Ecosystem services: an ecophysiological examination

Derek Eamus¹, Catriona M.O. Macinnis-Ng, Grant C. Hose, Melanie J.B. Zeppel, Daniel T. Taylor and Brad R. Murray

Institute for Water and Environmental Resource Management
Department of Environmental Sciences
University of Technology Sydney
PO Box 123
Broadway
NSW 2007
Australia

¹ Corresponding author: Derek.Eamus@uts.edu.au

Key words: Ecosystem services; carbon accounting; biodiversity, NPP, wetlands
1.0 Summary

This review aims to discuss ecosystem services, provide case studies at catchment and local scales and provide ideas for future research. Thus this review discusses the following:

1. Ecosystem services (ES) are those goods and services that are provided by or are attributes of ecosystems that benefit humans. Examples of ES include the timber derived from a forest, the prevention of soil and coastal erosion by vegetation and the amelioration of dryland salinity through prevention of rises in the water table by trees. The provision of ES globally is in decline because of a lack of awareness of the total economic value of ES in the public, policy and political fora.

2. Providing a scientific understanding of the relationships among ecosystem structure, function and provision of ES, plus determining actual economic value of ES, is the central challenge to environmental scientists (including triple bottom-line economists).

3. Some ES are widely dispersed throughout many different ecosystems. Carbon accumulation in trees and the contribution of biodiversity to ES provision, are two examples of highly dispersed attributes common to many ecosystems. In contrast, other ES are best considered within the context of a single defined ecosystem (although they may occur in other ecosystems too). Mangroves as “nursery” sites for juvenile fish is one example.

4. Examples of catchment-scale and local-scale provision of ES are discussed, along with future research issues for the nexus between ES and environmental sciences.

2.0 Introduction

Student numbers in Business and IT degrees are increasing as students pursue degrees with obvious economic links. In contrast, student numbers in science, including biology and ecology, are falling, partly because of the lack of perceived economic value of these topics. Ironic it is, then, to see that ecosystem services have been valued at between US$16 – 54 trillion per year (with an average of $33 trillion per year), more than the global gross national product (Costanza et al. 1997). It is doubly unfortunate that the study of ecology and ecophysiology are not perceived as contributing directly to national economies and policy development. Doubly unfortunate because not only is the study and funding of botanical research suffering, but also because the lack of understanding of the economic value of ecosystem services to economic health is causing long-term impoverishment of both the economy and ecology of developed and developing countries alike.
We present this review in 4 stages (sections 3 to 6). We begin by a) defining ecosystem services and b) considering issues pertinent to valuing ecosystem services in the marketplace. In doing so we aim to establish the importance of ecosystem services as a valuable way of thinking and to establishing a common currency among policymakers, managers, researchers and the public as to the value of natural systems. To highlight the broad applicability of this way of thinking, we provide case studies that cover a range of different ecosystem types and consider ecosystem services at both c) catchment (across several ecosystems) and d) individual ecosystem scales. These will provide examples of ecosystem services and illustrate how basic science in ecology and ecophysiology has illuminated our understanding of ecosystem services.

Our catchment scale (terrestrial) case studies have a distinctly Australian focus while our studies of particular ecosystems, which are mostly aquatic, have a more international flavour. We have taken this approach because there have been far fewer studies of aquatic ecosystem services in Australia compared to terrestrial ecosystem services and we argue that aquatic ecosystems are more universal across continents than terrestrial ecosystems. In the Australian context, terrestrial ecosystems are strongly influenced by the combination of low rainfall and low soil nutrients on a continental scale, making them highly unique (Eamus 2003). Freshwater ecosystems are influenced by these conditions to some degree (particularly if the water-body is ephemeral) but the elements of ecosystem structure and function are more similar between continents than those for terrestrial ecosystems, due to convergent evolution. Marine ecosystems are the most similar of ecosystems on a global scale because the lack of barriers allows dispersal of plants and animals over long distances (May 1992).

3.0 Defining ecosystem services

Ecologists use the phrases “ecosystem structure” and “ecosystem function”. Ecosystem structure refers variously to the aggregate of species composition, population and community structure and inter-relationships, climate, soils and plant form (or habit). Ecosystem function refers to system properties or processes occurring within and between ecosystems, such as nutrient recycling (Costanza et al. 1997). However, the concept of ecosystem services (or ecosystem goods and services) is a more recent development. Ecosystem goods and services (hereafter the two are deemed to be contained within the phrase ecosystem services (ES)) are those processes and attributes of an ecosystem (or part of an ecosystem) that benefit humans (Costanza et al. 1997). Alternatively, ES are transformations of natural assets (including molecules such as CO₂, timber, or
biodiversity) into products that have human-centred value (Cork et al. 2001). We shall not debate whether such an anthropocentric definition is sufficient or whether non-anthropocentric values (inherent values; Turner et al. 2003) should be included. In the absence of humankind, this debate would not occur and therefore it is the presence and activities of humans that generates the need for such a valuation.

Ecosystems undoubtedly produce ES. The list of ES that can be recognised is longer than might be anticipated and includes:

(1) soil formation;
(2) erosion control;
(3) regulation of water flow (surface, sub-surface and groundwater recharge);
(4) water purification;
(5) regional climate regulation (temperature and rainfall);
(6) carbon sequestration and global climate effects;
(7) recreation;
(8) pollination;
(9) waste disposal and treatment;
(10) food, timber, textiles and other resource production;
(11) genetic resources;
(12) cultural;
(13) nutrient recycling;
(14) pollution interception.

An easy way to think about an ES is to ponder the question: what would happen if a process did not occur across vast areas of the landscape? For example, what would happen if soil erosion went unchecked across 90% of the landscape? What would happen if nutrient recycling stopped for 100 years, globally? What would happen if woodlands and forests ceased transpiring water and absorbing carbon dioxide? Any attempt to address ES issues holistically will require integration of many disparate disciplines, including ecology, sociology, economics and others (Fig. 1). Furthermore, it is apparent that the services provided by one ecosystem can not be viewed in isolation from other ecosystems. Thus, the concept of metacommunities (Leibold et al. 2004) may be expanded upon to incorporate “metaecosystems”, considering the fundamental links among, and the non-independent functioning of, ecosystems (see section 6 for examples).
3.1 Some issues pertaining to ES

3.1.1 Should we attempt to put an economic value on ES?

Economies based on money dominate the means of exchange of goods and services between people and entities and consequently, to influence these economies requires monetary values to be assigned. The tragedy of the commons is the failure of common ownership of goods and services (often land and water) to manage these resources sustainably; oceanic fisheries are a classic example. Commonly owned resources are invariably degraded over time, and are a clear reason why we should put an economic value on ES. Furthermore, a lack of an economic value for ES partially explains why ES are in decline globally. But there are many other reasons why globally, the provision of ES are in decline and many reasons why we should put an economic value on ES. These are now discussed.

Why are ES in decline globally? Several reasons exist, including (Cork et al. 2001):

1) poor education levels of the public, managers and policy makers, about the link between ecology and economy, including:
   (i) an assumption that ES are infinite (for example, dumping of waste in the sea or the atmosphere because of its perceived ability to store and treat waste materials indefinitely);
   (ii) no understanding of the links between ecosystem structure, function and services;
2) the long-lead time between unacceptable behaviour by humans (for example, waste dumping or forest clearing) and ecosystem dysfunction (that is, loss of ES);
3) the belief that technology can remediate/compensate/overcome declines in the provision of ES;
4) few incentives in classic economic structures to invest in ES.

Why should we put an economic value on ES? There are four reasons: first, because results of classical ecological studies do not engage economic markets using a language that is able to cause change in that market. Whilst environmental sciences and ecology have convinced many of the “intrinsic value” of various attributes of ecosystems (usually the photogenic or cuddly ones), they have not caused sufficient responses from market economies for sufficient changes in practice to occur. Changes have been too slow, too localized and too poorly coordinated to effect the changes required for large-scale sustainable development of ecosystem resources. Second, by placing a
value on ES, we can engage in cost-benefit analyses of current and future activities and attempt to answer the question: if an ES is lost or seriously degraded, do the economic benefits justify the economic cost to the ES? Third, it can assist in deciding how to allocate finite resources (time, money) to competing demands within funding agencies, resource management agencies and others. Finally, Lawton (1999) has argued that ecology has yet to develop many laws that are universally applicable and that the laws, rules and mechanisms that underpin these patterns in ecology depend on the species complement and the specific environment in which those species occur. We tentatively suggest that applying an ES framework to studies of ecology may enhance our ability to formulate more widely applicable rules and may act as a catalyst to asking new questions and adopting new approaches to ecology. As an example of this we refer to the developing realisation that, from the perspective of vegetation water flux at catchment scales, a tree is a tree is a tree and consideration of species becomes superfluous (see below). We doubt that such a realisation would have developed from a purely ecological approach.

3.2 Some questions for ES research

If ES is accepted as an overarching philosophy within ecology, it raises new questions for research, including:

1. Which ecosystem(s)/component(s) is/are best at providing which ES?
2. What are the impacts of human activities on ES at local, regional and global scales?
3. What is the relationship between ES and ecosystem condition?
4. What is required to restore ES in degraded systems and how would we know when this has been achieved?
5. How interdependent are ES within an ecosystem and across ecosystems?
6. How much of ecosystem structure and function can be lost before ES are irretrievably lost?
3.3 Estimates of ES

It is clearly very difficult to value ES. However, many attempts have been undertaken in the past 10 years (e.g. Costanza et al. 1997; Jansson et al. 1999; Turner et al. 2003). Costanza et al. (1997) divide the world into 6 oceanic, coastal and estuarine ecosystems and 10 terrestrial ecosystems and identified 17 ES. For each ecosystem they assigned a dollar value for every relevant ES (no single ecosystem provides all 17 ES). The vexing question of how to assign the dollar value is not discussed further here, except to note that many methods for estimating values have been used in the past, including:

1) willingness-to-pay, whereby valuations are deduced from surveys of the public or through expert assessments of business or public’s imputed willingness to pay;
2) valuations of known ES that already have a market value (timber, for example);
3) the cost of a human-made substitutable good (for example the cost of providing clean water through desalination stations or sewage treatment plants at locations where potable water supplies are depleted/degraded);

4) implicit value; This is similar to (3) above. For example, forested catchments dampen flash floods and retain water for a long time (months), releasing it slowly into streams and rivers and as recharge to groundwater. In the absence of these forests, concrete flood drains, water storage facilities and sediment traps are required to protect down-stream sites. It is the value of the structures not built if the ES is maintained, that is assigned as the value of the ES.

5) willingness-to-accept compensation for loss of an ES;

6) valuation of the loss of economic activity directly arising from the loss of an ES (for example, the lost value of agricultural productivity where saline landscapes prevent agriculture productivity).

Costanza et al. (1997) produced global estimates of 17 ES. For example, atmospheric gas regulation was estimated to be valued at US$1.3 trillion per year, waste treatment was valued at US$2.3 trillion per year and nutrient cycling at US$17 trillion per year. It should be noted that the dollar value per se is not the most important feature, but it is the realization that the absence of such ES that will have a massive economic impact and that human welfare is inextricably linked to ecosystem health. Furthermore, the principle aim is not to provide a price tag on ES but to express the effect of a marginal change in the provision of the ES in terms of a rate of trade-off against other commodities (Turner et al. 2003). An interesting point to note is that as ES become more and more scarce, their value in classic economic theory will increase, leading to the erroneous but logical conclusion that maintaining ES at their best and most pervasive is less desirable than allowing them to decline, as this increases their economic value. Similarly, the willingness-to-pay concept also fails. For example, most people would be willing to forfeit all of their savings to maintain the supply of oxygen when asked: how much would you pay to maintain the oxygen producing capacity of all the chloroplasts in the world? Despite these logical and methodological frailties, we are in no doubt as to the importance and validity of the ES approach to guiding science, funding and decision making in the future.

Some ES are more dispersed across a range of ecosystems than others. We consider (section C) biodiversity to be a structural attribute underpinning many ES, while carbon sequestration, and regulation of groundwater levels are ES provided by many diverse ecosystems. Alternatively, we
may consider ES at the individual ecosystem scale and do so briefly in case studies (wetlands, riparian, seagrasses and mangroves) in section D.

4.0 Biodiversity, carbon flux and water flux as broad-scale ES across all terrestrial ecosystems

4.1 How ecosystem structure and function relate to ES

The goods and services (ES) we acquire from ecosystems are a product of natural functions and processes occurring within ecosystems (Daily et al. 1997). However, links between ecosystem function and ES are not necessarily straightforward. In some cases, several ecosystem functions are required for a particular ES; in other cases, a single ecosystem function contributes to more than one ES (Fig. 2). Ecosystem functions are carried out by the species inhabiting ecosystems. Thus, understanding how ecosystems are structured in terms of species richness and composition (i.e. species identity and abundance) is central to a comprehensive understanding of ES (Fig. 2). In particular, a question of increasing importance is: how does human-induced change in ecosystem structure impact on the ES upon which we depend? This research question is currently the focus of much speculation and interest among biologists, because there is considerable concern that changes to ecosystem structure due to habitat clearing, fragmentation and the introduction of alien species lead to the disruption of vital ES (Costanza et al. 1997).

Links between ecosystem structure and function have been well researched (see Tilman 1997; Chapin et al. 1998; Loreau et al. 2001; Engelhardt and Ritchie 2002; Naeem 2002; LeVeque and Mounolou 2003; Gaston and Spicer 2004; Statzner and Moss 2004). For convenience, ecosystem structure is usually represented as species richness (Tilman 1997). Species richness is a common measure of biodiversity because it is easily quantified, there is a lot of existing information on richness, it is a good surrogate for many other kinds of variation in biodiversity (e.g. genetic, organismal and ecological diversity), and it is a unit of practical management for legislation (Gaston and Spicer 2004).

A surprising amount of controversy and heated debate has been generated by studies exploring links between biodiversity and ecosystem function. This only emphasizes the importance and contemporary relevance of understanding these links for scientific, economic and social purposes (see Naeem 2002 for discussion). Overwhelmingly, it has proven very difficult to find unequivocal
support for any one of the proposed theoretical models linking changes in ecosystem function to changes in biodiversity over the others (Chapin et al. 1998; Loreau et al. 2001). Such models include the “diversity-stability” hypothesis; the “rivet” hypothesis; the “drivers-passengers” hypothesis and the “idiosyncratic” hypothesis. See LeVeque and Mounolou (2003) for a discussion of these. In general, however, Schwartz et al. (2000) found that much experimental work supports the notion that high species richness is required to maintain a high degree of ecosystem functioning. For example, the work of Tilman et al. (1996) in the Cedar Creek grasslands (North America) showed convincingly that plant biomass (productivity) increases with species richness. Consistent with this, Hector et al. (1999) demonstrated that decreased species richness was associated with low productivity in European grasslands. The advantage of these experimental manipulations is that confounding factors can be controlled for. Thus, despite other outcomes having been reported, there is rigorous experimental evidence for the importance of increased levels of biodiversity for ecosystem functioning (Gaston and Spicer 2004).

Apparent contradictions in the findings of different studies are probably due to issues such as experimental design and differences in spatial scales. These can be addressed appropriately in future work. For example, the design of some synthetic communities used in experiments testing links between ecosystem function and biodiversity has not incorporated randomly chosen taxa from the available species pool, a feature that can bias the outcomes of such studies (Chapin et al. 1998). In relation to spatial scale, the findings of observational studies contradict those of experimental studies because observational studies look at patterns across multiple sites while experimental studies examine patterns within a site (Naeem 2002). Publication bias might also be influencing our understanding of biodiversity and ES, with studies showing the importance of high levels of biodiversity being preferentially published (Kaiser 2000).

Despite controversy, important generalizations are emerging, namely:

(1) There is consensus that at least some minimum number of species (i.e. minimum level of biodiversity) is essential for ecosystem functioning and the provision of ES under conditions where the environment is not changing (Loreau et al. 2001). In some cases, a few dominant species may be enough to provide for a substantial level of ecosystem functioning, e.g. NPP in grassland ecosystems (Sala et al. 1995; Chapin et al. 1998). For instance, a seasgrass meadow dominated by one species may have equal ecosystem function to a mixed-species meadow (Duarte 2000).
(2) High species richness can minimize large reductions in ecosystem functioning by acting as a buffer against variation in environmental conditions. This is because species whose effects on ecosystem functions are similar may be differentially susceptible to extinction from the community under changing conditions in the environment. Hence, differential loss of species does not impact negatively on ecosystem services because loss of particular species is buffered by other species in the ecosystem (Chapin et al. 1998). However, recent theoretical work is showing that this “compensation effect” will vary depending on whether species go extinct randomly or in order of their sensitivity to a stress that intensifies over time (e.g. climate change) (Ives and Cardinale 2004). Mathematical simulations of food web structure indicate that when extinction is ordered, there tends to be greater resilience in the web (and hence compensation) because surviving species have greater average resistance to the stress (Ives and Cardinale 2004).

(3) The various functions performed and services provided by ecosystems exhibit a ceiling level set by abiotic conditions and the maximum amount of biodiversity (Naeem 2002).

(4) There are two contrasting views on how the identity of species in an ecosystem contributes to ecosystem functioning and ES. Species may be functionally equivalent to one another (redundant) or their function might be unique (Walker 1992; Naeem 1998). The maintenance of natural ecosystem functioning is probably reliant on a mix of a certain amount of redundancy (see point 2 above), and uniqueness among species.

(5) The effects of species on ecosystem function and ES may be multiplicative through their interactions with other species, or the effects of species may be additive (Power et al. 1996; Sala et al. 2000).

(6) Experimental studies have shown that high levels of biodiversity are important for ecosystem functioning. While there is much work yet to be done in translating these results to larger (landscape) scales, an appropriate management strategy would be to adopt the Precautionary Principle to conserve as much biodiversity as possible (Loreau et al. 2001). In this way, we will not inadvertently lose ES through loss of biodiversity.

4.1.1 Future research questions
While it is clear that a minimum number of species and hence ecosystem structure is important for ES, we are still far from a comprehensive understanding of the influence of ecosystem structure and loss of species on ecosystem function and hence ES. Because ecosystem functions can be involved in more than one ES, and because one ES may rely on several separate functions of an ecosystem (Fig. 2), there needs to be a concerted effort among biologists to understand better the links between ecosystem structure, ecosystem function and ES. Considering that the economic and social values of ES are increasingly being assessed (e.g. IACSEA 1998), it is likely that biologists will be required more and more to relate their ecosystem research to market-driven forces and social expectations. In addition, there needs to be recognition that:

(a) Ecosystem function (and hence ES) is not just a function of species richness. There is considerable diversity among the populations of individual species, which can be important for ES. Luck et al. (2003) have suggested that a focus of future work should be on “service-providing units” (SPUs). These SPUs provide a recognized ES at some temporal or spatial scale. For example, the entire population of a tree species sequesters carbon globally; regional populations of the species in agricultural areas utilise groundwater recharge thus ameliorating dryland salinity; and local populations provide food for livestock. However, the current suggestion from biologists tackling the issue of the link between biodiversity and ecosystem services is not to abandon traditional species-based approaches when assessing biodiversity decline, but rather, to give more attention to the role of population diversity and genetic differentiation among populations, and to consider the usefulness of the SPU concept (Luck et al. 2003).

(b) Organisms provide different ecosystem functions and services at different life history stages. For example, see discussion of forest regrowth and transpiration below.

(c) Contrary to expectation, human activities can result in both decreases and increases in species richness (Sax and Gaines 2003). Biodiversity is decreasing globally due to habitat destruction and the introduction of exotic species. For example, invasion by the exotic shrub Tamarisk (Tamarix sp.) reduced biodiversity of riparian habitats and the services those habitats provide (Zavaleta 2000).

At local and regional scales, losses of native species can be offset by the establishment of exotics, which can result in an increase in biodiversity at these scales. Thus, the complex nature of the link between biodiversity and ES becomes more complex, given that we now have to consider how
increases in biodiversity at local and regional spatial scales due to invading species will impact on the ES upon which we depend.

Figure 2. A simple illustration of how more than one ecosystem function is required to produce a particular ES, while a single ecosystem function can contribute to more than one ES. In this example of a wetland ecosystem, the ES of water quality is provided by three functions of the ecosystem operating in tandem (nutrient uptake, sedimentation, and water storage). The function of water storage is also required for the ES of flood mitigation. The link between ecosystem structure/biodiversity and ecosystem functioning is currently under much scrutiny from biologists.

4.2 Carbon sequestration by woodlands and forests

4.2.1 Introduction

Carbon fixation by vegetation fulfils three distinct ES. These are (a) it is the basis for crop and forest yield; (b) it is involved in climate regulation; and (c) it is the foundation of all other ES. The
first requires no further explanation. For the second, we accept, a priori, that large increases in atmospheric carbon dioxide concentration result in changes in global and regional climate and that maintaining a stable climate is a significant ES. Extremes in weather generate losses to agricultural production and increase insurance and other costs to human welfare; long-term changes in climate require adjustments in infrastructure and industry. For the third ES, we argue that understanding Net Primary Productivity (NPP) or Net Ecosystem Exchange (see Kirschbaum et al. 2001 for a discussion of productivity terms) is the foundation for all other terrestrial ES. In the absence of carbon fixation, all ES (and all terrestrial, freshwater and coastal ecology) grinds to a halt. Therefore, a discussion of carbon budgets and NPP is central to any basic understanding of all ES.

In order to contribute to research on ES, it is necessary to quantify net carbon gain (NPP). To-date, NPP has been modeled at global, continental and regional scales, while measurements are made at local scales. This section principally addresses the question: how big is the NPP of Australia, at continental, regional and local scales? It is important to note that because of the long residence time for carbon in terrestrial systems, small increases in NPP result in large increases in the sequestration of C in biomass and soils. Consequently, precise estimates of NPP are needed for carbon accounting purposes. Global estimates of C turnover are generally 20 – 60 y (Schimel et al 1994) but a recent analysis by Barrett (2002) concludes Australian terrestrial C has a turnover time of 78 y. Low soil water content, frequent fires (and so the formation of non-labile charcoal) and high C absorption capacity of Australia soils probably explain this (Barrett 2002).

Biology determines the global carbon cycle through production and turnover of organic matter (Field 1998). Production is via photosynthesis, turnover is through respiration and decay. NPP is the principle regulator of all ecological processes, both within and between trophic levels and ecosystems. NPP for terrestrial systems is theoretically simple to determine, but in practice is difficult, time consuming and expensive, especially for woody ecosystems, because of problems dealing with below-ground processes, long time-scales and considerable spatial and temporal variability in NPP. Consequently, modeling is often used to estimate regional or continental NPP (Cao and Woodward 1998).

4.2.2 Global, continental and regional estimates of NPP

Mean global estimates of NPP range from 44 to 66 Gt C yr\(^{-1}\) (Cramer et al 1999; Field et al. 1995). Using a simple modeling approach, and including discounts for water and temperature stress, Field et al. (1998) calculate an average NPP of land without permanent ice cover as 426 g of C m\(^{-2}\) y\(^{-1}\).
Multiplying this value by the area of Australia, yields a continental estimate of 3.24 Gt C y\(^{-1}\). This is an overestimate since much of Australia is desert with extremely low NPP. Cao and Woodward (1998) estimate an average NPP to be 422 g m\(^{-2}\) y\(^{-1}\), which yields an average Australian NPP of 3.21 Gt C y\(^{-1}\) which is a similarly overestimated value. De Fries (1999) estimates the NPP of Australian native vegetation to be 2 Gt C y\(^{-1}\).

Global models of terrestrial NPP show maxima at two latitudinal peaks: approximately 40 – 70° N and 10° N to 15° S, with peak values of about 0.3 Pg C per degree of latitude (Field et al. 1998; Cao and Woodward 1998). These spatial patterns reflect the combined distributional effects of rainfall, forest cover and deserts. Seasonal patterns of NPP are consistent with seasonal changes in temperature, rainfall and net radiation (Cao and Woodward 1998) and can be found in estimates of NPP for different regions of Australia.

Within these global models, values of NPP within Australia range from about 50 g C m\(^{-2}\) y\(^{-1}\) for central Australia, to about 850 – 900 g C m\(^{-2}\) y\(^{-1}\) for east coast regions and far north tropical Australia (Field et al. 1998) or up to 1000 – 1100 g C m\(^{-2}\) y\(^{-1}\) (Cao and Woodward 1998).

How do the global estimates (Cao and Woodward 1998; Field et al. 1998; DeFries 1999) compare with Australian models? Roderick et al. (2001) estimate Australian NPP to be about 3.2 Gt C y\(^{-1}\) (1 Gt = 1 Pg = 10\(^{15}\) g), and cite 3 other estimates ranging from 1.6 to 2.8 Gt C y\(^{-1}\). As argued above, estimates around 3 Gt C y\(^{-1}\) are likely to be overestimates. Wang and Barrett (2003) cite estimates of Australian NPP ranging between 1 and 3 Gt C y\(^{-1}\) whilst themselves estimating NPP at between 0.79 and 1.1 Gt C y\(^{-1}\) with a bimodal distribution in time. Thus, in northern Australia, NPP increases during the summer wet season and decreased in the winter dry season but in temperate Australia the peak is in October. A key finding from Roderick et al. (2001) is that productivity of vegetation increases substantially when the diffuse fraction of solar radiation increase due to cloud or pollution and the volume of shade within a canopy declines. Interestingly, in a comparative review of four approaches to modeling C gain by canopies, a sun-shade model performed the best at all spatial scales (Medlyn et al. 2003).

Can any of these model estimates be compared to field-based estimates for Australian ecosystems? This is difficult to achieve because (a) continental-scale estimates of NPP have relatively poor spatial resolution and assign average vegetation attributes across large areas; (b) field estimates provide only point (local) estimates of NPP and the resources required to provide far more field estimates are not readily available; and (c) there are only two comprehensive and detailed point estimates of NPP in Australia. Esser (1998) summarises about 12 estimates for Australian pastures,
eucalypt forest, mangrove, saltbush and desert shrubland. Values range from 30 - 40 g C m$^{-2}$ y$^{-1}$ (desert shrub and Banksia and Xanthorhea woodland) to 1100 – 1200 g C m$^{-2}$ y$^{-1}$ for pasture and eucalypt forest to 2915 g C m$^{-2}$ y$^{-1}$ for wetland and heathland. However, almost all studies cited (from the 1960s – 1970s) did not include below-ground processes and the assumption was made that below-ground NPP equaled above-ground NPP. Therefore these values should be viewed with caution.

The estimate of NPP (2.08 t C ha$^{-1}$ y$^{-1}$) for region H (monsoonal Australia excluding Queensland) of Wang and Barrett (2003) could be taken as an estimate for the NPP for north Australian savannas (Chen et al. 2003). Similarly, Wang and Barrett’s estimate of NPP for region D (southeastern Australia) was 2.05 t C ha$^{-1}$ y$^{-1}$ may approximate to a broadleaved forest around Canberra (Keith et al. 1997). Alternatively, Cao and Woodward (1998) calculate NPP for tropical savannas to be 6.6 tC ha$^{-1}$ y$^{-1}$ and NPP for temperate evergreen forest was calculated to be 6.98 tC ha$^{-1}$ y$^{-1}$. Do these values approximate field studies of NPP in Australia?

Surprisingly, there are only two comprehensive published studies of NPP in Australia, in tropical savannas (Chen et al. 2003) and temperate snowgum forest (Keith et al. 1997). NPP of the savanna was about 11 t C ha$^{-1}$ of which 8 ton C ha$^{-1}$ was below-ground productivity. Most of the fluxes occurred in the wet season, except for fluxes associated with fires, which occurred in the dry season. All measures of productivity (GPP, NPP and NEP) showed that C fluxes of north Australian savannas are tightly coupled to seasonal patterns of rainfall and soil moisture, a result in agreement with leaf (Prior et al. 1997; Eamus et al. 1999), tree (O’Grady et al. 1999; Eamus et al. 2000) and canopy (Eamus et al. 2001; Hutley et al. 2000) scale measurements. NEP in Chen et al. (2003) was estimated as 3.8 ton C ha$^{-1}$ y$^{-1}$. Using eddy covariance data at a single savanna site, Eamus et al. (2001) estimated NEP at 2.8 ton C ha$^{-1}$ y$^{-1}$. NEP is the difference between NPP and soil respiration (Wang and Barrett 2003). There are exceedingly few estimates of NEP in Australia (Wang and Barrett 203).

Keith et al. (1997) showed that for a mature snowgum (Eucalyptus pauciflora) forest 50 km west of Canberra, Australia, NPP was 7.65 t C ha$^{-1}$ y$^{-1}$. Peak basal area increment occurred between November to January and again in March and April. In contrast to the savanna site, 25% of the standing biomass was located below-ground (compared with 40% in savannas), a result not expected from consideration of the much larger annual rainfall at the savanna site. If we exclude heathland and mangroves, the root to shoot biomass ratio for Australian ecosystems is 0.2 to 0.4
(Snowdon et al. 2000), and rainfall is a poor predictor of root biomass (Snowdon et al. 2000), although root depth may be inversely correlated to site aridity (Eamus and Prior 2001).

Several conclusions are apparent from comparing modeled regional estimates of NPP with field measurements. These are:

1. There are surprisingly few (two) estimates of NPP for Australian ecosystems.
2. Seasonality of changes in NPP observed in field data is adequately captured in the models. Similarly, the change from summer peaks in NPP in tropical Australia to spring and autumn for temperate forest, is also captured in the models.
3. Allocation between above- and below-ground processes varies between sites but this difference is not immediately explained by differences in annual rainfall.
4. For both the savanna and snowgum forest, field measurements of NPP greatly exceed NPP calculated by the models. Two reasons may be proposed for this. First, the field studies may not have been carried out in the same type (structure) of ecosystems that were assumed to be representative of the entire region by the modelers. Second, the climate for the large-scale regions used by modelers may not accurately represent the actual climate of the field sites and if conditions at the field site were better (less restricted by water and temperature) than average large-scale climate assumed by the modelers, then actual NPP will exceed modeled NPP. Both probably apply.

Carbon uptake by terrestrial ecosystems is an ES because it contributes to stabilization of atmospheric composition and hence climate regulation and through production of timber and crop yield. Confusingly, Costanza et al. (1997) list stabilization of atmospheric composition and climate regulation as separate ES and provide a dollar value for each. Thus, forests (tropical and temperate) are estimated to provide climate regulation services valued at more than US$300 per hectare per yr and grasslands, rangelands and wetlands provide gas regulation services valued at more than US$400 per hectare per year (Costanza et al. 1997). It is clear, however, that ecology and related disciplines need to provide far more information about ecosystem structure, function, allocation patterns and light conversion efficiencies before the real supply of ES through C uptake can be accurately estimated at local, regional or continental scales.

Carbon trading on the stock market will soon start, with an estimated price of $10 – 30 per tonne of carbon. If the NPP of a site is 500 g C m\(^{-2}\) y\(^{-1}\) (= 5 t C ha\(^{-1}\)) then this puts a C trading value of $50
to $150 per hectare. From knowledge of NPP for disparate ecosystems and the trading price on the market for C, we can start to answer such questions as: which ecosystem is best at providing climate regulation and gas regulation? What is the cost : benefit ratio of degrading different ecosystems? How much degradation (loss of NPP) should be allowed before the lost value in C trading is too much? To-date, however, estimates of regional or continental-scale NPP differ by factors of 3, and plot-scale estimates differ significantly from model estimates, suggesting that our understanding of factors that regulate NPP at regional scales is still incomplete.

4.2.3 Future research

In relation to NPP and ES, the following research topics are suggested:

1. Can we define allocation rules for C within plants in different ecosystems? Friedlingstein et al. (1999) show how changes in the percentage allocation of NPP to below ground processes influences biomass accumulation and stress responses, but we do not have a convincing mechanistic understanding of allocation rules for trees in the field (Eamus 1996)

2. Using field data, what are the seasonal and annual NPPs for all the major biomes in Australia?

3. What mechanisms link variation in climate and soils to variation in NPP?

4. How can we reliably quantify the C storage of natural ecosystems of Australia?

The next section deals with the role of trees in catchment water balance and the ES associated with water fluxes through trees.

4.3 Trees and forests as regulators of water tables

Woodlands and forests, native and plantation, provide a major discharge path for water and therefore, have a major role in determining the hydrological balance of catchments. By acting as wicks and transporting water from soil/groundwater back into the atmosphere, they minimise groundwater recharge, thereby preventing or ameliorating the development of dryland salinity. Furthermore, forested catchments provide a more stable and cleaner water supply than water collected from urban or industrial catchments, therefore, the water requires far less treatment to make it suitable for human use. Forests also dampen the flow of water into rivers and streams and
thereby reduce the impact of floods, reduce soil erosion and sediment accumulation in streams and rivers and reduce nutrient input to these water bodies (see Riparian ES case study below). Therefore, trees provide at least three ecosystem services; the prevention or amelioration of dryland salinity; the stable provision of clean water; and mitigation of floods and soil and nutrient loss through surface flows.

4.3.1 Supply of potable water

2.2 million deaths, or 4% of all fatalities worldwide, are attributed to insufficient supplies of clean water and sanitation (Dudley and Stolton, 2003). Well-managed, forested catchments provide ES by supplying potable water. These catchments supply water that contains fewer pollutants, sediments and nutrients, and that requires significantly less treatment than water derived from catchments that are urbanised/industrialised, cleared or contain poorly managed forests (Dudley and Stolton, 2003).

Changes in forest cover affect the water yield of a catchment (Jones and Post, 2004; Lu et al. 2004). For example, increases in forest cover due to regrowth after clearing decreases the water yield of a catchment, as younger trees transpire more than mature forests. As the trees mature, water yield increases (Fig. 3) (Vertessy et al. 1995; 2001). Cleared forests allow more water to run off but water quality is significantly reduced because of suspended sediment, nutrients and debris.
Figure 3. Relationship between mean annual runoff and stand age from mountain ash forest catchments (after Kuczera 1985).

4.3.2. What do we need to know to manage and maintain supplies of clean drinking water from forested catchments?

To manage forests to provide potable water, it is necessary to understand interactions between climate, soils, disturbance and vegetation as these determine the quantity of water transpired and hence catchment water yield (Vertessy et al. 1995; Cornish and Vertessy 2001). Indeed, understanding the control of forest water use is central to determining the water balance of a site (Wullschleger et al. 1998) and the development of a mechanistic understanding of the regulation of tree water use has allowed calculations of tree water use to be scaled temporally and spatially, to estimate the water use of stands of trees, forests and catchments (Wullschleger et al. 1998). Scalars that have been successfully used to scale from individual tree to whole stands and forests include basal area, (O’Grady, 2000), stem diameter at breast height (Vertessy et al. 1995, 1997), and leaf area (Hatton et al. 1995).

The relationship between forest age and water yield is complex and determined by several interacting factors including leaf area index (LAI; Fig. 4a), transpiration rates of tree and understorey vegetation, sapwood area (Fig. 4b), soil and litter evaporation and tree interception. From knowledge of these factors an estimate of the water yield from a forest can be determined. Topography and climate also influence water use and must be examined when comparing different catchments (Barrett et al. 1996).
The Maroondah catchment (Victoria, Australia) supplies drinking water for Melbourne. The catchment is forested with Mountain Ash (Vertessy et al. 1995) and yields high quality water that requires minimal treatment. The Mountain Ash forest yields about 80% of the total water derived from the catchment runoff, and therefore understanding how forest water use varies with climate and forest age allows catchment managers to predict supply into the future. Figure 5 shows a catchment water balance for the Maroondah water supply catchment showing how runoff (water yield) varies with the age of the stand.
Figure 5. The proportion of run-off, tree transpiration, understorey transpiration and soil evaporation changes as a stand of mountain ash ages. Data from Vertessy et al. (1995).

The importance of forested catchments in the provision of this ES is demonstrated in New York, one of the most densely populated cities on the planet. The Catskill/Delaware catchment, provides the nine million residents of New York with 90% of their drinking water, approximately 1.3 billion gallons of water per day (Dudley and Stolton, 2003). It has been estimated that the cost of a plant to treat water (US$6-8 billion; annual running cost $300 million) to potable quality would be 7 times greater than protecting the forest. In contrast, the protection of the catchment will cost US$1 – 1.5 billion over ten years (Dudley and Stolton, 2003).

4.3.3 Prevention and amelioration of dryland salinity

Dryland salinity is a major environmental problem for Australia (SCSI, 2004). In 2001 there were 5.7 million ha of land at risk or affected by dryland salinity (NLWRA, 2001). The significance of the problem is demonstrated by the commitment of the federal government to spend $1.7 billion over seven years in the National Action Plan for Salinity and Water Quality (Standing Committee on Science and Innovation, 2004). Dryland salinity has significant negative impacts on agricultural land, roads and buildings, and biodiversity (NLWRA, 2001, Littleboy et al. 2001; Zeppel et al. 2003). Dryland salinity is estimated to cause $300 million of lost agricultural production in the
Murray Darling Basin alone whilst damage to NSW roads costs $9 m per year for classified roads (NLWRA, 2001). The loss in profits for the agricultural sector in WA, due to dryland salinity, is estimated at between $80 and $260 million per year. In Wagga Wagga, the local Council estimate the damage to infrastructure in the town would amount to $180 million over 30 years, with some residents already spending up to $20,000 to repair their homes (SCSI 2004).

The removal of deep-rooted, perennial native vegetation and its replacement with shallow rooted, annual crops has altered the hydrological balance away from neutrality (groundwater levels remain in equilibrium, neither rising nor falling over the medium term) to significant groundwater recharge. Forests therefore contribute to the management and prevention of dryland salinity by minimising groundwater recharge by transpiring almost all of the annual rainfall (Clarke et al. 2002; Kington and Pannell, 2003) or the lateral flow of water through landscapes (Timms et al., 2001). Returning trees to the landscape may be part of the solution to dryland salinity (George et al., 2001; Stirzaker et al. 2002; Walker et al. 2002).

4.3.4 What do we need to know to manage and maintain areas at risk or affected by dryland salinity?

To manage and maintain biodiversity and productivity of agricultural land in areas at risk or affected by salinity, we need to know the best locations to plant trees (Farrington and Salama, 1996; McJannet et al. 2000), and the effects of reafforestation or clearing on local and regional patterns of groundwater recharge (Schofield, 1990). When replanting on hillslopes to ameliorate dryland salinity, it is important to consider where to place the trees in relation to zones of discharge and recharge, the spacing between trees, and what configurations to use, for example block plantings, tree belts or alley cropping (Stirzaker et al. 2002). Groundwater depth and salinity are also important inputs to determining where to plant trees to reduce recharge.

Managing dryland salinity requires knowledge of the effects of temperature, rainfall and soil conditions (especially waterlogging and salinity) on the growth, water use and survival of different tree species (Bell, 1999; Marcar et al. 1995; Thorburn, 1996; Stirzaker, 2002). The amount of water transpired by trees, and hence diverted from groundwater recharge, is affected by root distribution, rainfall interception, and leaf area index of trees. Indeed, Hatton and Nulsen (1999) argue that effective control of catchment water balance will only be achieved by revegetation that
generates a leaf area index approximating that of the natural, pre-cleared state, and revegetation with either trees or plants with similar ecohydrological characteristics as trees is required.

Reforestation has successfully lowered water tables in saline areas in Queensland (Walsh et al. 1995), and Western Australia (Silberstein et al., 2002). Thus, a reforested valley in Western Australia had a substantially lowered saline groundwater table across the site, as well as a reduced average salinity of the groundwater (Bari and Schofield, 1992). However these examples are of relatively small-scale local areas, and additional methods may be required to reclaim large-scale regional aquifers (Silberstein et al. 2002). In addition, the amount of area within a catchment that needs to be forested may be up to 70-80% of the catchment (George et al., 1999; Hatton et al. 2002) so it is important to remember that the solutions for dryland salinity are not fast and simple (Hobbs et al. 2003; Kington and Pannell, 2003).

4.3.5 Future Research

Research needs to be focussed on examining new sustainable land and water use systems (SCSI, 2004). Further research is required examining the effects of different forests, plantations and crops on groundwater recharge and discharge. Currently, revegetation strategies mean that agricultural land must be transferred from crops to planted trees, so preferably these trees would allow some profit for the landholder. Further research needs to be conducted addressing which tree species will be economically viable, in addition to being able to grow, transpire and survive under different climatic conditions while lowering groundwater. Finally, there has been no consistent field based approach to assessing the impact of rising water tables, water logging and salinity on native vegetation (Cramer and Hobbs, 2002). Cramer and Hobbs provide suggestions for addressing this in Western Australia, yet there is a paucity of research on the impacts of salinity on native vegetation in eastern Australia (but see Briggs and Taws 2003). There is a lack of reliable, quantitative field data examining the effects of dryland salinity on terrestrial vegetation in eastern Australia (Briggs and Taws, 2003).

5.0 Ecosystem-specific examples of ES

In the sections above we considered ES that are provided by a range of ecosystems. However, other equally important ES may be specific to particular ecosystems. Here we consider some of the services provided by vegetative components of particular ecosystems and illustrate how basic
ecology and plant ecophysiology has contributed to our understanding and valuation of ecosystem services.

5.1 Riparian ecosystems

The riparian zone is the interface or ecotone between aquatic habitats and their terrestrial catchments (Boulton and Brock 1999). Riparian areas are adjacent to perennial, intermittent, and ephemeral streams, lakes and estuarine-marine shorelines, although are most commonly thought of as those areas adjacent to freshwater habitats such as rivers and wetlands (Committee on Riparian Zone Functioning and Strategies for Management et al. 2002) and are considered in that context here. Riparian zones are under threat, as vegetation is often cleared to improve access for stock to water, for logging, to reduce local flooding by improving channel carrying capacity, or to maximise available cropping space (Tockner and Stanford 2002). In parts of Europe and Asia, between 60 and 99% of the riparian corridor has been developed (Ravenga et al. 1998).

To survive in riparian zones, vegetation must adapt to the rise and fall of water levels, unstable substrata, flooding and anoxia (Naiman and Decamps 1997). Adaptations to these conditions include adventitious roots, stem buttressing and root flexibility. Plants may also possess air spaces (aerenchyma) in the roots and stems to survive anaerobic conditions (e.g. Cyperaceae and Juncaceae). Having strong and/or flexible roots and stems allows plants to cope with the shear stresses of high flows (Naiman and Decamps 1997).

The ES these ecosystems provide are many. Most notably, they provide services to:

1) maintain water quality by filtering or ‘buffering’ the input of sediment, nutrients and toxicants from the catchment;
2) stabilise banks from erosion, and
3) provide habitat and contribute organic matter to maintain aquatic ecosystems.

5.1.1 Filtering

The importance of riparian vegetation in filtering runoff has long been recognised (Muscutt et al. 1993; Hook 2003) and they are now key components of many agricultural best management practices as a means of managing non-point source pollution. Riparian buffer strips (also known as filter strips or vegetative filter strips) filter runoff entering adjacent water ways by increasing
infiltration of water to the soil, and decreasing the turbulence of runoff water, thus enhancing pollutant removal by sedimentation (Abu-Zreig et al. 2003). Because many pollutants (nutrients, pesticides, metals) are adsorbed to sediment/soil particles, riparian strips also effectively reduce the pollutants reaching aquatic environments. However, riparian buffer strips can also remove soluble nutrients (e.g. Patty et al. 1997). The efficiency of riparian buffer strips depends on numerous factors, but most notably, vegetation type and species, and buffer strip width.

The effectiveness of different plant species and type in removing nutrients and sediment has been determined. Lee et al. (2000) showed that a combination of grass and woody species removed larger amounts of nutrients and retained larger amounts of sediment than did grass strips alone. They suggest that deep-rooted woody species increase the infiltration capacity of the strip, however, the comparison of vegetation types in that study was confounded by differences in strip width.

Hook (2003) showed significant effects of vegetation type in sediment retention, but differences were dependent on the width of the buffer strip. For narrow strips, retention was significantly less in dry upland plots compared to either transitional or wetland plots, but for wider strips (6 m) there was no significant difference in the effectiveness of the vegetation types. The upland plots had a much lower vegetative biomass and density than the other 2 vegetation types; prompting the authors’ conclusion that vegetation density was a significant factor determining buffer strip efficiency.

Both forested and grass riparian buffer strips reduced (by up to 90%) nitrate-N concentrations in groundwater reaching an adjacent stream (Osborne and Kovacic 1993). However, on an annual basis, forested strips were more effective at reducing concentrations of nitrate-N than were grass strips, but were less efficient at retaining total and dissolved P (Osborne and Kovacic 1993). In their review, Lyons et al. (2000) concluded that grassy riparian zones might be better than wooded areas in filtering runoff and reducing bank erosion, but that woody species provided greater bank stabilisation. However, this is somewhat dependent on bank morphology and local hydrology. Indeed, maintaining the grassy riparian zones requires on-going management because successional processes will tend ultimately to favour woody species (Lyons et al. 2000). Deep-rooted woody species may also provide other benefits such as lowering groundwater tables (see above).
The inclusion of tall woody riparian zones provides for other ES not provided by grassy species. In particular, woody species provide stream shading, which may be useful for limiting microphyte weed growth (e.g. Bunn et al. 1998) and buffering stream temperature fluctuations (Castelle et al. 1994). The presence of tall riparian buffer strips can also reduce contamination of waterways by intercepting aerial drift from agricultural spraying (e.g. Ucar and Hall 2001; Felsot et al. 2003).

Increasing width of the buffer strip increases the removal of sediment and nutrients. Thus, Abu-Zreig et al. (2003) showed that buffer strip width was the critical factor affecting phosphorus removal from agricultural runoff. In that study, a 15 m wide strip removed 89% of the P. Increasing the width beyond 15 m was unlikely to improve sediment retention, but was likely to increase P removal (Abu-Zreig et al. 2003). Mickelson et al. (2003) showed an 87% reduction in sediment removal for 9.1 m strips, 16% more than for 4.6 m strips. Patty et al. (1997) also report 89% removal of P, but 100% removal of sediment over a grassy 18 m strip; smaller strips were much less efficient. Hook (2003) suggest that riparian buffer strips in rangelands should be at least 6 m wide. This suggestion is consistent with other studies, but generally, widths greater than 15 m are most effective (Castelle et al. 1994).

5.1.2 Erosion control

By limiting sediment influx and reducing bank erosion, riparian ecosystems provide a critical service in maintaining aquatic ecosystem health. High volumes of sediment entering streams can cause a loss of aquatic habitat and biodiversity, a decline in water quality, increased flooding in silted streams, and decreased water storage capacity, thereby reducing the availability of water resources.

Zaimes et al. (2004) demonstrated that intact riparian zones had significantly lower rates of stream bank erosion than grazed or cropped areas. Generally, the presence, density and type of stream bank vegetation influences bank erosion (Beeson and Doyle 1995; Harmel et al. 1999) with forested riparian zones subject to less erosion than grassed riparian zones (Harmel et al. 1999). Interestingly, there is some evidence to suggest forest age also influences erodability, with older forest less prone to erosion (Odegaard 1987, Zaimes et al. 2004). Considering the reduction in stream sedimentation by riparian zones due to both the interception of runoff and bank stability, the total stream sediment load could be reduced by approximately 80% by forested riparian buffers (Zaime et al. 2004).
Riparian zones provide other valuable ES, such as habitat for fish and aquatic invertebrates (Boulton and Brock 1999; Pusey and Arthington 2003). Riparian zones themselves are significant components of biodiversity at local and regional scales because riparian zones are often disproportionately species-rich compared to surrounding ecosystems (Nilsson and Svedmark 2002) and also serve as wildlife corridors (Mitsch and Gosselink 2000b). Riparian vegetation provides habitat for more bird species than any other vegetation association (Tockner and Stanford 2002). Riparian buffers also enhance the in-stream processing of both non-point and point source pollutants, thereby reducing the impact on downstream rivers and estuaries, but studies have yet to assess the extent and magnitude of the benefits this provides (Dosskey 2001).

Considering these ecosystem services provided by buffer strips in agricultural areas (not just as riparian zones), Rein (1999) showed the economic value of implementing 1 ha of buffer strip at around US$15000 over 5 years (based on buffers strip of 1 ha per 35 ha of cultivated land). Assuming that existing riparian zones do not incur the costs of planting or maintenance, the financial benefits they provide may be even greater than suggested above. However, as discussed above, considerations of buffer width and vegetative cover will greatly influence their effectiveness and the financial benefits they return. Zavaleta (2000) also valued riparian ecosystems of the US in response to invasion by the exotic shrub, Tamarisk (*Tamarix* sp.). Tamarisk consumes more water than native riparian species and contributes to increased stream sedimentation and, consequently, increased frequency and severity of flooding (Zavaleta 2000). Conservative estimates of Tamarisk impact are US$280-450 per ha which represents that portion of the value of riparian ecosystem services that has been lost. Clearly, the economic value of intact riparian ecosystems would be far greater than this.

5.2 *Freshwater and wetland ecosystems*

Like riparian ecosystems, wetlands span the divide between wholly aquatic and wholly terrestrial ecosystems and provide many similar ES. In contrast to riparian zones, however, wetlands have soils that are saturated during part of the vegetation-growing season, and support plants that are typical of saturated soils. Wetland ecosystems vary greatly in type, ecological function, and the ecosystem services they provide (Mitsch and Gosselink 2000a). Wetlands can be both marine and freshwater dominated, and include tidal marshes, fens and bogs, swamps and riverine macrophyte beds. Wetlands associated with riverine ecosystems are the focus of this case study (but see seagrass case study for marine-dominated example).
The ecological functions of wetlands include water storage, maintenance of surface and groundwater flows, biochemical cycling, retention of sediment and dissolved materials and provision of habitat (Mitsch and Gosselink 2000a). Aside from recreation and aesthetics, perhaps the most widely exploited services of wetland ecosystems are the ability to treat and improve water quality, and water storage/flood mitigation.

The ability of wetlands to remove nutrients, metals and other toxicants, and trap sediment (Johnston 1991), underlies their extensive use in water treatment facilities. Because nitrogen is important to eutrophication and health effects in drinking water, its removal from water by wetlands has been extensively studied. Three processes contribute to nitrogen retention by wetlands: denitrification, sedimentation and uptake by plants (Johnston 1991; Saunders and Kalff 2001). Denitrification involves anaerobic bacteria that release N to the atmosphere. Aquatic plants may take up and store N in their shoots and roots during the growing season, and by altering and reducing stream flow (see below), aquatic plants facilitate sedimentation and the incorporation of N in the sediment (Saunders and Kalff 2001).

Jansson et al. (1998) estimated that the potential nitrogen retention of existing wetlands in the Baltic Sea catchment could retain about 5-13% of the total annual N load. This represents a substantial N removal and reduces the eutrophication of the Baltic Sea. In the USA, Mitsch et al. (1999, cited in Mitsch and Gosselink 2000b) found that 3.4-8.8% of the Mississippi River Basin must be converted to wetlands or riparian forest in order to achieve a 50% reduction in the nitrogen loads entering the Gulf of Mexico by 50%.

At a smaller scale, Casey and Klaine (2001) demonstrated that wetlands were able to remove nitrogen and phosphorus from terrestrial runoff during storm events. Wetland sediments are important sinks for phosphorus (Casey et al. 2001), although the vegetation of the wetland can have significant effects on phosphorus dynamics by altering the redox potential of the sediment (Aldridge and Ganf 2003). The ability of plants to alter sediment conditions varies widely among species (e.g. Aldridge and Ganf 2003).

The physical presence of wetlands alters the flow and sediment dynamics of a water body. Macrophyte beds reduce current velocities both within and adjacent to beds, resulting in increased sedimentation and reduced turbidity (Madsen et al. 2001). The presence of macrophytes also
reduces the likelihood of sediment resuspension. Increased sedimentation and reduced turbidity provide ideal sediment and water clarity conditions to promote further macrophyte growth.

At a broader scale, wetlands capture floodwater and sediments and slowly release the water back to the river after flood passes. The role of macrophytes here is to slow down currents, increase transpiration and shade water (Mitsch and Gosselink 2000b). The economic value of wetlands in terms of flood mitigation alone was estimated at approximately US$1000 per ha (in 1990 $ values, Woodward and Wui 2001). However, the placement of wetlands within a catchment to maximise the benefits to flood control is subject to debate (see Mitsch and Gosselink 2000b), but provision of this service is largely restricted to floodplain wetlands (Bullock and Acreman 2003).

Wetlands also play important roles as habitat, nursery areas and refugia for aquatic life. For example, macrophytes reduce the impacts of pesticide contamination on aquatic systems, by either providing a refuge for fish (e.g. Napier 1992) or adsorbing toxicants from the water column (e.g. Brock et al. 1992). Wetlands also have their own intrinsic biodiversity value, which may ultimately influence their ability to provide key ecosystem services (e.g. Engelhardt and Richie 2002, but see the biodiversity discussion above for more detail).

Costanza et al. (1997) provided a global annual estimate of wetland services at US$4.9 trillion, which equates to approximately $14,785 ha/yr. Wetlands are behind only estuaries, seagrass beds and floodplains in their per hectare value. Interestingly, analysis by Woodward and Wui (2001) suggests that the per-hectare value of wetlands varies little with wetland size. They also recognised that any given wetland will not provide all the services attributable to wetlands, yet even those that might provide only a single service are valuable. For example, those which provide water quality improvements alone may be valued at over US$1000 ha/yr (in 1990 dollar values; Woodward and Wui 2001).

5.3 Future research needs

The ecosystem services described here for wetland and riparian ecosystems are those that are already identified and well described in the literature. The future for research in these systems is to identify and quantify the value of other services such as nutrient cycling, and the relative roles of various wetland types within a catchment. In the management of any ecosystem(s) we risk mismanaging the resource if we fail to acknowledge the interconnectedness of ecosystems and ES.
This is no more apparent than for riparian and wetland systems. So, for example, is the value of ES provided by a wetland made greater or does the system become more efficient in providing a service when adjoined by a functioning riparian zone? Which prompts the question, is the value of ES by adjoining ecosystems additive or multiplicative?

6.0 Seagrasses and mangroves

Seagrass and mangrove ecosystems occur throughout the world in coastal and estuarine zones. Seagrasses, by definition, live fully submerged in seawater, have an anchoring system, have hydrophilous pollination and are able to cope with high salinity (den Hartog 1970; Kuo 1982). The term mangrove refers to woody halophytes living at the interface of land and sea (Moberg and Rönnbäck 2003). Specialist morphological and physiological adaptations of mangroves include aerial roots, tidal dispersion of propagules, highly efficient nutrient retention mechanisms and the ability to also cope with high levels of salt (Duke et al. 1998; Alongi 2002). Seagrass meadows and mangrove forests are intimately linked, physically and functionally (Fortes, 1991) and both play an integral role in marine food chains (Kuo 1982; Alongi 2002).

Seagrasses are a highly productive component of the benthic ecosystem (West and Larkum 1982; Beer and Koch 1996). Their productivity is on a par with that of a marsh or coniferous forest (McComb et al. 1981; Beer and Koch 1996). Seagrass meadows act as estuarine filters, removing sediments and nutrients from coastal waters (Short and Short 1984; Short and Wyllie-Echeverria 1996), and provide shelter for juvenile fish species (Pollard, 1984; Burchmore et al. 1993; Carruthers and Walker 1997), and substrate for sessile plants and animals through substrate extension (den Hartog 1979; McComb et al. 1981). Seagrasses are used as a direct and indirect food source by crustaceans and other invertebrates, fish, turtles and dugongs (West and Larkum 1982; Montgomery and Targett 1992). Similarly, mangroves provide breeding areas and support food webs for birds, fish, crustaceans, shellfish, reptiles and mammals (Loneragan et al. 1997; Alongi 2002; Lal 2003). Mangroves are a renewable source of wood, produce oxygen, act as a carbon dioxide sink, trap sediments, pollutants and nutrients and protect the coast against erosion (Alongi 2002; Moberg and Rönnbäck 2003).

The global economic value of seagrass/algae beds is estimated to be $3,801 \times 10^9 \text{ yr}^{-1}, while that for tidal marsh and mangroves is $1,648 \times 10^9 \text{ yr}^{-1} (Costanza et al. 1997). These values do not take into account a number of well-known ecosystem services for these biomes. For seagrasses, gas regulation, disturbance regulation, erosion control, waste treatment, habitat, food production and
recreation should all be assigned an economic value (Short et al. 2000; Duarte 2002). For mangroves, unvalued services include gas regulation, water regulation, erosion control, soil formation, nutrient cycling and cultural uses (Lal 2003; Moberg and Rönnbäck 2003). Therefore the estimates provided by Costanza et al. (1997) are highly conservative. Despite the value of seagrasses and mangroves, destruction of habitat, particularly close to human population has been increasing over the last 30 years (Fortes 1991; Alongi 2003; Duarte 2002), largely due to resource exploitation and pollution.

Seagrass meadows improve water quality and cycle nutrients

Physiological studies have been vital in defining the role of seagrass meadows as estuarine filter systems. Seagrass communities alter current velocities, most significantly by creating a zone of reduced flow within the leaf canopy (Fonseca et al. 1983; Leadbetter 1986). This removes sediments and nutrients from coastal waters (Short and Short 1984; Short and Wyllie-Echeverria 1996) by encouraging the settling of fine particles (such as organic material) and prevents already settled particles from being resuspended and carried away (Leadbitter 1986). Furthermore, both nitrogen and phosphorus are taken up by leaves from the surrounding water, increasing nutrient removal and cycling (Short and Short 1984). Seagrass roots and rhizomes resist sediment erosion, promoting a tightly bound substrate (Zieman 1975; Leadbitter 1986). Vegetative reproduction and rhizome extension promote the physical stability and resilience of meadows (Procaccini et al. 1996).

Besides filtering nutrients from the water column, seagrass meadows aid in the return of nutrients to the food web. Aquatic angiosperms are unique, in that nutrients are absorbed through the roots (as in terrestrial plants) as well as through the leaves (as in macroalgae) and translocation of nutrients between the roots and leaves occurs depending on the site of uptake and the concentration of nutrients (Cambridge and Hocking 1997). In this way, Thalassia sp. accounts for much of the movement of cations, including Fe, Pb and Cd (Schroeder and Thorhaug 1980).

Nutrients are lost from seagrass meadows through leaching, the export of sloughed leaves and leaf fragments, nutrient transfer by foraging animals, denitrification and diffusion from the sediment. The mechanisms of nutrient gain include nitrogen fixation, sedimentation and nutrient uptake by leaves (Hemminga et al. 1991; Herbert 1999).
The true value of seagrasses as estuarine filters has been fully appreciated through physiological studies to find reasons for decline, particularly because seagrass loss is a compounding process. Once die-off begins, secondary effects such as resuspension of sediments, increased turbidity and reduced light penetration exacerbate the situation (Thayer et al. 1994), sometimes leading to autocatalytic decline (Larkum and West 1982).

Coastal eutrophication is one of the major factors leading the global declines in seagrasses (Short and Wyllie-Echeverria 1996; Duarte 2002). Excess nutrients stimulate growth of phytoplankton which reduces light penetration and promotes epiphytic macroalgae growth, which shades and suffocates seagrasses (Duarte 2002). Light availability has long been recognised as the major environmental factor in controlling distribution, growth and survival of seagrasses (Dennison 1987; Batuik et al. 1992). Minimum light requirements for seagrasses are higher than those for phytoplankton and macroalgae (Abal et al. 1994) due to physiological demand of living in anoxic sediments and the respiratory demand of roots (Goodman et al. 1995) and thus, higher concentrations of chlorophyll $a$, total suspended solids, dissolved nutrients and light attenuation coefficients were associated with shallower depth limits in Moreton Bay (Abal and Dennison 1996).

Reduction in the distribution of seagrasses reduces ecosystem services by reducing the area available for foodwebs and habitat. Areas without seagrass cover become highly turbid as sediments become suspended in the watercolumn and poor water quality leads to further decline in remaining seagrasses, further reducing their distribution and therefore value. Furthermore, morphological characteristics of seagrasses growing under low light can be altered, reducing their value as habitat. Seagrasses grown in low light have thinner leaves, lower rates of productivity (and therefore biomass), larger shoots (Abal et al. 1994) and lower shoot densities (Olesen 1996).

6.1 Productivity in mangroves and seagrasses

Rates of primary production in seagrasses and mangroves influence their ecosystem services. Generally, higher productivities enhance goods production by stimulating foodwebs and nutrient turnover (Lal 2003; Moberg and Rönnbäck 2003).

Seagrasses are highly productive ecosystems, even though they occur under low nutrient conditions (den Hartog 1979; Cambridge and Hocking 1997). Daily productivities are $8 \text{ g C m}^{-2} \text{ day}^{-1}$ in
Zostera sp. and 16 g C m$^{-2}$ day$^{-1}$ in Thalassia sp. (Jørgensen et al. 1981). The bulk of seagrass biomass is mineralised through detrital food chains (50%) and usually less than 20% is directly consumed by herbivores (Duarte and Cebrián 1996). Sediment storage accounts for 16% of the fixed carbon, while 34% is exported as dissolved organic matter, a vital nutrient source in coastal systems (de Boer et al. 2000). The organic matter provided by seagrasses initiates sulfate reduction and therefore maintains an active sulfur cycle in estuarine sediments (Zieman 1975; Lee and Dunton 2000). Dissolved free amino acids (DFAA) are also derived from seagrasses. Above a seagrass community, concentrations of DFAA were generally 2 to 5 times higher than those measured over deep-ocean areas and they were similar to values obtained for other highly productive marine environments (Jørgensen et al. 1981). These organic nutrients eventually feed prawns and other commercial fishes (Loneragan et al. 1997). Seagrasses also contributed DFAA to the sediment pore-water, thereby assisting the benthic infauna (Jørgensen et al. 1981).

Mangroves fix and store significant amounts of carbon and therefore make a vital contribution to global carbon budgets (Alongi 2002). Mangroves also make a significant contribution to coastal foodwebs (and therefore fisheries, Mumby et al. 2003). Earlier reported values of mangrove productivity were derived from measurements of light attenuation under the canopy but these rates are underestimates as they do not account for accumulation of biomass above ground (Alongi 2002). So productivities such as 1.4 g C m$^{-2}$ day$^{-1}$, reported by Upadhyay et al. (2002) may be only 10% of the actual photosynthetic production (Alongi 2002). A more accurate measure of mangrove productivity involves measuring light transmission and leaf photosynthesis (Ross et al. 2001; Alongi 2002). Therefore, best estimates of mangrove productivities suggest they can be as productive as seagrasses (15.5 g C m$^{-2}$ day$^{-1}$, Alongi 2002; 7.2 g C m$^{-2}$ day$^{-1}$, Ross et al. 2001).

Carbon fixed in mangrove ecosystems is budgeted in the following manner: decomposed within the system (40%), exported (30%), stored in sediments (10%) and consumed by herbivores (9%) (Duarte and Cebrián 1996). More recent studies suggest these values may underestimate the carbon stored in wood and eventually decomposed and the carbon stored in sediments or exported (Alongi 2002). None-the-less, these values indicate the contribution to detrital foodwebs which support higher-order consumers. Hence, mangroves adjacent to coral reefs in the Caribbean influence the fish community structure by enhancing the survivorship of juvenile fish and doubling the biomass of some commercially important fish species (Mumby et al. 2003).
A number of factors influence mangrove productivity. For instance, a fringe forest was more productive than a dwarf forest (Ross et al. 2001), productivity increases with increasing stand age (Alongi 2002) and productivity was higher in the lower estuary than the higher estuary (Chen and Twilley 1999). These physiological characteristics demonstrate the enhanced value of mature forests over juvenile forests and may indicate the influence of nutrient inputs from the mouth of an estuary over land-derived nutrients (Chen and Twilley 1999). Furthermore, a relatively pristine mangrove forest was more efficient in carbon processing than a disturbed one (Alongi 2002). These natural and human-induced associations demonstrate the need to manage mangrove forests for their carbon budgets and perhaps prioritise conservation of more productive systems.

If ES rely on the interactions between seagrasses and mangroves (Fortes 1991), the loss of ecosystem interactions can lead to the loss of ecosystem services derived from the connected ecosystems in the seascape (Moberg and Rönnbäck 2003). Therefore effective management of mangrove and seagrass ecosystems relies on a detailed understanding of the ecophysiological requirements of both ecosystems.

6.2 Future research questions

For the most effective management and conservation of coastal ecosystems, associations between mangrove and seagrass ecosystem services need to be quantified. For instance, do seagrasses adjacent to highly productive mangroves have higher productivities and more efficient nutrient cycling and do seagrass meadows adjacent to highly productive mangroves have different carbon allocation budgets to those adjacent to less productive mangroves? More broadly, linkages amongst interacting ecosystems (metaecosystems) require investigation to quantify ES provision (Fig. 6).

7.0 Conclusion

In this review, we have (1) defined and described ecosystem services, (2) argued that it is vitally important that we overcome inertia among environmental scientists to place economic values on ecosystem services, (3) discussed the important links between ecosystem structure, function and services, and (4) provided empirical examples of how ecophysiology has contributed substantially to our understanding of ecosystem services. We have also presented a set of research questions that need answering in order to provide a comprehensive understanding of ecosystem services. In doing so it has become apparent that the services provided by one ecosystem can not be viewed in isolation from other ecosystems. In this sense, the concept of metacommunities (Leibold et al.
2004) may be expanded upon to incorporate “metaecosystems”, considering the fundamental links among, and the non-independent functioning of, ecosystems.

It is our contention that the concept of ecosystem services provides a unifying language and approach for dialogue between environmental scientists, industry, economists, the public, policy makers and politicians. Given the current and impending ecological crises facing the globe, and the general degradation of the goods and services provided by natural ecosystems, we believe the unification of environmental, economic and social needs in the concept of ecosystem services provides an engaging approach to ensure an environmentally sustainable future. Until recently, there has been an unfortunate absence of a common language for communication between scientists and other stakeholders, which has mitigated against environmental sciences penetrating the minds of those that have their hands on the levers of industry, policy and management. It is imperative that transparent discussion among stakeholders takes place with a common language, and the language of ecosystem services offers a practical, yet scientifically based, way forward.
8.0 References


Dudley N, Stolton S (2003) 'Running pure: the importance of forest protected areas to drinking water. A research report for the World Bank/Alliance for Forest Conservation and Sustainable Use.' WWF.


Fonseca MS, Zieman JC, Thayer GW, Fisher JS (1983) The role of current velocity in structuring
eelgrass (Zostera marina L.) meadows. *Estuarine, Coastal and Shelf Science* 17, 367-380.


Jørgensen NOG, Blackburn TH, Henriksen K, Bay D (1981) The importance of *Posidonia oceanica* and *Cymodocea nodosa* as contributors of free amino acids in water and sediments of


Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD,


Figure 6. A conceptual model of interacting ES provided by terrestrial and aquatic ecosystems. A metaecosystem approach highlights the exchange of mass and energy between ecosystems in the provision of ES.
Bank stabilisation
Nutrient cycling
Retention of nutrients
Clean water supply

CO₂
H₂O
Pollutants and nutrients

Wettable falls, prevents dryland salinity

Nutrient cycling
Fine particles settle

High productivity supports detrital foodwebs