

SPECIES–AREA RELATIONSHIPS AND MARINE CONSERVATION

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Abstract. The species–area relationship (SPAR) was the central paradigm for the emerging science of reserve design in the 1970s and early 1980s. The apparent consistency of the SPAR for natural areas suggested that it could be used to predict the number of species that would be maintained within the isolated confines of a nature reserve. This proposed use of the SPAR led to heated debates about how best to partition space among reserves. However, by the end of the 1980s, the SPAR was no longer a central issue in reserve design. There was too much uncertainty about the underlying causes of the SPAR to trust that it would hold for reserves. The SPAR was also inappropriate for the design of single-species reserves and thus did not answer the traditional needs of wildlife managers. Ecologists subsequently focused their reserve-design efforts on the management of individual populations to reduce the probability of extinction and the loss of genetic variation. Nevertheless, because the SPAR does not require detailed knowledge of the requirements of individual species, it is still used to estimate local species richness and to predict the effects of habitat loss and fragmentation on biodiversity. These applications of the SPAR may be especially useful in the design of marine reserves, which often differ in purpose from conventional terrestrial reserves and may require fundamentally different approaches.

Key words: *biodiversity; marine reserves; reserve design; species–area relationship.*

INTRODUCTION

The species–area relationship (SPAR) represents one of the earliest quantitative models in biogeography. A relationship between the number of species (species richness) and land area for oceanic islands was noted as early as 1778 (Browne 1983). The relationship is typically nonlinear; so that an increase in area corresponds to less than a proportional increase in the number of species. Arrhenius (1921) is generally credited with the first quantitative formulation of the SPAR. He suggested the relationship had the general form of a power function: $S = cA^z$, where S is the number of species, A is area, and c and z are constants that are fitted to the data. The value of c depends on the units for area, but the exponential constant, z , is unitless. On a log-log plot, a species–area curve that follows this relationship appears as a line with slope z . The value of z has often been used to compare species–area curves across different spatial scales. In many cases, z falls within the range of 0.15 to 0.39 (May 1975), and it has been claimed that values for areas within continents tend to be lower than those for oceanic islands (MacArthur and Wilson 1963, 1967). For $z = 0.3$, this relationship is consistent with Darlington's rule that a tenfold increase in area corresponds to a doubling in the number of species (Darlington 1957). The number and variety of cases that were found to conform to this relationship was so impressive that it was called "one

of community ecology's few genuine laws" (Schoener 1976).

Several hypotheses have been proposed to explain the SPAR. They correspond to mechanisms that are not mutually exclusive, but instead represent successive levels of complexity. The most parsimonious is that the relationship is simply an effect of sampling (MacArthur and Wilson 1963, 1967). If organisms are distributed randomly in space, larger areas are likely to enclose greater numbers of organisms, which in turn are likely to include more species. With increased area, the total number of possible species (from the regional species pool) would be approached asymptotically with a consequent decrease in the rate at which additional species are encountered. This explanation for the SPAR, which has been called the "passive-sampling" or "random-placement" hypothesis, predicts a positive, but nonlinear relationship between the number of species and area. If species–abundance distributions are log-normal, a SPAR very similar to the Arrhenius relationship is expected (Preston 1962). Passive Sampling should always be considered the null hypothesis; unless it can be rejected, more complex explanations are unwarranted.

The "habitat-diversity" hypothesis emphasizes the effect of associations between species and habitats (Williams 1943, Lack 1969) on the SPAR. Larger areas are more likely to enclose more diverse types of habitat and therefore will include more species. The habitat-diversity hypothesis predicts a positive, nonlinear relationship between number of species and area, although it does not predict the exact form of the relationship.

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Both the passive-sampling and habitat-diversity hypotheses consider the species composition of a given area to be independent of the area's surroundings and therefore do not predict any effect of isolation. However, biogeographers have often observed a reduction in the number of species on more isolated islands and this suggests an additional mechanism contributes to the SPAR. The "equilibrium theory" of biogeography can explain both the effects of area and of isolation with a single mechanism. According to the equilibrium theory, the number of species within an area is a dynamic balance between the arrival of new species and the local extinction of species already present (Preston 1962, MacArthur and Wilson 1963, 1967). The theory predicts fewer species on more isolated islands, and more species on larger islands. The predictions follow by reasoning that increased isolation from sources of immigration should decrease the rate at which new species arrive, and that populations on larger islands should be less prone to extinction. These simple mechanisms appear to be quite reasonable, although it can be difficult to disentangle them entirely from effects of habitat. For example, larger islands are also likely to provide a greater diversity of habitats (Whitehead and Jones 1969), and remote, isolated islands may be subjected to climates that are different from those that are close to a mainland (Williamson 1981).

The initial enthusiasm for the equilibrium theory led some to the uncritical supposition that any data that appeared to fit the Arrhenius equation represented support for the theory. However, it was later shown that a variety of plausible mechanisms were consistent with the Arrhenius equation, and that species–area curves did not provide critical tests of the equilibrium theory (Connor and McCoy 1979). Furthermore, not all species–area relationships were adequately described by the Arrhenius equation, and a number of alternatives were suggested (Dony 1963, Connor and McCoy 1979).

One of the most troubling aspects of the early SPAR literature was a tendency to extrapolate from the results of experiments that were conducted on very small spatial scales to conclusions about mechanisms operating on scales several orders of magnitude greater. This may have reflected both practical constraints and an implicit belief in a single, universal SPAR. Small-scale studies provided greater opportunity for experimental manipulation, and for the inclusion of taxa that would have been difficult to survey over larger areas. The apparent faith in the scale-independence of the SPAR can be traced back to early explanations of the SPAR in terms of underlying log-series (Fisher et al. 1943, Williams 1943) or log-normal distributions of species abundance (Preston 1948, 1962), which were assumed to be independent of scale (Leitner and Rosenzweig 1997). However, it was later recognized that even at a single location, the SPAR was scale dependent (Palmer and White 1994) and there was likely to be a plurality of

mechanisms contributing to it (Connor and McCoy 1979, Williamson 1981). For very small areas of uniform habitat, passive sampling may be sufficient to explain the SPAR. For areas that extend across landscapes, the contribution of habitat diversity will be significant as well. For areas that enclose individual populations the SPAR is likely to be dependent on rates of population extinction and recolonization. At regional scales that encompass the ranges of species, evolutionary processes are important, along with the effects of climate, including energy available for production (Wright 1983), and geological history. These distinct scales of diversity are recognized in the definitions of Whittaker (Whittaker 1960). He defined the diversity of species within a habitat as "alpha diversity," the diversity among habitats as "beta diversity," and the diversity of a region as "gamma diversity." Early studies of the SPAR focused on patterns in beta diversity, such as the number of bird species inhabiting oceanic islands. However, the discussion of SPAR soon broadened to include virtually every spatial scale, sometimes with little apparent concern for how fundamentally they might differ.

In the 1970s and early 1980s, the SPAR and the equilibrium theory of island biogeography became central to the science of reserve design and led to the "single large or several small" (SLOSS) debate. The debate was over whether it was more effective to establish a single large reserve or a few smaller reserves of equal total area (reviewed in Shafer 1990). It began in 1975, when the SPAR was used to argue that larger reserves were preferable because they would maintain a greater number of species (Diamond 1975, May 1975). Simberloff and Abele (1975) criticized this argument by claiming that empirical studies of the SPAR were too ambiguous to support the idea that large reserves were optimal. They pointed out that, with values of z below 1 (which is almost always the case), the SPAR could be used to argue for several small reserves. A set of impassioned rebuttals quickly followed (Diamond 1976, Terborgh 1976, Whitcomb et al. 1976; the rebuttals were published together in *Science* later that year, along with Simberloff and Abele's [1976] reply. A common argument in these rebuttals was that not all species are alike in area requirements, and that some species will be preserved only in large reserves.

The issues raised by the SLOSS controversy are still discussed, although seldom in the simple terms of the original debate. A consideration of the SLOSS question must be based on more than just numbers of species. Some species (including many that are threatened) have a requirement for large areas and will always be lost from small reserves. Small reserves are also less likely to include rare species (Gaston 1994). Furthermore, local species extinctions do not occur randomly, so that over time the species compositions of small reserves

would be expected to converge, and thereby reduce the anticipated benefit of small reserves (Patterson and Atmar 1986). By the end of the 1980s, the equilibrium theory was no longer considered a paradigm for reserve design (Murphy 1989). A new focus of reserve design became the management of individual populations to prevent extinction and the loss of genetic variation (Soulé and Simberloff 1986). This "small population paradigm" led to a renewed appreciation of autecological studies, as opposed to theoretical predictions about changes in community composition. It was also argued that the SPAR had become irrelevant to the problem of reserve design, because "soon there will be no large sites left to set aside," and the only practical course of action will be "intensive stewardship and management" of small reserves (Simberloff 1988).

It is easy to gain the impression that the SPAR represented a hypothesis that was somehow falsified. However, it would be more accurate to portray the SPAR as a phenomenon that was too robust to be falsified by available data, and too general to be incompatible with any of the alternative theories that could explain it (Connor and McCoy 1979). In these respects, the SPAR may have been a poor tool to test theories about community structure, but it is not necessarily a poor tool to estimate or predict species richness. A SPAR is often used, sometimes implicitly, in contemporary discussions about the loss of biodiversity. In the introductory chapter of the seminal volume on this topic, Wilson (1988) discussed the problem of estimating extinction rates when the "vast majority of species are not monitored at all." He explained that extinction rates are "usually estimated indirectly from principles of biogeography," and cited Simberloff's (1984) application of the SPAR to project species losses due to tropical deforestation. In the same volume, Myers (1988) stated that "according to the theory of island biogeography, which is supported by abundant and diversified evidence, we can realistically expect that when a habitat has lost 90% of its extent, it will eventually lose half its species." A recent commentary on the implications of habitat reduction for worldwide extinction referred to the SPAR as "biodiversity's basic law" (Rosenzweig 1999).

THE SPAR AND MARINE CONSERVATION

Despite the shift away from the use of the SPAR as a principle for terrestrial-reserve design, it is still used for the estimation of local species richness and for the prediction of changes in biodiversity. In these applications, its value in marine conservation may be considerable. However, the SPAR has been less thoroughly studied in the marine realm than in terrestrial systems. During the time when the role of the SPAR in reserve design was being actively debated, its importance in the marine realm was seldom considered. For example, in a widely cited critique of SPAR studies, only four

of the one hundred studies examined were of marine fauna, and three of these were of decapod crustaceans within coral heads (Connor and McCoy 1979). Vermeij (1978) devoted only three paragraphs to the effects of area in his book *Marine Biogeography and Adaptation*, and used the equilibrium theory of island biogeography to conclude that for organisms with "high powers of dispersal," "effects of area are much less important." In general, marine biogeographers have been more concerned with dispersal from centers of origin (Briggs 1984), vicariance events (Pandolfi 1992), and sea level changes (McMannus 1985). Marine ecologists have been more inclined to explain species diversity in terms of disturbance (Connell 1978), energy limitations (Brown 1981) or as the outcome of an interplay between competition and predation within these habitats (Huston 1994). However our views of both the causes of the SPAR and its relevance to marine systems have broadened. The primacy of the equilibrium theory of island biogeography has been replaced by a pluralistic view, with the recognition that the SPAR is at least partly determined by passive sampling and habitat diversity (Williamson 1981). Furthermore, some of the processes that may contribute to a SPAR may be more important in marine systems than was once believed. It is now recognized that the distribution of species on many scales can be limited by dispersal, even if those species are dispersed as planktonic larvae (Gaines and Roughgarden 1985, Cornell and Karlson 1996, Smith and Witman 1999). This recognition has been reinforced by taxonomic work that has shown that some marine species that were once thought to be geographically widespread, and thus apparently not limited by dispersal, may actually consist of numerous cryptic species with restricted distributions (Knowlton 1993). It is thus worthwhile to examine some of the early criticisms of the application of the SPAR to reserve design, and consider how it may be used to good effect in the design of marine reserves.

Are protected areas equivalent to natural areas?

The value of the SPAR as a predictive tool for reserve design depends on the assumed equivalence between the areas used to establish an empirical SPAR and the areas that are to be protected. However, biogeographic models for natural areas might not apply to patches of protected habitat that are surrounded by unprotected areas. If the habitats inside and outside of an area are similar, individuals are likely to migrate between them. In contrast, an area surrounded by inhospitable habitat may be effectively isolated from migration (Terborgh 1975). Surrounding areas may also act as sources of "undesirable" species, including non-native species, "weeds," and species that are predators, pathogens, or parasites of protected species. Edge effects may also be of particular importance for areas of distinct habitat in marine systems (Farrell 1989, Be-

nedetti-Cecchi and Cinelli 1993) and foundation species such as corals modify the hydrodynamic features of adjacent habitats (Geister 1977). The transport of waterborne substances or organisms into areas may also be more pronounced at edges, although even large areas may fail to buffer drastic changes in the physical, chemical, or biological characteristics of water masses that pass through them. If edge effects are undesirable, large, compact areas may be favored to reduce the ratio of edge-to-area. However, if one purpose of a marine reserve is to enhance fisheries by exportation to surrounding areas, edge effects may be desirable (Allison et al. 1998).

Some uncertainties about differences between reserves and naturally isolated areas would be resolved if the boundaries of reserves coincided with these areas. The boundaries of marine reserves often coincide with natural islands, bays, or estuaries. These are likely to be more representative of natural isolates than a segment of coastal habitat fragment of forest or prairie that represents what was previously a much larger area. Thus for at least some marine reserves, the SPAR could be applied directly.

Have new approaches to terrestrial reserve design made the SPAR obsolete?

Just as there are fundamental differences between marine and terrestrial ecosystems, there are fundamental differences in the objectives, design, and implementation of marine vs. terrestrial reserves (Carr et al. 2003). Many of the refinements that have marked advances in terrestrial reserve design will be difficult to apply to marine reserves. We simply don't know as much about the distributions or individual requirements of the majority of marine species. We can contrast our extensive knowledge of the Northern Spotted Owl, which has permitted a sophisticated autecological approach to reserve design (Murphy and Noon 1992, Lamberson et al. 1994), with our relative ignorance of the barndoor skate, a noncommercial marine fish species that we have only recently noticed is near extinction (Casey and Myers 1998). It is also difficult for us to implement intensive management strategies, such as captive breeding, for marine species with extended pelagic stages (Hilborn 1998). The design of marine reserves may also be less driven by calls to protect the dwindling populations of species that are on the verge of extinction. Marine species often decline in ways that are not consistent with the small population paradigm developed for terrestrial reserves. The unit of decline for many terrestrial species is the population, and loss occurs through the destruction or fragmentation of their habitats (Ehrlich and Ehrlich 1981). In contrast, marine species may decline uniformly over large regions, and losses may be the result of widespread exploitation or habitat deterioration rather than the incremental loss of habitats (Carlton 1993, Vermeij 1993). Global extinc-

tions of marine species have been rarely observed, and may in fact be difficult to recognize. However although few recent marine extinctions have been reported, there are hundreds of species that have been described but not recorded over the past century (Carlton 1993), and it is likely that marine species are at much greater risk than has generally been believed (Carlton 1993, Roberts and Hawkins 1999). Marine species may persist in a state of very low abundance or "quasi-extinction," during which we may observe them only rarely (Carlton 1993).

The importance of area effects in the marine realm

Significant relationships between species number and area have been found in the marine realm at scales ranging from $<1 \text{ m}^2$ to $>100\,000 \text{ km}^2$. At spatial scales of square meters or square centimeters, the SPAR has been demonstrated for marine invertebrate communities associated with coral heads (Abele and Patton 1976), boulders (McGuinness 1984), rock walls (Smith and Witman 1999), mussel beds (Witman 1985), and artificial settling plates (Day 1977, Osman 1978, Anderson 1998). At these scales, passive sampling is likely to contribute to the positive relationships between area and species number (Osman 1977, McGuinness 1984). If the areas represent discrete patches of habitat (e.g., coral heads, boulders, or settling plates) patch size may be also be correlated with microhabitat diversity or may even define distinct habitat types. Size-dependent characteristics of habitats are not restricted to edge effects. For example, the size of a coral head may determine the size of the crannies that shelter cryptic fish or invertebrates (Abele and Patton 1976) or the size of a boulder may determine whether it remains anchored in one position, or rolls about in the surge (Sousa 1979). Because of these effects of patch size on habitat type, patches of different size may harbor qualitatively different species assemblages and small patches may sometimes contain more species than larger patches (Anderson 1998).

Seagrass beds may be considered as single habitats, although they typically extend over greater areas than the small habitat patches discussed above. McNeill and Fairweather (1993) surveyed fish and macroinvertebrates in natural and artificial seagrass beds specifically to address the SLOSS question. The areas of these beds ranged from 7.7 m^2 to 5800 m^2 for *Zostera capricorni*, 200 m^2 to $31\,000 \text{ m}^2$ for *Posidonia australis*, and 7.0 m^2 to 14 m^2 for the artificial beds. To provide the most direct answer to the SLOSS question, paired comparisons were made within sets that included two relatively small seagrass beds and one large bed of approximately the same total area. For beds of both species, numbers of fish and invertebrate species were significantly greater for two small beds. For the much smaller artificial seagrass beds, there were few significant differences between two small and one large bed, although this

may have resulted from the limited range of sizes that were investigated. The data provided in Table 1 of McNeill and Fairweather (1993) can be fit to the Arrhenius function for comparison with studies of the SPAR in other systems. For the smaller *Zostera* beds, the value of the exponent z is 0.27 ($P = 0.00003$) for fish, and 0.14 ($P = 0.0006$) for macroinvertebrates. These values are low but well within the range obtained for noninsular terrestrial systems. For the larger *Posidonia* beds, the estimates of z were -0.078 ($P = 0.02$) for fish and -0.049 ($P = 0.009$) for macroinvertebrates. The negative values indicate that areas of fixed size within larger beds had fewer species, possibly because positive edge effects were reduced. However, because only small portions of the larger beds were sampled, it is unlikely that they actually had fewer total species.

As with terrestrial systems, a SPAR for small areas of marine habitat should not be simply extrapolated to larger areas. However, SPARs for small areas may still be useful for the estimation of biodiversity. Because it is seldom practical to census every organism within an area much greater than 1 m², a sampling method is needed to estimate species richness, even within a single habitat. The relationship between the number of species and the number of individuals in a sample represents the passive sampling component of the SPAR. The observed relationship can be extrapolated to estimate the number of species expected in larger samples or complete areas of uniform habitat. Plots of species richness vs. numbers of individuals, known as "rarefaction curves," have long been used to compare species richness in benthic samples (Sanders 1968). However, a more generalized approach is to plot the number of species encountered against a measure of collection effort (such as search time) to produce a "species accumulation curve" (SCUM) or "collector's curve" (Colwell and Coddington 1995). Because only the number of different species is counted it is not necessary to record the occurrence of every individual. The asymptote of the SCUM can be used as an estimate of the actual number of species present at a single location (Colwell and Coddington 1995). A SCUM can also be used to determine if a particular sampling method is adequate, as exemplified by Smith and Witman's (1999) quadrat survey of benthic communities along a vertical rock wall. A SCUM for a single location should not be extrapolated to estimate species richness for areas that comprises diverse habitats. However SCUMs can be determined for a representative sample of habitats, and with estimates of complementarity (overlap) of the species assemblages, combined to estimate species richness for large areas (Colwell and Coddington 1995).

Marine reserves may coincide with the natural boundaries of individual islands or bays. For this reason, the study of marine fish assemblages in California

bays and estuaries by Horn and Allen (1976) is of particular interest. This study was based on lists of fish species that occur in 13 bays that provided good representation of much of the coastline. The area of the bays ranged from 22 ha to 121 ha, the lists were compiled from published surveys that included 224 species. Along with total surface area, other variables used in the analysis were latitude, distance to nearest bay, tidal range, annual rain fall, mouth width, and mean annual coastal temperature. The data closely fit a power function, with $z = 0.21$ ($r^2 = 0.93$, $P < 0.01$), a value that would be low for terrestrial biota on oceanic islands. In this respect, bays may be more analogous to semi-isolated terrestrial areas, such as peninsulas, into which immigration is restricted by the narrowness of their connection to a larger landmass. Of all the variables analyzed in a stepwise regression, only mouth width was significant and explained 53% of the variation in species number. Distance to the nearest next bay was not a significant variable. These findings are consistent with the supposition that the California continental shelf acts as a source pool for the species found in bays, and suggest that the widths of bay mouths may influence rates of immigration.

Although the fit of the power function to Horn and Allen's (1976) data might seem to imply that a simple mechanism distributes more or less species of fish into California bays, other factors are clearly at work in determining actual species compositions. A dissimilarity measure based on species composition separated the bays into two main clusters: northern and southern, divided by the well-known faunal boundary at Point Conception. Fish species could be divided by their distributions into "northern," "southern," and "widespread" species, although few species were strictly "northern" or "southern." It was also noted that, for the 55 species restricted to a single bay, 48 were from one of the four largest bays and none occur in the four smallest bays. Thus it appeared that the largest bays not only included more species, but may have also provided critical habitats not available in smaller bays.

The SPAR is seldom used to interpret patterns of marine biodiversity at regional or global scales, although the need to consider area effects as a marine "null hypothesis" has long been recognized (McCoy and Heck 1976, Schopf et al. 1978). For example, longitudinal gradients of species diversity in tropical reef fish are usually explained by either dispersal from a center of origin (McMannus 1985, Briggs 1992) or by the buildup of species in areas that are downstream in oceanic surface currents (Jokiel and Martinelli 1992). The effect of area is not usually considered although it explains 72% of the variance in species richness (Ormond and Roberts 1997). Regional variation in the generic diversity of reef building corals is also significantly correlated with continental shelf area, and even

more strongly with reef length (Fraser and Currie 1996).

Most estimates of worldwide biodiversity loss are based on the SPAR and the rate at which area is lost from tropical forests (Whitmore and Sayer 1992, Lawton and May 1995). The rationale given for this bias is that most species are thought to occur in this biome (Wilson 1988). However the number of species that inhabit marine benthic habitats may as great (Grassle and Maciolek 1992, Gray 1994). Although there is a widespread belief that marine species are relatively resistant to extinction (Roberts and Hawkins 1999) there is little evidence to support this and the rate at which marine biodiversity is being lost is presently unknown (Carlton 1993, Roberts and Hawkins 1999). In a recent volume devoted to “better estimates of impending rates of extinction” (Lawton and May 1995) both of the chapters that discussed marine taxa provided estimates of extinction rates from fossil data but not for modern communities (Jablonski 1995, Jackson 1995). The SPAR has been used to predict the loss of marine biodiversity that would result from faunal mixing (McKinney 1998). This approach was tested with a paleontological analysis of the change in marine biodiversity that followed the rise of the Isthmus of Panama. The isolating effect of the Isthmus coincided with a 45–60% increase in total biodiversity, which was consistent with the SPAR. Extrapolation of this to global scales led to the prediction that the number of marine species would decrease by 58% if worldwide biotic mixing occurred. Although I am not aware of any published predictions for global losses of marine biodiversity from habitat destruction based on the SPAR, such predictions could clearly be made with existing data for corals, reef fish and perhaps other groups.

CONCLUSIONS

The SPAR provides a robust, albeit coarse, means to characterize the distribution of species richness at any scale. As a principle for terrestrial-reserve design, the SPAR has been largely supplanted by the small-population paradigm and intensive-management strategies. For marine reserves where these strategies may be less appropriate, the SPAR may provide a useful tool for estimation of biodiversity and prediction of the number of species that are likely to be represented in a reserve. Although there have been few investigations of the SPAR across marine habitats, they suggest that it can generally be approximated by a power function with a relatively low exponent. This implies that to increase the representation of species in marine reserves, relatively large increases in area will be needed.

The reliability of the SPAR to predict the effects of habitat reduction and fragmentation in marine systems depends critically on underlying mechanisms. The passive-sampling and habitat-diversity hypotheses do not account for the effects of surrounding areas but exten-

sive degradation of marine habitats outside of protected areas could strongly influence communities within these areas (Carr et al. 2003), and open marine populations may be strongly dependent on external sources of recruitment (Caley et al. 1996, Allison et al. 1998).

Most estimates of the global loss in biodiversity are based on application of the SPAR to the tropical forest biome. Similar estimates are urgently needed for the marine realm. The species diversity of marine benthos may be as high as tropical forests, and the old notion that marine species are resistant to extinction may simply reflect our inability to detect extinctions among those groups that face the greatest risk. For groups that have been relatively well studied (e.g., tropical reef corals and fishes) it should be possible to generate these estimates now. It is unfortunate that the SPAR has not been investigated more extensively in the marine realm. Data that is already available for well studied groups can be used to determine the SPAR, and potential conservation applications should be considered. This use of existing data from potentially diverse sources also highlights the need for public databases of ecological and systematic surveys.

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LITERATURE CITED

- Abele, L. G., and W. K. Patton. 1976. The size of coral heads and the community biology of associated decapod crustaceans. *Journal of Biogeography* **3**:35–47.
- Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* **8**:S79–S92.
- Anderson, M. J. 1998. Effects of patch size on colonization in estuaries: revisiting the species area relationship. *Oecologia* **118**:87–98.
- Arrhenius, O. 1921. Species and area. *Journal of Ecology* **9**: 95–99.
- Benedetti-Cecchi, L., and F. Cinelli. 1993. Early patterns of algal succession in a midlittoral community of the Mediterranean Sea: a multifactorial experiment. *Journal of Experimental Marine Biology and Ecology* **169**:15–31.
- Briggs, J. C. 1984. Do centres of origin have a centre? *Paleobiology* **7**:305–307.
- Briggs, J. 1992. The marine East Indies: centre of origin? *Global Ecological and Biogeographical Letters* **2**:149–156.
- Brown, J. H. 1981. Two decades of homage to Santa Rosalia: towards a general theory of diversity. *American Zoologist* **21**:877–888.
- Browne, J. 1983. The secular ark: studies in the history of

- biogeography. Yale University Press, New Haven, Connecticut, USA.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**:477–500.
- Carlton, J. T. 1993. Neoextinctions of marine invertebrates. *American Zoologist* **33**:499–509.
- Carr, M. H., J. E. Neigel, J. A. Estes, S. Andelman, R. R. Warner, and J. L. Largier. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications* **13**:S90–S107.
- Casey, J. M., and E. A. Myers. 1998. Near extinction of a large, widely distributed fish. *Science* **281**:690–692.
- Colwell, R. K., and J. A. Coddington. 1995. Estimating terrestrial biodiversity through extrapolation. Pages 101–119 in D. L. Hawksworth, editor. *Biodiversity: measurement and estimation*. Chapman and Hall, London, UK.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**:1302–1310.
- Connor, E. F., and E. D. McCoy. 1979. Statistics and biology of the species–area relationship. *American Naturalist* **113**:791–833.
- Cornell, H. V., and R. H. Karlson. 1996. Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology* **65**:233–241.
- Darlington, P. 1957. *Zoogeography*. Wiley, New York, New York, USA.
- Day, R. W. 1977. Two contrasting effects of predation on species richness in coral reef habitats. *Marine Biology* **44**:1–6.
- Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* **7**:129–146.
- Diamond, J. M. 1976. Island biogeography and conservation: strategy and limitations. *Science* **193**:1027–1029.
- Dony, J. G. 1963. The expectation of plant records from prescribed areas. *Watsonia* **5**:377–385.
- Ehrlich, P., and A. Ehrlich. 1981. *Extinction: the causes and consequences of the disappearance of species*. Random House, New York, New York, USA.
- Farrell, T. M. 1989. Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. *Journal of Experimental Marine Biology and Ecology* **128**:57–73.
- Fisher, R. G., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**:42–58.
- Fraser, R. H., and J. Currie. 1996. The species richness–energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *American Naturalist* **148**:138–159.
- Gaines, S., and J. Roughgarden. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences (USA)* **82**:3707–3711.
- Gaston, K. J. 1994. *Rarity*. Chapman and Hall, London, UK.
- Geister, J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Pages 23–29 in *Proceedings of the Third International Coral Reef Symposium*. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA.
- Grassle, J. F., and N. J. Maciolek. 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *American Naturalist* **139**:313–341.
- Gray, J. S. 1994. Is deep sea species diversity really so high? Species diversity of the Norwegian continental shelf. *Marine Ecology Progress Series* **112**:205–209.
- Hilborn, R. 1998. The economic performance of marine stock enhancement projects. *Bulletin of Marine Science* **62**:661–674.
- Horn, M. H., and L. G. Allen. 1976. Numbers of species and faunal resemblance of marine fishes in California bays and estuaries. *Bulletin of the Southern California Academy of Science* **75**:159–170.
- Huston, M. A. 1994. *Biological diversity*. Cambridge University Press, Cambridge, UK.
- Jablonski, D. 1995. Extinctions in the fossil record. Pages 25–44 in J. Lawton and R. May, editors. *Extinction rates*. Oxford University Press, New York, New York, USA.
- Jackson, J. B. C. 1995. Constancy and change of life in the sea. Pages 45–54 in J. Lawton and R. May, editors. *Extinction rates*. Oxford University Press, New York, New York, USA.
- Jokiel, P., and F. J. Martinelli. 1992. The vortex model of coral reef biogeography. *Journal of Biogeography* **19**:449–458.
- Knowlton, N. 1993. Sibling species in the sea. *Annual Review of Ecology and Systematics* **24**:189–216.
- Lack, D. 1969. The numbers of bird species on islands. *Bird Study* **16**:193–209.
- Lamberson, R. H., B. R. Noon, C. Voss, and K. S. McKelvey. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conservation Biology* **8**:185–195.
- Lawton, J., and R. May, editors. 1995. *Extinction rates*. Oxford University Press, New York, New York, USA.
- Leitner, W. A., and M. L. Rosenzweig. 1997. Nested species–area curves and stochastic sampling: a new theory. *Oikos* **79**:503–512.
- MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* **17**:373–387.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- May, R. M. 1975. Island biogeography and the design of wildlife preserves. *Nature* **254**:177–178.
- McCoy, E. D., and K. L. Heck. 1976. Biogeography of corals, sea-grasses and mangroves: an alternative to the centre of origin concept. *Systematic Zoology* **25**:201–210.
- McGuinness, K. A. 1984. Species area relations of communities on intertidal boulders: testing the null hypothesis. *Journal of Biogeography* **11**:439–456.
- McKinney, R. L. 1998. On predicting biotic homogenization: species–area patterns in marine biota. *Global Ecology and Biogeography Letters* **7**:297–301.
- McMannus, J. 1985. Marine speciation, tectonics and sea-level changes in Southeast Asia. Pages 133–138 in C. Gabriele and M. Harmelin Vivien, editors. *Proceedings of the Fifth International Coral Reef Symposium*. Atenne Museum, Moorea, French Polynesia.
- McNeill, S. E., and P. G. Fairweather. 1993. Single large or several small marine reserves: an experimental approach with seagrass fauna. *Journal of Biogeography* **20**:429–440.
- Murphy, D. D. 1989. Conservation and confusion: wrong species, wrong scale, wrong conclusions. *Conservation Biology* **3**:82–84.
- Murphy, D. D., and B. R. Noon. 1992. Integrating scientific methods with habitat conservation planning: reserve design for northern spotted owls. *Ecological Applications* **2**:3–17.
- Myers, N. 1988. Tropical forests and their species: Going, going. . . ? Pages 28–35 in E. O. Wilson and F. M. Peter, editors. *Biodiversity*. National Academy Press, Washington, D.C., USA.
- Ormond, R. F. G., and C. M. Roberts. 1997. Biodiversity of coral reef fishes. Pages 216–257 in R. F. G. Ormond, J. D. Gage, and M. V. Angel, editors. *Marine biodiversity: patterns and processes*. Cambridge University Press, Cambridge, UK.

- Osman, R. W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs* **47**: 37–63.
- Osman, R. W. 1978. The influence of seasonality and stability on the species equilibrium. *Ecology* **59**:383–399.
- Palmer, M. W., and P. S. White. 1994. Scale dependence and the species–area relationship. *American Naturalist* **144**: 717–740.
- Pandolfi, J. M. 1992. Successive isolation rather than evolutionary centres for origination of Indo-Pacific corals. *Journal of Biogeography* **19**:593–609.
- Patterson, B. D., and W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* **28**:65–82.
- Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology* **29**:254–283.
- Preston, F. W. 1962. The canonical distribution of commonness and rarity. *Ecology* **43**:185–215, 410–432.
- Roberts, C., and J. Hawkins. 1999. Extinction risk in the sea. *Trends in Ecology and Evolution* **14**:241–246.
- Rosenzweig, M. L. 1999. Ecology—heeding the warning in biodiversity's basic law. *Science* **284**:276–277.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* **102**:243–282.
- Schoener, T. 1976. The species–area relation within archipelagos: models and evidence from island land birds. Pages 629–642 in H. J. Firth and J. H. Calaby, editors. *Proceedings of the XVI International Ornithological Congress*. Australian Academy of Science, Canberra, Australia.
- Schopf, T. J. M., J. B. Fisher, and C. A. F. Smith. 1978. Is the marine latitudinal diversity gradient merely another example of the species area curve? Pages 365–386 in B. Battaglia and J. A. Beardmore, editors. *Marine organisms: genetics, ecology and evolution*. Plenum, New York, New York, USA.
- Shafer, C. L. 1990. *Nature preserves: island theory and conservation practice*. Smithsonian Institution Press, Washington, D.C., USA.
- Simberloff, D. S. 1984. Mass extinction and the destruction of moist tropical forests. *Zhurnal Obschei Biologii* **45**: 767–778.
- Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* **19**:473–511.
- Simberloff, D. S., and L. G. Abele. 1975. Island biogeography theory and conservation practice. *Science* **191**:285–286.
- Simberloff, D. S., and L. G. Abele. 1976. Island biogeography and conservation: strategy and limitations. *Science* **193**:1032–1032.
- Smith, F., and J. D. Whitman. 1999. Patterns of species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment. *Ecology* **80**:51–69.
- Soulé, M. E., and D. Simberloff. 1986. What do genetics and ecology tell us about the design of nature reserves? *Biological Conservation* **35**:19–40.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields—the nonequilibrium maintenance of species diversity. *Ecology* **60**:1225–1239.
- Terborgh, J. 1975. Faunal equilibria and the design of wildlife preserves. Pages 369–380 in F. Golley and E. Medina, editors. *Tropical ecological systems: trends in terrestrial and aquatic research*. Springer-Verlag, New York, New York, USA.
- Terborgh, J. 1976. Island biogeography and conservation: strategy and limitations. *Science* **193**:1029–1030.
- Vermeij, G. J. 1978. *Biogeography and adaptation: patterns of marine life*. Harvard University Press, Cambridge, Massachusetts, USA.
- Vermeij, G. J. 1993. Biogeography of recently extinct marine species: implications for conservation. *Conservation Biology* **7**:391–397.
- Whitcomb, R. F., J. F. Lynch, P. A. Opler, and C. S. Robbins. 1976. Island biogeography and conservation: strategy and limitations. *Science* **193**:1030–1032.
- Whitehead, D., and C. Jones. 1969. Small islands and the equilibrium theory of insular biogeography. *Evolution* **23**: 171–179.
- Whitmore, T., and J. Sayer, editors. 1992. *Tropical deforestation and species extinction*. Chapman and Hall, London, UK.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**:279–338.
- Williams, C. B. 1943. Area and number of species. *Nature* **152**:264–267.
- Williamson, M. 1981. *Island populations*. Oxford University Press, Oxford, UK.
- Wilson, E. O. 1988. The current state of biodiversity. Pages 3–18 in E. O. Wilson and F. M. Peter, editors. *Biodiversity*. National Academy Press, Washington, D.C., USA.
- Witman, J. D. 1985. Refuges, biological disturbance and rocky subtidal community structure in New England. *Ecological Monographs* **55**:421–445.
- Wright, D. H. 1983. Species energy theory: an extension of species area theory. *Oikos* **41**:496–506.