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What do species do in intertidal systems?

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Abstract

There is a surprising lack of targeted research into the effects of loss of biodiversity on functioning of marine ecosystems. General theoretical models have been developed and these have been tested in terrestrial systems, particularly grasslands, and in mesocosms. Findings have been controversial, however, with debate focussing on the role of species diversity *per se* as opposed to the role of particular species from specific functional groups (functional diversity). Marine systems process materials and energy quite differently from terrestrial systems and have a high degree of functional diversity. Specific models may therefore need to be developed for marine systems and marine tests of general models could be valuable in resolving current ecological debates. Although targeted research is lacking, there is a considerable body of relevant work in intertidal systems and some of this research is reviewed here. Idiosyncratic effects of loss of species appear to be prevalent in intertidal systems and removals of more than one species often result in interactive effects, suggesting a high degree of complexity and unpredictability. However, it is thought that idiosyncratic effects are more likely to occur in systems with 'keystone' species than in systems with weak or diffuse effects of consumers. Intertidal systems, particularly rocky shores, provide an ideal model system for research into effects of loss of diversity on ecosystem function. In addition to distinguishing the roles of species and functional diversity, intertidal research could also characterise inter-trophic effects and relationships between the diversity of ecosystems and their stability and invasibility.

Keywords: intertidal, diversity, ecosystem function, functional groups, inter-trophic effects.

Introduction

The title of this review is derived from an influential paper by John Lawton which summarised some of the theories predicting what may happen to the functioning of ecosystems as species are lost from them (Lawton 1994). Given the currently high rate of loss of species, this issue has become one of the key areas of debate in ecology (Schwarz *et al* 2000; Tilman 2000). In this paper, I will first outline the sorts of ecosystem functions that have been considered in this context and present the main theories predicting how their rates are related to the numbers of species present. A case will be made for tests of these theories in marine systems and evidence from intertidal systems will be reviewed. Finally, I will discuss one attempt to provide a general predictive framework into which to fit these findings and will suggest some avenues for research in intertidal systems.

Effects of loss of species on ecosystem function

The functioning of ecosystems can be defined in many ways, but may broadly be thought of as the rate at which they process materials and energy (e.g. Díaz and Cabido 2001). Processes of interest thus include productivity (primary, secondary, etc.), decomposition, transfer of energy between trophic levels, nutrient retention, nutrient cycling, etc. Martinez (1996) sought to expand that definition to include ecological processes, such as recruitment,

predation, etc., but such processes have not usually been considered in this context and will generally be omitted from the current review.

From a human perspective, the functioning of ecosystems has become a focus of ‘sustainability science’, which supports conservation based on the value of ‘goods and services’ that ecosystems provide to mankind (Costanza *et al* 1997). International conventions such as the Rio Convention on Biodiversity oblige signatories to protect the biodiversity of systems, in part to maintain the integrity of their functions. This is based on the premise that the functioning of systems is related to their biodiversity, and it is this premise that has been intensely scrutinised in recent years.

Three main hypotheses are commonly cited to predict the relationship between biodiversity and ecosystem function (Figure 1). The redundancy hypothesis (Walker 1992), suggests that the loss of a large proportion of species in an ecosystem would have no effect on its functioning because many species are ‘redundant’ in terms of ecosystem function and their loss would be compensated for by other, similar species. However, a critical point would eventually be reached, at which all functional analogues would have been lost and there would then be a catastrophic decline in ecosystem function (Figure 1). This theory has been particularly controversial, with calls by conservationists for the abandonment of the term ‘redundancy’ due to the implication that some species are of no value and could be lost without consequence (e.g. Gitay *et al* 1996). Naeem (1998) and Yachi and Loreau (1999) have argued instead that we should think positively about the retention of redundant species as an essential component of ‘biological insurance’ against future changes in environmental circumstances.

Ehrlich and Ehrlich (1981) proposed the ‘rivet hypothesis’ that likens the species in an ecosystem to rivets in an aircraft – the loss of each one would have a small effect on the efficiency of the machine – and predicts a gradual decline in ecosystem function as species are lost until a critical point is reached and the aircraft (ecosystem function) crashes (Figure 1). This change in function is sometimes drawn as a step function, but is distinguished from the redundancy hypothesis by progressive change as species are lost, rather than no change until the critical point. It should also be noted that although these models are illustrated with a negative relationship between number of species and ecosystem function, this does not imply that the relationship is always negative (e.g. see Wardle *et al* 1997).

Finally, Lawton (1994) proposed that there would not be a smooth relationship between number of species and ecosystem function, but rather that the effects of losing a species would depend on the identity of the species lost and would vary ‘idiosyncratically’ from species to species (Figure 1).

Diverse systems are also thought to be more stable than less diverse systems and less vulnerable to invasion. These are long-standing ideas, which have again come to the fore in recent years and which have been the subject of renewed experimental research (e.g. McCann 2000; Naeem *et al* 2000; Prieur-Richard and Lavorel 2000; Lyons and Schwartz 2001). As with other aspects of research in this field, findings have been controversial and no consensus has yet been reached.

Evidence to date

Much of the field evidence for and against these ideas has been derived from terrestrial systems, including grasslands, soils and streams. This evidence has been reviewed elsewhere

(e.g. Naeem *et al* 1999; Schlöpfer and Schmid 1999; Tilman 1999; Bolger in press; Waide *et al* 1999; Wardle *et al* 2000; Ekschmitt *et al* 2001) and will not be considered in any detail here except to note some key findings and controversies. Among the most influential studies have been those of Tilman *et al* (1996) and Hector *et al* (1999), which showed positive relationships between the number of species of grasses and herbs and primary productivity, in apparent support for the rivet hypothesis. ‘Complementarity’ was proposed as a key mechanism to explain how more diverse assemblages can be more productive than monocultures; a diverse range of species with slightly different niches make fuller use of available resources than could any one species (Hector 1998).

These findings have provoked considerable controversy, however, with suggestions that the experimental designs and inferences are flawed (Aarssen 1997; Grime 1997; Huston 1997; Huston *et al* 2000). These authors argued that significant increases in productivity may not be attributable to diversity *per se*, but rather to one or two extremely productive species, which function very differently from the others. Probability dictates that the chances of including such species are increased in the high diversity treatments. This has been termed the ‘sampling’ (Tilman 1999) or ‘selection’ effect (Huston 1997). If it is indeed the underlying cause of the observed effects, then the evidence supports the idiosyncratic rather than the rivet hypothesis. Considerable effort has therefore been invested in developing experimental designs that distinguish the effects of species diversity from those of individual influential species - so called ‘functional diversity’ (e.g. see Tilman 1997; Leps *et al* 2001; Spaekova and Leps 2001).

The other main arena of investigation has been laboratory-based, in mesocosms. The Ecotron, for example, yielded some influential findings showing relationships between ecosystem processes and diversity of plants, herbivores and soil fauna (Naeem *et al* 1994). Mesocosms are very attractive as a tool for studying these processes – a particular strength being the opportunity to make accurate measurements of ecosystem functions and fully to control the species composition. Drawbacks, however, centre around the obvious artefacts in terms of loss of natural physical processes affecting ecosystem processes – e.g. variation in nutrient availability, climatic variation, etc. – and limits to the number and size of species that can be included (Lamont 1995). Because assemblages are compiled, rather than species deleted progressively from complete assemblages, diversity is generally lower in laboratory than in field experiments and laboratory experiments are less likely to detect unexpected roles of rare species. Laboratory studies also create an artificial medium for behavioural interactions and do not permit natural shifts in abundances of other species (e.g. compensation for loss of one species by immigration of others).

More field experiments are sorely needed to complement the progress being made in mesocosms by reducing those artefacts, while of course suffering drawbacks of their own, particularly relating to the difficulty of measuring ecosystem processes accurately (see below). The mixture of field and laboratory approaches used can make it difficult to synthesise a cohesive overview, but most authors agree that an integrated approach is most likely to lead to rapid progress (e.g. Schlöpfer and Schmid 1999; Díaz and Cabido 2001).

The bulk of the research to date has concentrated on the effect of diversity within a trophic level on functions of that level (e.g. manipulating diversity of plants to test effects on primary productivity). Schlöpfer and Schmid (1999) noted a particular lack of information about the effects of herbivore diversity on herbivory. Hence there have been calls for

research into effects of diversity at one trophic level on function of another (Naeem *et al* 1999).

The need for tests in marine systems

Responses of marine ecosystems to loss of biodiversity have not been extensively studied. In 1999, keyword combinations of the terms biodiversity, biological diversity, species diversity, species richness, stability, ecosystem stability, ecosystem function, productivity, yield and food web produced no relevant papers from the marine literature (Schläpfer and Schmid 1999), despite an already large body of work in other habitats. This is unfortunate for two main reasons. The first is that marine ecosystems are fundamentally different from their terrestrial counterparts (Steele 1985, 1991) and therefore models derived from terrestrial research may not apply to marine systems. For example, nutrient availability depends on oceanographic processes and dramatic variation can occur over relatively short time scales via upwelling events (e.g. Vasquez *et al* 1998). Unlike on land, where organisms are generally decomposed where they die, materials in marine systems are often transported away from where they were produced and decomposed elsewhere. Given such differences, marine environments will probably require tailor-made models to predict effects of loss of species on ecosystem function. Such models will need to be developed and tested in marine environments. Secondly, marine diversity is very different from that on land. In particular, the marine fauna is more diverse at higher taxonomic levels than is the terrestrial fauna (May 1994; Vincent and Clarke 1995; Ormond 1996). Twenty eight phyla are found in the marine environment, of which thirteen are endemic (Grassle *et al* 1991). This compares to eleven terrestrial phyla, of which only one is endemic (Grassle *et al* 1991). It therefore seems likely that marine systems have scope for greater functional diversity than terrestrial systems and may therefore be extremely valuable in settling the debate over the roles of species diversity versus functional diversity.

The role of intertidal systems

Intertidal systems, particularly rocky shores, are among the classic experimental model systems in ecology, with an extraordinary track record of influential research, including Kitching and co-workers' research in Lough Hyne, Co. Cork, Ireland (e.g. Kitching *et al* 1959), Connell's (1961) pioneering experiments on competition on Cumbrae, UK and Paine's (1974) keystone predator removal on the west coast of the USA. Intertidal systems have a high degree of functional diversity, they are accessible and experimentally tractable (Connell 1974; Paine 1977, 1994 and see McGrath, this volume) and, due to a long history of research, a considerable degree of essential background knowledge is available. They are also particularly pertinent in this context, as they are among the marine systems most threatened by man's activities and are therefore quite likely to suffer increased rates of local extinction in the coming years (Crowe *et al* 2000; Thompson *et al* 2002). It is therefore appropriate for research into effects of loss of biodiversity on marine ecosystem function to focus on intertidal systems.

Evidence to date from intertidal systems

Although there has been a considerable body of potentially relevant research in intertidal systems, surprisingly little research has been done to tackle these questions directly. There has, of course, been a wealth of research testing hypotheses about the roles of individual species in affecting community structure - the experiments on predation and competition mentioned above being classic examples. I will not deal with work on removals of individual species here because their relevance in the current context is not as great as multi-species

removals – without knowledge of how the system responds to loss of >1 species, it is not easy to differentiate among the redundancy, rivet and idiosyncratic hypotheses. Nevertheless, reviewing extensive bodies of separate single-species removals in the same system can yield considerable insight, as discussed below.

In this section, then, I will briefly review studies involving removals of two or more species at a time. Given the theme of the symposium, I have generally restricted the review to intertidal studies. However, some studies on shallow subtidal systems (seagrass beds) are included because the work specifically addressed the relevant hypotheses and the species involved have intertidal analogues.

Some of these studies were not originally conceived to test hypotheses about the relationship between biodiversity and ecosystem function. However, in measuring response variables such as cover or biomass of algae, the authors made it possible to infer likely impacts on primary productivity. In fact, very little of the experimental work actually measured rates of primary production directly (by measuring rates of accumulation of biomass and losses to grazing and other causes). This would be extremely difficult in intertidal systems, particularly exposed rocky shores, given the rapid advection of broken material and the difficulties of estimating consumption by grazers, particularly of microalgae (but see Epstein 1997; Thompson *et al* 1997; Middelburg *et al* 2000). The use of tractable surrogates is widespread in this context (Hector 1998; Waide *et al* 1999) and it can certainly be argued that impacts on the cover or biomass of macroalgae will undoubtedly alter the mechanism and magnitude of primary production. It should be noted, however, that in doing this we are extrapolating the link between the roles of species in affecting community structure to include the link between community structure and ecosystem function. This distinction is important and the latter link has rarely been tested in intertidal systems (Allison *et al* 1996).

In contrast to much of the research in other systems, a significant proportion of the relevant work in intertidal systems has been done on inter-trophic effects. The findings clearly indicate that the diversity of one trophic level (e.g. primary consumers) can affect the diversity and function of other trophic levels (e.g. primary producers). The majority of effects were idiosyncratic (Table 1, e.g. Scheibling 1994; Jernakoff and Nielsen 1997 and see Paine 2002). Perhaps this is not surprising, given the high incidence of strongly interacting ‘keystone’ species (and the inevitable bias of researchers towards manipulations of those species thought likely to have marked effects). Typically, the loss of strongly interacting species has dramatic effects and the effects of loss of other species are different and/or less dramatic (Table 1, and see Allison *et al* 1996). Thus, the identity of the species lost is of key importance. Given the predominance of high level, high functional diversity in marine systems, this may well be a characteristic feature of them. It is striking, however, that idiosyncratic effects were also found after removal of different species from within a functional group – grazing limpets: Beovich and Quinn (1992) found that only loss of *Siphonaria diemenensis* would lead to major effects on foliose algae (e.g. *Scytosiphon lomentaria*); removal of *Cellana tramoserica* had little effect. This difference was partly attributed to differences in radula morphology and feeding biology, such that only *Siphonaria* could graze mature foliose algae.

Functional groups are not always defined by trophic considerations. Ecosystem engineering (*sensu* Jones *et al* 1994) can provide another basis for classification and the importance of different ecosystem engineers also varies depending on the identity of the engineer. Emmerson and Raffaelli (2000) used microcosm experiments to test effects of diversity *per*

se and functional diversity of bioturbators (allogenic ecosystem engineers) on flux of ammonia from sediments into the water column. They found that different species had markedly different effects and also showed that complementarity could act in soft sediment marine systems as it does in terrestrial plant communities (see Hector 1998).

One of the main insights to emerge from manipulations of two or more species in orthogonal designs is that not only is the identity of the species lost important, but also the identity of the combinations of species lost. Differences in the effect of losing species *a* depending on the presence or absence of species *b* give rise to statistical interactions in analyses of response variables – hence the category *idiosyncratically interactive* in Table 1. This is an issue that has rarely been considered in other systems (see Lamont 1995). As an example, ephemeral algae grew on a north Cornwall (UK) shore only if limpets (keystone grazers) were absent or if mussels (autogenic ecosystem engineers) were present to provide a refuge from limpet grazing; where limpets were present and mussels absent, no ephemerals grew (Crowe *et al*, unpubl data). Table 1 also includes details of similar effects reported by Geller (1991), Scheibling (1994) and Navarrete and Menge (1996).

Not only is the identity of the species lost important, but also the structure of the community from which they are lost. Where studies were done at more than one site, results of experimental removals tended to differ from site to site. For example, the growth of ephemeral algae at a different Cornish shore from the one described above depended only on the presence of mussels, probably because the dominant ephemeral alga there was *Porphyra* spp., which was strongly associated with mussels. Barnacles did not provide an effective refuge for algae from grazing limpets on the Isle of Man (UK) (Johnson *et al* unpubl), but did in California (USA), where they were ineffective as a refuge from grazing by littorinids (Geller 1991). In this case, the value of barnacles as a refuge depended on the sizes of the grazing gastropods. Environmental conditions can also alter the effects of losing species. For example, Zedler *et al* (2001) found different effects of manipulating diversity of saltmarsh plants under different conditions of drought and nutrient availability. These findings indicate that effects of loss of biodiversity are ‘context dependent’, much like many other ecological phenomena (see also Allison *et al* 1996; Jonsson and Malmqvist 2000).

Very few studies (in any system) have considered more than one ecosystem function at a time. Zedler *et al* (2001) included recruitment and canopy architecture as ‘ecosystem functions’ (along the lines suggested by Martinez 1996) as well as accumulation of biomass and nitrogen. They found that different species were more important for different functions and indicated that biodiversity was therefore of key importance as the loss of any species could reduce efficiency of at least one ecosystem function.

Evidence from past research – a new synthesis

In the rush of research to test these new ideas in the current context, we must not forget the volume of research done on intertidal systems in the past. There have been large numbers of experimental removals of single species, geared largely to testing hypotheses about their roles in affecting community structure. Allison *et al* (1996) reviewed a section of the literature that related to the effects of secondary consumers on their prey as a basis for predicting effects of loss of biodiversity in coastal habitats. They proposed a predictive framework to help categorise the effects of loss of biodiversity, which I will outline here.

Their categories depended on the type of system from which species are lost. They differentiated among systems involving strong keystone predatory effects, strong diffuse

predatory effects and weak effects (see also Menge *et al* 1994). Strong keystone effects occur when a single predatory species exerts an overwhelming influence on prey species. The classic example is the exclusion of mussels from low tidal levels on rocky shores in northwest USA by *Pisaster ochraceus* (Paine 1974). Strong diffuse effects occur where several predatory species are each capable of influencing prey species, such as on the tropical rocky shores of Panama (Menge *et al* 1986). In systems where predators exert only weak effects, there may be other processes that override their influence. For example, on a sheltered shore that is repeatedly inundated by sand, predators are only a minor source of prey mortality (Menge *et al* 1994).

Where predators exert only weak effects, the loss of one or more species has little effect, because there was little combined effect of all the species and/or compensation is possible (Figure 2). Where diffuse effects occur, the loss of one or more predators can usually (but not always) be compensated for by the other strongly interacting predators present, either via a functional response or by an increase in abundance (Figure 2). Such systems contain a degree of redundancy, or biological insurance (Walker 1992; Allison *et al* 1996; Yachi and Loreau 1999). Idiosyncratic effects are most likely to occur in systems containing a keystone species (Figure 2) - or perhaps only two to three influential predators with markedly different functional roles and little scope for compensation.

General predictions in ecology inevitably carry a high degree of uncertainty. For example, in this context, compensation for loss of a species may not occur if compensating populations are strongly recruit-limited (see Gaines and Roughgarden 1985) or if the species lost was very specialised. These basic categories (i.e. systems involving either strong keystone, strong diffuse or weak influences of consumers) do, however, provide a helpful starting point for predicting effects of loss of species from ecosystems. It also remains, of course, to determine which category any given system fits into. For a number of well studied localities, this information is already available (e.g. see Allison *et al* 1996). However, for many others a targeted body of experimental research is required. Given the potentially significant consequences of losing as yet unidentified strong interactors, Allison *et al* (1996) recommend a conservative approach to management where there is uncertainty.

Directions for future research

Vitousek and Hooper (1993) have suggested that systems with relatively few species (<10) may offer the best opportunity to explore relationships between biodiversity and ecosystem function because in those systems, it should be possible to characterise the roles of each species in some detail. This was part of the rationale underlying Zedler *et al*'s (2001) research, which is among the most comprehensive studies to date. It seems likely, however, that systems of differing diversity may exhibit different patterns of response to species loss. For example, Schlöpfer and Schmid (1999) suggested that low diversity systems might be more likely to exhibit idiosyncratic effects and high diversity systems were more likely to contain redundant species. It should be possible to find intertidal systems with a range of degrees of diversity to test these ideas. Some specific hypotheses that require further work for which intertidal systems could be particularly amenable include:

1. Functional diversity is more important to ecosystem function than species diversity *per se*.
2. Loss of diversity at one trophic level affects the functioning of other trophic levels.
3. Loss of diversity will decrease stability.

4. There is a negative relationship between invasibility of ecosystems and species diversity (and/or functional diversity).

Tests of hypotheses 1 and 2 require experimental investigation, ideally using both mesocosms and field research. Such tests could benefit from the potentially high level of functional diversity available in marine systems. For example, manipulations of herbivores could include amphipods, gastropods, echinoderms and fish, all of which graze in different ways on a diverse and productive assemblages of marine plants.

Examinations of the role of functional diversity are hampered, however, by the lack of a universal system for classifying functional groups (Sullivan and Zedler 1999; Díaz and Cabido 2001). There is essentially a two tiered hierarchy of functionality. On the first tier, species can be grossly divided on the basis of trophic levels (primary producer, primary consumer, decomposer, etc.) or other broad roles, such as autogenic or allogenic ecosystem engineers (Jones *et al* 1994). Within each broad category, species can be further subdivided into functional groups on the basis of morphological, dietary or other characteristics. For example, intertidal primary producers can be divided into microalgae, crustose algae, foliose algae, articulated calcareous algae, etc. (e.g. see Steneck and Dethier 1994) and primary consumers include microalgal grazers, macroalgal grazers, epiphytic grazers, etc. Such classifications are extremely difficult to develop, however. This is partly because species group differently depending on the criteria used for classification (e.g. a classification based on trophic roles will differ from a classification based on engineering activities). Species perform many different functions and may often vary their function under different circumstances (e.g. the abalone *Haliotis roei* sometimes feeds on drift algae and sometimes grazes (Scheibling 1994)).

In general, investigations of different ecosystem functions are served best by different classifications of functionality. Sullivan and Zedler (1999) found that a classification of saltmarsh plants based on morphological and metabolic criteria did not predict a classification subsequently derived from experimental evidence of a range of ecosystem functions of the species. Although the loss of any given species may not have an effect on any one ecosystem function (e.g. productivity), this does not necessarily imply that it is not critical for other functions (e.g. nutrient retention). Ideally, therefore, it would be of value to measure more than one function at a time, an approach currently lacking in much of the relevant research (but see Naeem *et al* 1994, Zedler *et al* 2001).

The challenges involved in testing hypotheses 1 and 2 also include making more explicit tests of the link between changes in community structure (e.g. cover of macroalgae) and ecosystem functions (e.g. productivity) – see Allison *et al* (1996). This will require the development of elegant and effective methods for measuring ecosystem functions (e.g. productivity) in the field.

Incorporating treatments to simulate different environmental contexts (e.g. changes in temperature or disturbance regime) would make it possible to evaluate the biological insurance hypothesis, which proposes that different species may become important under different circumstances (Yachi and Loreau 1999). An alternative, although less equivocal approach to testing this hypothesis would be to run experiments for long enough periods to enable natural shifts in environmental context, or to find several geographically remote sites with similar assemblages under different natural regimes. For this, and for tests of hypotheses 3 and 4, concerted long-term research at large networks of sites is necessary. The

European Union is supportive of such networks and BIOMARE (www.biomareweb.org) is among several currently being established.

Concluding remarks

Perhaps unsurprisingly then, given the high degree of functional diversity in the marine fauna and flora, a considerable proportion of the research to date has provided evidence in support of the idiosyncratic hypothesis. Importantly, the use of spatially replicated factorial experiments has also indicated that effects of losing species can depend on the identities of combinations of species lost ('idiosyncratic interactions') and are context-dependent – varying from place to place, perhaps due to the composition of the communities from which they are lost. This supports the theoretical findings of Cardinale *et al* (2000). Loreau (2000) and Díaz and Cabido (2001) have also suggested that variation in environmental conditions among sites is likely to mask effects of diversity, for example where environmental conditions play a stronger role in determining ecosystem functions than species diversity (e.g. rates of productivity may primarily be affected by nutrient availability rather than diversity). In fact, environmental conditions strongly influence both diversity and function, such that relationships between ecosystem function and diversity may be correlative rather than causal (e.g. see Rosenzweig and Abramsky 1993; Huston 1997).

One would also expect to see temporal variations in environmental conditions and community composition, which might also influence the effects of loss of species on ecosystem function (see also Cardinale *et al*, 2000, Allison *et al* 1996). The influence of such temporal variation has rarely been tested in this context, particularly over long periods of time. This is an important omission and such data will be needed to determine the value of the biological insurance provided by so-called redundant species (Hector *et al* 2001).

It is also important to recognise that, with few exceptions (e.g. Zedler *et al* 2001), each experiment tends to focus on one ecosystem function. No amount of experimental research would be able to provide a basis to predict changes in all ecosystem functions as a consequence of loss of particular species. This again provides an important rationale for conserving species regardless of the degree of redundancy found in any given system in relation to any given function (Hector *et al* 2001). In pursuing this debate, it is worth noting that conservation of species can also be justified by their intrinsic and aesthetic worth; their functional roles simply build on this argument (Ghilarov 2000; Hector *et al* 2001). Nevertheless, tests of hypotheses about the role of biodiversity in ecosystem function provide an excellent opportunity to pursue basic research about fundamental ecological questions, while providing results which have valuable implications for conservation and management.

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Tables

Table 1. Summary of findings in relation to models relating biodiversity to ecosystem function of research in intertidal (and some shallow subtidal) systems in which loss of >1 species was simulated experimentally. Studies marked '†' were not done specifically to test hypotheses about effects of loss of biodiversity. Variables sampled can serve as surrogates for ecosystem functions (e.g. changes in algal cover or biomass indicate changes in primary productivity). In these cases, conclusions in relation to models of loss of biodiversity were not drawn by the authors of the original papers, but have been added by the current author.

System	Approach	Trophic level / functional group manipulated	Trophic level sampled	No of taxa manipulated	Response variables	Effects / <i>model supported</i>	Citations
Saltmarsh, southern California, USA	Field & greenhouse experiments – selective plantings	Primary producers (saltmarsh macrophytes)	Primary producers	8	- recruitment - canopy architecture - biomass and N accumulation	Different species important for different functions - <i>rivet / idiosyncratic</i>	Zedler <i>et al</i> 2001 Sullivan & Zedler 1999
Rocky shore, Western Australia†	Field experiment – manual removals	Herbivores (grazing gastropods)	Primary producers (macroalgae)	2	algal cover and biomass	Removal of limpets & chitons had strong effects, removal of abalone only effective in absence of limpets & chitons – <i>idiosyncratically interactive</i>	Scheibling 1994
Rocky shore, south eastern Australia†	Field experiment – cage enclosures	Herbivores (limpets)	Primary producers (foliose and encrusting algae)	2	cover of foliose and encrusting algae	Only one species of limpet affected growth of macroalgae - <i>idiosyncratic</i>	Beovich & Quinn 1992
Rocky shore, south western UK	Field experiment – manual removal	Herbivores (limpets) & ecosystem engineers (mussels)	Primary producers (macroalgae)	2	cover of macroalgae	Spatially variable interactive effects – <i>idiosyncratically interactive</i>	Crowe <i>et al</i> (unpubl.)

Continued overleaf

Table 1 *contd.*

Rocky shore, Isle of Man, UK	Field experiment – manual removal	Herbivores (limpets) & ecosystem engineers (barnacles)	Primary producers (macroalgae)	2	• cover of macroalgae	Little effect of ecosystem engineer, strong effect of herbivores – <i>idiosyncratic</i>	Johnson <i>et al</i> (unpubl.)
Rocky shore, northern California, USA †	Field experiment – paint / Tanglefoot exclosures	Herbivores (limpets and littorinids)	Primary producers	3 (not fully orthogonal)	• cover of macroalgae	Barnacles prevented reduction of algae by limpets but not littorinids – <i>idiosyncratically interactive</i>	Geller 1991
Soft sediment, Scotland & South Australia	Laboratory mesocosms	Bioturbators (Scotland: polychaete, amphipod, gastropod; Australia: 3 gastropods, ghost shrimp, cockle)	—	3	• release of ammonia (nitrogen cycling)	Biomass dependent effects; differences between species; multispecies more effective than single species (complementarity); functionally diverse more effective than functionally depauperate - <i>idiosyncratic</i>	Emmerson & Raffaelli 2000
Seagrass, eastern USA (shallow subtidal)	Outdoor mesocosms	Mesograzers (amphipods and isopods)	Primary producers, secondary producers	3	• epiphyte accumulation • seagrass biomass accumulation • secondary production	Different species had strongest effects on different functions – some apparent <i>redundancy</i> , some <i>idiosyncratic</i> effects	Duffy <i>et al</i> 2001

Continued overleaf

Table 1 *contd.*

Seagrass, eastern USA (shallow subtidal)†	Outdoor mesocosms	Mesograzers (amphipods)	Primary producers	2	• epiphyte biomass • seagrass biomass	Different effects of different grazers – <i>idiosyncratic</i>	Duffy & Harvilicz 2001
Seagrass, Western Australia (shallow subtidal)†	Field exclosures (some artefacts identified, but effects still detectable)	Mesograzers (amphipods and gastropod)	Primary producers	2	• periphyton biomass • epiphyte diversity and biomass • seagrass mortality	Mixed effects on periphyton; gastropods affected epiphyte biomass but not diversity, amphipods vice versa; seagrass mortality reduced by gastropods only – <i>idiosyncratic</i>	Jernakoff & Nielsen 1997
Rocky shore, northwestern USA	Manual removals	Predators (starfish, dogwhelks)	Filter feeders (mussels, barnacles)	2	• survival of filter feeders	Whelks only become important in absence of starfish, i.e. partially compensate for loss of keystone – <i>idiosyncratically interactive</i>	Navarrete & Menge 1996

Figure legends

Figure 1. Models of effects of loss of biodiversity on ecosystem function (modified from Lawton 1994).

Figure 2. Overall influence of a functional group and the effects of species loss. Solid bars represent the total effect of the group on the system; open bars represent the relative effects of individual species within the group. Panels on the left represent the system with all species within the group present, the middle panels represent the system with one species removed, the panels on the right represent the system with two species (species 1 and 3) removed. The three types of system are represented – weak effects, strong keystone effects (species 3 is the keystone) and strong diffuse effects. Figure from Allison *et al* (1996), used with permission from SCOPE 55, *Functional Roles of Biodiversity: A Global Perspective*, edited by Mooney, H.A., J. Hall Cushman, Ernesto Medina, Osvaldo e. Sala, and Ernst-Detlef Schulze, 1996, John Wiley & Sons Ltd, Chichester, UK.

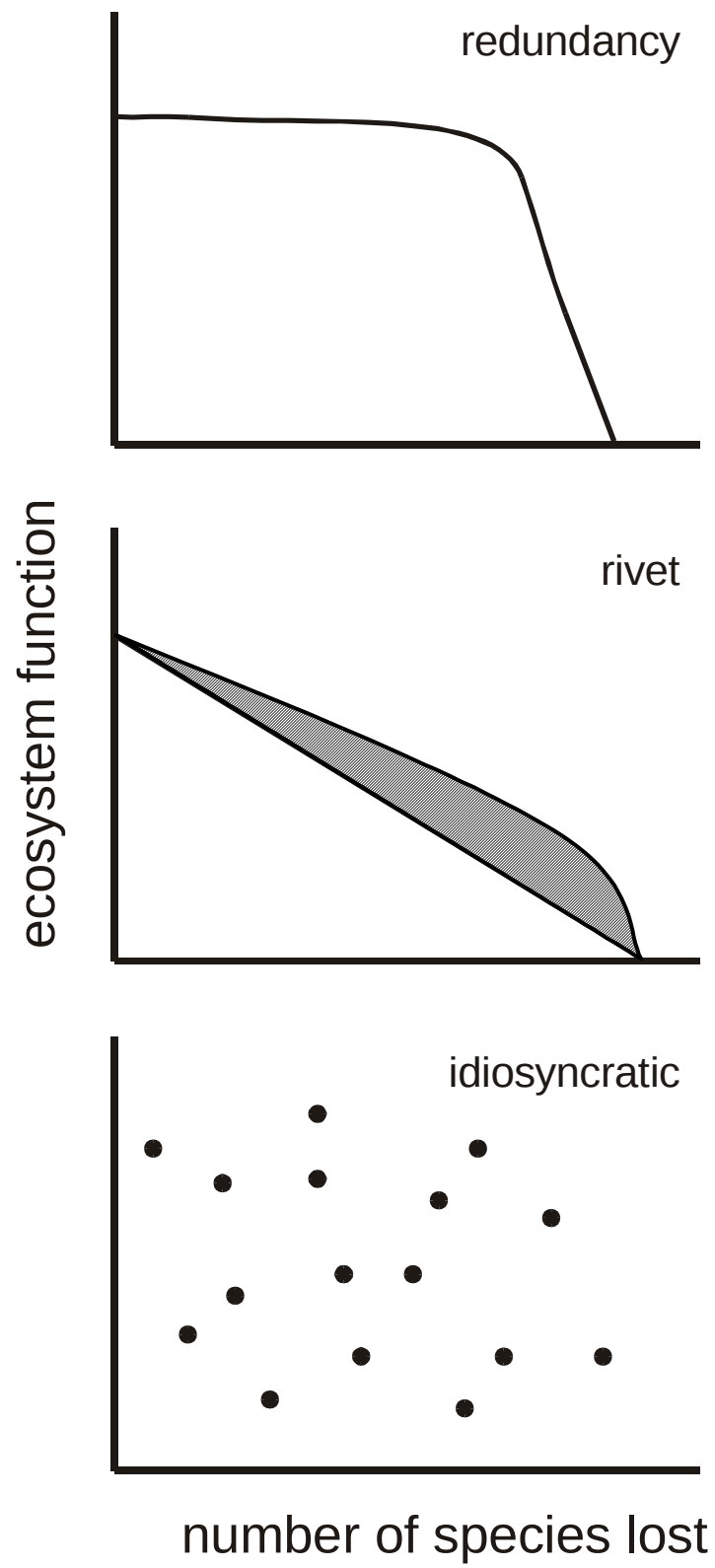


Figure 1.

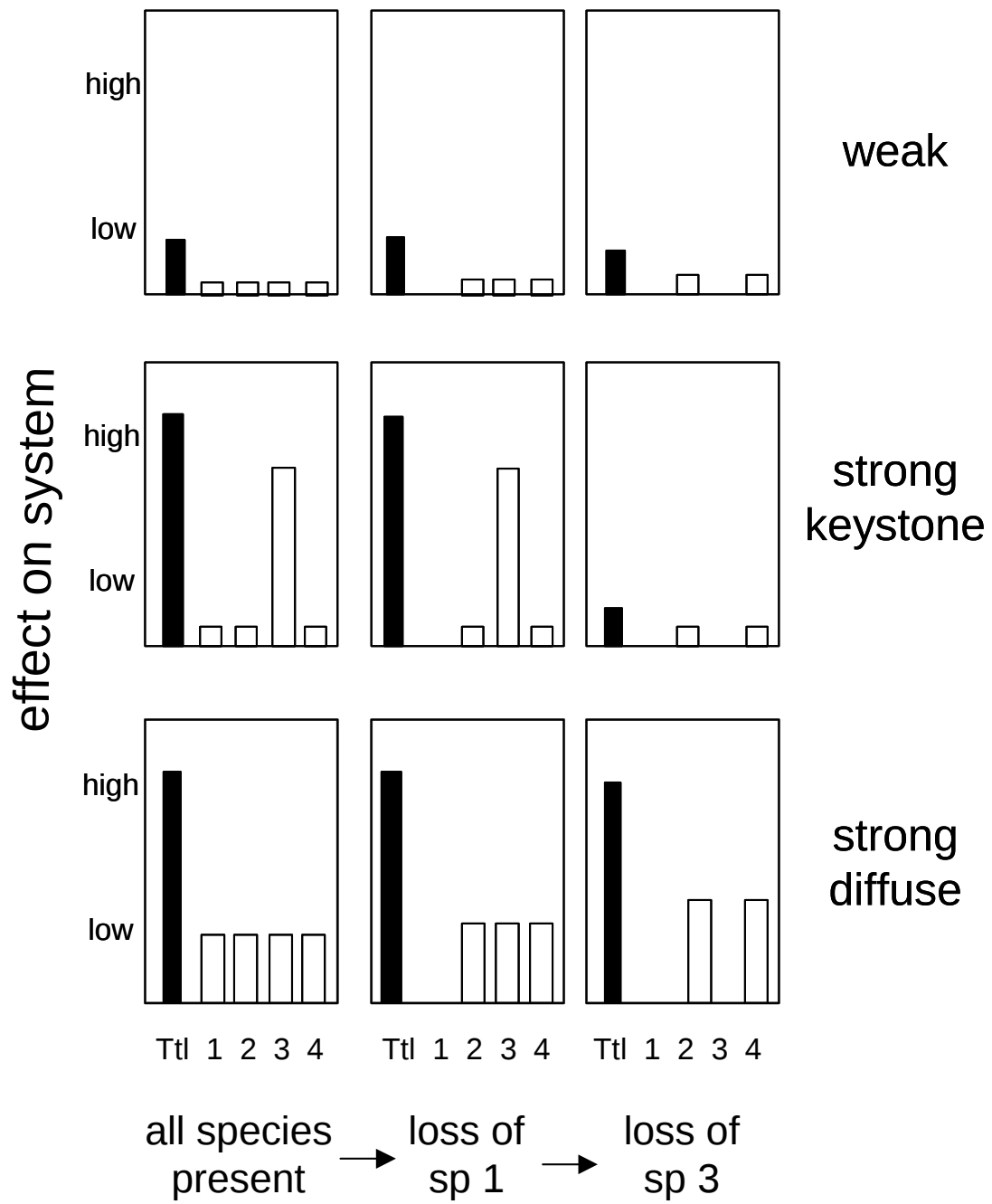


Figure 2