



Marine biodiversity and ecosystem services: an elusive link

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Abstract

Efforts to test the hypothesised positive link between ecosystem services and functions and biodiversity are increasing in order to forecast the consequences of the present erosion of biodiversity on ecosystem functions and to provide an additional basis for the conservation of biodiversity. These efforts have been, however, modest in marine ecosystems. An examination of seagrass communities, which are simple assemblages with a limited membership of about 50 species worldwide and < 12 species in any one community, provides, however, strong evidence for the existence of such positive link between species richness and ecosystem functions. Ecosystem functions are, however, dependent on the particular membership of the community, rather than its number, for the functions are species-specific properties. Yet evidence, is provided, that an increasing species richness should be, on average, linked to an increase in the functional repertoire present in the community, will lead to a more efficient use of resources and a greater capacity to ensure the sustainability of ecosystem functions under disturbance or ecosystem change. Closer examination indicates that the functional variability of mixed-species seagrass assemblages is correlated to the variability in species size, whereas species of similar size tend to show similar functional capacities and, therefore, a greater degree of functional redundancy. In addition, the demonstration of positive interactions in seagrass communities, which are also dependent on the presence of engineering species in the community that facilitate the growth of other species, provides increasing grounds to expect an enhanced functional performance of mixed communities over that expected from a simple additive contribution of the community members. Multispecific communities also hold, within the functional repertoire they contain, many unrealised functional potentials that may prove instrumental to ensure the sustainability of ecosystem functions in the presence of disturbance or a changing environment. The arguments offered, illustrated for the comparatively simple seagrass communities, provide strong reasons to expect a strong — if difficult to test experimentally — positive relationship between species diversity and the functions of marine ecosystems and, thereby, the services they yield to humanity. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Seagrass; Marine ecosystems; Ecosystem services

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1. Introduction

Present concern about the preservation of biological diversity is partially based on the belief that loss of biodiversity would result in the loss of ecosystem functions and the many services they provide to society (see Constanza et al., 1997). These services encompass a number of functions that derive from the interactions of the organisms with their environment, both physical and chemical, as well as their own value as food or raw materials (Table 1). Except for the values as food or raw materials, which are clearly species-specific, most functions are shared among many of the organisms present in any one community. Moreover, both the contribution to ecosystem functions and the viability as harvestable food or raw material of any one species seem to be very much dependent on the development of a significant abundance, for rare species can hardly have a significant impact on their environment or be reliable sources of food or raw materials for human populations. Hence, the link between biodiversity and ecosystem functions and services is not straightforward. Yet the test of these links is essential to demonstrate a significant ecosystem role for biological diversity (Tilman, 1997), which would provide reasons other than ethical for the preservation of biodiversity as a whole, rather than that of target species alone. The demonstration of this link has, therefore,

Table 1

Expected role of marine biodiversity in general, and that of seagrass communities in particular, in sustaining ecosystem functions, goods and services; the basis, structural or trophic, of the functions is indicated for seagrass communities; modified from Heip et al. (1998)

Ecosystem functions, services and goods	Role of biodiversity	Role of seagrass biodiversity	Basis
Ecosystem functions			
Primary production	High	High	Trophic
Carbon storage	Low	High	Trophic
Carbon flow	High	High	Trophic
Nutrient cycling	High	Moderate	Trophic
Ecosystem services			
Gas and climate regulation	Low/medium	Medium	Trophic
Disturbance regulation	High	High	Combined
Erosion and sedimentation control	Medium/high	High	Structural
Remineralisation	High	High	Trophic
Waste treatment	High	Low	Trophic
Biological control	High	Medium	Combined
Monitoring of global change and ecosystem health	High	High	Structural
Recreation tourism and education	High	High	Structural
Ecosystem goods			
Habitat and refuge	High	High	Structural
Food resources	High	High	Combined
Raw materials	High	Low	Structural
Genetic resources	High	High	Structural
Natural heritage	High	High	Combined

inspired research efforts of many scientists (see Tilman, 1997), and ranks highest in the agendas of international research programmes on biological diversity (e.g. *Diversitas*; <http://www.icsu.org/diversitas/>).

The investigation of the link between biodiversity and ecosystem functions typically involves the test of the null hypothesis that key ecosystem functions are independent of the number of species present in the community. Hence, the original question is in fact narrowed down to the test for the existence of functionally redundant species in natural communities. A species can be considered to be functionally redundant when the community contains functionally-analogous species, so that its disappearance from the community entails no measurable loss of functionality. Explicit experimental tests of this concept have been conducted in terrestrial ecosystems (e.g. Naeem et al., 1994; Tilman and Downing, 1994; Tilman et al., 1996) with some success. The experimental designs used included confounding factors, largely derived from the fact that the synthetic communities used were not composed of randomly drawn species. These confounding factors weakened the power of the experiments, so that the conclusive test of the link between species diversity and ecosystem functions and services remains an elusive goal.

Efforts to demonstrate such links in the marine environment have been far fewer, even though there is a widespread belief that they are strong (Table 1). The reasons for this are unclear, and may derive from a more limited concern about the consequences of species loss, due to the comparatively low probability of species losses in marine compared to terrestrial ecosystems, together with greater difficulties in conducting ecosystem-level experiments. Yet, the elucidation of the link between changes in species diversity and ecosystem functions and services is very relevant in marine ecosystems where an emerging biodiversity crisis is becoming apparent. The marine biodiversity crisis is most evident in the coastal zone, where losses of mangroves, coral reefs and seagrass beds are widespread (Fortes, 1988; Short and Wyllie-Echeverria, 1996), but it also extends to the pelagic, where the populations of large pelagic fish have been decimated (Pauly et al., 1998).

My goal here is to examine the relevance of the hypothesised link between species diversity and ecosystem functions and services for marine ecosystems. I shall base this examination on the particular type of ecosystem, seagrass meadows, with which I am most familiar. Seagrass beds are particularly well suited subjects for this task because (1) they are angiosperms — similar to the species used in some of the experimental tests of the link between species diversity and the functions of land ecosystems (e.g. Tilman and Downing, 1994; Tilman et al., 1996); (2) they encompass a limited set of species, with only about 50 closely-related species worldwide and no more than 12 species coexisting in any one community (Duarte, 2000); and (3) they are experiencing worldwide losses, with a substantial loss in cover (Short and Wyllie-Echeverria, 1996), providing direct empirical evidence of the changes in ecosystem functions and services upon biodiversity loss and rendering the elucidation of this link particularly important. The reader will, however, note that the arguments formulated are not derived from exclusive consideration of seagrasses, and can be, with minor adjustments, transferred to most other marine communities. Hence, while using seagrass communities as an example, I intend to provide quasiuniversal arguments in support of the hypothesised link between species diversity and the functional performance of marine communities.

2. Seagrass biodiversity

Seagrasses comprise a group of about 50 species of closely-related angiosperms, all of them belonging to two families of monocots, and comprising 12 genera (Duarte, 2000). Seagrasses are, therefore, amongst the poorest taxa, in terms of species membership, present in the sea. The paucity of species in the seagrass flora is reflected in a low species diversity in the communities they form, with about half of the meadows described in the literature being monospecific (Duarte, 2000). Two-thirds of the mixed-species meadows reported contain only two or three species, and the greatest species richness reported corresponds to a meadow containing 12 species (Duarte, 2000). Hence, the species diversity, as represented by the Shannon-Weaver index, of seagrass communities is generally low (range 0–1.5, Duarte, 2000), well below the values characteristic of communities of other marine organisms, which typically range between 1 and 4 (Margalef, 1980).

In addition to the low diversity of seagrass communities, the functional repertoire of the species present within the seagrass flora is limited. Seagrass species are physiologically similar, with similar functions (e.g. carbon and nutrient uptake, photosynthesis) and pathways, and also share a similar basic architecture (Duarte, 1991, Marbá and Duarte, 1998). The form repertoire of seagrasses is very narrow compared to the diversity of form and shapes present in all other groups of marine autotrophs, such that seagrass species are largely scaled models of a single growth plan (Duarte, 1991, Marbá and Duarte, 1998). Hence, the null hypothesis of functional redundancy, which would be conducive to an absence of relationship between species diversity and ecosystem functions, is, a priori, a plausible hypothesis in seagrass communities.

3. Functions of seagrass meadows: ecosystem services

The ecosystem-relevant functions seagrasses perform are consequences of their physiological functions, such as primary production and nutrient recycling, by which they provide food to consumers and trap carbon and nutrients, but are also dependent on their structural role (Table 1). Seagrasses form dense communities with a high biomass (mean biomass 460 g dw m⁻², Duarte and Chiscano, 1999), which offer habitat and refuge for a wide diversity of organisms. Hundreds of species are found living epiphytic on the leaves at any one meadow, and there is a large number of species that live in the refuge offered by the plant's canopies. Hence, seagrass communities harbour complex food webs maintaining high marine biodiversity through the combined trophic and structural roles they serve. Seagrasses are the main food sources of the dugong (*Dugong dugon*), the most threatened marine mammal. Indeed, seagrass meadows are habitats for many endangered species, such as the large Mediterranean bivalve *Pinna nobilis*, inhabiting *Posidonia oceanica* meadows. Many of the animals associated with seagrass meadows are of commercial importance, including prawns and other crustaceans, and fish. Hence seagrass meadows are important habitats for other species, thereby contributing to maintain marine biodiversity and the production of potential food for humans.

Although local use of seagrass for food is of relatively small importance, much of their high primary production is exported to adjacent ecosystems (Duarte and Cebrián, 1996) where it may be an important carbon source. In addition, much of the primary production of seagrasses is buried in the sediments (Duarte and Cebrián, 1996) as leaf material and, largely, as roots and rhizomes. All seagrass tissues, particularly below-ground ones, decompose slowly (e.g. Harrison, 1989; Enríquez et al., 1993), such that some of the carbon and nutrients in the tissues are buried for time scales of at least centuries. Hence, seagrass meadows tend to be autotrophic ecosystems (i.e. they produce more organic carbon than that used in the ecosystem), which are areas of net oxygen release and CO₂ and nutrient sinks (Hemminga and Duarte, 2000). For instance, carbon burial rates of 58 g C m⁻² year⁻¹ have been reported for the Mediterranean species *Posidonia oceanica* (Mateo et al., 1997), and the colonisation of sediments by the Mediterranean species *Cymodocea nodosa* has been reported to result in an accumulation of about 3.6 g N m⁻² year⁻¹ (Pedersen et al., 1997). Indeed, seagrass communities store, on average, 16% of their production in the sediments, representing a carbon storage of about 8 · 10¹³ g C annually globally, such that seagrass meadows, although representing only 1% of the primary production of the global ocean, are responsible for 12% of the net CO₂ uptake by oceanic biota (Duarte and Cebrián, 1996).

Seagrasses alter the environment they colonise in different ways. Their roots and rhizomes penetrate into the sediments releasing oxygen therein, which stimulates bacterial activity and attenuates the reduced condition of the sediments, thereby avoiding the accumulation of toxic compounds, such as sulfide (Terrados et al., 1999a). In addition, their canopies attenuate waves and dissipate turbulence, thereby reducing sediment resuspension and increasing the retention of sediments within the meadows (Gacia et al., 1999; Terrados and Duarte, 1999). In addition, part of the leaf litter they produce is washed ashore (e.g. 20 and 25% of the production of a Kenyan and an Australian seagrass meadows, Robertson and Hansen, 1982; Ochieng and Erfteimeijer, 1999, respectively). This leaf litter protects the shoreline from erosion during storms and serves as seed material for the formation of dunes (Hemminga and Nieuwenhuize, 1990). Hence, seagrasses are 'engineering species', which modify the physical and geochemical conditions in their environment, facilitating the life of other organisms in the community and protect both the beach and submarine sediments from erosion (Table 1).

4. Species loss in seagrass meadows: evidence for ecosystem consequences

Seagrass loss has been recorded frequently throughout the world (Short and Wyllie-Echeverria, 1996), so there is ample evidence of what its effects on the ecosystem are. Seagrass loss often occurs as catastrophic events, rather than gradual processes, for the initiation of seagrass loss triggers a number of negative effects (e.g. sediment reduction, sediment resuspension) which further accelerates their loss (Duarte, 1995). Hence, seagrass loss — similar to seagrass recovery — is often a self-accelerating process (Duarte, 1995). Basin-wide declines have been reported in the Atlantic and the

Mediterranean, and declining seagrass cover is now a worldwide problem (Short and Wyllie-Echeverria, 1996). The causes for seagrass decline include deterioration of water quality, largely resulting from eutrophication of siltation (Duarte, 1995; Terrados et al., 1998), but also include other, possibly climatic effects, and seagrass decline has been linked to temperature and sea level rise, and changes in the frequency of storms and hurricanes (e.g., Short and Wyllie-Echeverria, 1996; Marbá and Duarte, 1997). There are fewer reports of partial losses, involving only one or a few of the species in the community. Species erosion in seagrass communities has been reported in relation to siltation of SE Asian coastal ecosystems (Terrados et al., 1998), and long-term fertilisation experiments have documented changes in species frequency with increasing nutrient additions (Fourqurean et al., 1995). The sequences of species loss or decline in these studies was not random, but showed a similar pattern with the climax species, *Thalassia* species being most sensitive to the change in growth conditions (Fourqurean et al., 1995; Terrados et al., 1998). Moreover, the sequence of species loss as siltation of SE Asian coastal meadows proceeds was reproduced in the experimental assessment of the response of seagrass communities to burial (Duarte et al., 1997), further indicating that the sequences of species loss are not random.

Whatever the causes, the consequences of seagrass loss are well documented, at least for the case of meadow declines, and involve the loss of associated fauna, both in quantity and diversity, leading to fisheries decline, the deterioration of water quality, and sediment erosion followed by shoreline erosion (e.g. Duarte, 1995).

The consequences of partial losses involving single species, rather than entire meadows, are far less documented. For instance, loss of *Halophila*, and to a lesser extent, *Halodule* species involves reduced food availability to dugongs, whom preferably feed on these species. The paucity of documented consequences may largely reflect a poor observational (or experimental) basis, but may also reflect a relatively lack of evident effects of declining seagrass species diversity on ecosystem functions. There is, however, empirical evidence that some species, such as *Thalassia hemprichii* in SE Asian meadows, facilitate the development of mixed meadows, for other seagrass species (e.g. *Syringodium isoetifolium* and *Cymodocea rotundata*) are always found in association with it (Terrados et al., 1998). This observation suggests that loss of these species could have particularly negative effects on the community and the functions they perform. Hence, although the negative consequences of loss of seagrass meadows are well documented, there is little evidence on the consequences of the partial loss of diversity, involving the loss of one or a few species in the community.

5. Similar functions, different roles: are seagrass species equivalent?

While seagrasses share a common physiological basis and architectural design, their roles in the ecosystem differ considerably. The maintenance of seagrass populations depends largely on clonal growth, which in turn depends on the speed of horizontal extension of the species (Duarte, 1991a; Marbá and Duarte, 1998). The rate of seagrass species differs by a factor of 50 across species, from slow-growing ($< 10 \text{ cm year}^{-1}$)

species, such as *Posidonia oceanica*, to fast-growing ($> 5 \text{ m year}^{-1}$) species, such as *Halophila ovalis* and *Syringodium filiforme* (Duarte, 1991a, Marbá and Duarte, 1998). The horizontal extension rate is, together with other dynamic properties of the seagrass (such as shoot turnover and life span), negatively scaled to the size of the seagrass species (Duarte, 1991a; Vermaat et al., 1995; Marbá and Duarte, 1998). These size-dependent differences among species are largely responsible for differences in their roles in the community. In particular, large, slow-growing species generally act as climax species whereas small, fast-growing species tend to be colonizers (Duarte, 1991a; Marbá and Duarte, 1998). The slow turnover rate of slow-growing species allows them to reach high biomass in close meadows compared to the biomass achieved by closed stands of small, fast-growing species (Duarte and Chiscano, 1999). Moreover, large species have long-lived modules, which are also thick and tend to decompose very slowly. Hence, the persistence of seagrass material, and eventually the burial of the associated carbon in the sediments is linked to the size — and, therefore, life span and growth rate — of the species. Indeed, carbon accumulation in *Posidonia oceanica*, the slowest growing seagrass species, meadows is so high that this species is able to form reefs (Molinier and Picard, 1952). Hence, the storage of carbon in the sediments is linked to the size, and the role as pioneers or colonisers, of the seagrass species. Conversely, the tissues of small, fast-growing species are less fibrous, decompose faster and are more palatable than the fiber-rich tissues of slow growing species. Hence, small, pioneer species usually support high grazing pressure and transfer a greater fraction of their production up the food web, whereas grazing pressure on slow growing species is typically low (Cebrián and Duarte, 1995, 1997).

The role of seagrass species in the community is, therefore, ranked across a continuum from slow-growing, climax species that form meadows with high biomass and store significant amounts of carbon in the sediments, to fast-growing, pioneer species that develop stands with low biomass and experience high grazing pressure. This gradient corresponds to a gradient from a dominance of the structural role, in one hand, to the predominance of the trophic role in the case of fast-growing species.

The preceding discussion makes it clear that the functions and services provided by a given species richness in a seagrass community depend critically on the individual species involved. Hence, assemblages with a similar number of species, but with specific memberships drawn randomly from the regional seagrass flora, are likely to differ greatly in function, particularly depending on the balance between large and small species in the assemblage. Species with contrasting sizes tend to exploit different reservoirs of the same resources. For instance, the rhizosphere of mixed meadows is partially segregated by species, with small and large species tending to extend their rhizosphere in shallower and deeper layers of the sediments, respectively. In addition, the canopies of the species also exploit different parcels of the water column, such that mixed meadows develop multilayered canopies with small species being in the understory of the larger species. Not surprisingly, small species tend to show characteristics of shade-adapted plants, with thin leaves with high chlorophyll a concentrations and showing low compensation irradiances for photosynthesis and a high photosynthetic efficiency (Enríquez et al., 1995). Provided that seagrass communities are often resource-limited, a diversification of the resource pools exploited, such as that of mixed

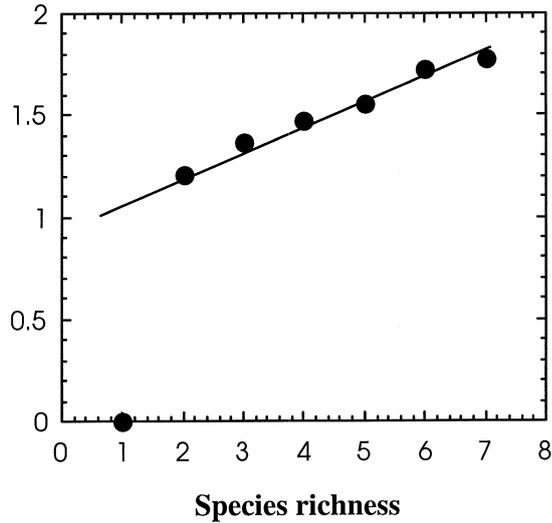
meadows of species with contrasting sizes, with their multilayered canopies and rhizospheres, achieve, must lead to a greater productivity. It is, therefore, not surprising that the mixed meadow at Silaqui Island (The Philippines), with seven species mixed together, is amongst the most productive yet studied (Duarte and Chiscano, 1999) despite being strongly nutrient limited (Agawin et al., 1996; Terrados et al., 1999b). This is also the most diverse seagrass stand that has been studied to any detail (see Vermaat et al., 1995, 1997; Agawin et al., 1996; Duarte et al., 1997, 1998, 2000; Terrados et al., 1998, 1999a,b), and provides, therefore, a convenient example of the link between species diversity and functional diversity.

The above discussion leads to the conclusion that species richness per se should have no direct relationship to the functional performance of the community, so that high species richness is not necessarily associated to a broad functional repertoire. Yet, high species richness is likely to be correlated with a greater performance by the community, simply because there must be a statistical tendency for the form and, therefore, functional repertoire present within the community to increase with increasing species richness. This functional variability must allow more thorough and efficient use of the resources present, as well as ensure that the performance remains high in the presence of a dynamic environment. To illustrate this point, I have produced, on the basis of the reported functional properties of the seven species present in the mixed Philippine meadow at Silaqui Island (from data in Vermaat et al., 1995, 1997), a simulation of the functional variability present in synthetic communities of increasing species richness produced by randomly assembling all possible combinations of species from the species pool present. The results from this simulation experiment clearly show that the average functional variability of the species present in the community significantly increases with increasing species richness (Fig. 1). While this is so, on the average, this is not necessarily the case for every possible combination, and there are specific combinations of species which do not lead to increased functional diversity over some possible assemblages with lower species richness (Fig. 1). Hence, high species diversity is a condition necessary, but not sufficient, to yield high functional diversity in seagrass communities.

6. Positive interactions in seagrass communities

The preceding discussion of the role of species diversity in providing functional diversity to the community assumes that the effect of high species diversity is additive. This is not necessarily the case, and positive interactions within the community could, if present, enhance the functional performance of the communities beyond that encountered by adding the functions of meadows of the individual species alone. Indeed, positive interactions in plant communities have received far less attention than negative, competitive interactions (Betness and Callaway, 1994; Hacker and Gaines, 1997), most likely because of the belief that resource limitation, which is widespread in plant communities, must enhance competitive interactions. Yet, recent evaluations suggest that positive interactions are more common in nature than expected, particularly when involving the presence of engineering species, which by altering the physical and

**Productivity variability
(coefficient of variation)**



**Horizontal extension variability
(coefficient of variation)**

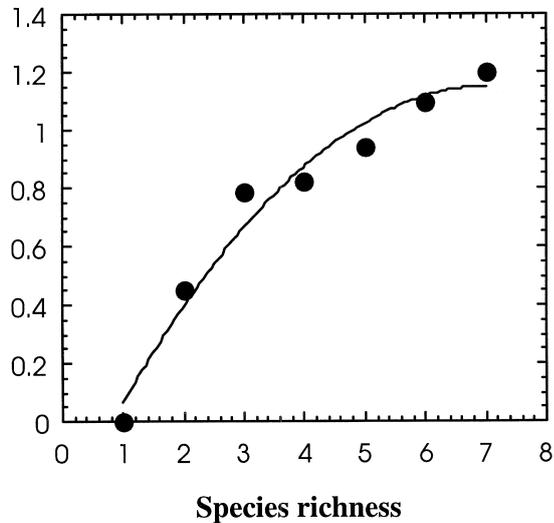


Fig. 1. Relationship between the average coefficient of variation in the horizontal rhizome extension rate (m year^{-1}) and the productivity (as turnover, year^{-1}) of randomly produced seagrass assemblages, generated by sampling all possible combinations of species from the species pool present in the mixed community growing in Silaqui Island (The Philippines). These are *Thalassia hemprichii*, *Enhalus acoroides*, *Cymodocea serrulata*, *Halodule uninervis*, *Cymodocea rotundata*, *Syringodium isoetifolium*, and *Halophila ovalis*. Data on species branching and horizontal rate from Vermaat et al. (1995).

chemical properties of the environment facilitate the presence of species that would otherwise be absent (e.g. Betness and Callaway, 1994; Hacker and Gaines, 1997).

Evidence of positive interactions in seagrass communities is suggested by the tendency for the average biomass of SE Asian communities to increase with increasing species richness (Fig. 2). Moreover, the increase in the biomass of multispecific assemblages is also linked to an increased evenness in the distribution of biomass, and therefore, resources, within the communities (Terrados et al., 1998). Together with the fact that the presence of the climax species, *Thalassia hemprichii*, is associated with greater species diversity, the positive effect of the presence of *Thalassia hemprichii* on the accompanying species was demonstrated experimentally (Duarte et al., 2000). Experimental removal of *Thalassia hemprichii* led to a declining trend of four of the six extant species, despite resource limitation in the community (Duarte et al., 2000). Hence, the biomass — and therefore the structural and trophic roles — of the community was not compensated by positive response of the extant species to removal of *Thalassia hemprichii* (Duarte et al., 2000). Hence, partial loss of seagrass diversity may negatively affect the diversity of associated organisms, but also lead to a further decline of seagrass species diversity in mixed meadows. However, the negative effects

Community biomass

(g DW m⁻²)

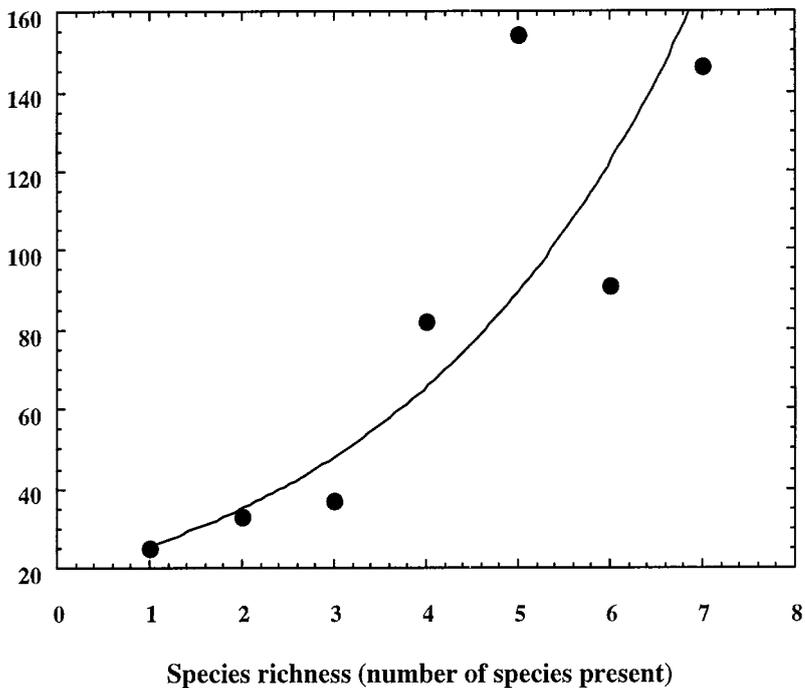


Fig. 2. Relationship between the average species richness of SE Asian seagrass communities and the average biomass the stands support. Data from Terrados et al. (1998).

associated to the experimental removal of *Thalassia hemprichii* were not observed when any other species were experimentally removed (Duarte et al., 2000). Furthermore, the experimental removal of species other than *Thalassia hemprichii* lead to a positive response of this species, regardless of the number of species removed, thereby compensating the biomass and, therefore, ecosystem functions of the community (Duarte et al., 2000). This experiment provided an insight into the nature of the interactions. In particular, it showed that the interactions between species were asymmetric, so that the development of the population of the dominant species, *Thalassia hemprichii*, was suppressed by resource competition with the other members of the community, whereas these benefitted from the presence of *Thalassia hemprichii*. Hence, the experiment provided additional evidence that there is no direct relationship between species richness and the maintenance of ecosystem functions — as indicated by community biomass — which depends, instead, on the specific membership of the community.

The demonstration of asymmetric interactions within mixed seagrass communities provides evidence that the loss of species richness will have contrasting effects on the functional performance of the community depending on the role, whether as a facilitator or a competitor, of the species lost. Hence, while some seagrass species play contrasting roles in mixed communities, largely because they exploit different pools of resources as a result of size differences, there is no evidence that species of comparable sizes perform different functions. These seagrass species of comparable size could, thus, be considered to be functionally redundant in the community.

7. Disturbance and the role of biodiversity in the maintenance of ecosystem functions

The perception of the functional role of species richness in the community depends on whether the communities examined are in approximate steady-state or experience intense dynamics. Seagrass communities are subject to frequent disturbance, whether anthropogenic (e.g. shoreline construction, eutrophication, mechanical damage) or natural (e.g. sand wave motion, storms and hurricanes/typhons, overgrazing). These disturbances may, if sufficiently strong, lead to partial or total loss of the seagrass community. The presence of multispecific species buffers the effects of disturbances, at least in the case of partial losses. A multispecific community is likely to contain a membership spanning a broad range in growth capacity and the capacity to survive disturbance (Vermaat et al., 1997). Disturbance may, depending on its particular magnitude and return time, decimate a subset of the species present, depending on their particular resistance to disturbance and their capacity to recover subsequently, which are species-specific traits (Duarte, 1991b; Marbà and Duarte, 1995). Moreover, the presence of a multispecific community generally provides the capacity for rapid colonisation of the gaps created by disturbance, followed by the subsequent colonisation by the slow-growing, climax species. Hence, some species may have a negligible contribution to the functioning of established communities, such as *Halophila ovalis*, which contributes only 0.03% of the biomass and 0.6% of the production of the Silaqui Island meadow (Vermaat et al., 1995). However, this species plays a critical role as colonizer of the gaps created by the

activity of burrowing shrimps or intense burial (Duarte et al., 1997). Similarly, small pioneer species have been reported to confer mixed meadows with the capacity to rapidly colonised gaps, thereby minimising the loss to ecosystem functions derived from the disturbance.

When longer time scales are considered, multispecific assemblages are likely to be more capable to respond to environmental change, in the sense of gradual trends (e.g. sea warming, sea level rise), than monospecific assemblages are, simply because, as emphasised earlier, the functional repertoire present within multispecific assemblages is likely to be, on average, greater than that of monospecific meadows.

8. Species diversity and the resilience of the functions of marine ecosystems

The discussion of the functioning of mixed seagrass meadows leads to the conclusion that the link between species richness and ecosystem functions and services is not a direct one. The reason is that the functional performance of the community is a property of the species present therein and not of their number. A few species, such as, for instance, *Trichodesmium* species, the main pelagic nitrogen fixer in the ocean, play key roles in marine environments which cannot be assumed by other species within the same community. In such cases, the functional performance of the community depends critically on the presence of these particular species, rather than the number of species per se. Conversely, functional redundancy does occur within communities, such as that involving closely-related (typically congeneric) species in seagrass communities. Loss of redundant species would lead to no measurable reduction in ecosystem functionality, despite a significant loss in genetic diversity.

However, an indirect relationship between species richness and ecosystem function can be postulated, whereby increased species richness is on average, in a statistical sense, likely to be linked to increased functional performance and the provision of more ecosystem services than those of monospecific communities. The reasons for this conclusion are twofold:

1. Multispecific assemblages have a greater probability of containing a greater functional diversity within its membership than those of species-poor assemblages, thereby providing more opportunities for efficient resource exploitation (Tilman, 1997). For instance, a randomisation simulation on the average number of trophic guilds present in a community of benthic invertebrates with increasing species richness is likely to support also an increase in functional diversity with increasing species richness. In communities richer in components than seagrass meadows, the relationship between function and species richness is likely to be asymptotic, as demonstrated experimentally for land species (Tilman, 1997).
2. Positive interactions within communities will enhance their functional performance, which will increase faster than expected from a simple additive consideration of the functional capacities contributed by the member species alone. Because positive interactions are increasingly recognised to be frequent in nature, particularly when involving engineering species (e.g. coral reefs, seagrasses, mangroves, spongi,

macroalgae in marine environments), a non-linear increase in ecosystem function with increasing species richness is also expected to occur.

Hence, ecosystem functions derive from properties intrinsic to the individual species present and their interactions, but the greater opportunities for enhanced functional performance and positive interactions derived from a greater number of species present in diverse communities leads to the expectation of a positive relationship between species richness and ecosystem functions.

In fact, the link between species richness and ecosystem function is likely to be strong (Tilman, 1997). The reason for this assertion is that any evaluation of the role of species diversity in the functional properties of natural communities based on examination of steady-state communities underestimates the potential offered by the pioneer species. Pioneer species are typically underrepresented members of established communities, but play an essential role in the recovery of ecosystem functions following disturbance. The warranty of the maintenance of functional performance associated to the presence of pioneer species in mixed communities represents a potential whose value is, unfortunately, increasingly realised in an ocean subject to strong anthropogenic forcing leading to change at both local and global scales. The importance of biodiversity in ensuring the sustainability of ecosystem functions after disturbances has been demonstrated experimentally in land ecosystems (Tilman and Downing, 1994), and should also hold in the marine ecosystem. The maintenance of the broadest possible genetic diversity ensures that the communities also contain the broadest possible functional capacities, even if many of these remain potential and are not realised in established communities. Hidden potentialities may, however, prove critical following disturbance or gradual changes in the environment inhabited by the communities.

The demonstration of a link between ecosystem function and services and species richness has remain elusive when tested for specific communities, except for a few clear demonstrations, such as outlined for seagrass communities. The arguments presented provide, however, strong reasons to expect this link to be a general rule in marine ecosystems, and call for conservation efforts to be increased to ensure the maintenance of marine biodiversity as a means of maintaining the functions of marine ecosystems and, thereby, the services they yield to humanity.

Acknowledgements

This is a contribution to the PREDICT project, funded by the INCO-DC programme of the European Commission (contract ERB3514PL972504). I thank Richard Warwick, editor in chief of *J. Exp. Mar. Biol. Ecol.*, for the invitation to write this essay, which has proven a stimulating task. [RW]

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