages at a minimum of two locations and across a minimum of two times. At least two locations are required because the taxonomic, functional or genetic composition of an assemblage at one location is compared with the taxonomic, functional or genetic composition of assemblage(s) at another/other location(s) to assess similarity. However, spatial comparisons alone are not enough to detect if homogenization and/or differentiation has occurred. At least two time periods are also required because both past and present data are essential for the detection of changes in the compositional similarity of species assemblages through time. Critical to the process of homogenization and differentiation are native species extinctions and exotic species colonizations (McKinney & Lockwood 1999; McKinney & Lockwood 2001; Rahel 2002; Olden & Poff 2003). Extinction and colonization are processes that occur through time, hence the need for two or more time periods to be considered.

An important question to ask of studies claiming to provide evidence for homogenization and/or differentiation is: Do these studies use data from at least two locations and from at least two time periods? From my literature search (Appendix 1), only one study investigating biotic homogenization of vegetation assemblages – Rooney *et al.* (2004) – has utilized floristic survey data collected in two time periods and replicated across space. This study provides the most reliable evidence for homogenization to date. The authors revisited sites sampled previously and resampled the actual plots used in an historical survey using the same (but note, more intensive) sampling methods. This approach is recommended because data are recorded at two distinct points in time and replicated across space, and the degree of homogenization that occurs in the time period can be clearly quantified (Olden & Rooney 2006). Two key factors should be considered when using a revisitation methodology. First, it is important to use the same sampling methodology in both time periods (e.g. same quadrat size, sampling at the same time of year, same sampling effort and intensity) (Olden & Rooney 2006). Second, sampling must be done in the same locations (Fischer & Stöcklin 1997) in order to avoid falsely recording a species as present or absent in the contemporary survey relative to the historic survey.

Other attempts to identify homogenization in plant assemblages have compared contemporary species lists detailing the presence (and/or absence) of both native and non-native species across space, without utilizing a revisitation methodology (e.g. Rejmánek 2000; McKinney 2004c; a; 2005; Kühn & Klotz 2006; McKinney 2006; Olden *et al.* 2006; Schwartz *et al.* 2006; Castro *et al.* 2007; Castro & Jaksic 2008a; b; Qian *et al.* 2008). Studies that have not used historical data have had to account for temporal changes in species compositions of assemblages where historical data are not available. Some studies have simply avoided the issue (as in McKinney 2005; 2006). Studies that do not make observations in both space and time, and only compare the compositional similarity of vegetation in one time period (as in Rejmánek 2000) can reveal important insights into changes in plant species turnover across space (i.e. β-diversity). However, such studies do not address the processes of biotic homogenization and differentiation.

To circumvent the problem of a lack of historical data, two reconstruction methods have recently been proposed (Olden & Rooney 2006). The first method partially reconstructs an historical species assemblage by removing exotic species from a species list of the contemporary assemblage, but makes no attempt to account for species loss due to extinction (e.g. Rejmánek 2000; McKinney 2004c; a; Kühn & Klotz 2006; Qian & Ricklefs 2006; Qian *et al.* 2008). Exotic species are removed from the contemporary list because it is assumed that these species would not have been present in the historical species assemblage. The second method reconstructs an historical species assemblage by both removing exotic species and adding extinct native species – standard reconstruction technique'. Extinct native species are added to the contemporary list of native species, to account for species loss due to regional or global extinction (e.g. Castro *et al.* 2007; Castro & Jaksic 2008a; b). Clearly, defining the time period that the reconstructed assemblage is intended to represent is paramount in such reconstruction, to ensure that assumptions about the timing of invasions and extinctions are as reliable as possible.

It comes as no surprise that there are shortcomings to both these reconstruction methods. In the first method, failure to take into account extinctions (if they have occurred) will obviously result in an incomplete historical assemblage. As a consequence, estimates of the degree to which homogenization has occurred will overstate the significance of the introduction of exotic species if extinctions have actually occurred (Olden & Rooney 2006).

In the case of the standard reconstruction technique, there are two significant shortcomings. The first shortcoming relates to the means by which regional scale contemporary floristic inventories are assembled. Regional scale inventories are compiled from individual herbarium records and/or local scale species inventories from individual locations within a region. Consequently, such inventories may simultaneously understate native species extinctions and overstate exotic species colonizations. By amalgamating local scale data into a regional inventory, a native species may be recorded as present even though it might have been extirpated from all but one location within the region. Correspondingly, an exotic species may be recorded as present although it may have colonized only one location within the region. As a result, regional species inventories may understate native species extinctions and at the same time overstate exotic species colonizations.

The second limitation of the standard reconstruction technique concerns the scale of the data used to reconstruct the species composition of historical species assemblages. Applying the technique is problematic if data sources are of a different spatial scale (e.g. local scale contemporary inventories of native and exotic species and regional scale contemporary inventories of extinct native species). If the standard reconstruction technique were employed in the example above, extinct native species would be added to the contemporary inventories of all locations within the region. Under the assumption that extinct native species were historically rare within a region, it is unlikely that these species were present in all locations across the region. Consequently, this would overstate native species extinctions.

Unfortunately, the above limitations of the standard reconstruction technique preclude the use of a wealth of contemporary datasets that could be employed to reconstruct the historical species composition of regions where historical data are unavailable. Consequently, there is a need for research into methods that might make these contemporary datasets available for studies of homogenization and differentiation.

1.2.5.2 Importance of targeting individual vegetation associations

Most empirical investigations of biotic homogenization in plant communities utilize data that have been pooled across many different and unspecified vegetation associations (Rejmánek 2000; McKinney 2004a; c; 2005; McKinney & Lockwood 2005; Kühn & Klotz 2006; McKinney 2006; Olden *et al.* 2006; Qian & Ricklefs 2006; Schwartz *et al.* 2006; Castro *et al.* 2007; Castro & Jaksic 2008a; b; Qian *et al.* 2008). Use of pooled datasets has revealed broad changes in compositional similarity between regional floras across space and through time. In particular, the use of pooled datasets has constrained our ability to make ecologically meaningful generalizations regarding patterns of biotic homogenization and differentiation. Such generalizations can only emerge by taking into account the types of vegetation assemblages involved in comparisons. Specifically, vegetation associations, based on a broadly used scheme (a good example for Australia is the classification approach advocated by Specht (1970)) can be employed as the base unit of comparison for studies of floral homogenization. My literature search revealed only two studies have investigated biotic homogenization in relation to specific vegetation associations, i.e. forest (Rooney *et al.* 2004; Schulte *et al.* 2007).

There is a pressing need for research to focus on individual vegetation associations because different vegetation associations may respond differently to a range of habitat alterations. As a consequence, the differing responses of vegetation types may affect the degree to which homogenization and differentiation are observed across vegetation associations. Although there is no firm evidence, it makes sense that, for instance, temperate grasslands would exhibit different responses to a particular habitat alteration to temperate forests, given the vastly different life histories of the plants involved. When vegetation associations are employed as the unit of comparison, and it emerges that some vegetation associations are more prone to biotic homogenization than others, two key questions arise: (i) What patterns of change in compositional similarity are evident both within and between different vegetation associations? (ii) What are the factors that might make one vegetation association more prone to homogenization and/or differentiation than another?

1.2.5.3 Importance of spatial and temporal scales

Patterns of homogenization and differentiation are affected by a complex set of factors. In particular, these patterns are likely to be affected by the spatial and temporal scales at which observations are made (Olden & Poff 2003; Cassey *et al.* 2006). The influence of invasions and extinctions on changes in species composition has been found to vary with spatial factors, such as spatial scale and the degree of initial spatial aggregation and distribution of native species populations (Cassey *et al.* 2006; Rooney *et al.* 2007). The use of pooled datasets, where the spatial scale of analysis is largely determined by the artificial boundaries of political regions, disregard the natural boundaries that give rise to historically distinct bioregions (Olden 2006). Consequently, such datasets have a tendency to underestimate homogenization because political regions are more likely to have a greater degree of initial similarity (Olden 2006).

It is therefore advisable that the basic spatial scale of comparison in floral homogenization studies should be defined by the natural boundaries of the vegetation association under examination. For example, if woodland is under investigation, the natural boundaries at the local scale might be the physical boundaries of a local watershed. At a regional scale, woodland within the natural boundaries of a regional catchment would be considered. At the next level of spatial scale one might consider woodland in a bioregion. Focusing investigations on multiple spatial scales based on natural boundaries of vegetation associations will likely yield ecologically meaningful results compared with analyses based on artificial boundaries.

The temporal scale of comparison is another significant and unexplored factor in homogenization studies of vegetation associations. The salient issue is that the species composition both within and between vegetation associations can be comprised of species that often have vastly different life spans. Within an association, the structural formation (sensu Specht 1970) is significant because the life span of the species composing the different structural elements can be substantially different. For example, woodland might be composed of a canopy of trees and a ground layer of grasses and herbs. Changes in the species composition of different structural elements within an association could take different amounts of time to emerge. A similar situation arises when comparing, for example, forest and grassland. The differences in life span of the dominant species, i.e. trees and grasses, are such that compositional change in forest could take centuries to become apparent (Delcourt *et al.* 1983), but only a few years in grassland.

1.2.5.4 Importance of identifying human-related and environmental drivers of patterns of homogenization and differentiation

Our current insight into patterns of homogenization and differentiation in plant species assemblages has largely been determined from macroecological studies of undefined vegetation associations at large spatial and long temporal scales (McKinney 2004a; c; Kühn & Klotz 2006; McKinney 2006; Olden *et al.* 2006; Qian & Ricklefs 2006; Schwartz *et al.* 2006; Castro *et al.* 2007; Castro & Jaksic 2008a; Qian *et al.* 2008). A growing number of studies have attributed the patterns of homogenization and differentiation to the process of urbanization (Kühn & Klotz 2006; McKinney 2006; Olden *et al.* 2006; Schwartz *et al.* 2006).

However, owing to the large spatial and long temporal scales at which these studies have been conducted, it is difficult to attribute observed patterns of homogenization and differentiation to specific human activities. Furthermore, specific factors, such as urban development and fragmentation, which are associated with the process of urbanization and can precipitate the species extinctions and colonizations that underlie patterns of homogenization and differentiation, often operate simultaneously (Williams *et al.* 2009). Consequently, it is difficult, if not impossible, to disentangle the effect of individual drivers of change in species composition. This situation is further complicated if different vegetation associations respond differently to a range of human-related habitat alterations (Section 1.2.5.2). As a result, there has been little progress in our understanding of the specific human-related activities coupled to the process of urbanization that might drive homogenization and differentiation within specific vegetation associations.

Moreover, there also has been little advancement in our understanding of how patterns of homogenization and differentiation might be associated with environmental drivers of change in plant species composition (Olden 2006). For instance, exotic species may colonize areas that have similar climatic conditions to that of their native range (Corlett 1992; Wu *et al.* 2004). If this is the case, patterns of homogenization and differentiation within a region might be associated with the climatic conditions tolerated by the same exotic species within their native range. Consequently, there is a need for research to now focus on how patterns of homogenization and differentiation within individual vegetation associations might be associated with both human-related and environmental factors.

1.2.5.5 Importance of species abundance

Homogenization studies have focused primarily on species colonization, i.e. the addition of a species to an assemblage, and/or extinction events, i.e. the removal of a species from an assemblage, as the principle drivers of change in species diversity (Lodge 1993; Brown 1995; Myers 1997; Vitousek *et al.* 1997). As a consequence, the three traditional definitions of biotic homogenization focus on the processes of colonization and extinction as discrete, stepwise events (McKinney & Lockwood 1999; Rahel 2002; Olden & Rooney 2006).

In reality, invasion and extinction are not stepwise events. Rather, increases and decreases in species abundance underpin the processes of colonization and extinction. Changes in species composition brought about by colonization involve increases in species abundance within a given time period. Similarly, changes in species brought about by extinction involve decreases in species abundance. In addition, changes in species composition can also be generated by the increases and/or decreases in the abundance of those species present in both the historical and contemporary observations.

Studies not employing abundance data do not take into account changes in the abundance of all species at all times contributing to biotic homogenization. This is best demonstrated by a study of a temperate forest understory assemblage in Wisconsin, USA (Rooney *et al.* 2004). The study used data that included both species composition and a measure of abundance (in this case, species density) for all species at all times. These data enabled the authors to use the Bray-Curtis Index (Bray & Curtis 1957) which allows for subtle changes in both species composition and abundance to contribute to overall taxonomic homogenization for all native and exotic species present at one or both times. The exotic species colonizations and native species extinctions were found by to be important contributors to increased taxonomic homogenization (Rooney *et al.* 2004). However, the use of species composition and abundance data in this study allowed for a deeper insight into the process of homogenization. For instance, the chief driver of taxonomic homogenization was native species that were common (i.e. widespread and highly abundant) in the historical survey, and went on to become more abundant in the same species assemblage in the contemporary survey (Rooney *et al.* 2004). Another study found that abundant exotic species classified as invasive were found to have a greater homogenizing effect spatially than less abundant non-invasive exotic species (McKinney & La Sorte 2007).

Inclusion of abundance data would be a useful advance in the study of homogenization and differentiation because it may allow for more subtle changes in plant species composition to be discerned (see Rooney *et al.* 2004). The data required include the abundance of all species present in both the contemporary and historical species inventories used to calculate compositional similarities from which levels of homogenization and differentiation are determined. However, the occurrence of both contemporary and historical inventories which record species abundance in the same locations is rare; thus there is an extremely limited opportunity to explore this issue in homogenization studies (Cassey *et al.* 2007). Fortunately, empirical evidence suggests there is a strong correlation in the scores calculated when comparing indices that calculate similarity based on species abundance and those that employ species occupancy records (see Section 1.2.3, McKinney & Lockwood 2005). In general, differences in similarity scores calculated by the two types of metric are small and the trajectory of change in similarity (i.e. homogenization or differentiation) is the same (Cassey *et al.* 2007).

1.3 Thesis rationale

1.3.1 Research significance

This thesis advances the study of taxonomic homogenization and differentiation in plant species assemblages by addressing the gaps in the research conducted to date. I have identified these gaps within the various components of the conceptual framework (see Section 1.2.5). These components are analogous to the ingredients of the recipe required for conducting studies of homogenization and differentiation in vegetation. Homogenization and differentiation studies can be heavily reliant on historical data and thus are at least partly dependent on the design of previous research used to gather that data. With this factor in mind, I consider some of these ingredients as essential and some as important but not essential to the study of plant homogenization.

The essential ingredients are:

(i) observations must be made in at least two locations and across at least two times (Section 1.2.5.1);
(ii) when primary historical data are unavailable, the use of a reconstruction methodology is required, at a minimum involving the standard reconstruction technique (Section 1.2.5.1);
(iii) a focus on individual vegetation associations is critical (Sections 1.2.5.1 and 1.2.5.2).

Where possible, the important (but not essential) ingredients to incorporate are:

(iv) utilization of a revisitation methodology (Section 1.2.5.1);
(v) investigation of change in species composition at a range of spatial and temporal scales (Section 1.2.5.3);
(vi) an attempt to identify the human-related and/or environmental drivers of observed patterns of homogenization and differentiation (Section1.2.5.4);
(vii) inclusion of some measure of abundance (Section 1.2.5.5).

1.3.2 Thesis aim and objectives

The overall aim of this thesis is to investigate the process of taxonomic homogenization and differentiation in individual vegetation associations in south-eastern Australia. With this aim in mind, this thesis operates within the broad framework of seven essential and important criteria required for studies of homogenization and differentiation in plant species assemblages (Section 1.3.1).

The four main objectives addressed in this thesis are:

1. To identify patterns of taxonomic homogenization and differentiation within individual vegetation associations at a range of spatial scales.
2. To explore how patterns of homogenization and differentiation within individual vegetation associations might be associated with specific human-related factors associated with land-use.
3. To explore how patterns of homogenization and differentiation within individual vegetation associations might be associated with environmental factors.
4. To develop an approach that addresses the shortcomings of existing techniques used to reconstruct the historical species composition of regions where historical data are unavailable.

1.3.3 Thesis structure

With the essential and important criteria required for study of plant homogenization and differentiation in mind (Section 1.3.1), this thesis addresses the thesis objectives using a combination of complementary research methods, i.e. macroecological, observational and modelling.

Chapter 1 provides a general introduction to the field of biotic homogenization and differentiation. This chapter reviews the theoretical and empirical literature on plant homogenization by way of identifying essential and important criteria to consider when conducting homogenization studies.

In **Chapter 2** the results of an observational study investigating the role of logging as a driver of homogenization in forest vegetation in the Southern Tablelands of south-eastern Australia are presented. The study was conducted at a catchment scale and uses previously-collected (historical) data and freshly-collected (contemporary) data spanning a period of almost four decades. This chapter has been submitted as a manuscript to *Austral Ecology* as: 'Biotic homogenization of forest vegetation in south-eastern Australia and the effects of habitat disturbance through logging', by Licari, D. and Murray, B.R.

Chapter 3 is a macroecological study that explores how patterns of homogenization and differentiation in woodland and forest vegetation are associated with human-related and geographic attributes of 20 conservation reserves located across south-eastern Australia. This study was conducted at a regional scale and covers a period of c. 220 years (i.e. since permanent European settlement of Australia).

The findings of a macroecological study, which employed a novel modelling approach to investigate patterns of homogenization and differentiation in 87 woodland and 51 forest locations situated within 20 conservation reserves across south-eastern Australia, are presented in **Chapter 4**. The study was conducted at a regional scale over a period of c. 220 years.

Chapter 5 is an observational study reporting on how patterns of homogenization and differentiation in 30 remnant grassland sites are related to patterns of urbanization across western Victoria, in south-eastern Australia. This study was conducted at a regional scale and covers a period of two decades.

The study in **Chapter 6** was also conducted at a regional scale, covering a period of two decades. This chapter presents the findings of an observational study that explored how patterns of homogenization and differentiation are associated with the human-related and environmental attributes of 30 remnant grassland sites situated in western Victoria, in south-eastern Australia.

A synthesis of findings from the previous chapters is provided in **Chapter 7**. This links the findings in an overarching discussion and makes recommendations for the direction of future research.

2 Biotic homogenization of forest vegetation in south-eastern Australia: the role of logging and fire regime

This chapter has been submitted as a manuscript to *Austral Ecology* as: 'Biotic homogenization of forest vegetation in south-eastern Australia: the role of logging and fire regime', by Licari, D, Murray, B.R. and Hose, G.C.

2.1 Introduction

The significance of the spatial dimension to the study of the plant species biodiversity of vegetation has long been recognised. Empirical work by ecologists and biogeographers has established the importance of investigating the spatial turnover of plant species (i.e. β-diversity, Whittaker 1972) as a critical metric of biodiversity (Whittaker 1960; Wilson & Shmida 1984; Nekola & White 1999; Qian *et al.* 2005; Qian 2008). Since the 1990's a small but growing literature on the study of biotic homogenization and differentiation (BHD) has emerged from the five decade-long tradition of the study of β-diversity (Lodge 1993; Brown 1995; Myers 1997; McKinney & Lockwood 1999). As a theoretical framework, BHD integrates study of the three key processes which underpin the global biodiversity crisis, namely: anthropogenic habitat alteration, native species extinctions and exotic species colonizations (Rahel 2002).

Effectively, the BHD approach examines how the taxonomic identity, functional or genetic characteristics of a community, change in both space and time (Olden & Rooney 2006). In taxonomic studies of BHD, change in plant species composition is assessed by determining change in β-diversity through time. These changes are quantified by the change in species similarity of pairs of stands between two time periods (Olden & Poff 2003). The β-diversity of vegetation assemblages may either decrease over time (i.e. become more similar or homogenized), increase over time (i.e. become less similar or differentiated), or may remain in stasis over time (Rahel 2000; Rahel 2002; Olden & Poff 2003; Castro & Jaksic 2008a).

Human activities such as land clearing and urbanization have contributed to increased rates of species extinction (Vitousek *et al.* 1997). Species have also colonized areas beyond their natural ranges as a result of human transport (Elton 1958; Lodge 1993). The dual processes of extinction and colonization have transformed the taxonomic composition of ecological assemblages around the world (Lodge 1993; Brown 1995; Myers 1997; McKinney & Lockwood 1999). Shifts in the relative importance of extinction and invasion events can generate either homogenization or differentiation (Rahel 2002; Olden & Poff 2003; 2004b; Cassey *et al.* 2006; Olden & Rooney 2006).

The majority of empirical studies of BHD in plant assemblages have been conducted in the northern hemisphere (but see Castro *et al.* 2007; Castro & Jaksic 2008a; b), and most have pooled data from multiple and undefined vegetation associations (McKinney 2004a; c; Kühn & Klotz 2006; McKinney 2006; Qian & Ricklefs 2006; Schwartz *et al.* 2006; Castro *et al.* 2007; Castro & Jaksic 2008a; b). As there is no reason to expect that distinct vegetation assemblages will behave similarly with respect to the dynamics of change in species composition, there is much scope for exploring the ecological underpinnings BHD in specific vegetation associations (e.g. forests, grasslands).

Here I examine the patterns of BHD in the native and exotic plant species composition of wet sclerophyll forest (WSF) across the Shoalhaven River catchment (Southern Tablelands) of south-eastern Australia. I consider the relative importance of disturbance history in relation to BHD by comparing areas that have been logged and/or burnt at different times over a period of four decades. Specifically, I address three questions: (1) Have vegetation assemblages become more or less similar over time? (2) Is the pattern of change related to disturbance history? (3) What contribution do native and exotic species have on patterns of vegetation change?

2.2 Methods

2.2.1 Study area

The study area within the Shoalhaven River catchment (Figure 2.1) is 600-1500 m above sea level and receives an average annual rainfall of 700-1300 mm (State Forests of New South Wales 1995). The climate of the study area is characterised by short, warm summers (average temperature 23-29° C) and long, cool winters (average temperature 7-13° C). Since European settlement of the area in the 1820s, the wooded vegetation that once covered the plains, river flats and lower slopes of the catchment has been mostly cleared for agriculture. Although most of the hilly, higher altitude areas have been logged since at least the 1860s, these areas remain under the cover of relatively undisturbed sclerophyllous woodland and forest vegetation (State Forests of New South Wales 1995). Large tracts of these wooded areas are now reserved for nature conservation or forestry. The overstorey of WSF assemblages in the study area are dominated by eucalypts such as *Eucalyptus cypellocarpa*, *E. fastigata, E. robertsonii* and *E. sieberi.* Assemblages are mostly tall open forests with a scattered shrub understorey and a moderately dense ground layer of herbs, ferns and graminoids.

2.2.2 Historical and contemporary vegetation surveys

A comprehensive floristic survey of 40 m × 40 m sites within 261 forest stands in the Southern Tablelands was conducted by M.P. Austin as part of a CSIRO survey in 1968-69 (Storey 1969). This 'historical' survey recorded the presence of all native and exotic vascular plant species in a stratified random sample of stands of dry, wet and montane sclerophyll forest (sensu Austin *et al.* Unpublished manuscript). Stratification of stands was based on elevation, topographic position and aspect. The historical survey was carried out in natural vegetation relatively undisturbed by logging (i.e. < 10% felling) or fire (i.e. not burnt in the previous 10 years). Each stand was surveyed once by two experienced botanists in either the spring or summer and sampling effort was kept constant at approximately two person-hours per stand.

Of the three forest types sampled in the historical survey, WSF was the most widespread in areas currently reserved for nature conservation and forestry (i.e. 57 of the original WSF 78 stands). I then focused on these 57 WSF

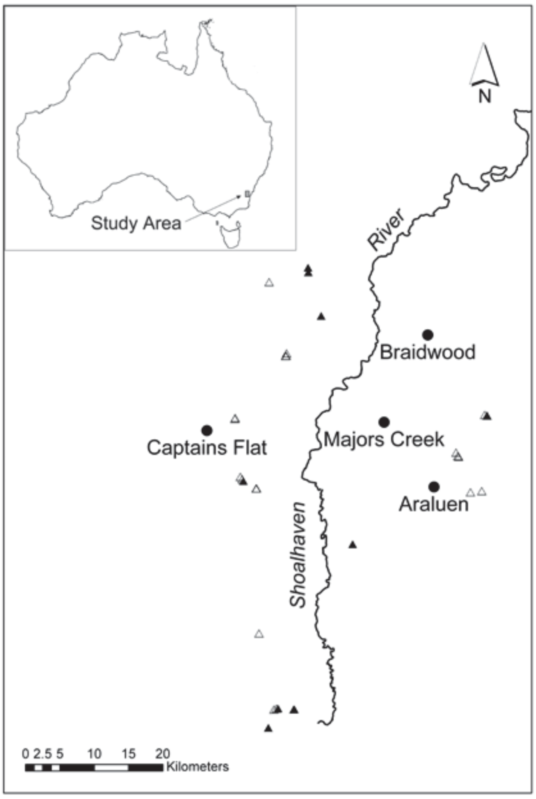

Figure 2.1 Location of the upper Shoalhaven River catchment of south-eastern Australia and the30 wet sclerophyll stands that were analysed in this study (▲ = unlogged, △ = logged).

stands in particular because of ease of access and there being reliable and long-standing records of logging and fire history for these stands.

Using GIS data (accessed from NSW National Parks & Wildlife Service and Forests NSW, 2007) and based on further ground-truthing I determined the logging and fire history of each stand in the period since the historical survey. To minimise the potentially confounding effects of both logging and relatively recent fire on plant species composition, stands which had been burnt by wildfire or by a prescribed burn in the 1998-2007 period (14 stands) or stands that could not be relocated and/or accessed (13 stands) were not considered further. From the sub-sample of 57 stands, my final design consisted of 30 stands, 10 unlogged and 20 logged stands within WSF (Figure 2.1). Of these 30 stands, in 14 of these stands there was no recorded fire since records began in 1938, in 11 stands there has not been a recorded fire since at least 1957 and in the remaining five stands there was no recorded fire after 1991 (Appendix 2).

Prior to conducting a contemporary floristic survey of these stands, I standardised taxonomic nomenclature in accordance with Harden (1992; 1993; 2000; 2002). More recent nomenclatural changes were sourced from the PlantNET website (Botanic Gardens Trust 2006a). In general, plant taxa were identified to species level in the historical inventories, however, in cases where a taxon was identified to a higher level in the taxonomic hierarchy (e.g. genus), the higher-level identification was retained.

Each stand was resurveyed in the spring and summers of 2007, mirroring the sampling methods of the historical survey as closely as possible. The contemporary survey was conducted within two weeks of the anniversary of the historical survey and recorded the presence of all native and exotic vascular plant species. Each 40 m × 40 m site within a forest stand was surveyed once by the same two observers who walked a systematic grid pattern and used consistent survey techniques. Sampling effort was kept constant at approximately two person-hours per site. Plant species that could not be readily identified in the field were sampled and then identified by botanists at the National Herbarium of New South Wales. Prior to statistical analysis of changes in vegetation composition, annual plant species (both native and exotic) were removed from consideration as this is considered the most conservative approach for determining overall assemblage-level changes (Williams *et al.* 2005b; Williams *et al.* 2006).

2.2.3 Similarity analysis

I used similarity analysis to compare historical and contemporary plant assemblages to determine if homogenization, differentiation or stasis had occurred. I initially determined changes in plant species composition of all 30 forest stands together. I then determined changes in plant species composition of the 10 unlogged stands and 20 logged stands separately. This procedure was performed for all species combined (i.e. native and exotic) as well as for native and exotic species assemblages separately.

I constructed separate species × stand matrices for both historical and contemporary assemblages using species presences and absences. The species

× stand matrices were then used to construct contemporary (J^C) and historical (J^H) stand × stand similarity matrices based on Jaccard's Index (Jaccard 1912; Koleff *et al.* 2003) in Microsoft Excel 2003. Change in Jaccard's index is commonly used in analyses of BHD (reviewed in Olden & Rooney 2006). Jaccard's index calculates the similarity between pairs of stands according to the following formula: $J_{ij} = \frac{n_{ij}}{n_i + n_j - n_{ij}}$ where n_i and n_j are the number of species present in the *i*th and *j*th stand respectively and n_{ij} is the number of species shared by both the *i*th and *j*th locations. The values computed by this index range from zero (no species in common) to one (all species in common).

I then calculated the observed Wilcoxon signed ranks test statistic (*Z*, henceforth, observed Wilcoxon *Z*-statistic) to determine the difference in the observed medians of the J^C and J^H similarity matrices (Wilcoxon 1945). Here, I calculated the observed Wilcoxon *Z*-statistic by comparing each cell in contemporary similarity matrix (J_{ij}^C) against the corresponding cell in the historical similarity matrix (J_{ij}^H). As the cells of Jaccard similarity matrices are not independent of each other (Nekola & White 1999), I used a novel approach to assess the significance of these patterns.

Using the same Monte Carlo permutation procedure as is used in the Mantel test (Mantel 1967; McCune & Grace 2002), I constructed an expected distribution of random Wilcoxon signed ranks test *Z*-statistics (henceforth, permuted Wilcoxon *Z*-statistic). The permutation process was conducted in *R* v2.8.1 and was repeated 10 000 times (Jackson & Somers 1989), giving a distribution of randomly permuted Wilcoxon *Z*-statistics. I then calculated the significance of the observed Wilcoxon *Z*-statistic using the procedure detailed in Manly (1997). Statistically significant positive values for the observed Wilcoxon *Z*-statistic indicate that the species composition of stands has become homogenized. In contrast, statistically significant negative values for the observed Wilcoxon *Z*-statistic indicate differentiation. Observed Wilcoxon *Z*-statistics which are not statistically significant indicate stasis in species composition.

Finally I calculated the observed mean change in similarity of Jaccard's Index as well as the standard error of the mean for every possible pairwise combination of stands in SPSS v14.0. The mean of the differences between all pairs (i.e. mean change in Jaccard's Index, $\Delta\bar{J}^{CH}$) was calculated to provide visual indication of the overall levels of homogenization and/or differentiation.

2.2.4 Occupancy analysis

The similarity analysis determines the magnitude and trajectory of change in β-diversity through time. However, the similarity analysis can not determine if either local extinction from and/or colonization of stands are responsible for the observed patterns of homogenization and/or differentiation. Consequently, for all 30 stands and both the unlogged and logged subsets of these stands I determined the change in the total number of stands in which each species was present (i.e. change in occupancy, $\%\Delta O$) for all species combined and for both the native and exotic species assemblages separately.

I first determined the occupancy of each species in both the historical and contemporary surveys (i.e. the total number of stands in which a species was found to be present). Then, I used the Wilcoxon signed ranks test (Wilcoxon 1945) in SPSS v14.0 to determine the direction and significance of change in occupancy for all species between the historical and contemporary surveys. Statistically significant increases in species occupancies indicated that more colonizations than local extinctions of species occurred across the catchment. Statistically significant decreases in species occupancies indicated that more local extinctions than colonizations of species occurred across the catchment. Statistically non-significant differences in species occupancies indicated colonizations and extinctions were equally important.

2.3 Results

2.3.1 Analysis of homogenization patterns for all species

The historical and contemporary surveys recorded a total of 192 plant species (184 native, 8 exotic) and 212 plant species (203 native, 9 exotic) respectively across the 30 stands. There was a significant increase in Jaccard's Index across all 30 stands indicating homogenization of forest vegetation between the historical and contemporary surveys ($\%\Delta\bar{J} = 14.9\%$, $P < 0.001$; Table 2.1;

Table 2.1 Changes in Jaccard's Indices and plant species occupancies across the 30 stands and across relevant subsets of stands for native and exotic species combined.

Stands	n^*	Change in Jaccard's Index		Wilcoxon Signed Ranks Test on change in Jaccard's Index		Change in species occupancy		Wilcoxon Signed Ranks Test on change in species occupancy	
		$\Delta\bar{J}$	$\%\Delta\bar{J}$	Z	$P^\dagger$	ΔO	$\%\Delta O$	Z	$P^\ddagger$
All stands	30	3.02×10^{-2}	14.9%	8.181	<0.001	161	17.2%	3.240	0.001
Unlogged stands	10	1.21×10^{-2}	6.9%	1.075	0.010	34	10.7%	1.642	0.100
Logged stands	20	3.90×10^{-2}	17.8%	6.386	<0.001	127	20.6%	3.347	0.001

$^*n$ refers to the number of stands. $^\dagger P$ value calculated by the permutation process outlined in the Methods section. ‡ P value calculated in SPSS v14.0.

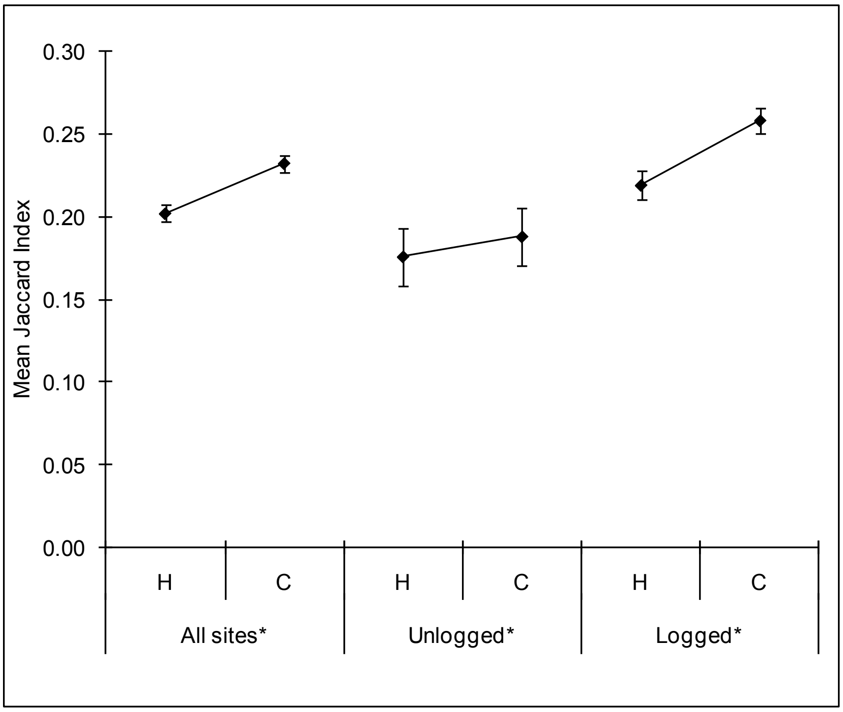

Figure 2.2 Mean Jaccard's Index (± SE) for the historical (H) and contemporary (C) assemblages for all species across the 30 stands and for subsets of these stands.

* indicates a significant difference between contemporary and historical assemblages, Table 2.1.

Figure 2.2). The median increase in occupancy was significantly greater than zero, suggesting that more species increased in occupancy than decreased between the two survey periods (%ΔO = 17.2%, P = 0.001; Table 2.1). This finding demonstrates the importance of colonization of stands over local extinctions in generating broad-scale homogenization across the catchment.

There was a significant increase in Jaccard's Index for both unlogged and logged stands between the two survey periods indicating that changes in species composition at both the 10 unlogged and 20 logged stands contributed to the pattern of homogenization observed across all 30 stands (Table 2.1; Figure 2.2). However, the change in species composition at the logged stands was of 2.5× greater magnitude than that of the unlogged stands (Unlogged: %$\Delta\bar{J}$ = 6.9%, P = 0.010; Logged: %$\Delta\bar{J}$ = 17.8%, $P < 0.001$; Table 2.1; Figure 2.2). For unlogged stands there was no significant increase in species occupancies for all species combined between the two survey periods indicating that both colonizations of and local extinctions from stands contributed to observed

Table 2.2 Changes in Jaccard's Indices and plant species occupancies across the 30 stands and across relevant subsets of stands for native and exotic species considered separately.

Stands	n^*	Species	Change in Jaccard's Index		Wilcoxon Signed Ranks Test on change in Jaccard's Index		Change in species occupancy		Wilcoxon Signed Ranks Test on change in species occupancy	
			$\Delta\bar{J}$	$\%\Delta\bar{J}$	Z	$P^\dagger$	ΔO	$\%\Delta O$	Z	$P^\ddagger$
All stands	30	Native	2.86×10^{-2}	13.7%	7.605	<0.001	144	15.9%	2.925	0.003
		Exotic	1.11×10^{-1}	197.0%	7.922	0.004	17	60.7%	1.720	0.085
Unlogged stands	10	Native	1.38×10^{-2}	7.8%	1.137	0.014	29	9.2%	1.387	0.165
		Exotic	7.41×10^{-4}	0.7%	0.137	0.086	5	100.0%	2.236	0.025
Logged stands	20	Native	3.68×10^{-2}	16.2%	5.831	<0.001	115	19.4%	3.138	0.002
		Exotic	1.35×10^{-1}	269.7%	6.732	0.002	12	52.2%	1.164	0.245

[*] n refers to the number of stands. [†] P value calculated by the permutation process outlined in the Methods section. [‡] P value calculated in SPSS v14.0

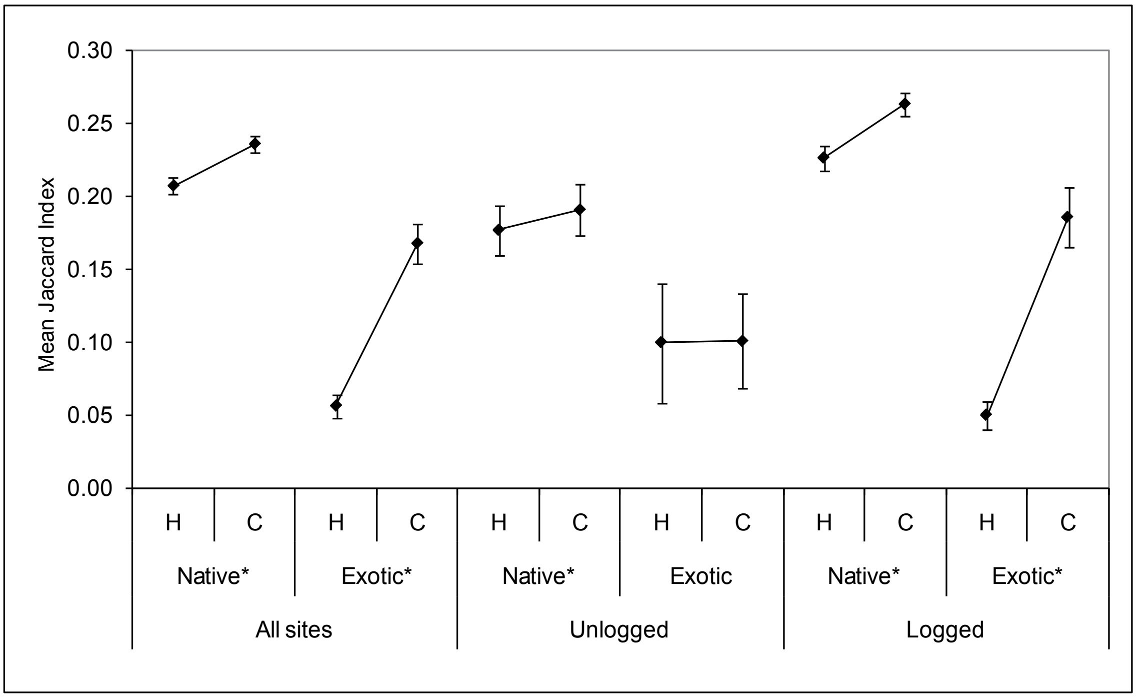

Figure 2.3 Mean Jaccard's Index (± SE) for the historical (H) and contemporary (C) assemblages for native and exotic species considered separately across the 30 stands and for subsets of these stands.

* indicates a significant difference between contemporary and historical assemblages, Table 2.2.

patterns of homogenization (%ΔO = 10.7%, $P = 0.100$; Table 2.1). However, a significant increase in species occupancies for all species combined in logged stands between the two survey periods again indicated that colonization of stands was relatively more important than local extinctions of species in generating homogenization for these stands (%ΔO = 20.6%, $P < 0.001$; Table 2.1).

2.3.2 Analysis of homogenization patterns for native and exotic species assemblages

Across all 30 stands, there was a significant increase in Jaccard's Index for both the native and exotic species assemblages indicating homogenization (Native: %$\Delta \bar{J}$ = 13.7%, $P < 0.001$; Exotic: %$\Delta \bar{J}$ = 197.0%, $P = 0.004$; Table 2.2; Figure 2.3). Native species occupancies increased significantly between the two survey periods, suggesting that colonization of stands by native species contributed to generating observed homogenization ($\%\Delta O = 15.9\%$, $P = 0.003$; Table 2.2). However, for exotic species both colonizations of and local extinctions from the 30 stands contributed to patterns of homogenization as there was no significant change in exotic species occupancies ($\%\Delta O = 60.7\%$, $P = 0.085$; Table 2.2).

In the 10 unlogged stands there was a significant increase in Jaccard's Index for native species but there was no significant change in Jaccard's Index for exotic species (Native: $\%\Delta\bar{J} = 7.8\%$, $P = 0.014$; Exotic: $\%\Delta\bar{J} = 0.7\%$, $P = 0.086$; Table 2.2; Figure 2.3). This finding indicates that only native species homogenized the species composition of unlogged stands. Interestingly there was no significant change in native species occupancies, indicating that both colonizations of and local extinctions of native species from unlogged stands produced observed patterns of homogenization ($\%\Delta O = 9.2\%$, $P = 0.165$; Table 2.2). As the change in Jaccard's Index for exotic species was not significant, the change in occupancy of exotic species was not considered further.

There was a significant increase in Jaccard's Index for both natives and exotics in the 20 logged stands suggesting that both native and exotic species contributed to the homogenization of these stands (Native: $\%\Delta\bar{J} = 16.2\%$, $P < 0.001$; Exotic: $\%\Delta\bar{J} = 269.7\%$, $P = 0.002$; Table 2.2; Figure 2.3). A significant increase in native species occupancies suggested that colonizations by native species contributed to the homogenization of logged stands ($\%\Delta O = 19.4\%$, $P = 0.002$; Table 2.2). Also, no significant change in exotic species occupancies indicated that both colonizations of and local extinctions of exotic from logged stands contributed to homogenization of logged stands ($\%\Delta O = 52.2\%$, $P = 0.245$; Table 2.2).

2.4 Discussion

My results demonstrate that WSF in the upper Shoalhaven River catchment of south-eastern Australia have become homogenized over a period of four decades. Both unlogged and logged stands throughout the catchment have become homogenized over the course of the study, with the colonization and extinction of both native and exotic plant species contributing to this. Colonization leads to homogenization when the same plant species are gained by assemblages that have historically different compositions (Rahel 2002; Olden & Poff 2003). Conversely, extinction generates homogenization when different plant species are lost from assemblages that are historically different, thereby further creating two similar contemporary assemblages (Rahel 2002; Olden & Poff 2003). Although much attention is often paid to the homogenizing effect of exotic plant species (e.g. McKinney 2004a; Qian & Ricklefs 2006), my results are similar to those of Rooney *et al.* (2004) who showed that both native and exotic plant species can contribute to homogenization in forests.

In unlogged stands, homogenization has been generated by both colonization by and local extinction of native species. The likely cause of these changes may be the low incidence of fire in the study areas relative to that of the surrounding landscape (State Forests of New South Wales 1995). Indeed, 90% of the unlogged stands have not been burnt since 1954 or earlier (Appendix 2). However, sclerophyllous eucalypt forest is adapted to fire and many species require fire to regenerate (Gill *et al.* 1981; Bradstock *et al.* 2002). Regeneration of forest following a natural disturbance such as wildfire or tree-fall (resulting in gap formation) follows a temporal sequence of natural phases in community assembly (Noble & Slayter 1981; Whitmore 1982; Attiwill 1994; Barnes *et al.* 1998; Thomas & Packham 2007). Consequently, changes in species composition have resulted from natural succession generated by the long inter-fire interval of unlogged WSF stands. Such changes have arisen independently of the logging regime. This result supports earlier work in dry sclerophyll forest which found that declines in plant species richness independent of any disturbance may represent a response to time since the last fire (Penman *et al.* 2008).

A key question is, does evidence for the current, long inter-fire intervals within the study area represent a change in the long-term, pre-European fire regime? Within the catchment there are no high resolution studies of recent (i.e. Holocene) microcharcoal deposits which might detail the long-term fire history of region. However, high resolution pollen and microcharcoal records at a number of mires approximately 70 km west of the catchment (Hope 2006; Hope & Clark 2008) and Bega Swamp approximately 80 km to the south-east of the catchment (Hope 2009, *pers. com.*) indicate that significant changes in fire regime since European settlement of the region. Microcharcoal deposition indicates regular fires up until European settlement (Hope 2003). Following settlement, microcharcoal initially increased following the loss of indigenous fire management practices and increased use of fire by pastoralists in some but not all of these swamps (Hope 2006; Hope & Clark 2008). However, following the creation of conservation reserves and the imposition of preventative and suppressive fire management practices, the frequency of fire has been reduced (Hope & Clark 2008).

In logged stands, homogenization has resulted from colonization of both native and exotic plant species, as well as local extinction of exotic plant species. In logged stands, changes in species composition might have resulted from either logging alone or, alternatively, an interaction of logging together with the long inter-fire interval. As with the unlogged stands, the logged stands have also experienced long inter-fire intervals. Most stands have not been burnt since 1957 or earlier (Appendix 2). However, given the significant level of disturbance created by modern logging practices it is possible that logging alone is responsible for changes in species composition.

Empirical evidence from WSF suggests that the natural phases of community succession are modified by logging (Ough 2001) and are frequently accompanied by changes in plant species composition and abundance (Hickey 1994; Chesterfield 1996; Murphy & Ough 1997; Ough 2001; Ough & Murphy 2004; Serong & Lill 2008). The largest changes in plant species composition tended to occur in the second and third decades following logging (Serong & Lill 2008). Thus, it is likely that homogenization of the stands in my study is closely linked to the disruption of the natural phases of community succession by logging.

Studies that have investigated the effect of major disturbance such as logging or wildfire in sclerophyllous forest have commonly used change in plant species richness (i.e. α-diversity) over time as the metric by which to measure changes in plant species biodiversity (e.g. Hickey 1994; Penman *et al.* 2008; Serong & Lill 2008). From a methodological perspective, plant species richness is important because it is relatively easy to measure and species is the unit most often used in conservation, management and legislation (Gaston & Spicer 2004). However, the results of my study suggest that change in α-diversity through time should not be the only metric by which to measure changes in plant species biodiversity. Indeed, the use of β-diversity, which measures change in plant species composition in both space and time, provides a rich description of change in plant species diversity and a is useful and reliable metric by which to measure change in biodiversity of multiple stands across a region.

However, patterns of homogenization and differentiation as measured by the change β-diversity over time are affected by a complicated set of factors. Change in β-diversity over time can be brought about by changes in species composition, and so varies according to identity and number of species that have become extinct from and/or colonized species assemblages and to a far lesser extent the species richness (i.e. α-diversity) of recipient species assemblages (Olden & Poff 2003). Also, the influence of extinctions and invasions on changes in species composition has been found to vary with spatial scale and the degree of initial spatial aggregation and distribution of species populations (Olden & Poff 2003; Cassey *et al.* 2006; Rooney *et al.* 2007). In addition to the spatial factors above, patterns of change in β-diversity over time are also likely to be affected by the temporal scale at which observations are made (Olden & Poff 2003).

I have shown here that WSF vegetation stands in south-eastern Australia have become more similar to each other (homogenized) over time. Homogenization has occurred irrespective of the disturbance regime, but the degree of homogenization was greater among logged compared to unlogged stands. In logged stands these changes were the cumulative result of colonization by natives and exotics as well as the local extinction of exotics. In unlogged stands changes were brought about by both the colonization and local extinction of natives. Having identified the patterns and causes of homogenization in WSF at a regional scale, there is a need to investigate patterns and at other spatial scales and in other vegetation associations.

3 Have human activities homogenized woodlands and forests of south-eastern Australia at a regional scale?

3.1 Introduction

Over the last two centuries, with pressure from human populations, industrialization and changing cultural practices, the resources of wooded regions around the world have been increasingly exploited (Williams 2003). Human activities, such as forestry and land clearing, have contributed to the extinction of native species (Vitousek *et al.* 1997). Facilitated by these human activities, colonization by exotic species also threatens areas of woody vegetation around the world (Liebhold *et al.* 1995; Krcmar-Nozic *et al.* 2000; Cox *et al.* 2001).

Changes in the composition of vegetation assemblages brought about by plant extinctions and colonizations may change the β-diversity, i.e. species turnover (Whitaker 1972), of wooded vegetation assemblages, i.e. woodland and forest, over time. The β-diversity of wooded vegetation may decrease becoming more similar (homogenized) over time (Olden & Rooney 2006), or, alternatively, the β-diversity of wooded vegetation may increase becoming less similar (differentiated) over time (Olden & Rooney 2006). However, it is also possible that β-diversity remains in stasis.

Studies that have pooled data from multiple and undefined vegetation assemblages have provided empirical support for homogenization (McKinney 2004a; c; Kühn & Klotz 2006; Qian & Ricklefs 2006; Schwartz *et al.* 2006; Castro *et al.* 2007; McKinney & La Sorte 2007; Castro & Jaksic 2008b), and differentiation (McKinney 2004a; 2005; Kühn & Klotz 2006; McKinney 2006; Qian & Ricklefs 2006), as well as stasis (Castro & Jaksic 2008a) in the species composition of vegetation assemblages. A number of the above studies have ascribed patterns of homogenization and differentiation to patterns of human population density and the process of urbanization (e.g. Kühn & Klotz 2006; McKinney 2006; Olden *et al.* 2006; Schwartz *et al.* 2006). However, apart from my study in Chapter 2, a limited number of studies from North America and Europe have investigated the underlying mechanistic effects of human activity on patterns of homogenization and differentiation in a specific vegetation association (e.g. wooded vegetation, as in Rooney *et al.* 2004; Schulte *et al.* 2007). Consequently, there has been scant advancement in our knowledge of how patterns of homogenization and differentiation in specific vegetation associations might be associated with environmental (Olden 2006), geographical or specific drivers of change associated with human land-use (e.g. change in human population density, settlement time). The purpose of this chapter is to address the above issue.

Patterns of homogenization and differentiation are likely to be affected by spatial factors including the degree of initial spatial aggregation, the distribution of native populations and spatial scale (Olden & Poff 2003; Cassey *et al.* 2006; Rooney *et al.* 2007). For instance, across Europe urban floras exhibit scale-related distribution patterns. When compared to native species, exotics introduced after 1500 AD demonstrate stronger distance decay patterns and higher β-diversity, however, exotics introduced before 1500 AD indicate weaker distance decay patterns and lower β-diversity (La Sorte *et al.* 2008). Furthermore, empirical evidence indicates that exotic species have a different impact on β-diversity than do native species depending on their geographic origin and time of introduction (Kühn & Klotz 2006). Exotic species introduced to Europe after 1500 AD exhibit a differentiating effect (i.e. higher change in β-diversity) whilst those introduced before 1500 AD have a homogenizing effect (i.e. lower change in β-diversity; Kühn & Klotz 2006). With these patterns in mind, here I also investigate if there are any patterns of homogenization and differentiation for both native and exotic that can be related to geographic distance.

As a continent relatively recently settled by Europeans, Australia provides a unique natural experiment by which to evaluate the generalities of trends in the processes of plant extinction and colonization that may ultimately lead to the homogenization of native wooded vegetation. In the relatively short time since European settlement in 1788, almost 45% of the original 728 000 km^2 area covered by woodland and forest vegetation in south-eastern Australia has been fully or partially cleared for human settlement, forestry and agriculture (National Land and Water Resources Audit 2001). Further changes to vegetation assemblages have been brought about by the naturalization of over 1700 exotic plant species and extinction of 36 native plant species (NSW Scientific Committee 2004; Botanic Gardens Trust 2006b) across the region.

Within the context of these fundamental changes to wooded vegetation in south-eastern Australia since European settlement, in this chapter I examine changes in plant species composition of at a larger spatial (continental) and longer temporal scale (c. 220 years) than in Chapter 2. Changes in plant species composition within woodland and forest vegetation in 20 conservation reserves across a broad region of south-eastern Australia are compared to determine if the processes of colonization and extinction have resulted in the species composition of these vegetation assemblages becoming more or less similar since European settlement. I have addressed the four questions below : (1) Has extinction of native plants and colonization by exotic plants generated homogenization, differentiation or stasis? (2) Are there differences between two different vegetation associations, woodland and forest, with respect to patterns of homogenization and differentiation? (3) Are there any relationships between patterns of homogenization and differentiation and the geographic distance separating reserves? (4) Are there geographic and human correlates of change in the taxonomic composition of woodland and forest assemblages in south-eastern Australia?

3.2 Methods

3.2.1 Plant species assemblages in woodland and forest

I first conducted a literature search for recent (post-1990) vegetation studies containing inventories of all vascular plant species of areas reserved for nature conservation (e.g. national parks and nature reserves) in south-eastern Australia. These inventories documented the presence of both native and exotic species. I focused on two vegetation associations, woodland and forest, because they are the most highly represented in this region. The classification of woodland and forest vegetation was based on life form, height and projected foliage cover of the tallest stratum (Specht 1970). Trees >5 m in height form the tallest stratum of both woodlands and forests, but the projected foliage cover of trees is <30% in woodlands and >30% forests.

The literature search allowed me to construct a database of contemporary woodland and forest species assemblages using inventories from a total of 20 conservation reserves (Figure 3.1; Appendix 3). These conservation reserves and the woodland and forest vegetation protected therein are representative of the remnant vegetation from the bioregions in which the reserves are located. From the detailed notes accompanying each inventory (Appendix 3) and other work in the region (Benson 1991; Hunter 2002a), it is likely that many of the woodland and forest remnants within these reserves have been affected to some extent by human activity.

Woodland assemblages in 20 reserves and forest assemblages in 12 reserves were used to assess patterns of change in the composition of vegetation. In general, the inventories I sourced for the contemporary databases identified plant taxa to species level. However, in cases where a taxon was identified to a lower level in the taxonomic hierarchy (e.g. subspecies, variety, form), the lower-level identification was retained if there was consistent usage of a lower-level name across all of the studies in which the taxon was cited. Prior to analysis, taxonomic nomenclature was standardized in accordance with Harden (1992; 1993; 2000; 2002). For more recent changes in nomenclature I consulted the PlantNET website (Botanic Gardens Trust 2006b).

The species composition of these contemporary assemblages was compared with historical assemblages. I employed a standard reconstruction technique (Rahel 2000; Marchetti *et al.* 2001; Taylor 2004; Castro *et al.* 2007; Castro & Jaksic 2008a) to reconstruct the historical species composition of woodland and forest assemblages in each reserve by both removing exotic species from the contemporary inventory and adding extinct native species.

Native species lost to extinction from woodland and forest vegetation in the study area were those gazetted under the NSW Threatened Species Conservation Act (NSW Scientific Committee 2004). Historical occurrences of extinct species in woodland and/or forest vegetation were determined from species habitat descriptions (Botanic Gardens Trust 2006b; Department of Environment and Conservation NSW 2006). The historical occurrence of an extinct species within the bioregion where a reserve is located (the IBRA scheme, Thackway & Cresswell 1995) was determined from herbarium records (Botanic Gardens Trust 2006b; Council of Heads of Australian Herbaria 2006).

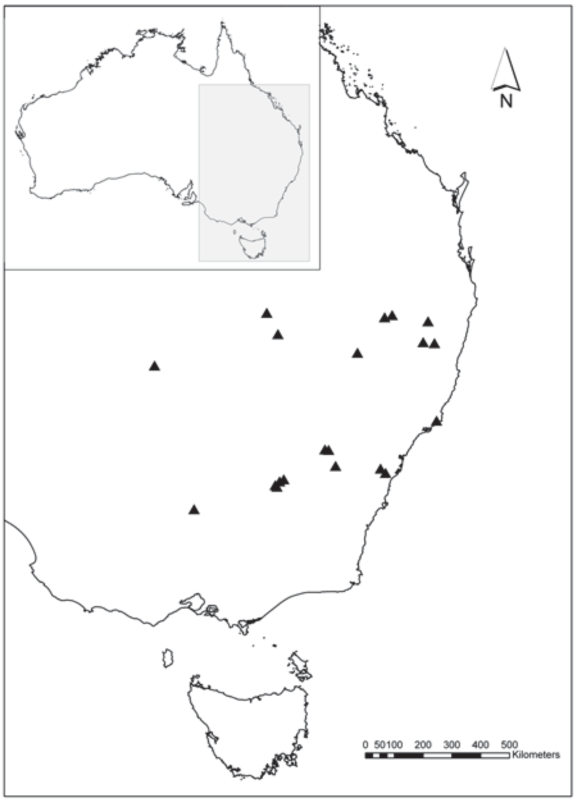

Figure 3.1. Location of the 20 conservation reserves in south-eastern Australia in which the woodlands and forests analysed in this study are located.

I assumed that if an extinct native species was found to occur in the woodland and/or forest vegetation of a specific bioregion, that species also occurred in the woodland and/or forest vegetation of a particular reserve in that bioregion. Extinct native species known to occur in vegetation types other than woodland or forest, and those extinct species known to have an extremely limited distribution and presumed not to have occurred at the selected reserves, were not added to inventories. For both woodland and forest assemblages I also constructed an inventory of only the native species occurring in each conservation reserve. These inventories were used in the statistical analyses to separate the effects of the extinction of native species and the colonization of exotic species in driving either homogenization or differentiation.

3.2.2 Human correlates of change in the species composition of assemblages

For each conservation reserve, I assembled data for two geographic variables (latitude and longitude) and two human variables (human population density and time since European settlement) that might be associated with temporal change in species composition of plant assemblages. I hypothesized that the variables latitude and longitude could act as surrogates for underlying climatic variables (e.g. temperature, precipitation) for which there are no records over the time scale of this study.

Assuming zero European human population density at the time of European settlement, I ascertained change in European human population density for the region surrounding each conservation reserve using data from the 2001 Census of Population and Housing in MapInfo Professional Version 7.0 (Australian Bureau of Statistics 2003). For each conservation reserve, I first determined the human population of each Census Collection District (CCD) whose centroid fell within a circular area of a 25 km radius of the centre of each reserve. I then determined the geographic area of each of these CCDs. Finally, I calculated the human population density by dividing the sum of the human population for all CCDs within the circular area by the total area of all CCDs (Appendix 3). Time since European settlement (settlement time) was calculated from records of settlement dates of the region surrounding each reserve accompanying contemporary species inventories or from local government records (Appendix 3).

3.2.3 Statistical analysis: Change in similarity

For woodland and forest vegetation I constructed species × reserve matrices for both contemporary and historical assemblages using the presence and absence of plant species. The species × reserve matrices were then used to construct reserve × reserve similarity matrices for the contemporary and historical assemblages separately. I employed Jaccard's Index (Jaccard 1912; Koleff *et al.* 2003) to create a Jaccard similarity matrix that reflected the compositional similarity between each pair of reserves. The values of Jaccard's Index range from zero (no species in common) to one (all species in common).

To assess temporal changes in the composition of assemblages, I calculated the difference between respective points in the historical and contemporary Jaccard similarity matrices. Positive values indicated that plant species composition of pairs of reserves have become homogenized, negative values indicated that assemblages have become differentiated and no change indicated stasis. The mean of the differences between all pairs (i.e. mean change in Jaccard's Index, $\Delta\bar{J}$) was calculated to assess overall levels of homogenization and differentiation.

As the cells of Jaccard similarity matrices are not independent of each other (Nekola & White 1999), I used a novel approach to assess the significance of these patterns. First I calculated the observed Wilcoxon signed ranks test statistic (Z) (henceforth, observed Wilcoxon Z-statistic) to determine the difference in the observed medians of the historical and contemporary Jaccard similarity matrices (Wilcoxon 1945). The same Monte Carlo permutation technique was then used as the Mantel test (Mantel 1967; Sokal 1979; McCune & Grace 2002) to construct an expected distribution of random Wilcoxon signed ranks test Z-statistics (permuted Wilcoxon Z-statistic). To construct the expected distribution I simultaneously permuted the rows and columns of the historical Jaccard similarity matrix and recalculated the permuted Wilcoxon Z-statistic. The permutation process was repeated 10 000 times (Jackson & Somers 1989), giving a distribution of randomly permuted Wilcoxon Z-statistics. Permutations were conducted in Microsoft Excel 2003 using the PopTools v2.7.5 add-in (Hood, 2006). PopTools uses the Mersenne Twister pseudo-random number generator (Matsumoto & Nishimura 1998), thus avoiding the documented problems with Microsoft Excel 2003's built-in pseudo-random number generator (Knfisel 1998; McCullough & Wilson 2005).

3.2.4 Statistical analysis: Geographical distance and patterns of change in similarity

For both woodland and forest vegetation I assessed the effect of geographical distance between reserves on observed patterns of homogenization and differentiation. The distance (km) between each pair of reserves was calculated, then for each pair of reserves the change in similarity (i.e. change in Jaccard's index, $Ln\Delta J$) was log-transformed (Ln plus 1). Next, simple linear regression was used to calculate the rate of change in Jaccard's index per unit distance (i.e. the slope of the regression line). Given that the cells of Jaccard similarity matrices are not independent of each other, I used randomization to assess the significance of the simple regression models (Nekola & White 1999). The significance of these patterns was determined using Mantel tests (Manly 1997) with 9 999 permutations (Jackson & Somers 1989) performed in Microsoft Excel 2003 using the PopTools v2.7.5 add-in (Hood, 2006).

3.2.5 Statistical analysis: Geographic and human correlates of patterns of change in similarity

For the geographic (longitude and latitude) and human (human population density and settlement time) variables, I assessed the effect of those variables on observed patterns of change in similarity. For each pair of reserves, the change in similarity (i.e. change in Jaccard's index, $Ln\Delta J$) was first log-transformed (Ln plus 1). For the longitude, latitude and settlement time, simple linear regression was used to calculate the rate of change in Jaccard's Index per unit difference in longitude and latitude settlement time between reserves. For human population density I first log-transformed (Ln plus 1) the difference in human population density before using simple linear regression to calculate the rate of change in Jaccard's Index per unit difference in the logarithm of human population density. Mantel tests (Manly 1997) with 9 999 permutations (Jackson & Somers 1989) performed in Microsoft Excel 2003 using the PopTools v2.7.5 add-in (Hood, 2006) were used to determine the significance of each regression.

3.3 Results

3.3.1 Native plant extinctions and exotic plant colonizations

Woodland vegetation across south-eastern Australia was colonized by 225 exotic plant species and an estimated 18 native plant species have become extinct since European settlement (Table 3.1). In the same time period, forest vegetation was colonized by 138 exotic plant species, while only 11 native plant species have become extinct (Table 3.1).

Table 3.1 Historical and contemporary species richness for the native, exotic and total floras of woodland and forest assemblages in this study.

Association/flora	Historical Species Richness	Contemporary Species Richness
Woodland		
Native	1449	1431
Exotic	0	225
Total	1449	1659
Forest		
Native	1173	1162
Exotic	0	138
Total	1173	1300

3.3.2 Analysis of homogenization and differentiation patterns

Analysis of observed composition patterns for all species revealed a significant decrease in similarity of both woodland ($\%\Delta\bar{J} = -4.82\%$, $P<0.001$, Table 3.2) and forest vegetation ($\%\Delta\bar{J} = -2.83\%$, $P<0.001$; Table 3.2), suggesting that the composition of both vegetation types have become differentiated since European settlement.

There was a significant decrease in Jaccard's Index for both natives ($\%\Delta\bar{J} = -1.57\%$, $P<0.001$; Table 3.2), and exotics ($\%\Delta\bar{J} = -3.30\%$, $P<0.001$; Table 3.2) in woodland assemblages, indicating that both the extinction of native plant species and colonization of exotic plant species have contributed to differentiation of woodland vegetation. However, in forest vegetation there was a significant decrease in Jaccard's Index for natives ($\%\Delta\bar{J} = -2.80\%$, $P<0.001$; Table 3.2) but not exotics ($\%\Delta\bar{J} = -0.03\%$, $P>0.05$; Table 3.2). This result suggests that only the extinction of native plant species has been the principal contributor to differentiation of forest vegetation.

3.3.3 Analysis of geographic distance and patterns of change in similarity

In woodland vegetation, change in Jaccard's Index significantly increased with geographic distance between pairs of reserves for native and exotic species together ($r^2 = 0.109$, $P<0.001$), and for native ($r^2 = 0.095$, $P<0.01$) and exotic ($r^2 = 0.054$, $P<0.01$) species separately (Table 3.3, Figure 3.2). Similarly, the change in Jaccard's Index in forest vegetation significantly increased with geographic distance between pairs of reserves for native and exotic species together ($r^2 = 0.078$, $P<0.05$) and for native ($r^2 = 0.101$, $P<0.05$) species separately (Table 3.3, Figure 3.2). However, there was no significant relationship between change in Jaccard's Index and geographic distance between pairs of reserves for exotic species ($r^2 = 0.011$, $P>0.05$) in forest vegetation (Table 3.3, Figure 3.2).

These results suggest that, although overall the species composition of woodland and forest vegetation have become differentiated since European settlement, pairs of reserves become homogenized at an exponential rate with increasing geographic distance between reserves.

3.3.4 Geographic and human correlates and patterns of change in similarity

In woodland vegetation, change in Jaccard's Index significantly increased for natives with longitudinal ($r^2 = 0.064$, $P<0.05$) and latitudinal ($r^2 = 0.034$, $P<0.05$) separation between pairs of reserves (Table 3.4). However, there was no significant relationship between change in Jaccard's Index and human population density ($r^2 = 0.019$, $P>0.05$) or settlement time ($r^2 = 0.013$, $P>0.05$) for natives (Table 3.4). For exotics, change in Jaccard's index also significantly increased with longitudinal separation ($r^2 = 0.049$, $P<0.05$), but there was no significant relationship with latitudinal separation ($r^2 = 0.007$, $P>0.05$), human population density ($r^2 = 0.002$, $P>0.05$) or settlement time ($r^2 = 0.018$, $P>0.05$; Table 3.4).

In forest vegetation there was no significant relationship between change in Jaccard's Index and any of the geographic or human variables for

Table 3.2 Observed change in Jaccard's Index, permuted Wilcoxon *Z*-statistic and observed Wilcoxon *Z*-statistic for all species, native species and exotic species in both woodland and forest vegetation.

Association	n	Species	Observed change in Jaccard's Index		Permuted Wilcoxon *Z*-statistic			Observed Wilcoxon *Z*-statistic	
			$\Delta\bar{J}$	$\%\Delta\bar{J}$	$\bar{Z}$	$P_{2.5}$	$P_{97.5}$	Z	P
Woodland	20	All	-4.58×10^{-3}	−4.82%	−0.594	−1.081	−0.121	−6.575	<0.001
		Native	-1.49×10^{-3}	−1.57%	−0.194	−0.671	0.278	−5.744	<0.001
		Exotic	-3.09×10^{-3}	−3.30%	−0.393	−0.888	0.079	−5.046	<0.001
Forest	12	All	-3.26×10^{-3}	−2.83%	−0.240	−0.806	0.295	−1.739	<0.001
		Native	-3.23×10^{-3}	−2.80%	0.034	−0.525	0.596	−3.058	<0.001
		Exotic	-3.43×10^{-5}	−0.03%	−0.271	−0.826	0.264	−0.021	0.348

Sample size '*n*' refers to the number of conservation reserves.

Table 3.3 Simple regression of change in similarity ($\Delta Ln\bar{J}$) against geographic distance (km) separating reserves for all species, native species and exotic species in both woodland and forest vegetation.

Association	n	Species	Simple regression model			Mantel Test
			Intercept	Slope	r^2	P
Woodland	190	All	-1.01×10^{-2}	2.64×10^{-6}	0.109	<0.001
		Native	-3.55×10^{-3}	4.73×10^{-6}	0.095	0.002
		Exotic	-6.55×10^{-3}	7.90×10^{-6}	0.054	0.008
Forest	66	All	-1.00×10^{-2}	1.66×10^{-5}	0.078	0.045
		Native	-8.42×10^{-3}	1.28×10^{-5}	0.101	0.018
		Exotic	-1.55×10^{-3}	3.69×10^{-6}	0.011	0.464

Sample size ‘*n*’ refers to the number of pairwise comparisons of conservation reserves.

natives (Table 3.4). Similarly, there was no significant relationship between change in Jaccard’s Index and longitude, human population density and settlement time for exotics (Table 3.4). However, there was a significant relationship between change in Jaccard’s Index and latitude ($r^2 = 0.054$, $P<0.05$; Table 3.4).

3.4 Discussion

The results of this study demonstrate that the species composition of woodland vegetation in 20 conservation reserves and forest vegetation in 12 conservation reserves that span the breadth of south-eastern Australia have become differentiated since European settlement. Further, woodland and forest vegetation have experienced different rates of change in species composition (Table 3.2). It is evident that the patterns of native plant extinction and exotic plant colonization, which have resulted in differentiation of woodland and forest vegetation, are different in similar types of wooded

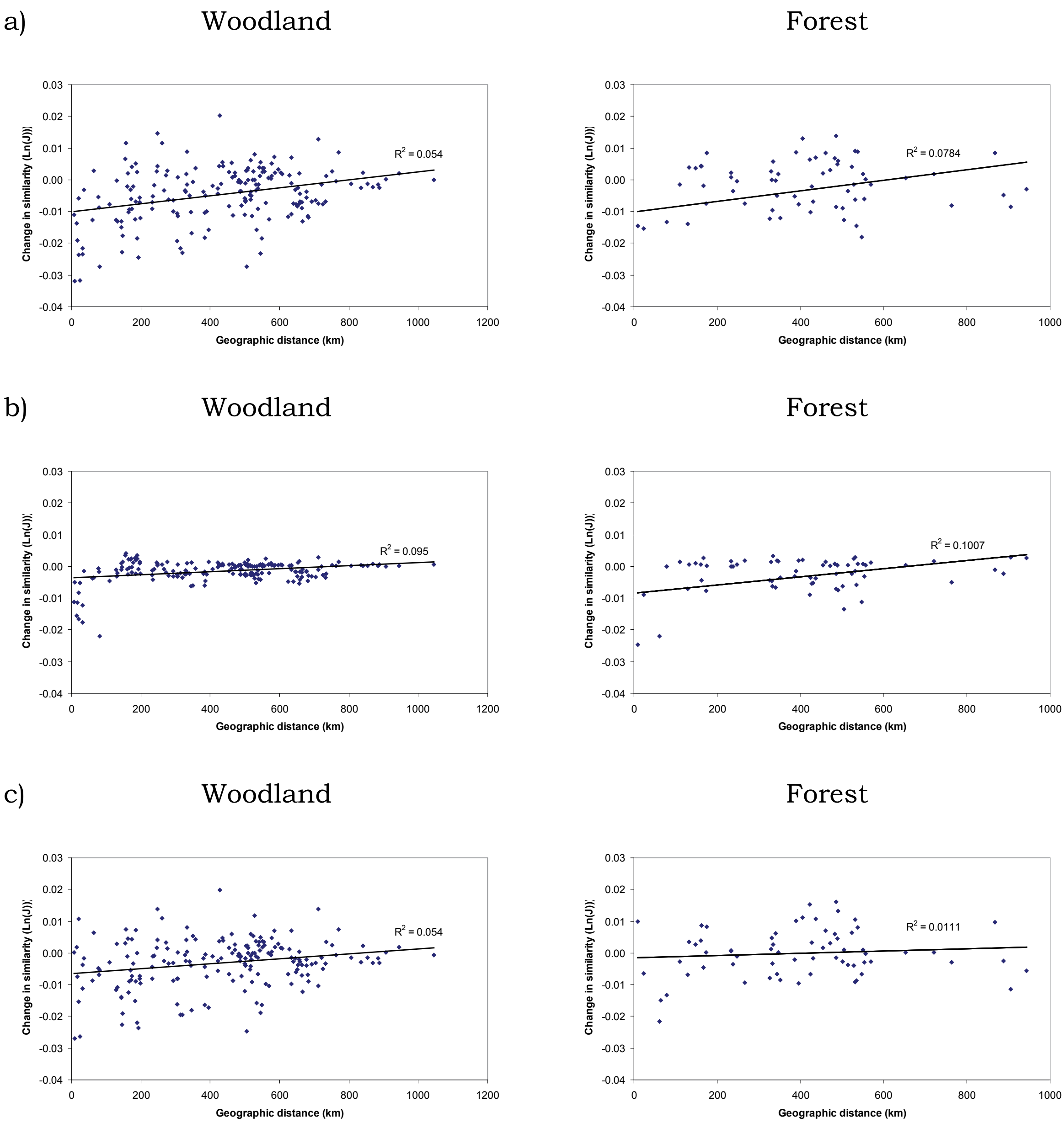

Figure 3.2 Change in similarity (ΔLnJ) since European settlement plotted against geographic distance (km) separating reserves for a) all species; b) native species; and c) exotic species in both woodland and forest vegetation.

Table 3.4 Simple regression of change in similarity (ΔLnJ) for native and exotic species in both woodland and forest vegetation.

Association	n		Native species				Exotic species			
			Simple regression model			Mantel Test	Simple regression model			Mantel Test
		Independent variable*	Intercept	Slope	r^2	P	Intercept	Slope	r^2	P
Woodland	190	LON	-2.70×10^{-3}	4.21×10^{-4}	0.064	0.010	-5.45×10^{-3}	8.12×10^{-4}	0.049	0.014*
		LAT	-2.38×10^{-3}	3.42×10^{-4}	0.034	0.030	-4.01×10^{-3}	3.43×10^{-4}	0.007	0.218
		lnPD	-1.98×10^{-3}	2.74×10^{-4}	0.019	0.198	-3.43×10^{-3}	1.73×10^{-4}	0.002	0.688
		ST	-1.96×10^{-3}	2.68×10^{-5}	0.013	0.262	-1.94×10^{-3}	-6.84×10^{-5}	0.018	0.220
Forest	66	LON	-5.65×10^{-3}	1.28×10^{-3}	0.035	0.174	-2.07×10^{-3}	1.08×10^{-3}	0.033	0.190
		LAT	-4.64×10^{-3}	6.13×10^{-3}	0.014	0.346	-2.42×10^{-3}	1.05×10^{-3}	0.054	0.044
		lnPD	-2.89×10^{-3}	-2.08×10^{-4}	0.002	0.722	-1.90×10^{-3}	1.01×10^{-3}	0.054	0.128
		ST	-4.98×10^{-3}	8.76×10^{-5}	0.033	0.370	1.87×10^{-5}	-4.14×10^{-6}	0.000	0.918

* Independent variables are longitude (LON), latitude (LAT), human population density (PD) and settlement time (ST). Sample size ‘*n*’ refers to the number of pairwise comparisons of conservation reserves.

vegetation. Both the extinction of native plant species and colonization by exotic plant species contributed to differentiation of woodland vegetation across the region. However, only the extinction of native species contributed to the differentiation of forest vegetation. My findings indicating that woodland and forest vegetation have become differentiated are supported by empirical evidence for differentiation at regional and continental scales from data pooled across unspecified vegetation types (McKinney 2004a; 2005; Kühn & Klotz 2006; Qian & Ricklefs 2006). My results also suggest that pooling data across different and unspecified vegetation types may obscure actual patterns of change in plant species composition.

In this study I used the standard reconstruction technique to reconstruct the species composition of the woodland and forest assemblages at the reserves that are the subject of this study. Consequently, I used data sources of a different spatial scale because these were the only data available (i.e. reserve scale contemporary inventories of native and exotic species and bioregional scale inventories of extinct species). As a result, my findings may overstate species extinctions and thus need to be interpreted with care (See Section 1.2.5.1). Also note, I explicitly address the above issue in Chapter 4). Rather than providing an absolute estimate of change, I draw conclusions on the trajectory of change in similarity of species composition over time in woodland and forest vegetation at the reserves in question.

In woodland, the propensity of both native plant extinctions and exotic plant colonizations to differentiate the species composition of reserves is promoted by shorter geographic distance between reserves, i.e. reserves that are closer together are more differentiated than those further apart (Figure 3.2, Table 3.3). Evidence for the differentiating effect of exotic species for areas that are closer together has also been found at continental and global scales (Rejmánek 2000; McKinney 2004a; Pyšek & Richardson 2006; Qian & Ricklefs 2006). In forest, the tendency of native plant extinctions to differentiate the species composition of reserves is also promoted by shorter geographic distance between reserves (Figure 3.2, Table 3.3).

When comparing two assemblages, species extinctions and colonizations can lead to either increasing or decreasing similarity in plant species composition (Rahel 2000; Rahel 2002; Olden & Poff 2003). Extinctions produce differentiation when the same species become extinct from assemblages that are historically similar, thereby creating two dissimilar contemporary assemblages. Extinctions produce homogenization when different species become extinct from historically dissimilar assemblages, thereby creating two similar contemporary assemblages. My results for both woodland and forest suggest that the same native species may have become extinct from reserves that are closer together, whilst different native species may have become extinct from reserves that are further apart. In contrast, colonizations generate differentiation when different species colonize assemblages that are historically similar, thus producing two dissimilar contemporary assemblages. Colonizations create homogenization when the same species colonize assemblages that are historically dissimilar, resulting in two similar contemporary assemblages. My results for woodland indicate that different exotic species colonized reserves that are closer together, whilst the same exotic species colonized reserves that are further apart.

Theoretical work suggests that alterations to natural habitats by human activities facilitate homogenization and differentiation (Rahel 2002). There is also a growing body of empirical evidence that links human-related environmental attributes, such as human population density, urbanization and land-use, to patterns of homogenization and differentiation in plant assemblages (Kühn & Klotz 2006; McKinney 2006; Olden *et al.* 2006; Qian & Ricklefs 2006; Schwartz *et al.* 2006; Schulte *et al.* 2007). Notwithstanding that most of the studies above used data pooled across unspecified vegetation associations (with the notable exception of Schulte *et al.* 2007), it would be logical to suggest that these results could be also generalized to an individual vegetation association.

However, the evidence from the above empirical studies raises the question: Why is human population density and settlement time not associated with changes in species composition in this study? In the context of this study, it is noteworthy that that human population density and settlement time are surrogates for human activities which could not be measured at the large spatial and long temporal scale of this study. From notes accompanying the contemporary inventories, it is clear that the woodland and forest assemblages that are the subject of this study have been subject to different types, intensities and durations of specific land-uses since European settlement (Appendix 3). Furthermore, these woodland and forest assemblages may also be affected by the alteration of landscape scale processes, which covary with land-use, since European settlement. For example, the disruption of natural fire and flooding regimes may also affect the species composition of woodland and forest vegetation. Thus different land-use histories of woodland and forest assemblages might be at least partly responsible for the observed levels of differentiation.

Although the tendency of native plant extinctions and exotic plant colonizations to differentiate the species composition of woodland is not associated with the human-related attributes of reserves, differentiation is associated with the geographic attributes of reserves (Table 3.4). The differentiating effect of native plant extinctions is associated with smaller longitudinal and/or latitudinal separation between reserves. Native plant extinctions from reserves that are closer together in longitudinal and/or latitudinal separation have a greater differentiating effect than those reserves further apart. However, the differentiating effect of exotic plant colonizations in woodland is only associated with longitudinal separation between reserves; exotic plant colonizations of reserves that are closer together in longitude have a greater differentiating effect than those reserves which have greater longitudinal separation. The propensity of native plant extinctions to differentiate forest vegetation is not associated with either geographic or human-related attributes of conservation reserves. However, latitudinal separation was found to be significant in the distribution of exotic plant species in forest (Table 3.4), even though exotic plant colonizations were not shown to be significant in differentiating forest vegetation (Figure 3.2, Table 3.3).

It comes as no surprise that change in the β-diversity of native and exotic floras of woodland vegetation over time can be associated with latitudinal separation of the conservation reserves that are the subject of this study. In temperate regions, the β-diversity of both native and exotic plant species has been found to decrease with increasing latitude (Qian *et al.* 2005; Qian 2008). Although almost 30 mechanisms purported to explain the origin of latitudinal gradients in species diversity have been proposed (Rohde 1992), the ecological basis of latitudinal gradients has proven difficult to determine (Sax 2001). However, I hypothesize that the underlying climatic gradient that relates to change in the β-diversity of the native and exotic floras of woodland vegetation over time with latitudinal separation is related to incident solar radiation.

Although the effect of latitudinal gradients on various measures of species diversity is well recognized (Sax 2001), the effect of longitudinal gradients on species diversity is not as well documented. In North America, the β-diversity of exotic plants has been strongly associated with a precipitation gradient over longitude (Qian & Ricklefs 2006). Yet, within the study area the β-diversity of native woodlands is strongly correlated with minimum winter temperature along a west–east gradient (Hunter 2005a). Thus it is likely that the underlying climatic gradient that associates change in the β-diversity of the native flora of woodland vegetation over time with longitudinal separation is also related to minimum winter temperature.

Notwithstanding the specific climatic gradient(s) that might be associated with latitude and longitude, the process by which extinctions and colonizations have a tendency to differentiate woodland vegetation in reserves with smaller latitudinal and/or longitudinal separation warrants explanation. First I need to assume that woodland vegetation in reserves with smaller latitudinal and/or longitudinal separation have relatively more similar climatic conditions and historical native species composition than those with larger latitudinal and/or longitudinal separation. Then the processes of native plant extinction and exotic plant colonization can now be addressed in turn.

If extinct native species were rare and rarity is correlated with small geographic range, reserves with smaller latitudinal and/or geographic separation were more likely to share the same extinct native species than those with larger latitudinal and/or geographic separation. Extinction of the same species from reserves with historically similar species composition (because they are closer together) makes the species composition of these reserves relatively less similar, i.e. more differentiated. Extinction of different species from reserves that historically had dissimilar species composition (because they are farther apart) makes the species composition of these relatively more similar, i.e. less differentiated, because these reserves share relatively more common and widespread native plant species.

One might expect reserves with smaller latitudinal separation to have similar climatic conditions and so they might be colonized by the same exotic species. My results indicating that reserves with smaller latitudinal separation are more differentiated than those further apart are therefore counterintuitive. However, these findings can be explained by the mode of colonization by exotic plants and the geographic range of exotic plants. Reserves with smaller latitudinal separation, having been colonized by different exotic plant species, suggest a sporadic colonization process, perhaps related to the different land-use histories of reserves. Reserves with larger latitudinal separation are less differentiated, i.e. relatively more homogenized, and therefore have been colonized by the same exotic species. The exotic species found in reserves that are farther apart are likely to be abundant invasive exotic species, with broad ecological niches and a wide geographic range (McKinney & La Sorte 2007).

My findings for woodland vegetation provide support for the idea that the process of homogenization might follow a temporal sequence starting from an initial phase of differentiation caused by the sporadic invasion of exotic species, through to homogenization as dominant invaders progressively become widespread and endemic native species gradually become extinct (Olden 2006). Indeed, since European settlement of the study area, the process of invasion has been relatively more important than extinction, at least at a regional scale. In this time period more than 1700 exotic plants have become naturalized , while only 36 native plant species have become globally extinct (NSW Scientific Committee 2004; Botanic Gardens Trust 2006b). Considering the large number of native plant species that are now considered at risk of extinction in the study area (563 species listed as threatened, NSW Scientific Committee 2004), it is very likely that the extinction of native species will need to be carefully considered in future studies of homogenization and differentiation in the area. However, the temporal sequence for forest vegetation is less clear. The observed results suggest that forest vegetation might be in the initial phase of differentiation and thus is becoming more differentiated by the extinction of native species and sporadic colonization of exotic species.

3.5 Conclusion

It is apparent that patterns of native plant extinction and exotic plant colonization, which underpin the process of homogenization and differentiation, are different in similar types of wooded vegetation. The differing patterns of extinction and colonization in both woodland and forest vegetation are related to climatic gradients that underlie the latitudinal and longitudinal separation of the conservation reserves, and the distribution and range size of extinct native species and exotic plant species. Although change in β-diversity in both woodland and forest vegetation could not be related to human population density and settlement time, it is likely that the differing land-use histories of conservation reserves also has been a causal factor in the process of differentiation.

Studies that address patterns of homogenization and differentiation in contrasting vegetation types are now required. Techniques that reconstruct the species composition of historical species assemblages from the composition of contemporary species assemblages have been successfully applied in studies where data for native species extinctions and exotic plant colonizations are available at large scales (e.g. Schwartz *et al.*, 2006; Castro *et al.*, 2007). However, contemporary species inventories are frequently available at smaller spatial scales. It would be profitable to now develop more sophisticated techniques to model the historical species composition of specific vegetation assemblages.

4 A stochastic model for reconstruction of historical species assemblages: A test in woodland and forests of south-eastern Australia

4.1 Introduction

The most reliable evidence for homogenization comes from studies using both historical and contemporary species inventories derived from vegetation surveys that record the presence and/or abundance of species at specific locations (e.g. Rooney *et al.* 2004, Chapter 2). Nonetheless, for macroecological studies of homogenization and differentiation, historical inventories at large spatial and long temporal scales are generally not available (however, see Vellend *et al.* 2007). In studies at large spatial and long temporal scales, therefore, a reconstruction technique (standard reconstruction technique) has been employed to estimate the taxonomic composition of historical species assemblages (Rahel 2000; Marchetti *et al.* 2001; Taylor 2004; Castro *et al.* 2007; Castro & Jaksic 2008a; b).

Regional scale studies of floristic homogenization and differentiation have relied on the standard reconstruction technique to reconstruct the historical composition of native species assemblages (e.g. Castro *et al.* 2007; Castro & Jaksic 2008a; b). The technique reconstructs an historical native species assemblage of a region in two steps. Exotic species occupancy records are first removed from the contemporary inventory of native and exotic species because it is assumed that exotic species would not have been present in the historical assemblage. Extinct native species occupancy records are then added to the contemporary inventory of native species to account for extinctions; these species are assumed to have been present in the historical assemblage.

However, the use of the standard reconstruction technique has two significant limitations. The first relates to the method by which regional scale contemporary inventories of native and exotic species are compiled. Such regional scale inventories, assembled from local scale species inventories and/or herbarium records from individual locations within a region, may understate native species extinctions and overstate exotic species colonizations. The process of pooling such local scale data into a regional inventory may allow a native species to be recorded as occupying the region even though it may have become extinct from all but one location within the region. Similarly, an exotic species may be recorded as occupying the region even though it may have colonized only one location. Consequently the compilation process may simultaneously understate native species extinctions and overstate exotic species colonizations (see Section 1.2.5.1).

The second limitation relates to the scale of the data used to reconstruct the composition of historical species assemblages within a region. The standard reconstruction technique cannot be applied when data sources are of a different spatial scale (e.g. local scale contemporary inventories of native and exotic species and regional scale contemporary inventories of extinct native species). If the technique were applied to the example above, extinct native species occupancy records would be added to the contemporary inventory of all locations within the region. Assuming that extinct native species were regionally rare and therefore did not occupy all locations across the region, this would overstate native species extinctions (see Section 1.2.5.1). The conundrum posed by this limitation is: How might we allocate extinct native species occupancy records without overstating extinctions? A modelling approach is the most obvious way to address this challenge.

In this chapter I address this challenge by employing a stochastic modelling approach to reconstruct the composition of historical species inventories of 87 woodland and 51 forest locations from a broad region across south-eastern Australia (Figure 3.1). The historical species inventories were reconstructed from data sources at a different spatial scale, namely local scale contemporary inventories of native and exotic species and a regional scale contemporary inventory of extinct native species. My aim is to make available local scale contemporary inventories of native and exotic species to macroecological investigations of homogenization and differentiation.

Two models were used to reconstruct historical species inventories for each woodland and forest location because the findings might be sensitive to the number of extinct native species used to reconstruct the historical inventory. For Model 1, the extinct native species added to the contemporary inventory of each location were those species known to be extinct. For Model

2, I used the extinct native species above, plus those species threatened with extinction. Threatened species were included because these species may have become extinct from individual locations within a region. My results might also be sensitive to the number of extinct (and threatened) native species occupancy records added to the contemporary inventory of native species for each woodland and forest location. For both models, three sensitivity levels were defined; these were based on the number of extinct (and threatened) species occupancy records added to the contemporary inventory of native species for each woodland and forest location.

For both models and at all three sensitivity levels the historical species composition of individual locations were reconstructed by first removing exotic species occupancy records from the contemporary inventory. A Monte Carlo procedure was used to assign each extinct native species a regional frequency of occupancy value based on the random sampling of a probability distribution, allocate occupancy records to individual locations, and calculate a sample historical similarity matrix. I used the values for each cell in the sample historical similarity matrix to calculate a modelled historical similarity matrix. Finally, similarity analysis was used to determine modelled change in similarity for all species (native and exotic) and native species, and to determine observed change in similarity for exotic species.

Modelled estimates of homogenization and differentiation for all species (native and exotic), and native species based on the two models described above and at three levels of sensitivity for each model, for both woodland and forest, are presented here. As well there are observed estimates of homogenization and differentiation.

4.2 Methods

4.2.1 Contemporary plant species assemblages in woodland and forest

The contemporary inventories of native and exotic species from floristic studies of the 20 conservation reserves used in Chapter 3 are used in this chapter (Figure 3.1, Appendix 3). The methods used to classify vegetation as either woodland or forest and standardize taxonomic nomenclature are consistent with those outlined in Section 3.2.1.

Woodland and forest assemblages at 87 and 51 locations respectively were isolated from the floristic studies of these 20 conservation reserves. A database of the contemporary inventories of native and exotic species for each of these locations was then constructed. The 87 woodland and 51 forest locations were used to model patterns of change in the composition of vegetation at a local scale. I compared the species composition of these observed local contemporary assemblages with modelled local historical assemblages.

4.2.2 Stochastic modelling approach

The stochastic modelling approach was conducted in three stages. (1) An inventory of extant native and extinct native species that might have become extinct from individual locations was assembled, the parameters of the log-series probability distribution estimated (henceforth, log-series) and then distribution calculated. (2) A Monte Carlo procedure was used to reconstruct the historical inventory of native species and calculate the modelled historical similarity matrix. (3) Change in similarity and the significance of the changes was determined. The methodological details of each of these three stages are now addressed in turn (also see flow chart in Appendix 4).

4.2.2.1 Stage 1: Assembly of a regional inventory of extinct native species and calculation of the log-series

First the log-series and the parameters by which this distribution is defined are described. A clear explanation of these parameters is required because the parameters of the log-series are the data inputs of my modelling approach. The log series distribution takes the form $\mathrm{\alpha x}, \frac{\mathrm{\alpha x}^2}{2}, \ldots \frac{\mathrm{\alpha x}^\mathrm{n}}{\mathrm{n}}$ (Equation 4.1) and this estimates expected frequency of occurrence of extinct native species for each category of n regional occurrences. The parameters of the distribution α and x are constants with $\propto > 0$ and $0 < x < 1$ (Pielou 1975). The parameter x is estimated by solving the equation $\frac{S}{N} = \frac{(1-x)}{x[-\ln(1-x)]}$ (Equation 4.2) where S is the total number species and N is the total number of occupancies of these species (Magurran 2004). The parameter $\propto$ is estimated from the equation

$\propto = \frac{N(1-x)}{x}$ (Equation 4.3) (Magurran 2004). I chose the log-series because this distribution might be a good fit for the historical distribution of extinct native species. The log-series has been found to provide a good description of the distribution of metacommunities and has been employed in modelling of homogenization and differentiation (Hubbell 2001; Cassey *et al.* 2006).

Before any modelling was started, I determined whether the contemporary distribution of native species in both woodland and forest was a good fit against the log-series. I assumed that if there was a good fit, the log-series would also be a good fit for the historical distribution of extinct native species and thus an appropriate choice for the modelling approach. The calculation of the cumulative log-series distribution for both woodland and forest was based on the total number of contemporary native species and the total number of occupancies of these species across the region. G-tests were used to determine whether the contemporary species distribution of native species in both woodland and forest locations was a good fit against the log-series. I found no statistically significant difference between the expected cumulative log-series distribution and the observed cumulative distribution of contemporary native species (Woodland: $G_{1,86} = 7.447,\ p < 0.001$; Forest: $G_{1,50} = 1.020,\ p < 0.001$), therefore the log-series is an appropriate choice for my modelling approach.

In the context of the modelling approach for both woodland and forest, *S* was defined as the total number of extinct native species. As calculation of the log-series is sensitive to *S* (see Equation 4.2), two different models were defined to determine the total number of extinct native species that might have occurred in woodland and forest vegetation across the region. This was done so the modelling approach would provide a range of estimates of homogenization and/or differentiation across the region.

The first more conservative model (Model 1) used a regional inventory of extinct native species lost from both woodland and forest across the region. The second more speculative model (Model 2) used the same inventory as for Model 1 plus an inventory of species threatened with extinction. Species threatened with extinction were included because these species might have become extinct from individual woodland and forest locations across the region. The following descriptions of methods refer to both Model 1 and Model

2 for both woodland and forest vegetation. However, for brevity I only refer to woodland vegetation under Model 2 in the text.

The identity and total number of species of extinct and threatened species (*S*) was determined as follows. Native species lost to extinction from woodland vegetation in the study area were those gazetted as 'presumed extinct', henceforth extinct, and 'endangered' or 'vulnerable', the latter two also referred to as extinct, unless I explicitly intend the reference to these species as threatened (NSW Scientific Committee 2004). Historical occurrences of extinct and threatened species within the bioregion surrounding each reserve (the IBRA scheme, Thackway & Cresswell 1995; Environment Australia 2000) were determined from herbarium records (Botanic Gardens Trust 2006b; Council of Heads of Australian Herbaria 2006). Historical occurrences of an extinct and threatened species in woodland were determined from species habitat descriptions (Harden 1992; 1993; 2000; 2002; Botanic Gardens Trust 2006b; Department of Environment and Conservation NSW 2006).

If an extinct or threatened species was found to occur within the area surrounding each reserve within a given bioregion and known to occur in woodland vegetation, I assumed that it was possible for that species to occupy all woodland locations within that bioregion. If an extinct or threatened species was known to have extremely limited distribution (e.g. a species known only to occur in one remote valley) I presumed this species could not to have occupied the research woodland locations and so was not included in the regional inventory. This procedure yielded an S of 229 extinct native species in woodland vegetation (Table 4.1).

The parameter N from the log-series was calculated. In the context of my modelling approach, for both woodland and forest, N was defined as the total number of occupancies of extinct native species across the region (see Equation 4.2). Using the same procedure used to determine the number of extinct and threatened native species above, I first determined the maximum number of possible regional occupancies of an extinct or threatened species prior to European settlement. The maximum number of possible regional occupancies of an extinct or threatened native species (N^{Max}) is defined as equal to the sum of all the bioregions in which an extinct species occurred

Table 4.1 Total number of extinct native plant species (S) and the number of total regional occupancies (N) for both woodland and forest vegetation and for both Model 1 and Model 2.

Model	Association	S	N*			
			N^{Max}	$N^{20\%}$	$N^{15\%}$	$N^{10\%}$
Model 1	Woodland	18	245	49	37	25
	Forest	11	171	34	26	17
Model 2	Woodland	229	4355	871	653	436
	Forest	336	6620	1324	993	662

* N^{Max} is the maximum number of possible occupancies of extinct species. $N^{20\%}$, $N^{15\%}$and $N^{10\%}$ are the three sensitivity levels of occupancy of extinct native species.

multiplied by the number of woodland locations in each bioregion. This procedure yielded $N^{Max}$of 4355 possible occupancies of extinct native plant species in woodland (Table 4.1).

Extinct species were assumed to have been regionally rare and occupying a smaller percentage of the maximum possible number of woodland locations. I define rare species as those found within the first quartile of proportional occupancies across the region (Gaston 1994). Calculation of the log-series is also sensitive to the total number of regional occupancies of extinct and threatened native species (N) that might have occupied locations across the region (Equation 4.2), therefore, I defined three sensitivity levels for the total number of regional occupancies of extinct native plant species as a percentage of N^{Max}: $N^{10\%}$, $N^{15\%}$and $N^{20\%}$respectively. At the $N^{10\%}$, $N^{15\%}$and $N^{20\%}$ sensitivity levels, this calculation yielded 436, 653 and 871 occupancies of extinct species respectively in woodland vegetation (Table 4.1). These three sensitivity levels were defined so that both Model 1 and Model 2 would also provide a range of estimates of homogenization and/or differentiation in the region based on the number of regional occupancies of extinct native species.

The calculated estimates for S and N for woodland under Model 2 at three sensitivity levels (i.e. $N^{10\%}$, $N^{15\%}$and $N^{20\%}$), allowed the solution of Equation 4.2 to obtain an estimate for parameter x (Magurran 2004). Equation

4.3 gave an estimate for parameter ∝. Finally, the expected log-series frequency distribution of the number of occupancies of extinct native species across the region at three sensitivity levels was calculated (Equation 4.1).

4.2.2.2 Stage 2: Reconstruction of the historical inventory and calculation of the modelled historical similarity matrix

For woodland under Model 2 at all three sensitivity levels, I reconstructed the historical inventory of extant native and extinct native species and calculated a modelled historical similarity matrix. The modelled historical similarity matrix was used as part of the statistical analysis to calculate change in similarity and thus estimate the degree of homogenization and/or differentiation.

To reconstruct the historical inventory, exotic species were first removed from the contemporary inventory of native and exotic species. The regional inventory of extinct native species identified in Section 4.2.2.1 was added to the contemporary inventory of native species and a Monte Carlo procedure with 10 000 iterations was used to allocate the regional frequency of occupancy to each extinct native species. I used the inverse transform sampling method to allocate each extinct species with an expected frequency of occupancy for each Monte Carlo iteration. The inverse transform sampling method generated a sample regional frequency of occupancy at random from the log-series calculated in Section 4.2.2.1. For each extinct species, frequency of occurrence was allocated under the constraint that the number of occurrences across the region were less than or equal to the maximum number of locations in which that species might have occurred.

The number of regional occupancies of an extinct species to individual woodland locations were randomly allocated under the constraint that species could only be added to the locations where an extinct species could possibly have occurred (identified in Section 4.2.2.1). For example, if an extinct species could occupy a maximum number of 11 woodland locations and that species was randomly assigned a regional frequency of occupancy of five from the log-series distribution, then five presence records were allocated to the 11 woodland locations at random. Once regional occupancies for each extinct native species had been allocated to individual woodland locations, the process of reconstructing a sample historical inventory of extant native and extinct native species was complete.

I used the historical inventory to calculate a sample historical similarity matrix using Jaccard's index (Jaccard 1912; Koleff *et al.* 2003); methods were consistent with those outlined in Section 3.2.3. For each Monte Carlo iteration, I then sampled every combination of pairs of locations in the Jaccard similarity matrix. For each pair of locations, the mean Jaccard's index value was calculated from the 10 000 iterations. Finally, the mean Jaccard's index value of each pairwise comparison was used to construct a modelled historical Jaccard similarity matrix.

4.2.2.3 Stage 3: Determination of change in similarity and testing significance of change

Using methods consistent with those outlined in Section 3.2.3, similarity analysis was used to determine increases, decreases or no change in the similarity of species composition of woodland under Model 2 at all three sensitivity levels, allowing a contemporary inventory of only the native species occurring in each woodland location to be constructed. Exotic species were removed from the contemporary inventory of native and exotic species. I used the inventory of native species in the statistical analyses to separate the effects of the extinction of native species and the colonization of exotic species in driving change in similarity over time. Change in similarity was calculated for all species (native and exotic species combined), native species only, and exotic species only. Finally, the permuted Wilcoxon Z-statistic test (outlined in Section 3.2.3, but calculated in R v2.8.1) was used to determine the statistical significance of change.

4.3 Results

For both Model 1 and Model 2, analysis of change in similarity was calculated from the observed contemporary similarity matrix and the modelled historical similarity matrix (modelled result). Under Model 1, the modelled historical similarity matrix was calculated from the reconstructed historical inventory of extant native and extinct native species. The modelled historical similarity matrix for Model 2 was calculated from the reconstructed historical inventory of extant native as well as extinct and threatened native species.

4.3.1 Analysis of modelled change in similarity for all species

4.3.1.1 Model 1

The average of the permuted Wilcoxon *Z*-statistic distribution was negative at all three sensitivity levels in woodland vegetation ($N^{10\%}$, $\bar{Z} = -0.505$; $N^{15\%}$, $\bar{Z} = -0.483$; $N^{20\%}$, $\bar{Z} = -0.492$; Table 4.2). These values for the average permuted Wilcoxon *Z*-statistics suggested that we can expect native species extinctions and exotic species colonizations to differentiate woodland vegetation. The modelled results indicate a highly significant decrease in similarity ($P < 0.001$) at all three sensitivity levels ($N^{10\%}$, $Z = -11.916$; $N^{15\%}$, $Z = -12.048$; $N^{20\%}$, $Z = -12.232$; Table 4.2).

In forest vegetation, the average of the permuted Wilcoxon *Z*-statistic distribution for all species was also negative at all three sensitivity levels ($N^{10\%}$, $\bar{Z} = -0.034$; $N^{15\%}$,$\bar{Z} = -0.054$; $N^{20\%}$,$\bar{Z} = -0.089$; Table 4.3). These results suggested that, at random, we can expect native species extinctions and exotic species colonizations to differentiate forest vegetation. My modelled results revealed a highly significant decrease in similarity ($P < 0.001$) at all three sensitivity levels ($N^{10\%}$,$Z = -4.843$; $N^{15\%}$,$Z = -4.952$; $N^{20\%}$, $Z = -5.349$; Table 4.3). The results for Model 1 suggested that when considered together, native species extinctions and exotic species colonizations differentiate the species composition of both woodland and forest vegetation.

4.3.1.2 Model 2

The average of the permuted Wilcoxon *Z*-statistic distribution for all species was positive in woodland vegetation at all three sensitivity levels ($N^{10\%}$, $\bar{Z} = 1.145$; $N^{15\%}$, $\bar{Z} = 0.889$; $N^{20\%}$, $\bar{Z} = 0.056$; Table 4.2). My findings indicated that by random chance alone native species extinctions and exotic species colonizations can be expected to homogenize woodland vegetation. Under Model 2, the modelled results revealed a highly significant increase in

Table 4.2 Modelled and observed changes in Jaccard's Index, permuted Wilcoxon *Z*-statistics and observed Wilcoxon *Z*-statistics for all species, native species and exotic species in woodland vegetation.

Species	Model	Sensitivity	Permuted Wilcoxon Z-Statistic				Modelled/observed change in mean Jaccard Index		Modelled/observed Wilcoxon Z-Statistic	
			$\bar{Z}$	$P_{2.5}$	$\tilde{Z}$	$P_{97.5}$	$\Delta\bar{J}$	$\%\Delta\bar{J}$	Z	P
All species	Model 1	$N^{10\%}$	−0.505	−1.230	−0.504	0.227	-1.15×10^{-3}	−1.86%	−11.916	<0.001
		$N^{15\%}$	−0.483	−1.217	−0.482	0.256	-1.14×10^{-3}	−1.84%	−12.048	<0.001
		$N^{20\%}$	−0.492	−1.246	−0.492	0.252	-1.17×10^{-3}	−1.89%	−12.232	<0.001
	Model 2	$N^{10\%}$	1.145	0.405	1.143	1.897	1.64×10^{-3}	2.78%	7.532	<0.001
		$N^{15\%}$	0.889	0.148	0.884	1.645	1.14×10^{-3}	1.92%	7.491	<0.001
		$N^{20\%}$	0.056	−0.679	0.050	0.832	-2.54×10^{-4}	−0.42%	4.138	<0.001
Native	Model 1	$N^{10\%}$	0.112	−0.625	0.109	0.826	2.06×10^{-4}	0.33%	46.170	<0.001
		$N^{15\%}$	0.129	−0.588	0.123	0.840	2.15×10^{-4}	0.35%	41.838	<0.001
		$N^{20\%}$	0.118	−0.609	0.111	0.839	1.84×10^{-4}	0.30%	38.016	<0.001
	Model 2	$N^{10\%}$	1.721	0.983	1.709	2.480	3.00×10^{-3}	5.07%	42.169	<0.001
		$N^{15\%}$	1.462	0.728	1.460	2.200	2.50×10^{-3}	4.19%	32.190	<0.001
		$N^{20\%}$	0.639	−0.103	0.639	1.368	1.10×10^{-3}	1.81%	21.431	<0.001
Exotic	–	–	−0.612	−1.330	−0.610	0.105	-1.36×10^{-3}	−2.18%	−13.264	<0.001

Table 4.3 Modelled and observed changes in Jaccard's Index, permuted Wilcoxon *Z*-statistics and observed Wilcoxon *Z*-statistics for all species, native species and exotic species in forest vegetation.

Species	Model	Sensitivity	Permuted Wilcoxon Z-Statistic				Modelled/observed change in mean Jaccard Index		Modelled/observed Wilcoxon Z-Statistic	
			$\bar{Z}$	$P_{2.5}$	$\tilde{Z}$	$P_{97.5}$	$\Delta\bar{J}$	$\%\Delta\bar{J}$	Z	P
All species	Model 1	$N^{10\%}$	−0.034	−0.903	−0.028	0.840	-3.00×10^{-4}	−0.30%	−4.843	<0.001
		$N^{15\%}$	−0.054	−0.938	−0.053	0.819	-3.64×10^{-4}	−0.36%	−4.952	<0.001
		$N^{20\%}$	−0.089	−0.959	−0.091	0.790	-4.74×10^{-4}	−0.47%	−5.349	<0.001
	Model 2	$N^{10\%}$	1.442	0.588	1.432	2.342	4.34×10^{-3}	4.50%	16.625	<0.001
		$N^{15\%}$	0.971	0.144	0.970	1.807	3.07×10^{-3}	3.13%	14.277	<0.001
		$N^{20\%}$	0.136	−0.695	0.134	0.969	3.11×10^{-4}	0.31%	8.413	<0.001
Native	Model 1	$N^{10\%}$	0.053	−0.813	0.053	0.901	1.55×10^{-4}	0.15%	25.127	<0.001
		$N^{15\%}$	0.037	−0.822	0.034	0.905	9.09×10^{-5}	0.09%	20.052	<0.001
		$N^{20\%}$	−0.011	−0.870	−0.010	0.841	-1.92×10^{-5}	−0.02%	13.168	<0.001
	Model 2	$N^{10\%}$	1.510	0.654	1.500	2.393	4.80×10^{-3}	4.97%	24.385	<0.001
		$N^{15\%}$	1.051	0.223	1.044	1.892	3.52×10^{-3}	3.60%	17.245	<0.001
		$N^{20\%}$	0.236	−0.575	0.231	1.061	7.66×10^{-4}	0.76%	9.991	<0.001
Exotic	–	–	−0.079	−0.956	−0.074	0.785	-4.55×10^{-4}	−0.45%	−5.488	<0.001

similarity ($P < 0.001$) at all three sensitivity levels ($N^{10\%}$, $Z = 7.532$; $N^{15\%}$, $Z = 7.491$; $N^{20\%}$, $Z = 4.138$; Table 4.2).

For the analysis of all species in forest vegetation under Model 2, the average of the permuted Wilcoxon *Z*-statistic distribution was also positive at all three sensitivity levels ($N^{10\%}$, $\bar{Z} = 1.442, N^{15\%}$, $\bar{Z} = 0.971$; $N^{20\%}$, $\bar{Z} = 0.136$; Table 4.3). Thus at random, native species extinctions and exotic species colonizations can be expected to homogenize forest vegetation under Model 2. The modelled results for all species found a highly significant increase in similarity ($P < 0.001$) at all three sensitivity levels ($N^{10\%}$, $Z = 16.625$; $N^{15\%}$, $Z = 14.277$; $N^{20\%}$, $Z = 8.413$; Table 4.3). In contrast to Model 1, my modelled results for Model 2 indicated that native species extinctions and exotic species colonizations homogenize the species composition of both woodland and forest vegetation.

4.3.2 Analysis of modelled change in similarity for native species

4.3.2.1 Model 1

Under Model 1, the average of the permuted Wilcoxon *Z*-statistic distribution was positive for native species in woodland vegetation at all three sensitivity levels ($N^{10\%}, \bar{Z} = 0.112; N^{15\%}, \bar{Z} = 0.129$; $N^{20\%}, \bar{Z} = 0.118$; Table 4.2). These findings suggested that we can expect the extinction of native species to homogenize woodland vegetation by random chance alone. There was a highly significant increase in similarity ($P < 0.001$) in my modelled results for woodland at all three sensitivity levels ($N^{10\%}, Z = 46.170$; $N^{15\%}, Z = 41.838$; $N^{20\%}$, $Z = 38.016$; Table 4.2).

In forest vegetation, under Model 1 the average of the permuted Wilcoxon *Z*-statistic distribution was positive at the lower two sensitivity levels ($N^{10\%}, \bar{Z} = 0.053$, $N^{15\%}$, $\bar{Z} = 0.037$; Table 4.3), indicating that at random we can expect the extinction of native species to homogenize forest vegetation at both the $N^{10\%}$ and $N^{15\%}$ sensitivity levels. However, the average of the permuted Wilcoxon *Z*-statistic was negative at the $N^{20\%}$ sensitivity level for Model 1 suggesting that native species extinctions differentiate forest vegetation ($N^{20\%}$, $\bar{Z} = -0.011$; Table 4.3). My modelled results indicated a highly significant increase in similarity ($P < 0.001$) at all three sensitivity levels ($N^{10\%}$, $Z = 25.127$; $N^{15\%}$, $Z = 20.052$; $N^{20\%}$, $Z = 13.168$; Table 4.3). The modelled results under Model 1 indicated that native species extinctions homogenize the species composition of both woodland and forest vegetation.

4.3.2.2 Model 2

In woodland vegetation, under Model 2 the average of the permuted Wilcoxon *Z*-statistic distribution was positive at all three sensitivity levels ($N^{10\%}$, $\overline{Z} =$ 1.721, $N^{15\%}$, $\bar{Z} =$ 1.462; $N^{20\%}$, $\bar{Z}$ = 0.639 Table 4.2). These results indicated that under this model we can expect the extinction of native species to homogenize woodland vegetation at all three sensitivity levels by random chance alone. Examination of my modelled results also revealed evidence for homogenization, with a highly significant increase in similarity ($P < 0.001$) at all three sensitivity levels ($N^{10\%}$, $Z = 42.169$; $N^{15\%}$, $Z = 32.190$; $N^{20\%}$, $Z = 21.431$; Table 4.2).

Under Model 2, the average of the permuted Wilcoxon *Z*-statistic distribution was positive for forest vegetation at all three sensitivity levels ($N^{10\%}, \bar{Z} =$ 1.510; $N^{15\%}, \bar{Z} =$ 1.051; $N^{20\%}, \bar{Z} = 0.236$; Table 4.2). The above findings indicated that at random we can expect the extinction of native species to homogenize forest vegetation under Model 2. Analysis of my modelled results found a highly significant increase in similarity ($P < 0.001$) at all three sensitivity levels ($N^{10\%}, Z = 24.385$; $N^{15\%}, Z = 17.245$; $N^{20\%}$, $Z = 9.991$; Table 4.2). In concurrence with the findings for Model 1, my modelled results for Model 2 also indicated that native species extinctions homogenize the species composition of both woodland and forest vegetation.

4.3.3 Analysis of observed change in similarity for exotic species

In woodland vegetation, the average of the permuted Wilcoxon *Z*-statistic distribution was negative ($\bar{Z} = -0.612$; Table 4.2), indicating that at random we can expect exotic species colonizations to differentiate woodland vegetation. Analysis of my observed results determined a highly significant decrease in similarity ($Z = -13.264$, P<0.001; Table 4.2).

Similarly, the average of the permuted Wilcoxon Z-statistic distribution was also negative for forest vegetation ($\bar{Z} = -0.079$; Table 4.3). This result also suggested that exotic species colonizations can also be expected to differentiate forest vegetation by random chance alone. My observed results for forest vegetation also found a highly significant decrease in similarity for exotics ($Z = -5.488$, P<0.001; Table 4.3). These findings indicated that exotic species colonizations have had a differentiating effect on both woodland and forest vegetation across south-eastern Australia since European settlement.

4.4 Discussion

Patterns of observed homogenization or differentiation are largely dependent on the degree of historical similarity of assemblages under comparison, as well as the identity and number of species that have become extinct from or have colonized a particular assemblage (Olden & Poff 2003). We cannot be certain of the historical similarity or identity and number of native species extinctions at individual woodland and forest locations that are the subject of this study because the species composition of these locations was not surveyed in two time periods. In the context of the investigation of patterns of homogenization and differentiation, it is important to preface any discussion of my modelled results with a note on the limitation of this and indeed all approaches which reconstruct or model historical data. Consequently, I temper interpretations of my results with this limitation in mind.

My modelled results allow me to draw qualified conclusions on the trajectory of change in species composition of native species since European settlement. In my analysis for all species, my modelled results for both woodland and forest are best interpreted as a range of estimates of homogenization between Model 1 and Model 2. The modelled results indicated a range of change in similarity for woodland (from −1.89% to 2.78%) and for forest (from −0.47% to 4.50%) since European settlement (Table 4.2, Table 4.3).

Of particular interest is how native plant extinctions in both woodland and forest result in homogenization for both Model 1 and Model 2. The modelled results for change in similarity of native species consistently indicated homogenization of woodland vegetation for both Model 1 and Model 2. However, the modelled change in similarity for Model 2 is an order of magnitude higher than that of Model 1 (Table 4.2). In forest vegetation, the modelled change in similarity indicated homogenization at the $N^{10\%}$ and $N^{15\%}$

sensitivity levels and differentiation at the $N^{20\%}$ sensitivity level for Model 1 (Table 4.3). However, the modelled results for change in similarity of native species consistently indicated homogenization of forest vegetation for Model 2 (Table 4.3). Consistent with my results for woodland vegetation, the modelled change in similarity in forest vegetation for Model 2 is an order of magnitude larger than that of Model 1 (Table 4.3).

In this chapter my modelling approach has precluded me from examining the influence of native species colonizations on patterns of homogenization and differentiation. However, my findings from Chapter 2 indicate that human-related disturbance in forest at a catchment scale has promoted native species colonizations which in turn has generated homogenization over a period of almost 40 years. If such changes in plant species composition were to persist over a longer time scale, it is possible native species colonizations may further promote homogenization of the woodland and forest locations across south-eastern Australia.

However the results from this chapter contrast with those from Chapter 3, which indicated that native species extinctions have a tendency to differentiate both woodland and forest vegetation. In both this chapter and Chapter 3 I based my investigations on contemporary floristic inventories for woodland and forest vegetation from the same conservation reserves. Consequently these two studies have been conducted at the same spatial scale. In Chapter 3 I employed the standard reconstruction technique and my investigations were conducted with sampling units of a relatively large area, i.e. conservation reserves, at a relatively coarse grain size. However, in this chapter I used a stochastic modelling approach to reconstruct the historical composition of native species assemblages and conducted my investigations with sampling units of a relatively small area, i.e. localised woodland and forest assemblages within conservation reserves, at a relatively fine grain size. The contrasting findings for native species between this chapter and Chapter 3 may have arisen from differences in the granularity (i.e. grain size) of investigation and/or the method used to reconstruct the historical species assemblages. Although it is not possible to disentangle the effects of granularity and type of reconstruction method, I address these two issues in turn.

Grain size has been noted as a factor that might affect the results of investigations of homogenization and differentiation, however, this issue remains uninvestigated (Olden 2006). The obvious way by which grain size may affect the results of an investigation is by the influence of species-area relationships. Investigations conducted at large spatial grain size will tend to contain larger numbers of species than those conducted at a small grain size (MacArthur & Wilson 1967). For instance, let us compare the spatial similarity of a pair of nominal locations at a large grain size and at a small grain size, but hold the separation distance between the two locations constant. The spatial similarity of the two locations at the large grain size may appear more similar than the same two locations at a small grain size because there is a greater chance of sharing the same species. Furthermore, as larger areas are likely to support greater habitat diversity, at a large grain size there is a greater probability of recording species colonizations and lower probability of species extinctions (Olden 2006). In contrast, at a small grain size there is a smaller probability of recording species colonizations and a larger probability of observing species extinctions.

The fundamental difference between the standard reconstruction technique I employed in Chapter 3 and the modelling approach I adopted in this chapter is the underlying assumption about species extinctions. Under the standard reconstruction technique I assumed that if an extinct native species was known to occur in the woodland vegetation of a specific bioregion, for instance, that the same species also occurred in the woodland vegetation of a particular reserve in that bioregion (See Section 3.2.1). Extinctions would therefore tend to generate differentiation because the same species have become extinct from historically similar assemblages, thereby creating two dissimilar contemporary assemblages. However, under the modelling approach I relaxed the above assumption. Here, I assumed that if an extinct native species was known to occur in the woodland of a particular bioregion then, based on the sampling of the log-series distribution, the same species occurred in some but not necessarily all of the woodland locations of that region. In this case extinctions would tend to generate homogenization because different species have become extinct from historically dissimilar assemblages, thereby creating two similar contemporary assemblages.

In contrast to my findings for native species, my results for exotic species indicated that exotic species colonizations have a differentiating effect on the species composition of woodland and forest vegetation. Moreover, my results indicated that the differentiating effect of exotic plant colonizations in woodland vegetation is almost an order of magnitude greater than that in forest vegetation (Table 4.2; Table 4.3). The propensity of exotic species to differentiate the species composition of plant species assemblages is supported by empirical evidence at large spatial scales from data pooled across unspecified vegetation types (Rejmánek 2000; Chapter 3; McKinney 2004a; 2005; Kühn & Klotz 2006; Pyšek & Richardson 2006; Qian & Ricklefs 2006).

It is clear from my results for both woodland and forest vegetation that it is profitable to investigate patterns of homogenization and differentiation in specific vegetation types. My findings indicated that for all species and native species, the trajectory and potential range of change in the species composition between Model 1 and Model 2 for both woodland and forest is similar in magnitude (Table 4.2; Table 4.3). These results suggest that native species extinctions have had a similar homogenizing effect in both woodland and forest vegetation. In contrast, my results indicated exotic species colonizations have a greater differentiating effect in woodland vegetation than forest vegetation (Table 4.2; Table 4.3). These findings suggest that the pooling of data across indeterminate vegetation types may mask actual patterns of change in plant species composition. However, the question remains, what factors might underlie the differences between the responses of the two vegetation associations?

Several causal factors could be implicated in generating observed differentiation in these vegetation associations, including land-use history since European settlement; the different processes and mode of invasion/extinction; time since invasion and extinction events began as a result of human activities and residence time of exotic plant species in new regions. Below, I discuss each of these potential mechanisms in turn.

Theoretical work suggests that alterations to natural habitats by human activities facilitate homogenization and differentiation (Rahel 2002). Empirical research in unspecified vegetation associations indicates that the process of urbanization and increasing human population density are drivers of homogenization (McKinney 2006; Olden *et al.* 2006; Schwartz *et al.* 2006).

However, my results from Chapter 3 indicate that change in human population density is not an important determinant of patterns of homogenization and differentiation for woodlands and forests in the study region. In this study only 11 woodland and 7 forest locations are located within or close to areas of significant human population size and density (Appendix 3). In the case of these 18 locations, all were located within the greater Sydney metropolitan area (Australia's largest city). Consequently, the patterns of homogenization and differentiation evident in this study are likely to have come about as a result of factors other than human population size and density. Although detailed historical land-use data for the locations in this study are not available, it is likely that the woodlands and forests have been subject to different associations, intensities and durations of specific land-uses since European settlement (Appendix 3). Covarying with land-use is the alteration of landscape scale processes since European settlement. For example, the disruption of natural fire and flooding regimes across a range of locations may have affected the species composition of woodlands and forests. Thus different land-use history in different woodland and forest locations might be at least partly responsible for the taxonomic differentiation of these plant species assemblages (also see Section 3.4).

Theoretical modelling of homogenization suggests that temporal changes in taxonomic similarity of species assemblages could come about as a result of different processes of invasion and extinction (e.g. extinction independent of invasion or extinction followed by invasion); the historical distribution of native species populations across habitats; and the mode of species invasion and extinction (e.g. widespread invasion by species associated with agriculture) (Cassey *et al.* 2006). Without some form of revisitation methodology, it is not possible to know what sequence of invasion and extinction processes have been in operation to bring about observed levels of differentiation. However, as the woodlands and forests in this study have been subject to different land-use history since European settlement (Appendix 3), the observed patterns of differentiation may have resulted from differences in invasion and extinction processes and/or the mode of species invasion and extinction in different locations. For example, woodland locations that have experienced heavy grazing might have experienced widespread invasion of exotic species associated with agriculture. Similarly, logging in forest locations may have contributed to the extinction of rare native species populations.

Differences in time since invasion and extinction events began may affect observed levels of homogenization or differentiation among regions of the world. For example, North America, where most homogenization studies have focused (Appendix 1), was first permanently settled by Europeans c. 390 years ago. In contrast, the Australian woodland and forest locations assessed in this chapter were settled by Europeans only 160–210 years ago (Appendix 3). However, my findings from Chapter 3 suggest that settlement time is not a significant driver of patterns of homogenization and differentiation for woodlands and forests in the study region.

Nevertheless, covarying with time since European settlement is the abundance and residence time of exotic plant species. The homogenizing effect of exotic species has been found to be positively associated with relative abundance (McKinney & La Sorte 2007). Residence time of exotic species has been found to be a predictor of abundance in south-eastern Australia (Hamilton *et al.* 2005), as well as an important factor in determining the homogenizing or differentiating effect of exotic species (Kühn & Klotz 2006). Thus exotic plant species may not have been resident within the study area for a sufficient time to become locally abundant enough to generate homogenization.

Any discussion of the magnitude and course of change in the similarity of the vegetation assemblages in this chapter requires me to address the choice of metric by which the estimates of change have been calculated (i.e. Jaccard's index). It is well established that widely applied similarity indices, which calculate similarity based on species occupancy but do not account for species abundance, are biased because rare and abundant species are treated equally (Wolda 1981; 1983; Magurran 2004; e.g. Jaccard's and Sørensen's indices, Chao *et al.* 2006). For example, Jaccard's index generally calculates lower levels of similarity when compared to indices that take into account species abundance (i.e. biased downward; Fisher 1999; Chao *et al.* 2006). This is particularly an issue when comparing assemblages with a high proportion of rare species and high species richness (Chao *et al.* 2006).

Although my findings do not lend themselves to comparing the relative merits of different types of similarity metrics, the modelled results for both woodland and forest do suggest that Jaccard's index is influenced by a high proportion of rare species. For native species, the difference in results between

Model 1 and Model 2 suggests that greater numbers of extinct species do promote greater level of homogenization (Table 4.2, Table 4.3). Further, if the number of extinct native species is kept constant, lower numbers of species occupancies further promote homogenization (see. $N^{10\%}$, $N^{15\%}$and $N^{20\%}$ levels of sensitivity, Table 4.2, Table 4.3).

Notwithstanding concerns about the downward bias of similarity metrics based on species occupancy, empirical evidence also suggests that there is strong correlation in the scores calculated when comparing the two classes of similarity metrics (McKinney & Lockwood 2005). Generally, differences in similarity scores calculated by the two types of metric are not large and the course of change in similarity (i.e. homogenization or differentiation) is the same (Cassey *et al.* 2007). Further, in purely practical terms the availability of both contemporary and historical inventories which record species abundance are rare (Cassey *et al.* 2007). However, given that this issue is of concern, my modelling approach addresses this issue appropriately because it: (1) tests two models based on the number of extinct native species used to reconstruct the historical species inventory; and(2), for both models, tests three levels of sensitivity based on the number of extinct native species occupancies.

4.5 Conclusion

It is not surprising that the overall change in similarity for all species brought about by native species extinctions and exotic species colonizations is highly dependent on the number of plant species that have become extinct and the number of historical occurrences of these extinct species across the region. The two models tested in this study indicated that native plant extinctions are likely to have had a homogenizing effect on the plant species composition of woodland and forest locations. This study confirmed that exotic plant colonizations have had a differentiating effect on the plant species composition of 87 woodland and 51 forest locations across south-eastern Australia.

Applying a stochastic modelling approach such as the one presented in this chapter holds promise for macroecological investigations. My stochastic modelling approach provides a valuable method by which to evaluate patterns of homogenization and differentiation, particularly for investigations conducted at large spatial and long temporal scales where historical vegetation survey data are incomplete or unavailable. However, it is important that the findings of such studies be interpreted conservatively and in a way that recognizes the limitations of such approaches.

5 Homogenization and differentiation of native grassland vegetation of south-eastern Australia along an urban–rural gradient

5.1 Introduction

Most of our current understanding of patterns of homogenization and differentiation in plant species assemblages has been gleaned from studies of undefined vegetation associations at large spatial and long temporal scales (McKinney 2004a; c; Kühn & Klotz 2006; McKinney 2006; Olden *et al.* 2006; Qian & Ricklefs 2006; Schwartz *et al.* 2006; Castro *et al.* 2007; Castro & Jaksic 2008a). Although it is difficult to attribute observed patterns of homogenization and differentiation to specific human activities with large spatial and long temporal scales, the process of urbanization has been implicated as an underlying driver of change (Kühn & Klotz 2006; McKinney 2006; Olden *et al.* 2006; Schwartz *et al.* 2006).

Few studies have investigated homogenization and differentiation in specific vegetation associations and all of these have focused on wooded vegetation (Rooney *et al.* 2004; Schulte *et al.* 2007, Chapters 2, 3 and 4). My results from Chapters 3 and 4 indicated that it is profitable to focus research on specific vegetation associations because different associations, i.e. woodland and forest, can exhibit different patterns of change in plant species composition. Given this, it is possible that other vegetation types may also demonstrate variable patterns of homogenization and differentiation.

When compared to forest, for example, grassland might display different patterns of homogenization and differentiation simply as a result of the vastly different life span of the dominant species, trees and grasses respectively. The differences in life span are such that changes in species composition of forest may take centuries to manifest (Delcourt *et al.* 1983), but only a few years or decades in grassland. Furthermore, forest and grassland may be subject to pressure from a different range of human activities, such as logging vs. agriculture, which could lead to different trajectories of change. Although a number of studies have investigated long-term change in the species composition of native grasslands across North America, Europe and Australia, none have examined patterns of homogenization and differentiation (Leach & Givnish 1996; Fischer & Stöcklin 1997; Williams 2005; Williams *et al.* 2005b; Bennie *et al.* 2006).

In this chapter I redress this gap by investigating patterns of homogenization and differentiation in remnant native grassland vegetation across western Victoria, south-eastern Australia (Figure 5.1). Prior to European settlement for agriculture in the 1830s, the native vegetation of western Victoria was almost exclusively temperate grassland, extending across an area of 8 000–10 000 km^2 (Barlow & Ross 2001). However, since European settlement, human activities have had a significant effect on the native grasslands of this region. Significantly, more than 99% of the original extent of these grasslands has been lost to agriculture and urban development (Stuwe 1986; Barlow & Ross 2001; Williams *et al.* 2005a). Remnant native grasslands now generally survive as isolated patches in rail easements, roadside verges, town commons and cemeteries within a rural or urban landscape matrix (Williams *et al.* 2005b; Williams *et al.* 2006).

With such a large loss to the original spatial extent of these native grasslands it is not surprising that these losses have wrought significant changes in plant species composition. Previous work on native grasslands in the region indicates that increasing levels of urbanization and longer maximum fire intervals increase extinction risk in this vegetation association (Williams *et al.* 2006). Furthermore, urbanization increases the likelihood of extinction of native species with a specific suite of functional traits (Williams *et al.* 2005b). However, the above studies examined change in local species richness of native species (i.e. α-diversity). Accordingly, in this chapter I extend the work of Williams *et al.* (2005b; 2006), addressing how patterns of homogenization and differentiation (i.e. change in β-diversity) in both native and exotic species in native grassland vegetation are associated with patterns of urbanization.

The floristic composition of the 30 remnant grassland sites that are the subject of this study was first sampled in 1984 (Stuwe 1986). Fourteen sites were resampled in 2001 (species inventories from Williams *et al.* 2005b) and I sampled a further 16 sites in 2007 giving a total of 30 sites from which to assess homogenization. These sites are situated along a 280 km urban–rural gradient ranging from the urban suburbs of Melbourne in the east, across tracts of agricultural land to Hamilton in the west. To determine the effect of urbanization on patterns of homogenization and differentiation, I have compared urban, peri-urban and rural sites, addressing the following three questions: (1) Have colonization and extinction generated homogenization, differentiation or stasis (i.e. no change in species composition)? (2) What patterns of change in vegetation composition are evident across the urban-rural gradient? (3) What effect have native and exotic species had on patterns of change in plant species composition?

5.2 Methods

5.2.1 Study area

The study area is within the Victorian Volcanic Plain bioregion, which has a climate characterized by warm summers (average temperature 20–27° C) and cool winters (average temperature 3–10° C) (Taylor *et al.* 2003). Most of the region receives an average annual rainfall of 500–700 mm, which gradually decreases along a south-west to north-east gradient (Conn 1993; Taylor *et al.* 2003). Basaltic lava flows have given rise to the flat or undulating plains and fertile soils which characterize the region. Given the mild climate, good rainfall, low relief and fertile soils, most of the region is particularly suited to intensive agriculture (Taylor *et al.* 2003).

The ground layer of the native grasslands that were once common across western Victoria is generally dominated by the tussock forming *Themeda triandra*, which is widespread across Australia (Stuwe 1986). However, perennial native grasses from the genera *Austrodanthonia*, *Austrostipa*, and *Poa* are also common amongst the *Themeda* tussocks, as are herbs from Asteraceae, Fabaceae, Liliaceae and Orchidaceae (Stuwe 1986; McDougall *et al.* 1994; Vranjic 2008).

5.2.2 Historical and contemporary vegetation surveys

A regional floristic survey of 211 remnant grassland sites located across the Victorian Volcanic Plain was conducted by J. Stuwe in the spring and summer

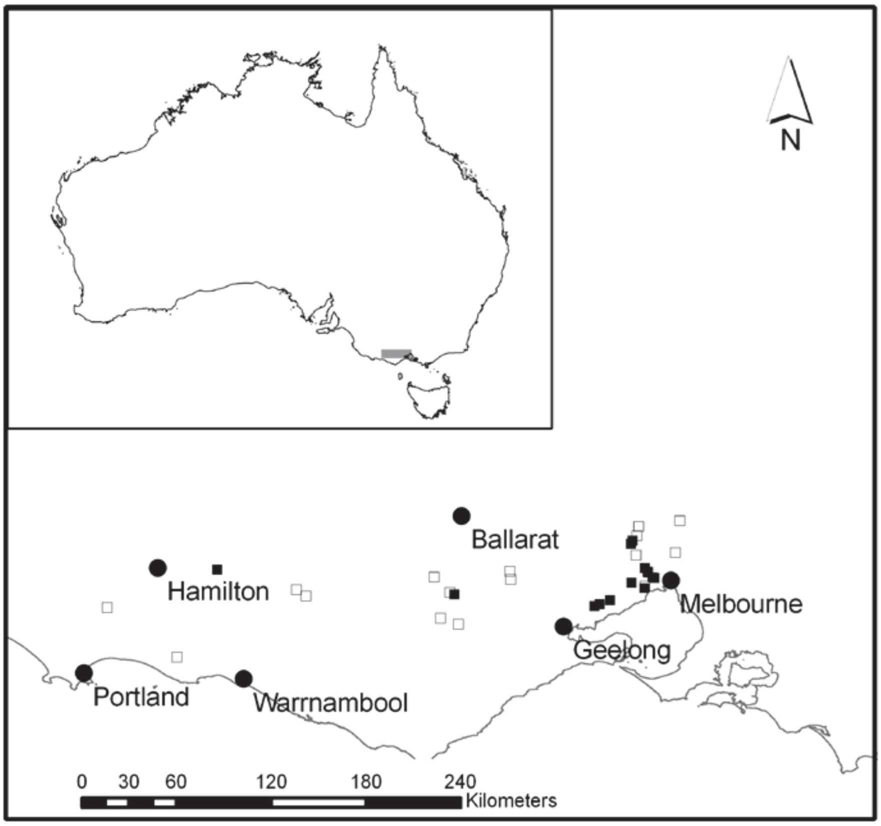

Figure 5.1 Location of the 30 native grassland sites that were analysed in this study (■= Sampled in 1984 and 2001, □ = Sampled in 1984 and 2007).

of 1984–85 (Stuwe 1986).This comprehensive regional survey, the 'historical' survey, recorded the presence of all native and exotic vascular plant species at each remnant grassland site, as well as the cover-abundance of all native and exotic vascular plant species within a 4 m x 2 m quadrat at each site.

Prior to conducting a contemporary floristic survey, the identity and location of each remnant grassland site was confirmed by consulting detailed notes and the original site maps accompanying the historical survey. I also standardized taxonomic nomenclature in accordance with Walsh and Stajsic (2007). In general, the historical survey identified plant taxa to species level, however, if a taxon was identified at a higher level in the taxonomic hierarchy (e.g. genus), the higher-level identification was retained in the contemporary survey.

A sub-sample of 30 remnant grassland sites located across the region was re-surveyed. Fourteen of these sites were re-surveyed by N.S.G. Williams and J. W. Morgan in the spring and summer of 2001 (Williams 2005; Williams *et al.* 2005a; Williams *et al.* 2006). The remaining 16 of these sites were re-surveyed by D. Licari and N.S.G. Williams in the summer of 2007. Both the 2001 and 2007 contemporary surveys recorded the presence of all native and exotic vascular plant species. The sampling methods employed in both the 2001 and 2007 contemporary surveys mirrored the sampling methods of the historical survey as closely as possible. Each site was surveyed using consistent survey techniques and was sampled by walking a systematic grid pattern. Here, I note that the different sampling intervals (i.e. 14 sites sampled in 1984 and 2001 and 16 sites sampled in 1984 and 2007) and the effects of the ongoing drought in the early years of the century have the potential to confound my results.

Recording a species as absent in a contemporary survey when it is indeed present (i.e. a false absence) has been raised as an issue for studies that employ floristic survey data from two time periods to assess change in the plant species composition (Fischer & Stöcklin 1997; Kéry 2004; Olden & Rooney 2006). To overcome this, in addition to implementing the consistent survey techniques detailed above, I also adopted a conservative approach to the plant species included in this statistical analysis of changes in assemblage composition. First, both native and exotic annual plant species were removed from consideration prior to statistical analysis, because this is considered the most conservative approach for determining overall assemblage-level changes (Williams et al. 2006; Williams et al. 2005). Then, specimens/samples from *Austrodanthonia*, *Austrostipa*, *Juncus*, *Wahlenbergia* and the Orchidaceae were identified to only the genus level because of the challenges posed by identifying these taxa in the field. Finally, samples of plant species that could not be identified in the field were identified by botanists at the National Herbarium of New South Wales.

5.2.3 Quantifying urbanization

Urbanization was quantified based on the human population density of the area surrounding each remnant grassland site. Human population density should be a good surrogate for the human activities that might affect the species composition of native grassland vegetation. Additionally, human population density is relatively easy to source and quantify and has been used in other studies of homogenization and differentiation (e.g. Olden *et al.* 2006; Schwartz *et al.* 2006).

The human population density of the area surrounding each remnant grassland site prior to the 1984 historical survey was determined using population data from the 1981 Census of Population and Housing (Australian Bureau of Statistics 1981). First human population density (persons km^{-2}) within a circular area of 5 km radius of the centre of each site was determined according to the method outlined in Section 3.2.2. Based on these human population density data, I then classified nine sites as urban (>200 persons km^{-2}), five sites peri-urban (10–200 persons km^{-2}) and 16 sites as rural (<10 persons km^{-2}) (Table 5.1).

5.2.4 Statistical analysis

When compared to the historical survey, there was an increase in the number of native species found in the contemporary survey of all remnant grassland sites. This indicates that in comparison to the historical survey, the historical survey undersampled the native species composition of the 30 sites. Furthermore, it suggests that the conservative precautions I adopted to minimise recording false absences were successful. Consequently I assumed that if a native or exotic species was recorded as present in the historical survey and recorded as absent in the contemporary survey, that the species had become extinct from a given site. However, from the perspective of recording species colonizations, undersampling in the historical survey raises the possibility of recording false colonizations. A false colonization would arise when a species is present in the contemporary survey and is recorded as absent in the historical survey, but is actually present historically.

In the instance of native species, it is safe to assume that if a perennial native species, recorded as absent in the historical survey of a remnant grassland site, was recorded as present in the contemporary survey, then it was actually present in 1984–85. Most perennial native species common in temperate grassland either lack dispersal mechanisms (McIntyre *et al.* 1995; Williams *et al.* 2005b) or are only able to disperse over very short distances (Morgan 1995). Species with poor dispersal capability would consequently

Table 5.1 Urbanization categories and numbers of sites per urbanization category for remnant grassland sites sampled in 1984/2001 and 1984/2007 based on the 1981 human population density of the area surrounding each site.

Sampling dates	Total	Urbanization Category		
		Urban	Peri-urban	Rural
1984/2001	14	7	3	4
1984/2007	16	2	2	12

have difficulty moving between isolated patches of remnant grassland vegetation (Andrén 1999). Given that the 30 grassland remnants that are the subject of this study are essentially isolated 'islands', it is unlikely that these native species could recolonize grassland remnants in the time between the historical and contemporary surveys (Williams *et al.* 2005b; Williams *et al.* 2006). Additionally, re-establishment from a soil seed bank is also unlikely because most perennial native species only form short-lived soil seed banks (Morgan 1995; Lunt 1996; 1997; Morgan 1998a). As recolonization by native species is unlikely, one could correct for undersampling of native species with a method akin to the standard reconstruction technique (see Section 1.2.5.1), by adding the list of those species found only in the contemporary survey to the historical inventory of native species.

Given that native species were found to have been undersampled in the historical survey when compared to the contemporary survey, it is safe to assume that exotic species were also undersampled in the historical survey. It is therefore likely there were exotic species actually present historically but not recorded in the historical survey. However, the technique to correct for undesampling of native species proposed above cannot be applied to correct for undersampling of exotic species because this technique does not account for exotic species colonizations.

It is reasonable to assume that at least some of the remnant grassland sites that are the subject of this study were colonized by additional exotic species between the historical and contemporary surveys because most of these sites are located in close proximity to roads and human settlement. It is well documented that motor vehicles are a dispersal vector for the propagules of exotic species and that the areas adjacent to roads are favourable for the establishment and growth of exotic species (see references in Forman & Alexander 1998; Tromulak & Frissell 2000; Harrison *et al.* 2002; Gelbard & Belnap 2003). Furthermore, colonization of native vegetation by exotic species at small scales has been associated with close proximity to human settlement (Batainoff & Franks 1998; Magee *et al.* 1999; Sullivan *et al.* 2005) and at larger scales with higher human population densities (Pyšek *et al.* 2002). The problem posed by this situation is: How might we allocate exotic species occupancy records in a manner which corrects for undersampling of exotic species and does not over- or understate exotic species colonizations?

This situation is similar to the one encountered in Chapter 4, where I reconstructed the pre-European historical inventory of woodland and forest locations across south-eastern Australia. In that study I adopted a stochastic modelling approach based on the log-series distribution to allocate native species occupancy records without overstating native species extinctions (Section 4.2.2), employing a stochastic modelling approach based on the log-series distribution. Here a similar approach is adopted to compensate for oversampling of exotic species in the contemporary survey.

Modelling was conducted in four stages: (1) The historical inventory of all remnant grassland sites was corrected for native species found to be present in contemporary inventories and presumed to have occurred historically; (2) A regional inventory of exotic species possibly present historically was assembled, the parameters of the log-series estimated and then the distribution calculated; (3) A Monte Carlo approach was used to correct the historical inventory of exotic species and determine the modelled historical similarity matrix; and (4) Change in similarity was estimated and the significance of the changes determined. The techniques I adopted at each stage are now addressed in turn.

5.2.4.1 Stage 1: Assembly of the inventory of native species possibly present historically and correction of the historical inventory

For each remnant grassland site I corrected for false colonization by native species. If a native species was recorded as present in the contemporary survey of an individual grassland site but recorded as absent in the historical survey of that site, it was assumed that species was present historically. For each remnant grassland site, an inventory of those native species found to be present in the contemporary survey but recorded as absent in the historical survey was assembled; these species were added to the historical inventory of each site.

5.2.4.2 Stage 2: Assembly of the regional inventory of exotic species possibly present historically and calculation of the log-series

Initially I assumed, if an exotic species was recorded as present in the contemporary survey but recorded as absent in the historical survey of an individual grassland site, it was possible for that species to have been present historically at that site (these species are referred to as 'possibly present'). The description of the methods used to correct for false colonization below refer to the detailed description of the log-series and the parameters which define this distribution (Section 4.2.2.1).

The parameter S is defined as the total number of exotic species that were possibly present historically at all 30 remnant grassland sites across the region (see Equation 4.2). For each remnant grassland site, I compared the contemporary and historical inventories to assemble a list of the exotic species that were possibly present historically. These individual lists were consolidated into a regional list of those exotic species, yielding an S of 92 exotic species.

The parameter N from the log-series was calculated, with N defined as the total number of historical occupancies of exotic species that were possibly present historically across the region (see Equation 4.2). The maximum number of regional occupancies of exotic species that were possibly present historically (N^{Max}) was defined as the total number of exotic species occupancies in the contemporary surveys but recorded as absent in the historical survey of all 30 sites. This procedure yielded an N^{Max} of 380 occupancies of exotic species that were possibly present historically (Table 5.2).

It was assumed that, when compared to the contemporary survey, exotic species were undersampled in historical surveys by the same ratio as native species were undersampled across the region. For the 30 remnant grassland sites I calculated the proportion by which native species were

Table 5.2 Total number of exotic plant species possibly present historically (*S*) and the number of total regional occupancies of these species (*N*) for the 30 remnant grassland sites.

S	N*			
	N^{Max}	$N^{33\%}$	$N^{43\%}$	$N^{53\%}$
92	380	125	162	201

* N^{Max} is the maximum number of possible occupancies of exotic plant species possibly present historically. $N^{33\%}$, $N^{43\%}$and $N^{53\%}$ are the three sensitivity levels of occupancy of these species.

undersampled across the region. The number of native species occupancies for those species found only in the contemporary surveys (O_N^C) was divided by the number of native species occupancies for those species found in both the historical and contemporary surveys (O_N^{CH}) (i.e. $\frac{O_N^C}{O_N^{CH}} = \frac{553}{650} = 0.851$; Table 5.3). The number of exotic species occupancies that were possibly present historically was determined by multiplying the number of exotic species occupancies in both the historical and contemporary surveys (O_E^{CH}) by the above ratio. This yielded 162 exotic species occupancies that were possibly present historically (i.e. $\frac{O_N^C}{O_N^{CH}} \times O_E^{CH} = \frac{553}{650} \times 191 = 162$; Table 5.3).

Given that there is a level of uncertainly about the number of exotic species that possibly occupied the 30 remnant grassland sites historically, I tested the sensitivity of the correction model around the number of exotic species occupancies. Three sensitivity levels were defined so that the model to correct for false colonization would also provide a range of estimates of homogenization and/or differentiation of remnant grassland sites based on the number of regional occupancies of exotic species that were possibly present historically.

The initial estimate of the number of exotic species that were possibly present as a percentage of N^{Max} (100 × 162/380 = 43%) was defined as the $N^{43\%}$ sensitivity level. A lower and an upper sensitivity level were defined as 43% ±10% , $N^{33\%}$ and $N^{53\%}$respectively. The number of occupancies of exotic species that were possibly present historically at the $N^{33\%}$ and $N^{53\%}$ sensitivity levels (125 and 201 respectively; Table 5.2) were then calculated. Finally, for

Table 5.3 Total number of plant species occupancies for both the historical and contemporary surveys across all 30 remnant grassland sites.

Species	Survey	Species occupancy	
		Historical survey	Contemporary survey
Native	Both surveys	650	650
	Historical survey only	371	-
	Contemporary survey only	-	553
	Total	1021	1203
Exotic	Both surveys	191	191
	Historical survey only	93	-
	Contemporary survey only	-	380
	Total	284	571

all three sensitivity levels, $N^{33\%}$, $N^{43\%}$and $N^{53\%}$: (1) Equation 4.2 was solved iteratively to obtain an estimate for parameter x (Magurran 2004); (2) Equation 4.3 was solved to obtain an estimate for parameter $\propto$; and (3) The expected log-series frequency distribution of the number of occupancies of exotic species that were possibly present across the region at three sensitivity levels (Equation 4.1) were calculated.

5.2.4.3 Stage 3: Correction of the historical inventory and calculation of the corrected historical similarity matrix

The historical inventories of all 30 remnant grassland sites were corrected for undersampling of native and extinct native species and a corrected historical similarity matrix calculated at all three sensitivity levels. The corrected historical similarity matrix was used as part of my statistical analysis to calculate change in similarity and thus estimate the degree of homogenization and/or differentiation.

The historical inventory was corrected by first adding occupancy records for the native species found to be present in contemporary surveys but not found in the historical survey, identified in Section 5.2.4.1, to the historical inventory. Then the regional inventory of exotic species possibly present historically, identified in Section 5.2.4.2, was added to the historical inventory. A Monte Carlo procedure with 10 000 iterations was used to allocate the regional frequency of occupancy to each exotic species possibly present historically. For each Monte Carlo iteration, I used the inverse transform sampling method to generate sample numbers from the log-series at random and to then allocate each extinct species with an expected frequency of occupancy. The inverse transform sampling method generated a sample regional frequency of occupancy at random from the log-series calculated in Section 5.2.4.2.

For each exotic species possibly present historically, the regional frequency of occupancy was allocated under the constraint that the number of occupancies across the region was less than or equal to the maximum number of locations in which that exotic species might have occurred. The number of regional occupancies of an exotic species possibly present historically were randomly allocated to individual grassland sites under the constraint that species could only be added to the locations where an exotic species possibly present historically might have occurred (identified in Section 5.2.4.2). Once regional occupancies for each exotic species possibly present historically were allocated to individual remnant grassland sites, the correction of the sample historical inventory of native and exotic species was complete.

The historical inventory was used to calculate a sample historical similarity matrix using Jaccard's index (Jaccard 1912; Koleff *et al.* 2003); methods were consistent with those outlined in Section 3.2.3. I then sampled every combination of pairs of remnant grassland sites in the Jaccard similarity matrix for each Monte Carlo iteration. The mean Jaccard's index value from the 10 000 iterations was calculated for each pair of sites and the mean Jaccard's index value of each pairwise comparison was used to construct a corrected historical Jaccard similarity matrix.

5.2.4.4 Stage 4: Determination of change in similarity and testing of significance of change

Similarity analysis was used to determine increases, decreases or no change in the similarity of species composition of the 30 remnant grassland sites at all three sensitivity levels, using methods outlined in Section 3.2.3. The change in similarity for all species (native and exotic species combined), native species only, and exotic species only, the 'modelled results', was calculated. Finally, I determined the statistical significance of change, the 'expected results', using the permuted Wilcoxon *Z*-statistic test outlined in Section 3.2.3 (but calculated in *R* v2.8.1).

5.3 Results

5.3.1 Analysis of change in similarity for all species

The average of the permuted Wilcoxon Z-statistic distribution was positive at all three sensitivity levels for all species for all 30 remnant grassland sites across the region ($N^{33\%}$, $\bar{Z} = 1.150$; $N^{43\%}$, $\bar{Z} = 1.102$; $N^{53\%}$, $\bar{Z} = 0.985$; Table 5.4). Positive values for the average permuted Wilcoxon Z-statistics indicated that we can expect native species extinctions and exotic species extinctions and colonizations to homgenize grassland vegetation. However, there was no significant change in similarity ($P > 0.05$) for my modelled results at all three sensitivity levels ($N^{33\%}$, $Z = 1.409$; $N^{43\%}$, $Z = 1.399$; $N^{53\%}$, $Z = 1.258$; Table 5.4, Figure 5.2). These findings suggested that the species composition of grassland vegetation across all 30 sites is in stasis.

The average of the permuted Wilcoxon *Z*-statistic distribution for all species was positive for the nine urban grassland sites at all three sensitivity levels ($N^{33\%}$, $\bar{Z} = 1.948$; $N^{43\%}$, $\bar{Z} = 1.910$; $N^{53\%}$, $\bar{Z} = 1.837$; Table 5.5). My findings indicated that native species extinctions and exotic species extinctions and colonizations can be expected to homogenize these urban grassland sites by random chance alone. The modelled results revealed a significant increase in similarity ($P < 0.05$) at all three sensitivity levels indicating that the species composition of urban grassland sites has become homogenized ($N^{33\%}$, $Z = 2.714$; $N^{43\%}$, $Z = 2.730$; $N^{53\%}$, $Z = 2.683$; Table 5.5; Figure 5.2).

For the five peri-urban sites, the average of the permuted Wilcoxon *Z*-statistic distribution was positive for all species at all three sensitivity levels ($N^{33\%}$, $\bar{Z} = 1.422$; $N^{43\%}$, $\bar{Z} = 1.424$; $N^{53\%}$, $\bar{Z} = 1.397$; Table 5.6). These findings suggested that we can expect native species extinctions and exotic species extinctions and colonizations to homogenize these peri-urban grassland sites

Table 5.4 Modelled and observed changes in Jaccard’s Index, permuted Wilcoxon *Z*-statistics and observed Wilcoxon *Z*-statistics for all species, native species and exotic species in all 30 grassland sites.

Species	Sensitivity	Permuted Wilcoxon *Z*-Statistic				Modelled/observed change in mean Jaccard Index		Modelled/observed Wilcoxon *Z*-Statistic	
		$\bar{Z}$	$P_{2.5}$	$\tilde{Z}$	$P_{97.5}$	$\Delta\bar{J}$	$\%\Delta\bar{J}$	Z	P
All species	$N^{33\%}$	1.150	0.693	1.152	1.619	5.80×10^{-3}	1.88%	1.409	0.264
	$N^{43\%}$	1.102	0.650	1.102	1.559	5.63×10^{-3}	1.83%	1.399	0.204
	$N^{53\%}$	0.985	0.534	0.979	1.458	5.04×10^{-3}	1.63%	1.258	0.244
Native	–	−4.526	−5.104	−4.515	−4.009	-2.84×10^{-2}	−8.17%	−11.129	0.000
Exotic	$N^{33\%}$	14.356	13.644	14.332	15.170	1.35×10^{-1}	81.27%	16.213	0.000
	$N^{43\%}$	14.098	13.383	14.076	14.944	1.29×10^{-1}	74.86%	16.287	0.000
	$N^{53\%}$	13.716	13.002	13.694	14.529	1.22×10^{-1}	68.08%	16.259	0.000

Table 5.5 Modelled and observed changes in Jaccard's Index, permuted Wilcoxon *Z*-statistics and observed Wilcoxon *Z*-statistics for all species, native species and exotic species in nine urban grassland sites.

Species	Sensitivity	Permuted Wilcoxon *Z*-Statistic				Modelled/observed change in mean Jaccard Index		Modelled/observed Wilcoxon *Z*-Statistic	
		$\bar{Z}$	$P_{2.5}$	$\tilde{Z}$	$P_{97.5}$	$\Delta\bar{J}$	$\%\Delta\bar{J}$	Z	P
All species	$N^{33\%}$	1.948	1.630	1.913	2.463	3.78×10^{-2}	10.58%	2.714	0.016
	$N^{43\%}$	1.910	1.599	1.881	2.416	3.66×10^{-2}	10.22%	2.730	0.010
	$N^{53\%}$	1.837	1.520	1.803	2.337	3.48×10^{-2}	9.65%	2.683	0.012
Native	–	−0.805	−1.347	−0.782	−0.342	-1.87×10^{-2}	−4.64%	−1.661	0.002
Exotic	$N^{33\%}$	4.855	4.474	4.819	5.228	2.04×10^{-1}	95.72%	4.678	0.506
	$N^{43\%}$	4.826	4.426	4.788	5.228	1.92×10^{-1}	85.62%	4.694	0.674
	$N^{53\%}$	4.775	4.364	4.725	5.228	1.80×10^{-1}	75.79%	4.662	0.776

Table 5.6 Modelled and observed changes in Jaccard's Index, permuted Wilcoxon *Z*-statistics and observed Wilcoxon *Z*-statistics for all species, native species and exotic species in five peri-urban grassland sites.

Species	Sensitivity	Permuted Wilcoxon *Z*–Statistic				Modelled/observed change in mean Jaccard Index		Modelled/observed Wilcoxon *Z*–Statistic	
		$\bar{Z}$	$P_{2.5}$	$\tilde{Z}$	$P_{97.5}$	$\Delta\bar{J}$	$\%\Delta\bar{J}$	Z	P
All species	$N^{33\%}$	1.422	0.943	1.351	2.064	4.29×10^{-2}	12.92%	2.064	0.054
	$N^{43\%}$	1.424	0.943	1.351	2.064	4.18×10^{-2}	12.56%	2.064	0.064
	$N^{53\%}$	1.397	0.943	1.351	2.064	4.03×10^{-2}	12.05%	2.064	0.070
Native	–	−0.403	−0.943	−0.331	−0.025	-1.24×10^{-2}	−3.25%	−0.535	0.406
Exotic	$N^{33\%}$	2.778	2.778	2.778	2.778	2.04×10^{-1}	117.76%	2.778	0.000
	$N^{43\%}$	2.778	2.778	2.778	2.778	1.97×10^{-1}	109.29%	2.778	0.000
	$N^{53\%}$	2.778	2.778	2.778	2.778	1.88×10^{-1}	99.08%	2.778	0.000

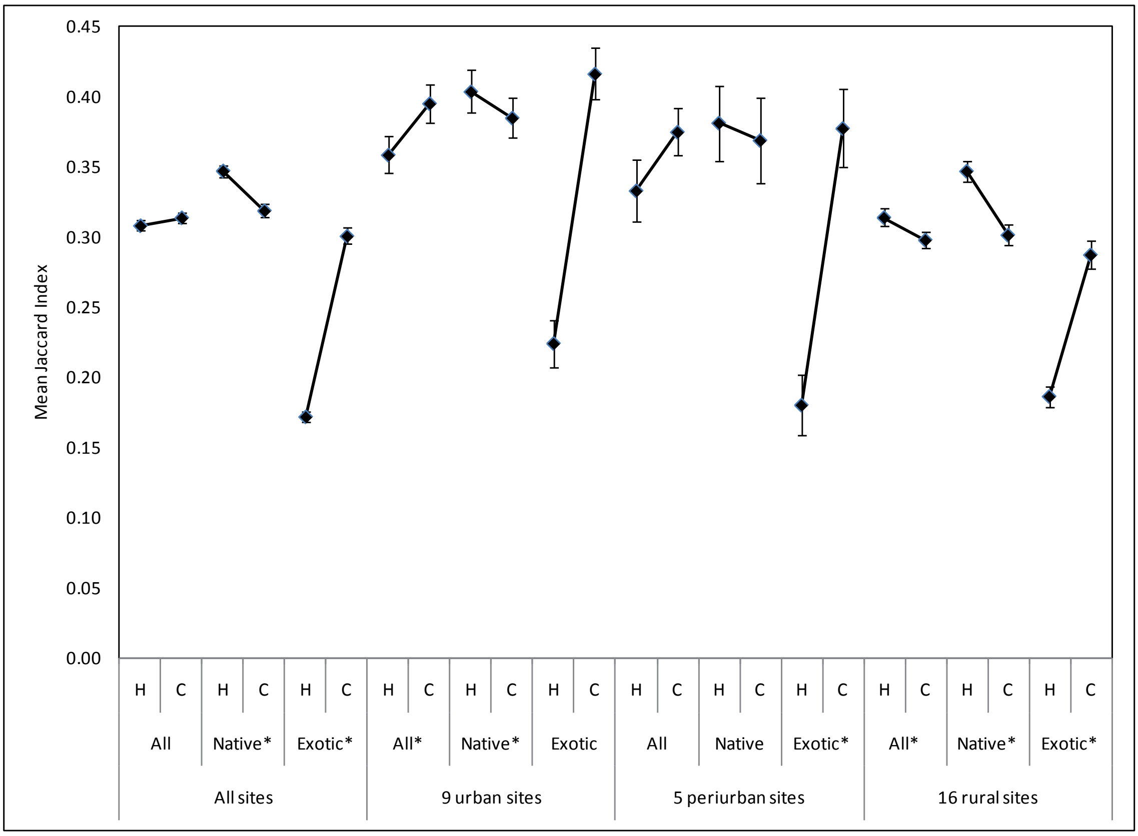

Figure 5.2 Mean Jaccard's index (±SE) for the historical (H) and contemporary (C) remnant grassland assemblages for all species considered together (i.e. native and exotic) as well as native and exotic species considered separately across the 30 sites and for subsets of these sites.

* indicates a significant difference between contemporary and historical assemblages. Figure reflects results for the $N^{43\%}$ sensitivity level from Table 5.4 to Table 5.7

by random chance alone. There was no significant increase in similarity ($P > 0.05$) in my modelled results for these sites at all three sensitivity levels ($N^{33\%}, Z = 2.064$; $N^{43\%}, Z = 2.064$; $N^{53\%}$, $Z = 2.064$; Table 5.6; Figure 5.2). These results indicated that the species composition of grassland vegetation at these peri-urban sites is in stasis.

In the 16 rural grassland sites, the average of the permuted Wilcoxon Z-statistic distribution was negative at all three sensitivity levels ($N^{33\%}$, $\overline{Z} = -1.856$; $N^{43\%}$, $\bar{Z} = -1.862$; $N^{53\%}$, $\bar{Z} = -1.899$; Table 5.7, Figure 5.2), indicating that at random we can expect native species extinctions and exotic species extinctions and colonizations to differentiate grassland vegetation. My

Table 5.7 Modelled and observed changes in Jaccard's Index, permuted Wilcoxon *Z*-statistics and observed Wilcoxon *Z*-statistics for all species, native species and exotic species in 16 rural grassland sites.

Species	Sensitivity	Permuted Wilcoxon Z−Statistic				Modelled/observed change in mean Jaccard Index		Modelled/observed Wilcoxon Z−Statistic	
		$\bar{Z}$	$P_{2.5}$	$\tilde{Z}$	$P_{97.5}$	$\Delta\bar{J}$	$\%\Delta\bar{J}$	Z	P
All species	$N^{33\%}$	−1.856	−2.351	−1.843	−1.419	-1.61×10^{-2}	−5.12%	−4.286	0.000
	$N^{43\%}$	−1.862	−2.364	−1.848	−1.432	-1.60×10^{-2}	−5.09%	−4.320	0.000
	$N^{53\%}$	−1.899	−2.406	−1.888	−1.463	-1.62×10^{-2}	−5.16%	−4.399	0.000
Native	–	−4.229	−4.834	−4.213	−3.713	-4.55×10^{-2}	−13.11%	−8.141	0.000
Exotic	$N^{33\%}$	6.840	6.143	6.787	7.809	1.05×10^{-1}	57.85%	8.306	0.004
	$N^{43\%}$	6.730	6.051	6.684	7.686	1.01×10^{-1}	54.08%	8.390	0.002
	$N^{53\%}$	6.544	5.887	6.498	7.466	9.60×10^{-2}	50.13%	8.372	0.000

modelled results indicated highly significant decrease in similarity ($P < 0.001$) at all three sensitivity levels, suggesting that the grassland vegetation at rural sites has become differentiated ($N^{33\%}$, $Z = -4.86$; $N^{43\%}$, $Z = -4.320$; $N^{53\%}$, $Z = -4.399$; Table 5.7; Figure 5.2).

5.3.2 Analysis of change in similarity for native species

For native species across all 30 remnant grassland sites the average of the permuted Wilcoxon *Z*-statistic distribution was negative ($\bar{Z} = -4.526$; Table 5.4, Figure 5.2). These results indicated that we can expect native species extinctions to differentiate grassland vegetation by random chance alone. Examination of my modelled results also revealed evidence for differentiation. There was a highly significant decrease in similarity in sites across the region, signifying differentiation of the native component of grassland vegetation across the region ($Z = -11.129$, $P < 0.001$; Table 5.4; Figure 5.2). For the nine urban grassland sites, the average of the permuted Wilcoxon *Z*-statistic distribution was negative ($\bar{Z} = -0.805$; Table 5.5), indicating that at random we can expect the extinction of native species to differentiate urban grassland vegetation. My modelled results determined a highly significant decrease in similarity ($\bar{Z} = -1.661$, $P < 0.01$; Table 5.5; Figure 5.2), which indicated that the native flora of urban grassland remnants has become differentiated.

The average of the permuted Wilcoxon *Z*-statistic distribution for all species was negative for the five peri-urban grassland sites ($\bar{Z} = -0.403$; Table 5.6), indicating that, by random chance alone, native species extinctions can be expected to differentiate the species composition of these sites. However, the modelled results revealed no significant change in similarity ($\bar{Z} = -0.403$, $P > 0.05$ Table 5.6; Figure 5.2), suggesting stasis in the species composition of native species at these peri-urban sites.

Analysis of native species for the 16 rural sites indicated the average of the permuted Wilcoxon *Z*-statistic distribution was negative ($\bar{Z} = -4.229$; Table 5.7; Figure 5.2). Thus at random, native species extinctions can be expected to also differentiate the remnant grassland vegetation of these rural sites. The modelled results for native species determined a highly significant decrease in similarity ($\bar{Z} = -8.141$, $P < 0.001$; Table 5.7; Figure 5.2), indicating that the native component of the grassland flora at rural sites has become differentiated.

5.3.3 Analysis of change in similarity for exotic species

The analysis of exotic species for all 30 remnant grassland sites indicated the average of the permuted Wilcoxon *Z*-statistic distribution was positive at all three sensitivity levels ($N^{33\%}$, $\bar{Z} = 14.356$, $N^{43\%}$, $\bar{Z} = 14.098$; $N^{53\%}$, $\bar{Z} = 13.716$; Table 5.4; Figure 5.2). Thus at random, exotic species extinctions and colonizations can be expected to homogenize the vegetation of remnant grassland sites across the region. The modelled results for all species found a highly significant increase in similarity ($P < 0.001$) at all three sensitivity level, suggesting that the exotic component of the flora has become homogenized across the region ($N^{33\%}$, $Z = 16.213$; $N^{43\%}$, $Z = 16.287$; $N^{53\%}$, $Z = 16.259$; Table 5.4; Figure 5.2).

For the nine urban sites, the average of the permuted Wilcoxon *Z*-statistic distribution was positive for all species at all three sensitivity levels ($N^{33\%}$, $\bar{Z} = 4.855$; $N^{43\%}$, $\bar{Z} = 4.826$; $N^{53\%}$, $\bar{Z} = 4.775$; Table 5.5). These findings suggested that we can expect exotic species extinctions and colonizations to homogenize these urban grassland sites by random chance alone. There was a no significant increase in similarity ($P > 0.05$) in my modelled results for these sites at all three sensitivity levels ($N^{33\%}$, $Z = 4.678$; $N^{43\%}$, $Z = 4.694$; $N^{53\%}$, $Z = 4.662$; Table 5.5; Figure 5.2). This result indicated that the exotic species composition of grassland vegetation at these urban sites is in stasis.

At all three sensitivity levels, the average of the permuted Wilcoxon *Z*-statistic distribution was positive for the five peri-urban grassland sites ($N^{33\%}$, $N^{43\%}$, $N^{53\%}$, $\bar{Z} = 2.778$; Table 5.6; Figure 5.2), indicating that we can expect exotic species extinctions and colonizations to homogenize these grassland sites. My modelled results indicated highly significant increase in similarity ($P < 0.001$) at all three sensitivity levels ($N^{33\%}$, $N^{43\%}$, $N^{53\%}$, $\bar{Z} = 2.778$; Table 5.6; Figure 5.2). Accordingly, the modelled results indicated that exotic species composition of peri-urban grassland vegetation has become homogenized.

For the 16 rural sites, the average of the permuted Wilcoxon *Z*-statistic distribution for exotic species was positive at all three sensitivity levels

($N^{33\%}$, $\bar{Z} = 6.840$; $N^{43\%}$, $\bar{Z} =$ 6.730; $N^{53\%}$, $\bar{Z} = 6.544$; Table 5.7; Figure 5.2). Consequently, exotic species extinctions and colonizations can be expected to homogenize these sites by random chance alone. There was a highly significant increase in similarity ($P < 0.01$) for my modelled results at all three sensitivity levels, signifying that the exotic species composition of rural sites has become homogenized ($N^{33\%}, Z = 8.306$; $N^{43\%}, Z = 8.390$; $N^{53\%}$, $Z = 8.372$; Table 5.7; Figure 5.2).

5.4 Discussion

Floristic studies that employ a revisitation methodology, using historical and contemporary species inventories derived from vegetation surveys, to investigate changes in plant species composition resulting from both extinctions and colonizations face a methodological dilemma. The dilemma is apparent because the means by which such studies can minimise recording both false absences and false colonizations is mutually exclusive. The most effective way to minimise the recording of false absences is to systematically oversample sites under investigation in the contemporary survey. Indeed some authors recommend between two and four separate sampling visits to address this issue (Kéry *et al.* 2006). However, in an effort to minimise false absences, it is likely that systematic oversampling of sites in the contemporary survey (cf. historical survey) may also inadvertently lead to the recording of false colonizations. Applying a stochastic modelling approach to correct for relatively different sampling intensity between historical and contemporary surveys shows great potential as a method by which the recording of both false absences and false colonizations can be minimised.

We can be certain of the identity and number of some of the exotic species that historically occupied the sites that are the subject of this study because these exotic species were found to be present in the historical survey. However, we cannot be certain of the identity and number of all the exotic species that were present at the time of the historical survey because, relative to the contemporary surveys, the historical survey undersampled the species composition of grassland vegetation across the region. Nevertheless, I am confident that my model presents ecologically meaningful results as well as providing a means by which to address the issue of relatively different sampling intensity between the historical and contemporary surveys. However, the modelled results need to be interpreted with care. Accordingly, rather than provide an absolute estimate of change in grassland vegetation, I can draw conclusions on the trajectory of change in species composition at the 30 remnant grassland sites.

Before the expected and modelled results are discussed, it is pertinent to note that the sites that are the subject of this study were sampled over two different time intervals, i.e. 14 sites sampled in 1984 and 2001 and 16 sites sampled in 1984 and 2007. Consequently, observed patterns of change in species composition of these two sets of sites may result from two factors. The first is the different time interval over which the remnant grassland sites were sampled, 17 and 23 years respectively. Given that homogenization and differentiation are both spatial and temporal processes, it follows that the time interval over which the process is measured may affect observed results (Olden & Poff 2004b). Longer time intervals between surveys favour greater numbers of both extinctions and colonizations. The trajectory of change resulting from native species extinctions (i.e. differentiation) and exotic species colonizations and extinctions (i.e. homogenization) is consistent across the study region.

The second factor is changes in species composition may result from different processes of change operating in different locations on the urban–rural gradient. For example, rural sites may be grazed by domestic animals but it is unlikely that urban sites would be under grazing pressure. However, it is not possible to disentangle the temporal effect of survey interval on the species composition of grassland vegetation from the effect of the varying processes which may operate along the urban–rural gradient. Notwithstanding this caveat, I am confident that the primary factor affecting changes in plant species composition is the level of urbanization of the area surrounding each site (Williams *et al.* 2005b; Williams *et al.* 2006).

5.4.1 Expected changes in species composition

In my analysis of all species, both native and exotic species considered together, my model predicted we can randomly expect the species composition of all 30 sites, the nine urban sites and five peri-urban sites to become homogenized (Table 5.4 to Table 5.6). In contrast my model predicted differentiation of the species composition of grassland vegetation at the 16 rural sites (Table 5.7). The findings for all species are underpinned by the changes in species composition we can expect to occur in the native and exotic floras separately.

For all 30 sites and subsets of these sites, my model predicted that at random we can expect native species extinctions to differentiate the species composition of grassland vegetation (Table 5.4 to Table 5.7). In contrast, we can consistently expect exotic species extinctions and colonizations to homogenize the species composition of grassland vegetation across the region by random chance alone (Table 5.4 to Table 5.7). Consequently, the findings for all 30 sites and subsets of these sites above (Table 5.4 to Table 5.6), indicated that we can expect exotic species extinctions and colonizations to have a relatively greater effect on the species composition of grassland vegetation than native species extinctions by random chance alone. For the 16 rural sites we can expect native species extinctions to have a relatively greater effect on species composition than exotic species extinctions and colonizations (Table 5.7).

5.4.2 Modelled changes in species composition

In my analysis of all species, my modelled results revealed a complex pattern of stasis, homogenization and differentiation in the species composition of grassland vegetation (Table 5.4 to Table 5.7). An explanation of these varying patterns requires an understanding of the changes in species composition that have occurred in the native and exotic floras separately. Patterns of observed homogenization or differentiation are largely dependent on the degree of historical similarity of assemblages under comparison, as well as the identity and number of species which have become extinct from or have colonized assemblages (Olden & Poff 2003).

Theory suggests that plant species extinctions and colonizations can generate either increasing or decreasing similarity in species composition (Rahel 2000; Rahel 2002; Olden & Poff 2003). Extinctions create homogenization when different species become extinct from historically dissimilar assemblages, in so doing producing similar contemporary assemblages. Differentiation is generated by extinctions when the same species become extinct from historically similar assemblages, thus creating dissimilar contemporary assemblages. Colonizations generate homogenization when the same species colonize historically dissimilar assemblages, thus creating similar contemporary assemblages. In contrast, colonizations produce differentiation when different species colonize historically similar assemblages, thereby generating dissimilar contemporary assemblages. The modelled results of stasis, homogenization and differentiation for all 30 sites and subsets of these sites are addressed in turn below.

When native and exotic species are considered together, my analysis indicated stasis, i.e. no significant change in species composition, in the species composition of all 30 sites ($P > 0.05$; Table 5.4). However, modelled results indicated a significant change in the species composition of both the native and exotic components of the flora ($P < 0.001$; Table 5.4). These findings suggested that for all 30 sites the relative change in species composition resulting from native species extinctions and exotic species extinctions and colonizations is opposite in trajectory but similar in magnitude. Consequently, the results indicated that species composition change has been driven by a combination of: (a) extinctions of native species which were relatively widespread across the region historically; (b) extinctions of exotic species that were relatively restricted in distribution within the region historically; and (c) widespread colonizations of the same exotic species across the region.

The analysis for all species indicated a trend toward homogenization of the species composition of the grassland vegetation at the nine urban sites. In the case of these sites the underlying changes in the composition of native and exotic species are particularly complex. The modelled results indicated a significant change in the species composition of the native component of the flora ($P < 0.01$; Table 5.5). Changes in species composition resulting from native species extinctions, which were relatively widespread across urban sites historically, set a course toward differentiation. There were also changes resulting from exotic species extinctions and colonizations that had a tendency to homogenize the species composition of grassland vegetation. Although the changes resulting from exotic species extinctions and colonizations were not statistically significant ($P > 0.05$; Table 5.5), the homogenizing effect of these changes was large enough in magnitude to buffer the differentiating effect of native species extinctions. Paradoxically, this buffering effect set the species composition of grassland vegetation at these urban sites on a course towards homogenization.

In the case of the five peri-urban sites, the analysis for all species also indicated stasis in the species composition of these sites (Table 5.6). However, for these sites there was significant change in the species composition of the exotic component ($P < 0.001$; Table 5.6) but not the native component of the flora ($P > 0.05$; Table 5.6). I note that the small sample size (n = 5) may have reduced the power of this analysis and thus these results need to be interpreted with care. This result indicated that extinctions of exotic species that were relatively restricted in distribution within peri-urban sites historically, as well as widespread colonizations of the same exotic species across the peri-urban sites, have driven change in the species composition of the exotic flora. Although statistically significant, this finding suggested that the magnitude of change in similarity in peri-urban sites resulting from changes in the exotic component of the flora was not large enough to affect the species composition of these sites on the whole.

For the 16 rural sites, the analysis for all species indicated that the species composition of grassland at these sites has become differentiated (Table 5.7). My modelled results for these rural sites indicated a significant change in the species composition of both the native and exotic components of the flora ($P < 0.01$; Table 5.7). The relative change in species composition resulting from native species extinctions and exotic species extinctions and colonizations is opposite in trajectory. However, for these rural sites the magnitude of change in the native flora was greater than that of the exotic flora. This indicates that extinctions of exotic species that were relatively restricted in distribution across the region, as well as widespread colonizations by the same exotic species, were partly responsible for driving changes in species composition. However, the main driver of change in species composition was extinctions of native species that were relatively widespread across the region in 1984.

5.4.3 Urbanization and change in species composition

My findings from this study revealed that change in species composition of grassland vegetation resulting from native species extinctions is associated with the level of urbanization of sites. This result is not entirely unexpected, as previous studies within the region have found relatively clear-cut relationships between native species extinctions and the degree of urbanization. The extinction risk of native species in grassland vegetation has been found to be associated with the degree of urbanization (Williams *et al.* 2006). Indeed, the likelihood of local extinction of native species is higher in urban sites than peri-urban or rural sites (Williams *et al.* 2005b). Notwithstanding that the change in species composition of the native species component of the flora for peri-urban sites was not significant (Table 5.6), the differentiating effect of native species extinctions is greater in magnitude for rural sites than it is for urban sites.

In the case of exotic species, there were obvious differences in the magnitude of homogenization associated with exotic species extinctions and colonizations for the different categories of urbanization. Change in the species composition of the exotic component of urban grassland vegetation was not statistically significant ($P > 0.05$; Table 5.5). However, in peri-urban sites there was a highly significant level of change of a very high magnitude ($P < 0.001$; Table 5.6). Similarly, in rural sites a highly significant level of homogenization of a high magnitude was also detected ($P < 0.01$; Table 5.7).

At first glance, my findings do not have an immediately obvious explanation. One might expect urban sites would be more prone to homogenization than rural sites because urban sites are likely to be under the influence of a range of factors favouring exotic species colonizations. For instance, the close proximity of urban sites to roads and vehicle traffic could create favourable conditions for the dispersal of and colonization by exotic species (see references in Forman & Alexander 1998; Tromulak & Frissell 2000; Harrison *et al.* 2002; Gelbard & Belnap 2003). Indeed, within the study region, exotic species have been found to invade roadside edges and replace native species of urban remnant grasslands (Morgan 1998b). With closer proximity to human settlement, urban grasslands might be more prone to exotic species colonizations resulting from the escape of exotic species from gardens or the dumping of garden waste (Batainoff & Franks 1998; Sullivan *et al.* 2005).

The factors likely to favour exotic species colonizations that I have described above are all spatial in nature. However, homogenization is both a spatial and temporal process (Olden & Rooney 2006), so it is also necessary to take into account the temporal element of change. Given that the urban grassland sites that are the subject of this study are located within long-established urban areas, it is likely many exotic species were already present at the time of the historical survey. Consequently, at the time scale of this study, recording changes in the species composition of the exotic flora that were large enough to be statistically significant would require: (a) large numbers of extinctions of narrowly distributed exotic species across many of the urban sites; and/or (b) large numbers of new colonizations of the same exotic species. Clearly, the changes in species composition brought about by exotic species extinctions and colonizations have not been large enough to generate statistically significant levels of change within urban grassland sites.

I propose that we are indeed likely to see the highest level of change in exotic species composition at peri-urban sites for two reasons. First, the areas immediately surrounding these sites are likely to experience the highest degree of land-use change over the course of this study. At the time of the historical survey, the peri-urban sites that are the subject of this study were located in areas at the margin of urban development. In the time since the historical survey, much of the farmland surrounding these sites has been subdivided and developed for human settlement. Consequently, the spatial factors described above that are likely to favour exotic species colonizations and thereby promote homogenization have become prevalent. Second, the suite of exotic species present at these sites at the time of the historical survey was likely to be those associated with agriculture. As the areas surrounding these sites have become more urbanized, colonizations by new exotic species are more likely to be those exotic species associated with urban areas, e.g. those associated with garden escapes or dumping of garden waste. Accordingly, it is these new exotic species colonizations that are likely to drive homogenization within peri-urban sites.

Given that the rural sites that are the subject of this study are not situated in close proximity to human settlement, it is not unexpected that the magnitude of homogenization associated with exotic species extinctions and colonizations is smaller than that of peri-urban sites. However, the magnitude of these changes is both high and statistically significant (Table 5.7). These findings suggested that the proximity of many of these rural sites to roads and perhaps occasional grazing by sheep may be associated with the turnover of exotic species in the remnant grassland vegetation of rural sites.

5.4.4 Other factors affecting change in species composition

Although in this study I explicitly associated patterns of homogenization and differentiation to patterns of urbanization, it is likely factors other than urbanization may also contribute to native species extinctions in remnant grasslands. For instance, long-term studies in grassland vegetation indicate that habitat fragmentation is at least partly responsible for the decline in abundance and extinction of native species (Leach & Givnish 1996; Fischer & Stöcklin 1997; Bennie *et al.* 2006). Native species extinctions in calcareous grasslands in continental Europe have been associated with small population size resulting from habitat fragmentation (Fischer & Stöcklin 1997). In North America, native species extinctions in prairie have been associated with the suppression of landscape scale fires resulting from habitat fragmentation (Leach & Givnish 1996).

Given that many Australian vegetation associations are adapted to fire (Bradstock *et al.* 2002), changes to fire regimes in grassland remnants might also contribute to changes in species composition of native grassland across the region. For example, within the study region, native species extinctions in grassland vegetation has been associated with longer maximum inter-fire intervals (Williams *et al.* 2006). In grasslands dominated by *Themeda triandra,* the biomass of the dominant grass increases up to six years following fire (Morgan & Lunt 1999). As both living and dead biomass of the *Themeda* tussocks accumulates after a fire, recruitment and survival of inter-tussock species declines (Lunt & Morgan 2002). Eventually, if the inter-fire interval exceeds 11 years, shading by accumulated litter kills inter-tussock species and any remaining *Themeda* tussocks (Morgan & Lunt 1999). Without a persistent soil seed bank, re-establishment of inter-tussock species from a soil seed bank is unlikely and extirpation of these species becomes irreversible (Morgan 1995; Lunt 1996; 1997; Morgan 1998a; Lunt & Morgan 2002).

It is also likely that lack of fire may promote exotic species colonizations across the region. Exotic plant species have been found in greater abundance in long-unburnt areas of native grassland (Lunt & Morgan 1999). Maintenance and restoration of healthy *Themeda* swards have been found to confer a degree of resistance to exotic species colonizations (Lunt & Morgan 2002; Prober & Lunt 2009). Fire has been found to suppress exotic annual species (Prober & Lunt 2009), probably due to the depletion of the soil seed banks of these species (Prober *et al.* 2005).

5.5 Conclusion

Change in the species composition of remnant grassland vegetation across western Victoria, brought about by native species extinctions and exotic species extinctions and colonizations, have created complex patterns of homogenization and differentiation. The results of this study also indicated that native species extinctions and exotic species extinctions and colonizations create the opposite effect in native grassland vegetation. Native species extinctions have a tendency to differentiate grassland vegetation, whilst exotic species extinctions and colonizations have a tendency to homogenize grassland vegetation.

Furthermore, this study confirms that patterns of homogenization and differentiation are associated with the initial level of urbanization of the areas surrounding remnant grassland sites across the region. In this study I postulate that patterns of homogenization and differentiation might be driven with change in the level of urbanization, and change in fire regime, as well as other factors. For example, the relationship of observed patterns of homogenization and differentiation to environmental conditions remains largely unexplored. What is now required is examination of how factors described above might be directly responsible for changes in the species composition of native grassland vegetation.

6 Human-related and environmental correlates of homogenization and differentiation in native grassland vegetation of south-eastern Australia

6.1 Introduction

A growing number of studies of homogenization and differentiation have focused on the role of urbanization as a driver of change in vegetation (Kühn & Klotz 2006; McKinney 2006; Olden *et al.* 2006; Schwartz *et al.* 2006, Chapter 5). However, with the exception of Chapter 5 in this thesis, these works are macroecological studies conducted at large spatial and long temporal scales for undefined vegetation associations. As a result, little progress has been made in our understanding of specific human-related activities associated with the process of urbanization that might drive homogenization and differentiation within specific vegetation associations. Furthermore, there has been negligible advancement in our understanding of potential environmental drivers of homogenization and differentiation (Olden 2006, however see Chapter 3). This chapter addresses the relationship between a range of human-related and environmental variables that I hypothesize might be associated with homogenization and differentiation within a specific vegetation association along an urban–rural gradient.

The findings from Chapters 3 and 4 indicated that different vegetation associations, such as woodland and forest, can display varying patterns of homogenization and differentiation. In Chapter 5, I addressed whether patterns of homogenization and differentiation were associated with patterns of urbanization. The results from Chapter 5 revealed that even within a specific vegetation association (i.e. grassland), species extinctions and colonizations can generate a complex mosaic of change in the species composition of vegetation. I postulated that homogenization and differentiation of grassland vegetation over the course of the study was associated with change in human-related site attributes over the same time interval, i.e. the level of urbanization and fire regime, 1984–2007.

In this chapter, I determine if patterns of homogenization and differentiation amongst the same 30 remnant grassland sites examined in Chapter 5 can be related to both change in the level of urbanization and change in fire regime. Here change in human population density is the metric 'human density' by which to determine change in the level of urbanization. This metric is used because population density data are relatively easy to source and quantify, and may be a good surrogate for the human activities that might affect the species composition of native grassland vegetation.

Change in fire regime is also examined as a specific driver of change in the composition of this vegetation association. Change in fire regime for grassland sites across the region is quantified as the 'maximum inter-fire time interval' of an individual site over the course of the study. In grasslands dominated by *Themeda triandra,* such as those discussed in Chapter 5, declines in the survival of native species and greater abundance of exotic species are associated with long inter-fire intervals (Morgan & Lunt 1999; Lunt & Morgan 2002; Williams *et al.* 2006; Prober & Lunt 2009). Indeed, maximum fire intervals have been found to explain local extinction of native species in grassland located within the study region (Williams *et al.* 2006). As well as investigating how human-related site attributes might drive homogenization and differentiation in grassland vegetation, I also address how environmental site attributes might also drive change.

In Chapter 3 the patterns of homogenization and differentiation in the woodland and forest vegetation of conservation reserves across south-eastern Australia were related to the geographic location of reserves. I proposed that differences in latitude and longitude amongst conservation reserves might be associated with changes in underlying environmental gradients (e.g. incident solar radiation). In this chapter a more direct approach is used to explore the influence of a range of environmental site attributes that might be associated with patterns of homogenization and differentiation; I investigate how solar radiation, temperature and precipitation are associated with changes in species composition.

An historical floristic survey conducted in 1984 sampled the native and exotic species composition of vegetation at the 30 remnant grassland sites examined in Chapter 5 (Stuwe 1986). Contemporary surveys undertaken in 2001 (Williams 2005; Williams *et al.* 2005a; Williams *et al.* 2006) and 2007 resampled the native and exotic species composition of 14 and the other 16 sites respectively. These historical and contemporary surveys were used to determine the level of homogenization and differentiation for all 30 grassland sites, as well as urban, peri-urban and rural subsets of these sites for all species (i.e. native and exotic species combined), native species only, and exotic species only. These results are now employed to determine the effect of human-related and environmental site attributes on patterns of homogenization and differentiation for all 30 grassland sites and all subsets of these sites. Here the questions are:

(1) Can patterns of homogenization and differentiation be associated with human-related correlates of change in the species composition, i.e. change in population density, maximum fire interval?

(2) Can patterns of homogenization and differentiation be associated with environmental correlates of change in the species composition, i.e. solar radiation, temperature and precipitation?

6.2 Methods

6.2.1 Site classification

The subsets of the 30 remnant grassland sites were classified as urban, peri-urban and rural based on the population density (persons km^{-2}) of the area surrounding these sites prior to the 1984 historical survey. Employing the same method outlined in Section 5.2.3, nine sites were determined as urban (>200 persons km^{-2}), five peri-urban (10-200 persons km^{-2}) and 16 rural (<10 persons km^{-2}).

6.2.2 Quantifying change in human-related site attributes

Following the methodology outlined in Section 5.2.3, I quantified change in the level of urbanization based on the change in population density of the area surrounding each remnant grassland site. To quantify change in population density, I first ascertained the historical population density within a circular area of 5 km radius from the centre of each remnant grassland site prior to the historical survey in 1984 (Williams *et al.* 2006), using data from the 1981 census (Australian Bureau of Statistics 1981). For each remnant grassland site, the contemporary population density of the same circular area above was determined at approximately the same time as the contemporary surveys were undertaken. For the 14 sites sampled in 2001 and for the 16 sites I sampled in 2007, population data from the respective 2001 census and 2006 census were used (Australian Bureau of Statistics 2001; 2006). The method outlined in Section 3.2.2 in ArcGIS v9.0 was used to calculate both the historical and contemporary population density above. Change in population density at each remnant grassland site was determined by subtracting the historical from the contemporary population density (Appendix 5).

Fire history was measured by the maximum fire interval (years) because native species extinctions in grassland vegetation within the study region are associated with long intervals between fires (Williams *et al.* 2006, also see discussion in Section 5.4.4). For the 14 sites sampled in 1984 and 2001, the maximum fire interval over the same period was determined from records in Williams *et al.* (2006). For the 16 sites sampled in 1984 and 2007 I used the same method described in Williams *et al.* (2006) to determine the maximum fire interval over the same period.

A number of sources were used to compile a fire history of each site. These included: (a) the field notes taken at the time of the historical and contemporary surveys, as well as field notes from other grassland researchers who also surveyed individual sites; (b) records and reports from local and state government agencies, as well as other agencies responsible for management of these remnant grassland sites (e.g. local cemetery trusts); and (c) the oral fire history of each site determined from interviews with long-term members of the Country Fire Authority brigade responsible for fire management at each site. Although fire records have not been documented in a consistent manner across the region, I am confident the compiled history of prescribed burning and wildfire for each site is thorough (Appendix 5).

6.2.3 Modelling of environmental site attributes

I modelled the value of a range of climatic parameters I hypothesized might be associated with change in the native and exotic species composition of the 30 remnant grassland sites (see Section 3.4). For each site the value for annual mean radiation (Mj m^{-2} day^{-1}), maximum temperature of the warmest period (° C), minimum temperature of the coldest period (° C) and annual precipitation (mm) using BIOCLIM v5.1 (henceforth referred to as 'solar radiation', 'maximum temperature', 'minimum temperature' and 'precipitation' respectively; Appendix 5) was determined. For a given location of known latitude, longitude and elevation, BIOCLIM can interpolate up to 35 climatic parameters based on meteorological data (Houlder *et al.* 2001). In Australia, interpolations are generated from the long-term monthly averages of climate variables at more than 900 temperature stations and 11,000 precipitation stations across the country (Busby 1991).

6.2.4 Statistical analysis

The effect of the above human-related and environmental site attributes on patterns of homogenization and differentiation across all 30 sites and subsets of these sites were assessed for all species, native species only, and exotic species only. For brevity in the description of methods, I only refer to the analysis of all species for all 30 sites.

Data from Chapter 5 were employed to construct a similarity matrix that reflected change in the composition of all species between the historical and contemporary surveys. The historical similarity matrix for all species and for all 30 sites (See Section 5.2.4.4) was assembled first, then the observed contemporary similarity matrix. Finally, a matrix that reflected the change in similarity between surveys by subtracting each cell in the historical matrix from the corresponding cell in the contemporary matrix was calculated. Before describing the assessment method for how patterns of homogenization and differentiation might be associated with the human-related and environmental site attributes, the choice of historical similarity matrix needs further explanation.

When compared to the historical survey, both native and exotic species were oversampled in the contemporary surveys of all 30 sites across the region in the Chapter 5 study. Consequently, a stochastic modelling technique was used to compensate for oversampling. This technique corrected the observed historical inventory of all 30 remnant grassland sites across the region by adding exotic species that possibly occupied these sites historically. Then a corrected modelled historical similarity matrix was calculated. Given that there was a level of uncertainly about the number of exotic species that possibly occupied the 30 sites historically, I calculated a range of estimates for the modelled historical similarity matrix based on three sensitivity levels. These sensitivity levels were based on the number of regional occupancies of exotic species that were possibly present historically. The modelled historical similarity matrix determined for the $N^{43\%}$ sensitivity level is used here. I consider this modelled historical similarity matrix for the $N^{43\%}$ sensitivity level to be my best estimate of the actual historical similarity matrix because the calculation of the matrix for the $N^{43\%}$ sensitivity level was based on the observed levels of oversampling (see Section 5.2.4).

A similarity matrix reflecting change in population density in the area surrounding each site between the historical and contemporary surveys was then constructed,. For each pair of sites, I first log-transformed the difference in population density between pairs of sites for both the historical and contemporary time period (Ln plus 100). Then for each pair of sites, the Bray-Curtis index (Bray & Curtis 1957) was used to calculate both an historical and a contemporary similarity matrix for population density. Values of the Bray-Curtis index range from zero (no change in population density for both sites between surveys) to one (exactly the same change in population density for both sites between surveys). Finally, I calculated a matrix that reflected the change in similarity in population density by subtracting each cell in the historical matrix from the corresponding cell in the contemporary matrix.

The Bray-Curtis index (Bray & Curtis 1957) was used for all other human-related and environmental site attributes to determine a similarity matrix based on the value of a given attribute for each pair of sites. For example, in the case of the solar radiation attribute, the values of the Bray-Curtis index range from zero (zero solar radiation at both sites, the null case) to one (exactly the same value for solar radiation at both sites).

Finally, the correlation (r) between each human-related and environmental variable and the change in similarity of composition of all species across all 30 sites was determined. The significance of these patterns was assessed using Mantel tests (Manly 1997) with 9 999 permutations (Jackson & Somers 1989) performed in Microsoft Excel 2003 using the PopTools v2.7.5 add-in (Hood 2006).

6.3 Results

6.3.1 Relationship of human-related and environmental variables to change in similarity for all species

For all 30 remnant grassland sites across the region, change in similarity of species composition of all species and change in similarity of population density were found to be negatively correlated ($r = -0.311$, $P < 0.001$; Table 6.1). However, the change in species composition of all species was not statistically significant for the 30 sites and thus will not be considered further ($P > 0.05$; Table 6.1). For all other subsets of these sites, urban, peri-urban and rural, there was no significant relationship between change in similarity of species composition and change in similarity of population density ($P > 0.05$; Table 6.2 to Table 6.4). Similarly, for all 30 sites and subsets of these sites, there was no significant relationship between changes in similarity of composition of all species and similarity of maximum fire interval ($P > 0.05$; Table 6.1 to Table 6.4).

There was no statistically significant relationship between change in the similarity of species composition of all species and similarity in maximum annual temperature for the 30 grassland sites ($P > 0.05$; Table 6.1). When the nine urban grassland sites were considered separately, there was a negative correlation between change in similarity of species composition for all species and similarity in maximum annual temperature ($r = -0.466$, $P < 0.05$; Table 6.2). However, there was no significant relationship between change in the similarity of species composition of all species and similarity in maximum temperature for the five peri-urban and 16 rural sites ($P > 0.05$; Table 6.3, Table 6.4). Similarly, for all 30 sites and subsets of these sites, there was no significant relationship between change in similarity of composition of all species and similarity of minimum temperature and precipitation ($P > 0.05$; Table 6.1 to Table 6.4).

Table 6.1 Correlation between change in similarity of species composition and human-related and environmental variables for all species, native species and exotic species across 30 grassland sites.

Species	Human-related/environmental variable	r	P
All	ΔLn Population density	−0.311	0.000
	Maximum fire interval	0.146	0.220
	Annual mean radiation	0.150	0.184
	Maximum temperature of warmest period	0.209	0.094
	Minimum temperature of coldest period	0.016	0.830
	Annual precipitation	0.146	0.186
Native*	ΔLn Population density	−0.237	0.028
	Maximum fire interval	0.151	0.190
	Annual mean radiation	0.106	0.328
	Maximum temperature of warmest period	0.103	0.388
	Minimum temperature of coldest period	−0.015	0.850
	Annual precipitation	0.104	0.320
Exotic*	ΔLn Population density	−0.163	0.200
	Maximum fire interval	0.063	0.570
	Annual mean radiation	0.184	0.100
	Maximum temperature of warmest period	0.238	0.044
	Minimum temperature of coldest period	0.077	0.308
	Annual precipitation	0.155	0.146

* indicates a significant difference in the species composition of contemporary and historical assemblages at the $N^{43\%}$ sensitivity level from Table 5.4 to Table 5.7.

6.3.2 Relationship of human-related and environmental variables to change in similarity of native species

For native species, change in similarity of species composition and change in similarity of population density were found to be negatively correlated for all 30 grassland sites (r=−0.237, $P < 0.05$; Table 6.1). However, there was no significant relationship between change in similarity of population density and change in similarity of native species composition when urban, peri-urban and rural sites were considered separately ($P > 0.05$; Table 6.2 to Table 6.4).

Table 6.2 Correlation between change in similarity of species composition and human-related and environmental variables for all species, native species and exotic species across nine urban grassland sites.

Species	Human-related/environmental variable	r	P
All*	ΔLn Population density	−0.220	0.364
	Maximum fire interval	−0.171	0.538
	Annual mean radiation	−0.097	0.842
	Maximum temperature of warmest period	−0.466	0.034
	Minimum temperature of coldest period	−0.172	0.686
	Annual precipitation	−0.214	0.582
Native*	ΔLn Population density	−0.294	0.170
	Maximum fire interval	−0.181	0.498
	Annual mean radiation	−0.135	0.706
	Maximum temperature of warmest period	−0.437	0.050
	Minimum temperature of coldest period	−0.104	0.876
	Annual precipitation	−0.259	0.390
Exotic	ΔLn Population density	−0.023	0.948
	Maximum fire interval	−0.154	0.600
	Annual mean radiation	0.002	0.908
	Maximum temperature of warmest period	−0.362	0.162
	Minimum temperature of coldest period	−0.273	0.326
	Annual precipitation	−0.012	0.824

* indicates a significant difference in the species composition of contemporary and historical assemblages at the $N^{43\%}$ sensitivity level from Table 5.4 to Table 5.7.

Furthermore, there was no significant relationship between change in similarity of species composition and similarity of maximum fire interval for all 30 sites and subsets of these sites for native species ($P > 0.05$; Table 6.1 to Table 6.4). Similarly, there was no significant relationship between change in similarity of native species composition and similarity of maximum temperature, minimum temperature and precipitation for all 30 sites and subsets of these sites ($P > 0.05$; Table 6.1 to Table 6.4).

Table 6.3 Correlation between change in similarity of species composition and human-related and environmental variables for all species, native species and exotic species across five peri-urban grassland sites.

Species	Human-related/environmental variable	*r*	*P*
All	ΔLn Population density	0.503	0.158
	Maximum fire interval	0.130	0.872
	Annual mean radiation**	–	–
	Maximum temperature of warmest period	0.464	0.144
	Minimum temperature of coldest period	0.037	0.822
	Annual precipitation	0.082	0.868
Native	ΔLn Population density	0.274	0.496
	Maximum fire interval	0.640	0.148
	Annual mean radiation**	–	–
	Maximum temperature of warmest period	−0.063	0.822
	Minimum temperature of coldest period	0.055	0.740
	Annual precipitation	−0.254	0.628
Exotic*	ΔLn Population density	0.628	0.084
	Maximum fire interval	−0.346	0.334
	Annual mean radiation**	–	–
	Maximum temperature of warmest period	0.773	0.008
	Minimum temperature of coldest period	0.063	0.892
	Annual precipitation	0.442	0.320

* indicates a significant difference in the species composition of contemporary and historical assemblages at the $N^{43\%}$ sensitivity level from Table 5.4 to Table 5.7. ** indicates annual mean radiaion for peri-urban sites was the same for all peri-urban sites, thus correlation was not possible.

6.3.3 Relationship of human-related and environmental variables to change in similarity of exotic species

There was no significant relationship between change in similarity of exotic species composition and change in similarity of population density, as well as the similarity of maximum fire interval for all 30 sites and all subsets of these sites ($P > 0.05$; Table 6.1 to Table 6.4). For the 30 sites considered together and

Table 6.4 Correlation between change in similarity of species composition and human-related and environmental variables for all species, native species and exotic species across 16 rural grassland sites.

Species	Human-related/environmental variable	r	P
All*	ΔLn Population density	−0.182	0.408
	Maximum fire interval	0.098	0.546
	Annual mean radiation	0.101	0.220
	Maximum temperature of warmest period	0.089	0.632
	Minimum temperature of coldest period	0.054	0.740
	Annual precipitation	0.100	0.414
Native*	ΔLn Population density	−0.345	0.052
	Maximum fire interval	0.076	0.622
	Annual mean radiation	0.052	0.544
	Maximum temperature of warmest period	0.041	0.820
	Minimum temperature of coldest period	0.088	0.546
	Annual mean moisture index	−0.132	0.418
Exotic*	ΔLn Population density	0.194	0.326
	Maximum fire interval	0.066	0.638
	Annual mean radiation	0.108	0.262
	Maximum temperature of warmest period	0.136	0.354
	Minimum temperature of coldest period	0.027	0.836
	Annual precipitation	0.113	0.334

* indicates a significant difference in the species composition of contemporary and historical assemblages at the $N^{43\%}$ sensitivity level from Table 5.4 to Table 5.7.

the five peri-urban sites the change in similarity of exotic species composition and maximum temperature were positively correlated (30 sites: $r = 0.238$, $P < 0.05$; five peri-urban sites: $r = 0.773$, $P < 0.01$; Table 6.1, Table 6.3). However, for the nine urban and 16 rural sites there was no significant relationship between change in similarity of exotic species composition and similarity of maximum temperature ($P > 0.05$; , Table 6.4). Similarly, for all 30 sites and subsets of these sites there was no significant relationship between change in similarity of exotic species composition and similarity of minimum temperature and precipitation ($P > 0.05$; Table 6.1 to Table 6.4).

6.4 Discussion

6.4.1 Human-related attributes and change in species composition

Across all 30 remnant grassland sites, change in population density was found to be negatively correlated with differentiation resulting from native species extinctions (Table 6.1). However, there was no association between patterns of homogenization and change in population density for exotic species for the 30 sites across the region. Similarly, for all subsets of these sites and for all species, native species only and exotic species only, there was no statistically significant association between patterns of homogenization and differentiation and change in population density. My results indicated that at a regional scale change in population density is a good surrogate by which to quantify the human activities which may affect the species composition of native grassland vegetation along an urban–rural gradient. At least for regions where such data have been regularly and consistently collected over a long period, it is a particularly valuable surrogate because these data are relatively inexpensive to both source and process.

At the scale of the 30 remnant grassland sites across the region, change in population density may be a surrogate for change in propagule pressure. Propagule pressure is a measure of the number of exotic individuals entering an area outside of their native range (Carlton 1996). Propagule pressure estimates both propagule size, i.e. the number of individuals in a single release event, and propagule number, i.e. the number of distinct release events (Lockwood *et al.* 2005). Consequently, propagule pressure increases as the propagule size and/or number increases (Lockwood *et al.* 2005).Reflecting a wide range of human activities (Pyšek & Richardson 2006), propagule pressure is considered a critical element in successful colonization by exotic species (Richardson 1999; Rejmanek 2000; Lockwood *et al.* 2005). However, for studies involving whole exotic floras and conducted at large spatial scales, propagule pressure has proven particularly difficult to measure (Lonsdale 1999). As exact quantitative metrics for propagule pressure are rarely available (Pyšek & Richardson 2006), human population size or density has served as a surrogate for propagule pressure in empirical studies (Pyšek *et al.* 2002; McKinney 2004b; Taylor & Irwin 2004).

However at smaller spatial scales, such as the urban, peri-urban and rural subsets of the 30 sites, other surrogates may more effectively quantify the changes in human activities that might drive change in the species composition of vegetation along an urban–rural gradient. The urban–rural gradient across the study region has been quantified by road density (Williams *et al.* 2005b; Williams *et al.* 2006), the ratio of persons per unit urban land-cover, a landscape shape index and dominant land-cover (Hahs & McDonnell 2006). These metrics might be better surrogates for human activities because they may more effectively reflect site proximity to roads, vehicle traffic, and human settlement, factors known to favour colonization by exotic species (Batainoff & Franks 1998; see references in Forman & Alexander 1998; Magee *et al.* 1999; Tromulak & Frissell 2000; Harrison *et al.* 2002; Gelbard & Belnap 2003; Sullivan *et al.* 2005). Surrogates for human activity such as those above might more effectively quantify change in human activities but these data are relatively more expensive to both source and process in terms of time and resources. Furthermore, given that historical and contemporary data are both required to determine change in any one of these metrics, such long-term historical data may prove difficult to source.

Fire interval has long been thought to be a major driver of dynamics of grassland condition and composition. In North America, the suppression of landscape scale fires resulting from habitat fragmentation has been linked to native species extinctions in prairie (Leach & Givnish 1996). In Australia, fire interval has been noted as a major driver of the local dynamics of *Themeda triandra* dominated grassland composition since Stuwe and Parsons (1977). Frequent fire promotes healthy vegetation structure which in turn promotes native species diversity (Morgan & Lunt 1999; Lunt & Morgan 2002). Healthy *Themeda* swards have been found to suppress exotic annual species as well as bestow a level of resistance to exotic species colonizations (Lunt & Morgan 2002; Prober & Lunt 2009). Moreover, previous work in grassland vegetation across the region indicates that maximum fire interval is a good predictor of change in α-diversity (i.e. species richness) resulting from native species extinctions at individual sites over time (Williams *et al.* 2006). It is therefore surprising that no statistically significant associations between similarity in maximum fire interval and change in β-diversity (i.e. species turnover, Whittaker 1972) over time across the study region have emerged.

Just as human population density represents a gradient in human-related activity, it is reasonable to consider that the maximum fire interval of sites represents an environmental gradient across the study region. Measures β-diversity were originally developed to examine changes in biodiversity over environmental gradients (Whittaker 1960). Consequently, I postulate that similarity in maximum fire interval does not predict change in β-diversity over time because of the pattern of fire across the region does not constitute a measureable environmental gradient over the temporal and spatial scale of this study. Given that maximum fire interval does not exhibit a measureable gradient it is reasonable to suggest that the pattern of maximum fire interval across the region is stochastic in nature. Notwithstanding native species extinction risk in grassland remnants across the study region is not associated with habitat fragmentation *per se* (Williams *et al.* 2006), the disruption of landscape-scale fires by habitat fragmentation (as in Leach & Givnish 1996) may have nullified any gradient in maximum fire interval that might have existed when grassland vegetation was in an unfragmented state.

6.4.2 Environmental attributes and change in species composition

At large spatial scales the β-diversity of both native and exotic plants has been related to climatic gradients. The β-diversity of exotic plants has been strongly correlated with a continental scale longitudinal precipitation gradient in North America (Qian & Ricklefs 2006). In Australian native woodlands, β-diversity is strongly associated with minimum winter temperature along a west–east gradient at similar spatial scale (Hunter 2005a). However, the 30 remnant grassland sites that are the subject of this study are all located within the Victorian Volcanic Plain bioregion, the boundaries of which are based on the predominant landscape-scale environmental attributes of the region (Thackway & Cresswell 1995; Environment Australia 2000). The broad pattern across the Victorian Volcanic Plain is one of gradual change in climate (Taylor *et al.* 2003). One might therefore predict that the environmental attributes of sites may not be associated with patterns of homogenization and differentiation on the whole. Indeed, it is more surprising that patterns of homogenization and differentiation are associated with an environmental site attribute (i.e. maximum temperature). I now address the relationship between patterns of homogenization and differentiation and each of the environmental attributes, solar radiation, maximum temperature, minimum temperature and precipitation in turn.

The intensity of insolation at the Earth's surface is principally a function of the angle of incidence of solar radiation resulting from differences in latitude (Pidwirny 2006). For the remnant grassland sites in this study, there is <1° range in latitude (Appendix 5). It is therefore not surprising that, for all species, native species only and exotic species only across all 30 sites and subsets of these sites, there is no statistically significant relationship between incident solar radiation and patterns of homogenization and differentiation.

Patterns of homogenization resulting from exotic species extinctions and colonizations are positively correlated with maximum temperature for all 30 sites as well as peri-urban sites (Table 6.1, Table 6.3). Changes in exotic species composition also have a tendency to homogenize grassland vegetation at rural sites (Table 6.4, but see Table 5.7). However, there was no statistically significant relationship between maximum temperature and patterns of homogenization at rural sites (Table 6.4). This result is particularly significant because it indicates that the changes in exotic species composition in the subset of peri-urban sites have been large enough to generate statistically significant levels of homogenization across all 30 sites.

These findings support the proposition that colonization by a new suite of exotic species associated with urban areas has driven homogenization at peri-urban sites (see Section 5.4.3). In Australia, the vast majority of exotic species found to be invasive in native vegetation were originally introduced for ornamental horticulture (Groves *et al.* 2005). It follows that many of the exotic species that have colonized peri-urban sites over the course of this study are likely to be of horticultural origin and therefore more likely to be associated with urban areas. Furthermore, exotic species may colonize areas that have similar climatic conditions to that of their native geographic range (Corlett 1992; Wu *et al.* 2004). Consequently, I postulate that homogenization is positively correlated with maximum temperature because the maximum temperature of these peri-urban sites is within the range of temperatures tolerated by these exotic species within their native geographic range.

Homogenization in the composition of all species in urban grassland sites is negatively correlated with maximum temperature (Table 6.2). Given this result, one might predict that changes in native and/or exotic species composition might also be associated with maximum temperature. However there was no statistically significant correlation between change in either native species composition or exotic species composition and maximum temperature (Table 6.2). The results from Chapter 5 indicated homogenization in the species composition of all species, but differentiation in the native species composition of urban grassland sites (Table 5.5). There were also changes in exotic species composition, which had a tendency to homogenize the composition of all species, but these changes were not large enough in magnitude to be statistically significant (Table 5.5). However, the homogenizing effect of change in exotic species composition was large enough to buffer the differentiating effect of change in native species composition. Overall, this resulted in homogenization of the species composition of all species (see Section 5.4.3). It is clear that homogenization in the composition of all species in urban grassland sites is predicated by a complex series of underlying changes in both native and exotic species composition. As a consequence, there is no clear-cut explanation for my finding that homogenization in the composition of all species is associated with the maximum temperature for urban grassland sites (Table 6.2).

Although maximum temperature was found to be associated with the tendency of exotic species to homogenize grassland vegetation, no such relationship emerged for minimum temperature. This is an interesting result given that patterns in β-diversity woodland have been found to be associated with minimum temperature in south-eastern Australia (Hunter 2005a). For all 30 sites and subsets of these sites and for all species, native species only and exotic species only, there was no correlation between patterns of homogenization and differentiation and minimum temperature. However, the lack of association of homogenization with minimum temperature in peri-urban sites is a particularly important finding in and of itself. Assuming that peri-urban sites have been colonized by exotic species originating from geographical areas with similar temperature conditions, my findings that homogenization of exotic species composition is associated with maximum but not minimum temperature is particularly valuable. This result provides circumstantial evidence that the exotic species that have colonized peri-urban sites might have originated in geographical areas with warmer rather than cooler climates.

Although average annual precipitation in the region ranges from 450–840 mm, most of the region receives average annual precipitation of 500–700 mm (Conn 1993; Taylor *et al.* 2003). Rainfall across the region gradually decreases along a south-west to north-east gradient (Taylor *et al.* 2003). As a result, it is not unexpected that across all 30 sites and subsets of these sites and for all species, native species only and exotic species only, that there is no statistically significant association between precipitation and patterns of homogenization and differentiation.

To date, the prediction of patterns of homogenization and differentiation within specific vegetation associations has proven elusive (but see Olden *et al.* 2006). My findings that patterns of homogenization and differentiation can be associated to human-related and environmental site attributes provide a glimpse into how we might be able to employ such attributes as part of a predictive framework. Both human-related and environmental site attributes may be considered filters that act to determine the species and plant trait assembly of vegetation along an urban–rural gradient (Diaz *et al.* 1998; 1999; Williams *et al.* 2009). Investigation of how patterns of change in the composition of specific plant traits (e.g. height, growth form) in both space and time are associated with human-related and environmental attributes may provide a way forward for future work to predict patterns of homogenization and differentiation.

6.5 Conclusion

The findings of this study represent a significant advance in the study of homogenization and differentiation in vegetation. My results demonstrated that a different set of factors may be associated with changes in native species composition when compared to changes in exotic species composition. At the regional scale the tendency for native species extinctions to differentiate the species composition of grassland vegetation is associated with change in human population density. This finding suggests that, at least at a regional scale, change in human population density is a useful surrogate for the human activities affecting the species composition of native grassland vegetation. However, at smaller spatial scales, it may be profitable to employ surrogates for human activity (i.e. proximity to roads, vehicle traffic and human settlement) that more directly reflect the human activities which might contribute to native species extinctions and exotic species extinctions and colonizations. In contrast, the tendency for exotic species extinctions and colonizations to homogenize the species composition of grassland vegetation is associated with maximum temperature at both regional and smaller spatial scales. This particular environmental variable has provided an understanding of the suite of exotic species that have driven homogenization of grassland vegetation across the region. Furthermore, the direct association of an environmental variable to patterns of homogenization and differentiation provides a valuable insight into how the study of plant functional traits might more effectively predict patterns of homogenization and differentiation.

7 General discussion

7.1 Were the aims and objectives of this thesis met?

The overall aim of this thesis was to examine the processes of taxonomic homogenization and differentiation in individual vegetation associations in south-eastern Australia. In this thesis I investigated this issue in three vegetation associations, woodland, forest and grassland, across a wide area of south-eastern Australia and at a range of spatial and temporal scales. In broad terms the overall aim of this thesis was fulfilled.

Four specific objectives were examined; these addressed the gaps in the published literature on homogenization and differentiation in plant species assemblages. Each of these specific objectives are addressed separately below:

1. *To identify patterns of taxonomic homogenization and differentiation within individual vegetation associations at a range of spatial scales.*

This specific objective was achieved by investigating patterns of taxonomic homogenization and differentiation within forest, woodland and grassland vegetation at a range of spatial and temporal scales.

In forest and woodland vegetation, patterns were examined at a continental scale over a period of c. 220 years (Chapters 3 and 4). For the continental-scale study of forest and woodland I examined patterns of homogenization and differentiation at two different grain sizes. In Chapter 3 patterns were investigated at a conservation reserve grain size, while in Chapter 4 these patterns were investigated at a local assemblage grain size. In forest vegetation, patterns were also examined at a catchment scale spanning a period of almost 40 years (Chapter 2). The results of these three chapters revealed a complex mosaic of patterns of homogenization and differentiation within forest and woodland vegetation across south-eastern Australia.

At the larger continental scale and at the conservation reserve grain size, native species extinctions differentiated the species composition of native species in both forest and woodland vegetation (Chapter 3). However, at a continental scale and at the local assemblage grain size (Chapter 4), my stochastic models consistently indicated that native species extinctions promoted homogenization in both forest and woodland vegetation. The contrasting patterns for native species extinctions between Chapters 3 and 4 can be attributed to the grain of investigation (i.e. conservation reserve vs. local assemblage) and/or the method by which the historical species assemblages were reconstructed (i.e. standard reconstruction technique vs. stochastic model).

In Chapter 2, I found that native species colonizations resulting from logging homogenized the species composition of native species in forest. This result for native species concurs with that of Chapter 4 and contrasts with that of Chapter 3. However, note the revisitation methodology employed in Chapter 2 takes into account both native species extinctions and colonizations. In Chapters 3 and 4 the standard reconstruction technique and the stochastic model respectively were used to reconstruct the historical species composition of forest assemblages. Both these reconstruction techniques only account for native species extinctions but do not account for native species colonizations. Notwithstanding differences in the grain size, spatial scale and temporal scale at which the studies of Chapters 2, 3 and 4 were conducted, it is not possible to decouple these spatial and temporal differences from the differing methods used to assess change in species composition between the historical and contemporary time periods.

At a continental scale and at the conservation reserve grain size, exotic species colonizations were also found to have a differentiating effect in woodland vegetation, but no statistically significant effect was found for exotic species in forest vegetation (Chapter 3). Furthermore, my observations at a continental scale and at the local assemblage grain size suggested that exotic species colonizations promoted differentiation in both forest and woodland vegetation (Chapter 4). The contrasting results for exotic species colonization of forest between Chapters 3 and 4 indicated that exotic species colonizations of forest have been idiosyncratic at a continental scale. Furthermore, the grain size at which these two studies were conducted is responsible for the observed differences in the effect of exotic species in forest.

In Chapter 2 I found that both exotic species extinctions and colonizations in forest had a homogenizing effect. This result contrasts with the result for forest vegetation for both Chapters 3 and 4. There are obvious differences in the grain size, spatial scale and temporal scale at which the studies of Chapters 2, 3 and 4 were conducted. However, it is not possible to disentangle these differences in scale from the methods used to assess change in species composition. Both exotic species extinctions and colonizations are taken into account by the revisitation methodology employed in Chapter 2. However, in Chapters 3 and 4 the standard reconstruction technique and the stochastic model respectively were used to reconstruct the historical species composition of forest assemblages. The reconstruction techniques employed in Chapters 3 and 4 only account for exotic species colonizations but do not account for exotic species extinctions.

In grassland vegetation, I examined patterns of homogenization and differentiation at a regional scale (i.e. western Victoria) and (by *defacto*) at the spatial scale of the urban, peri-urban and rural sites situated within the regional study (Chapter 5). Across the whole region, native species extinctions in grassland vegetation promoted differentiation in native species composition. In contrast, exotic species extinctions and colonizations promoted homogenization of the exotic species composition of grassland sites. However, the composition of all species remained in stasis.

For urban sites, the emergent patterns of homogenization and differentiation were even more complex. Native species extinctions promoted differentiation in the native species composition. Exotic species extinctions and colonizations promoted homogenization in the exotic species composition, but these patterns of change were not statistically significant. Even though the changes in compositional similarity brought about by exotic species colonizations were not statistically significant, I reasoned these changes were large enough to buffer the opposite differentiating effect of native species extinctions. This buffering effect brought about the unexpected finding that the species composition for all species became homogenized. In peri-urban sites, exotic species extinctions and colonizations homogenized the exotic species composition, but did not have an overall effect on the composition of all species. Finally, in rural sites, native species extinctions promoted differentiation in the native species composition whilst exotic species extinctions and colonizations homogenized the exotic species composition. Driven by the differentiating effect generated by native species extinctions, the species composition for all species became differentiated in rural sites.

Notwithstanding that my investigations were undertaken at a range of spatial and temporal scales, my findings for forest, woodland and grassland vegetation demonstrated diverse and complex patterns of homogenization and differentiation within each vegetation association. Consequently, my empirical results supported theoretical assertions that patterns of homogenization and differentiation are affected by the spatial and temporal scales and indeed the grain size at which observations are made (Olden & Poff 2003; Cassey *et al.* 2006; Olden & Rooney 2006). My results also provided the first comprehensive evidence that patterns of homogenization and differentiation can vary between different vegetation associations. These findings also provided circumstantial support for my proposition that different vegetation associations may respond differently to a range of habitat alterations (Chapter 1). However, a thorough test of this proposition would require examination of multiple vegetation associations at the same spatial and temporal scale.

2. *To explore how patterns of homogenization and differentiation within individual vegetation associations might be associated with specific human-related factors associated with land-use.*

I met this objective by investigating the effect of a range of human-related factors associated with land-use (Chapters 2, 3, 5 and 6). In Chapter 2 I found that logging promoted homogenization of forest in the Southern Tablelands of south-eastern Australia. I then addressed how patterns of homogenization and differentiation in woodland and forest at a continental scale across south-eastern Australia might be associated with patterns of human population density and settlement time (Chapter 3). However, no statistically significant association was detected between patterns of homogenization and differentiation and these human-related factors.

In Chapter 5 I addressed how patterns of homogenization and differentiation in grassland vegetation related to the level of urbanization along an urban–rural gradient. My findings for this chapter (detailed in the previous section) revealed complex patterns of homogenization and differentiation for urban, peri-urban and rural sites across western Victoria. These findings were examined on how change in human population density and maximum fire interval might be associated with patterns of homogenization and differentiation in the same grassland vegetation (Chapter 6). I found that at the regional scale change in patterns of differentiation in native species composition could be associated with changes in human population density. However, for all other subsets of sites within the region and for all species, native species only and exotic species only no statistically significant association emerged. Similarly, patterns of homogenization and differentiation could not be associated with maximum fire interval for all sites across the region, as well as for urban, peri-urban and rural sites.

3. *To explore how patterns of homogenization and differentiation within individual vegetation associations might be associated with environmental factors.*

I met this objective in the studies wherever it was possible to explore the above aim. In Chapter 3 I found that patterns of homogenization and differentiation in the woodland (20 reserves) and forest vegetation (12 reserves) could be associated with geographical attributes of the conservation reserves in which the vegetation was located. For woodland change in compositional similarity of both native and exotic species could be associated with longitudinal separation of reserves and for native species could also be associated with latitudinal separation of reserves. These geographic attributes could be related to underlying climatic factors (i.e. minimum annual temperature). In Chapter 6 I related patterns of homogenization and differentiation to a range of four climatic attributes of sites, solar radiation, maximum temperature, minimum temperature and precipitation. Interestingly, I found that homogenization resulting from exotic species extinctions and colonizations in all sites and peri-urban sites was positively correlated with maximum temperature.

4. *To develop an approach that addresses the shortcomings of existing techniques used to reconstruct the historical species composition of regions where historical data are unavailable.*

In Chapter 4 I presented a stochastic model that enabled me to reconstruct the historical species assemblages of 87 woodland and 51 forest locations situated over of a broad region of south-eastern Australia. Development of this technique allowed me to address a significant issue that restricted the use of the standard reconstruction technique; the application of the standard reconstruction technique is problematic if data sources are of a different spatial scale. My stochastic model represents a significant methodological advance in the study of taxonomic homogenization and differentiation. This model makes available local scale contemporary inventories of native and exotic species to macroecological investigations of homogenization and differentiation, something not available previously.

Moreover, in Chapter 5 I demonstrated that this stochastic model also has further application, where I employed this model to compensate for differential sampling intensity between the historical and contemporary floristic surveys. This additional application of my stochastic model is a further (and unexpected) methodological advance because it demonstrates that given explicit assumptions, data of varying quality can also be employed in studies of homogenization and differentiation. Therefore, this aim has been met and indeed, exceeded.

7.2 Were the criteria for study of taxonomic homogenization and differentiation met?

By way of the conceptual framework presented in Chapter 1, I identified a number of gaps in the investigations conducted to date of taxonomic homogenization and differentiation in plant species assemblages. I also proposed that studies of homogenization and differentiation need to be conducted within a framework of essential criteria: (i) observations must be made in at least two locations and across at least two times; (ii) when primary historical data are unavailable, the use of a reconstruction methodology is required (at a minimum involving the standard reconstruction technique); and (iii) focus on individual vegetation associations is critical. In addition to these essential criteria, I also proposed that where possible, four important (but not essential) criteria also be met: (iv) utilization of a revisitation methodology; (v) investigation of change in species composition at a range of spatial and temporal scales; (vi) an attempt to identify the human-related and/or environmental drivers of observed patterns of homogenization and differentiation and; (vii) inclusion of some measure of abundance.

For each of the individual investigations within Chapters 2 to 6 I met the essential criteria and indeed exceeded these standards by also incorporating the important criteria where possible. The studies within Chapters 2 to 6 all focused on individual vegetation associations and were conducted in at least two locations and across at least two times and at a range of spatial and temporal scales (meeting criteria (i), (iii) and (v)). Owing to a large spatial and long temporal scale, historical data were not available for Chapters 3 and 4, so I employed a reconstruction methodology (criterion (ii)). For Chapters 2, 5 and 6 I exceeded criterion (ii) by employing a revisitation methodology (criterion (iv)). Additionally, for Chapters 2, 3, 5 and 6 I identified human-related and environmental drivers of patterns of homogenization and differentiation (criterion (vi)). Unfortunately, for Chapters 2, 5 and 6 the available historical survey data were at the level of plant species occupancy and not species abundance. Consequently, criterion (vii) could not be met.

7.3 Future research directions

7.3.1 Predicting homogenization and differentiation

The findings of this thesis indicate that the dynamics of taxonomic homogenization and differentiation, both within and between individual vegetation assemblages, are complex. These dynamics arise out of a range of factors, including the spatial and temporal scales at which taxonomic studies are conducted and the interplay of human-related and environmental drivers of change in species composition. The prediction of patterns of homogenization and differentiation has been addressed at a continental scale for undefined vegetation assemblages (Olden *et al.* 2006). However, given the complexity of the dynamics involving species extinctions and colonizations that underpin patterns of homogenization and differentiation, it comes as no surprise that the prediction of such patterns within specific vegetation associations has not been addressed in the published literature to date.

Human-related habitat alteration has long been identified as a key driver of the process of homogenization and differentiation (Lodge 1993; Brown 1995; Vitousek *et al.* 1997; McKinney & Lockwood 1999). Indeed, my investigations of forest and grassland vegetation provided strong empirical support for this notion (Chapters 2, 5 and 6). Furthermore, my findings indicated patterns of homogenization and differentiation can also be attributed to environmental factors (Chapters 3 and 6). When considered together, the ability to attribute patterns of homogenization and differentiation to human-related and environmental factors provides an indication that future research might be able to be conducted under an *a priori* predictive framework rather than the *post hoc* mechanistic framework I employed in this thesis. This raises the question: What might be required of future studies that would enable prediction of patterns of homogenization and differentiation?

Human-related and environmental factors can be thought of as filters which act to determine the assembly of species and plant functional traits within a vegetation association (Diaz *et al.* 1998; 1999; Williams *et al.* 2009). Therefore, future studies targeting the prediction of patterns of homogenization and differentiation might profit from how human-related and environmental factors can be related to plant functional traits.

7.3.2 Assessing homogenization and differentiation using functional traits

It is not surprising that studies of homogenization and differentiation in plant species assemblages have on the whole focused on taxonomic changes in plant species composition. Such taxonomic changes, measured by changes in compositional similarity of assemblages over space and time, have yielded vital information on shifts in ecosystem structure through time and across space. Ultimately, however, it is not just changes in ecosystem structure that are worthy of attention in a conservation and management context. Ecosystem structure generates ecosystem functioning, and healthy ecosystem functioning provides the ecosystem services used by humans (Murray *et al.* 2006). Consequently, there is recognition that, in addition to taxonomic homogenization and differentiation, functional elements of vegetation assemblages are also a vital consideration (Olden & Poff 2004a; Olden *et al.* 2004; Smart *et al.* 2006; Wiegmann & Waller 2006; Winter *et al.* 2008).

Notwithstanding the theoretical treatment of functional homogenization and differentiation (Olden *et al.* 2004), quantitative evidence for functional homogenization and differentiation in both space and time has been largely circumstantial (e.g. Rooney *et al.* 2004; Wiegmann & Waller 2006; Winter *et al.*

2008). However, a recent study in undefined vegetation assemblages at a coarse grain (i.e. 1.0 km^2 grid cells) in Great Britain has found evidence for functional homogenization across a range of plant functional traits (Smart *et al.* 2006). Nevertheless, formal examination of functional homogenization and differentiation in both space and time and within specific vegetation associations remains an unaddressed issue in the published literature to date.

7.4 Final conclusion

In this thesis I investigated the patterns and causes of taxonomic homogenization and differentiation within forest, woodland and grassland vegetation across south-eastern Australia at a range of spatial and temporal scales. Doing so I met all objectives and conducted my analyses within a framework of essential and important criteria. Given the paucity of investigations within individual vegetation associations in the literature to date, I believe that this thesis makes a meaningful and significant contribution to the fields of plant ecology and biogeography.

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Appendix 1

List of empirical investigations that have examined biotic homogenization in plant species assemblages. With minor exceptions (e.g. Rejmánek 2000), these studies have examined changes in species and/or trait composition in both space and time. Studies are listed in chronological order.

Location	**Coverage**	**Findings**	**Reference**
North America	Plant species lists for 30 states and provinces	Exotics decrease compositional similarity of proximal regions in space. In contrast, exotics increase compositional similarity of regions further apart.	Rejmánek (2000)
Wisconsin, USA	Plant species composition and abundance in the understorey of 62 temperate forest stands	Homogenization caused by extinction of rare native species, invasion of exotic species, and native species that were abundant in the historic survey becoming more abundant in the same locations in the contemporary survey.	Rooney *et al.* (2004)
USA	Plant species lists for 20 parks and reserves	Exotics had a minor propensity to differentiate the locations that were studied. Patterns of homogenization and differentiation were associated with exotic species richness. Comparisons of areas with low exotic species richness tended toward differentiation, and areas with high exotic species richness tended toward homogenization.	McKinney (2004a)
USA	Plant species lists for 20 parks and reserves	Exotics were found to homogenize the locations under investigation because they were more commonly shared among locations.	McKinney (2004c)
USA	Plant species lists for eight cities	Non-indigenous native species were found to have a greater homogenizing effect than exotic species. Exotics tended to increase differentiation of urban floras.	McKinney (2005)
USA	Plant species lists for eight cities and 20 parks and reserves	Exotic and native plant species demonstrated similar patterns in evenness of species abundance (i.e. the degree to which species abundance is evenly distributed between natives and exotics). Consequently the numbers of native and exotic species shared among localities decreased with separation distance and latitudinal separation. The floras of urban habitats tended to be more homogenized than parks and reserves.	McKinney & Lockwood (McKinney & Lockwood 2005)
Germany	Plant species composition for 130 km^2 grid cells	Native species and exotic species introduced before the year 1500 demonstrated homogenization in 'most urbanized', 'less urbanized' and 'rural' areas. Exotic species introduced after 1500 promoted differentiation in the same areas.	Kühn & Klotz (2006)
California, USA	Plant species lists for 58 counties along human population density gradient	Flora of urban counties demonstrated homogenization resulting from the extinction of rare, endemic species and the invasion of common exotic species.	Schwartz *et al.* (2006)
North America	Plant species lists for 63 states and provinces in USA and Canada	Used a Monte Carlo approach to combine a scenario-based conceptual model with an approximation of species invasions and extinctions to predict future homogenization patterns for five taxonomic groups (fish, birds, mammals, plants, and reptiles and amphibians). Of the five taxa studied, the	Olden *et al.* (2006)

		greatest level of homogenization was predicted for plants. Results suggested that invasions of exotic species may be a more important driver of homogenization than extinctions of both historically-shared and historically-unshared plant species. Eastern North America was predicted as a plant homogenization 'hotspot' (i.e. with areas likely to exhibit future patterns of homogenization).	
USA	Plant species lists for eight cities and 18 parks and reserves	The floras of urban localities demonstrated a higher degree of homogenization than the flora's more natural areas (parks and reserves). Non-indigenous native plant species were found to homogenize urban floras whilst exotic species tended to differentiate urban floras.	McKinney (2006)
North America	Total native and exotic floras for states and provinces of the USA and Canada	Exotic plant species were found to have a tendency to differentiate the floras of neighbouring regions, but homogenize regions further apart.	Qian and Ricklefs (2006)
Great Britain	Plant species lists for 1572 plots within 238 1km^2 grid squares	Determined that temporal declines in α-diversity were associated with differentiation in plant species composition. Concurrently, as α-diversity declined over time, plant species assemblages became more similar across a range of plant traits (i.e. specific leaf area, canopy height, seed bank longevity and seed dispersal vector).	Smart *et al.* (2006)
South-eastern Pacific	Floras for six islands including Easter Island and five islands from the Desventuradas and Juan Fernández Archipelagos	Found that the effect of native plant extinction on homogenization is relatively small in comparison to the effect of exotic species. Invasion of exotic species was driving homogenization of island floras, albeit at a slow rate.	Castro *et al.* (2007)
Europe and USA	Seven urban floras in Europe and eight urban floras in the USA within the temperate deciduous forest biome	Within Europe, exotic species originating from within the region had a homogenizing effect whilst exotic species originating from outside the region had a differentiating effect. Within the USA, however, there was no substantial evidence to suggest that exotic species originating from within the USA played a greater homogenizing effect than those species originating from outside the USA. Between the two continents, the species interchange was largely from Europe to the USA. Exotic species introduced to Europe before the year 1500 promoted homogenization within Europe, within the USA between Europe and the USA. Exotic species introduced from outside the two continents had a lesser homogenizing effect.	La Sorte *et al.* (2007)
USA	Compared the tree composition and structural metrics of mixed broadleaved-coniferous forest across the Laurentian Mixed Forest Province within three states	Since European settlement of the region, there was a marked shift in species composition from conifer and mixed conifer-deciduous forest to deciduous species alone.	Schulte *et al.* (2007)
Chile	Floras for 13 administrative regions of continental Chile	Determined that there was stasis in the species composition at both national and regional scales. These results differ to those found in the Northern Hemisphere, and the authors postulated that the trajectory of change in species composition may differ between hemispheres.	Castro and Jaksic (2008a)
South-eastern Pacific	Floras for six islands including Easter Island and five islands from the Desventuradas and Juan Fernández Archipelagos. Included present but non-naturalized exotic species	Confirmed previous findings (Castro *et al.* 2007) for floristic homogenization across the six islands.	Castro and Jaksic (2008b)
USA	Compared the floras of counties within two states (California and	Within Florida, exotic species had a strong differentiating effect. However, in California exotic species had both a homogenizing and differentiating effect. Comparison of county pairs indicated	Qian *et al.* (2008)

	Florida)	that exotic species differentiated counties closer together but homogenized counties further apart.	
Germany	Ploidy level (a genetic trait) of native and exotic plants within 130 km^2 grid cells at three spatial scales	At the largest spatial scale (i.e. the whole country), exotic species were found to homogenize ploidy levels of the flora. At the smallest spatial scale (i.e. within grid cells), exotic species were found to differentiate ploidy levels. However, this study employed a ‘space for time’ approach to analyse trait homogenization within contemporary species pools of native and exotic species rather than making a comparison between historical and contemporary species pools.	Winter *et al.* (2008)

Appendix 2

Details of the stand location, logging status, fire history and tenure of each of the 30 stands that are the subject of this study.

Stand No.	Latitude (S)	Longitude (E)	Logging status	Fire history (Year of fire event)	Tenure
83	35.428	149.629	UL	No mapped fire	Tallaganda SCA
121	35.371	149.607	UL	No mapped fire	Tallaganda SCA
122	35.365	149.606	UL	No mapped fire	Tallaganda SCA
139	35.552	149.900	UL	1938	Monga NP
151	35.647	149.511	UL	1954	Tallaganda SF
220	35.726	149.690	UL	No mapped fire	Deua NP
227	35.944	149.603	UL	No mapped fire	Deua NP
228	35.945	149.602	UL	No mapped fire	Deua NP
234	35.944	149.577	UL	1989	Tallaganda SF
235	35.970	149.562	UL	No mapped fire	Deua NP
84	35.481	149.575	L	1957	Tallaganda SF
86	35.478	149.576	L	1957	Tallaganda SF
87	35.481	149.574	L	1957	Tallaganda SF
95	35.564	149.496	L	No mapped fire	Tallaganda SF
96	35.656	149.533	L	1954	Tallaganda SF
97	35.566	149.495	L	No mapped fire	Tallaganda SF
137	35.552	149.900	L	1938	Monga NP
140	35.551	149.896	L	1938	Monga NP
141	35.385	149.545	L	1981	Tallaganda NP
148	35.656	149.532	L	1954	Tallaganda SF
149	35.645	149.510	L	No mapped fire	Tallaganda SF
150	35.641	149.507	L	No mapped fire	Tallaganda NP
159	35.653	149.877	L	No mapped fire	Monga NP
201	35.607	149.856	L	1957	Monga NP

202	35.651	149.895	L	No mapped fire	Monga NP
203	35.602	149.852	L	1957, 1991	Monga NP
204	35.606	149.855	L	1957, 1991	Monga NP
231	35.945	149.570	L	1989	Tallaganda SF
233	35.944	149.574	L	1989	Tallaganda SF
236	35.846	149.543	L	No mapped fire	Tallaganda SF

Key to abbreviations: Unlogged (UL); Logged (L); National Park (NP); State Conservation Area (SCA); State Forest (SF).

Appendix 3

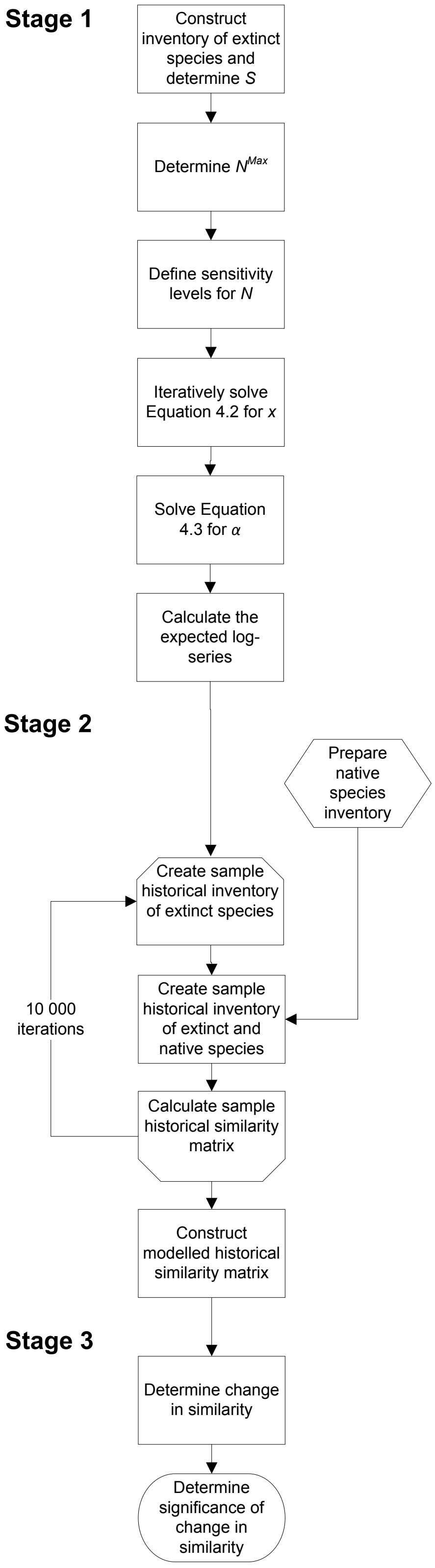
Details of the reserve name, the number and type of vegetation associations, reference, biogeographic region (based on the IBRA scheme) and geographic and human variables for the conservation reserves where the woodlands and forests detailed in this paper are located. Key to abbreviations: latitude (LAT); longitude (LON), human population density (PD); settlement time (ST); National Park (NP); Nature Reserve (NR); State Recreation Area (SRA); Voluntary Conservation Area (VCA).

Name	Vegetation association	Reference	Bio-region	LAT (degrees)	LON (degrees)	PD (persons km^{-2})	ST (years)
Arakoola NR	Woodlands – 4 Forests – 1	Hunter (2003)	BBS, NAN	29.2220	150.749	0.220	163
Barton NR	Woodlands – 5 Forests – 1	Lembit and Skelton (1998)	SEH	33.3165	148.887	21.102	152
Bents Basin SRA	Woodlands – 10 Forests – 7	Benson *et al.* (2002)	SB	33.9544	150.619	323.384	178
Big Bush NR	Woodlands – 2	Porteners (2001)	NSS	34.3632	147.424	2.755	151
Boginderra Hills NR	Woodlands – 3	Lembit and Skelton (1998)	NSS	34.2774	147.620	2.761	148
Copperhannia NR	Woodlands – 6 Forests – 2	Lembit and Skelton (1998)	SEH	33.8578	149.215	0.559	168
Culgoa NP	Woodlands – 6	Hunter (2005b)	DRP	29.0820	147.068	0.015	156
Guy Fawkes NP	Woodlands – 11 Forests – 7	Watson *et al.* (2000)	NET, NNC	30.0943	152.200	0.204	160
Ingalba NR	Woodlands – 2	Porteners (2001)	NSS	34.4860	147.410	2.611	151
Ironbark NR & Bornhardtia VCA	Woodlands – 5 Forests – 3	Hunter and Hunter (2003)	NET	30.3320	149.901	4.671	112

Kwiambal NP	Woodlands – 7 Forests – 1	Hunter *et al.* (1999)	NAN	29.1550	150.982	0.390	178
Mount Annan	Woodlands – 1	Benson and Howell (2002)	SB	34.0646	150.769	292.257	182
Mount Canobolas SRA	Woodlands – 3 Forests – 2	Hunter (2002b)	SEH	33.3480	149.001	19.212	165
Myall Lakes NP	Woodlands – 3 Forests – 9	Hunter and Alexander (2000)	NNC	32.4320	152.368	3.653	184
Narran Lake NR	Woodlands – 2 Forests – 2	McGann *et al.* (2001)	DRP	29.7490	147.418	0.081	154
Paroo Darling NP	Woodlands – 8	Westbrooke *et al.* (2003)	ML	30.7858	143.426	0.008	151
Pucawan NR	Woodlands – 2	Porteners (2001)	NSS	34.4451	147.344	3.325	151
Warra NP & Wattleridge VCA	Woodlands – 2 Forests – 4	Hunter (2005b)	NET	29.9990	151.951	0.339	171
Washpool NP	Woodlands – 3 Forests – 12	Hunter (1998)	NET, NNC	29.3480	152.101	0.202	158
Zara Enclosure	Woodlands – 2	Stafford and Eldridge (2000)	RIV	35.1714	144.704	0.081	148

Appendix 4

Flow chart of the stochastic modelling approach outlined in Section 4.2.2.



Identify and determine the total number of extinct species (*S*)

Determine the maximum number of possible regional occupancies of an extinct species (N^{Max})

Define appropriate sensitivity levels for *N* (e.g. $N^{10\%}$, $N^{15\%}$, $N^{20\%}$)

Calculate the expected log-series frequency distribution for sensitivity levels of *N*

Remove exotic species from the contemporary regional inventory of extant native and exotic species

Create sample historical inventory of extinct species by allocating a sample regional frequency of occupancy at random from the log-series to each extinct species

Add sample historical regional inventory of extinct species to the contemporary regional inventory of extant native species

Calculate a sample historical similarity matrix using and sample every combination of pairs of locations in the matrix

For each pair of locations calculate the mean similarity value from the sample of 10 000 iterations. Construct the modelled historical similarity matrix from these mean values

Construct an inventory of extant native species only and determine change in similarity using method outlined in Section 3.2.3

Determine the statistical significance of change using the permuted Wilcoxon Z-statistic test outlined in Section 3.2.3

Appendix 5

Site attributes of 30 remnant native grassland sites across western Victoria

Key	Attribute	Key	Attribute
A	Site number (Stuwe 1986)	H	Maximum fire interval (years)
B	Site name	I	Annual mean radiation (Mj m^{-2} day^{-1})
C	Soil parent material (B = Basalt, S = Sedimentary)	J	Maximum temperature (° C)
D	Urbanization category (U = Urban, P = Peri-urban, R = Rural)	K	Minimum temperature (° C)
E	Human population density (1981) (persons km^{-2})	L	Annual precipitation (mm)
F	Human population density (2001) (persons km^{-2})	M	Annual mean moisture index (0 (dry) to 1 (saturated))
G	Human population density (2006) (persons km^{-2})		

A	B	C	D	E	F	G	H	I	J	K	L	M
Sites sampled in 1984/2001												
1	Evans Street Native Grassland Reserve, Sunbury	B	P	66.3	353.1	–	6	15.7	25.8	3.4	572	0.57
2	Diggers Rest – Sunbury Rail Reserve	B	U	682.0	1144.6	–	9	15.7	25.7	3.4	577	0.58
34	Rokewood Cemetery	S	R	1.4	4.8	–	7	15.6	26.4	3.3	570	0.61
60	Manor Rail Reserve	B	P	105.6	105.4	–	9	15.7	24.9	4.6	505	0.48
74	Braybrook Rail Reserve	B	U	1436.0	1704.9	–	10	15.5	25.8	4.5	592	0.55
75	O'Brien Park Matthews Street, Sunshine	B	U	1396.0	1379.5	–	8	15.5	25.8	4.5	589	0.55
77	Denton Avenue Grassland Reserve, Sunshine North	B	U	1525.1	1474.4	–	16	15.6	25.9	4.4	571	0.53

85	Slough Estates	B	U	730.7	801.1	–	16	15.6	25.6	4.7	562	0.52
97	St Albans Rail Reserve	B	U	1068.7	1789.1	–	6	15.6	25.8	4.2	569	0.54
98	Truganina Cemetery	B	P	46.3	143.1	–	7	15.7	25.5	4.5	538	0.50
101	St Albans Road Rail Reserve, Sunshine North	B	U	1485.9	1538.7	–	10	15.6	25.8	4.4	573	0.54
107	Dunkeld Flora Reserve	B	R	0.8	0.7	–	9	15.4	25.2	3.6	687	0.67
61a	Little River Rail Reserve A (North side of tracks)	B	R	2.6	12.6	–	10	15.8	24.7	4.6	492	0.47
61b	Little River Rail Reserve B (South side of tracks)	B	R	3.2	12.6	–	13	15.8	24.7	4.6	486	0.47
Sites sampled in 1984/2007												
4	Raes Road Council Reserve	B	P	60.0	–	180.2	10	15.7	25.7	3.2	592	0.60
5	Melbourne–Lancefield Road Rail Reserve, Clarkefield	B	R	7.9	–	40.3	5	15.7	25.6	3.0	612	0.63
8	Cooper St, Somerton	B	U	775.5	–	722.2	9	15.4	26.0	4.0	651	0.63
22	Bolac Plains Road via Woorndoo	B	R	0.9	–	0.6	1	15.6	25.2	3.6	609	0.63
25	Woorndoo–Dundonnell Road via Woorndoo	B	R	0.8	–	0.5	1	15.5	25.2	3.7	615	0.64
31	Cressy Rail Reserve	B	R	0.5	–	0.0	22	15.5	26.1	3.6	570	0.60
38	Cape Clear–Rokewood Road via Rokewood	S	R	1.4	–	5.3	15	15.6	26.4	3.3	568	0.60
43	Pretty Hill Flora Reserve	B	R	2.6	–	2.3	9	15.1	22.9	5.3	758	0.69
58	Elaine–Blue Bridge Road Railway Reserve, Elaine	B	R	2.1	–	1.5	5	15.3	24.7	2.8	700	0.74
64	Calder Rail Reserve	B	P	22.6	–	461.1	20	15.7	25.8	3.8	559	0.54
66	Beveridge Rail Reserve	B	R	6.2	–	8.9	17	15.5	26.0	3.2	693	0.69
80	Laverton North Grassland Reserve, Altona North	B	U	801.4	–	716.0	5	15.6	25.6	4.7	567	0.53
99	Midland Highway Rail Reserve, Elaine	B	R	3.4	–	3.4	6	15.3	24.8	2.9	686	0.73
104	Cape Clear Cemetery	S	R	4.1	–	1.0	20	15.8	27.1	3.5	506	0.53

105	Cressy Trotting Track	S	R	1.7	–	1.1	2	15.6	26.4	3.6	556	0.59
151	Condah Cemetery	B	R	1.5	–	0.9	11	15.2	24.2	4.5	756	0.68