

But is it progress? On the alleged advances of conservation biology over ecology

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Abstract As conservation biology has developed as a distinct discipline from ecology, conservation guidelines based on ecological theory have been largely cast aside in favor of theory-independent decision procedures for designing conservation reserves. I argue that this transition has failed to advance the field toward its aim of preserving biodiversity. The abandonment of island biogeography theory in favor of complementarity-based algorithms is a case in point. In what follows, I consider the four central objections raised against island biogeographic conservation guidelines, arguing that they fail to undermine the credibility of this framework as a conservation tool. At best, these objections call for a more careful application of this framework to conservation problems, not its wholesale abandonment. At the same time, complementarity-based algorithms are biased in favor of networks of small reserves containing non-overlapping species. These conditions threaten to promote inbreeding depression, genetic drift and other factors that increase a population's risk of extinction. Therefore, recent developments in the field of conservation biology have arguably not contributed to its ultimate aim of preserving the maximum amount of biodiversity in the long run.

Keywords Biodiversity · Complementarity · Conservation biology · Ecology · Island biogeography theory · Philosophy of ecology

Introduction

Conservation biology was established in the mid-1980s as a practical discipline dedicated to the preservation of the earth's remaining biodiversity (Sarkar 2005). Since its inception, this field has struggled to define its relationship to the “pure” science of ecology.

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Ecologists are renowned for developing highly abstract mathematical models of ecosystem structure and function. The relevance of these models to “real world” conservation issues is often far from obvious. To make matters worse, questions about the scope and empirical adequacy of ecological models have generated considerable controversy within the discipline. Such academic disputes threaten to undermine ecology’s authority in the public policy arena. As Otto Frankel and Michael Soulé explain in their pioneering textbook *Conservation and Evolution*:

Conservation biology should operate differently from normal (adversary) science. Progress in the latter is usually via the vehicle of competition: somebody proposes a theory; somebody else challenges it and proposes another; battle lines are drawn and schools (armies) gather around the protagonists, many of whom cling to their pet theories even as they die... Conservationists cannot afford the luxury and excitement of adversary science. The weakness of this parochial style of intellectual progress is that years or decades may pass before a clear resolution is reached and before timid technocrats or politicians decide that action will not bring a storm of criticism (1981: 97).

The solution proposed by Soulé was to conceptualize conservation biology as a “crisis discipline”. In part, this title called for a relaxation of the epistemic standards endorsed by most academic ecologists: “In crisis disciplines,” Soulé explained, “one must act before knowing all the facts; crisis disciplines are thus a mixture of science and art, and their pursuit requires intuition as well as information” (1985, 727). To this end, Soulé and his colleagues developed a simple set of guidelines for designing conservation reserves which drew heavily on island biogeography theory and population genetics (described below). Though admittedly controversial, these guidelines had the backing of the best *available* ecological theory and data (Soulé and Wilcox 1980; Frankel and Soulé 1981). This reliance on ecology as guide for conservation directives conformed with these authors’ image of conservation biology, “as a science [that] is not strictly ‘pure’ but neither is it purely ‘applied’” (Soulé and Wilcox 1980 cited in Murphy 1990: 203).

However, even this qualified appeal to ecology would soon come under attack (Gilbert 1980; Margules et al. 1982; Zimmerman and Bierregaard 1986; Simberloff and Cox 1987; Simberloff 1988; Caughley 1994). Island biogeography theory and population genetics were faulted for a lack of adequate empirical support. Critics also played up the stochastic and historically contingent nature of ecological systems. The law-like generalizations offered by ecologists were seen as too simplistic to describe the messy, idiosyncratic systems conservationists sought to preserve. Instead of general conservation guidelines, these critics argued that conservation decisions should be grounded in rigorous “autoecological” (case-by-case) investigations of particular systems (Simberloff 1988; see also Caughley 1994, for a more detailed discussion). Astonishingly, these authors seemed oblivious to the impracticality of their suggestions, ignoring the considerable time, effort and financial costs associated with the autoecological approach—it is hardly surprising that this approach has been adopted in only handful of cases.

The negative part of the critique against theoretically informed conservation biology has been much more influential. By the mid 1990s conservationists had all but abandoned the conservation guidelines based on island biogeography theory and population genetics. But instead of rigorous autoecological studies, something much less scientifically grounded emerged in their place. Conservation biology has become dominated by various “fast and frugal” place prioritization algorithms for designing conservation reserves (Justus and Sarkar 2002). These algorithms involve the iterative application of simple decision rules to

a network of candidate bio-reserves. For example, these algorithms often rank a site according to its “complementarity value” or the number of species the site contains which are not already represented elsewhere in the network. As Sahotra Sarkar (2005) notes, complementarity-based algorithms have little basis in ecological science: they pay no attention to minimum viable population sizes, they ignore the threat of inbreeding depression and genetic drift in small populations, and they are insensitive to the relationship between reserve size and species richness. However, the emergence of these algorithms in place of ecologically motivated guidelines is often regarded as a significant advance in the field (Justus and Sarkar 2002; Garson and Justus 2003; Sarkar 2005). One advantage of these algorithms is that they rely on a minimal amount of ecological data, requiring only rough estimates of which species inhabit a network of candidate reserves (Justus and Sarkar 2002). Another advantage is that any candidate reserve, however small, can be ranked according to this decision procedure. A further benefit is that conservation managers can incorporate economic and political considerations into the reserve planning process, for example, by comparing the social or monetary costs and benefits of different reserve networks.

Despite these practical advantages however, the adoption of complementarity-based algorithms in place of theoretically motivated conservation guidelines has arguably not advanced the field of conservation biology. My argument for this thesis follows two steps. In the following section I draw on the conservation guidelines based on island biogeography theory as a case study. The four central objections raised in opposition to these guidelines are, I argue, far from conclusive. At best, these objections call for the more cautious application of island biogeography theory to conservation biology, not its wholesale abandonment. In section three I argue that the core principle on which most place prioritization algorithms are based—the principle of complementarity—is not ecologically sound. Taken on its own, without the addition of further ecological considerations, this principle has the potential to select for a network of reserves that place the species within them at *greater risk of extinction in the long run* than a system of reserves based on island biogeography theory. Therefore, although conservation biology has become a more readily applied discipline, the field has not progressed toward its ultimate aim of preserving the maximum possible biodiversity in the long run.

The rise and fall of island biogeography theory

Since the mid 19th century ecologists have recognized that the number of species inhabiting a given geographic area tends to increase proportionally with its size (Rosenzweig 1995). This relationship is described with the equation $S = cA^z$, where the number of species inhabiting a region (S) is equal to its area (A) multiplied by a taxon specific constant (c) raised to the power of an “extinction coefficient” (z). Although this pattern admits of some exceptions, the “species/area rule” has been demonstrated to obtain for a wide range of taxa inhabiting a variety of regions (*ibid*). Two processes are thought to underlie this pattern. Firstly, larger geographic areas typically contain a more diverse array of habitat types or “niches” than smaller ones (Hamilton et al. 1963). Secondly, individual habitats tend to be larger, capable of supporting more sizable populations, when located in a large as opposed to a small bioregion (Nilsson et al. 1988). All things being equal, larger populations are more extinction-prone than relatively small ones over the long term.

In 1967 Robert McArthur and Edward Wilson placed the species/area rule within a broader theoretical context. The equilibrium theory of island biogeography proposes that

the number species inhabiting a geographically isolated area or “island” is maintained in a state of dynamic equilibrium by two opposing forces: immigration and extinction. Larger islands are expected on this theory to both attract more stray migrants and enjoy lower extinction rates than comparatively smaller ones. All things being equal, the theory proposes, the number of species inhabiting an island is maintained at an equilibrium level proportional to its size. MacArthur and Wilson further noted that islands located in close proximity to a mainland migration source are exceptions to this rule: since they are regularly swamped with migrants, near-shore islands should contain higher species numbers than expected from their size alone. One of the most compelling experiments supporting this theory was conducted by Daniel Simberloff, Wilson’s graduate student. Simberloff created several mangrove islands of different sizes (hacking them into shape with a chainsaw) and removed all the insects inhabiting them. He then recorded the rates of insect recolonization on those islands, finding that species richness eventually reached an equilibrium level proportional to each island’s size and its distance from the mainland (Simberloff and Wilson 1969).

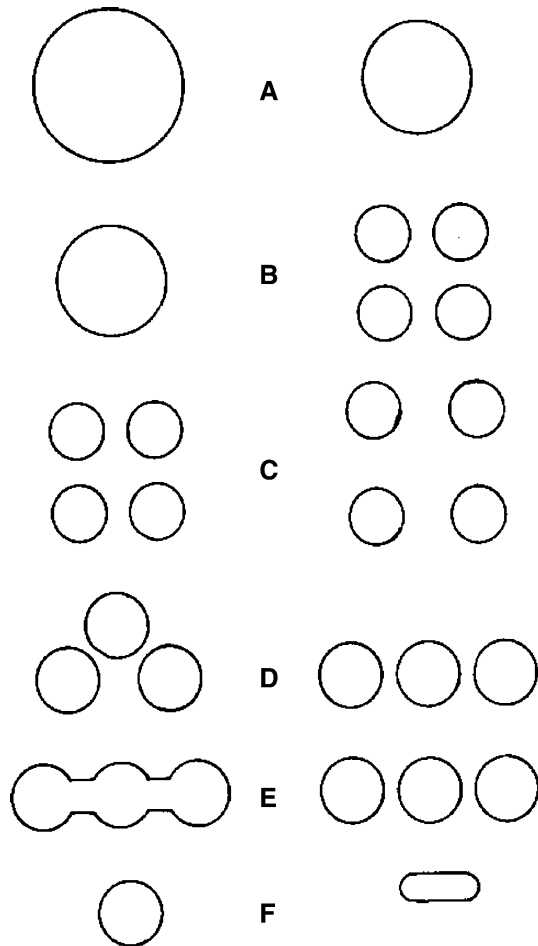
Over the following decade island biogeography theory was readily adopted by conservationists and policy makers. The theory offered several explicit guidelines for how terrestrial reserves—conceptualized as islands—ought to be designed to maximize the preservation of biodiversity. The list of recommendations included a preference for large reserves over small ones, single contiguous reserves over a network of small isolated regions of equivalent area, the location of reserves in close proximity rather than scattered far apart, and the establishment of corridors between small reserves to facilitate migration (see Fig. 1). By the early 1980s these guidelines (hereafter the “IBT guidelines”) had become enshrined in introductory textbooks, they appeared in *World Conservation Strategy* (1980), and were even endorsed by the World Bank (Simberloff 1988).

However, by the mid 1980s the IBT guidelines had come under severe attack (Gilbert 1980; Margules et al. 1982; Zimmerman and Bierregaard 1986; Simberloff and Cox 1987; Simberloff 1988; Caughley 1994). Among their harshest critics was none other than Simberloff himself. His central complaint was that the IBT guidelines were being adopted too zealously: “they have often been uncritically applied and viewed as laws rather than as approximate guidelines, as originally intended” (1988: 475). Four central objections to these guidelines were raised by Simberloff and critics. Firstly, they maintained that island biogeography theory lacks adequate empirical support to serve as a basis for conservation directives. Secondly, they objected that the species/area rule is not a law of nature, as some of its proponents had suggested. Third, it was argued that terrestrial reserve networks are disanalogous to islands, so even if island biogeography were true, its application to most conservation decisions is limited. Finally, these authors faulted the IBT guidelines for failing to provide direction on other conservation objectives besides the maximization of species richness. Let us consider each objection in turn.

Objection 1: The IBT guidelines lack adequate empirical support

One of the central criticisms raised by Margules, Higgs and Rafe against the IBT guidelines was that, “any conservation implications based on the equilibrium theory of island biogeography are doubtful because the theory itself is unsubstantiated” (1982: 117). Drawing on F.S. Gilbert’s (1980) critique of island biogeography theory, these authors point out that evidence in favor of the species/area relationship does not automatically support the dynamical process outlined by MacArthur and Wilson. To demonstrate the truth

Fig. 1 Island biogeography theory generated six guidelines for the design of conservation reserves. In each case the design on the *left* is seen as preferable to the one on the *right* (adapted from Margules et al. 1982)



of the equilibrium theory, Gilbert argued, one must further show that species richness on islands remains constant over time and that there is a high rate of species turnover. In a review of approximately 25 studies, Gilbert identified only one case—Simberloff’s mangrove study—in which all three conditions were satisfied. Based on this assessment, Margules et al. conclude that, “the clear message is that the equilibrium theory of island biogeography is insufficiently validated to support its application to conservation” (1982: 118).

Perhaps the first thing to point out in reply to this objection is that only a subset of the IBT guidelines are based on the equilibrium theory proper. The other recommendations (A, B and potentially E, Fig. 1) follow from the species/area rule alone. Specifically, the recommendations that larger reserves are preferable to small ones and that single interconnected reserves are preferable to isolated regions of equal size require only that species richness increases with area, not that species numbers on islands are constant or in dynamic equilibrium. This point weakens the objection, because the species/area rule was relatively well established by this time. So, even if this argument against island biogeography theory was sound, it does not call for the wholesale rejection of the IBT guidelines as Margules et al. suggest.

A second consideration to bear in mind when evaluating Gilbert's critique is that the relevant data for testing the equilibrium theory are extremely difficult to obtain. This theory is an easy target for anyone adopting extremely high standards of scientific confirmation. If species richness is a dynamic property, then an accurate estimate of its mean value requires numerous samples taken over an extended period of time. Several of the studies criticized by Gilbert were apparently unable to meet this onerous demand, relying instead on just two or three snapshots taken over relatively short time intervals. Determining whether islands incur a high species turnover rate poses a similar challenge, requiring species composition data over many generations. In his attempt to measure turnover rates on the Californian Channel Islands, Jared Diamond (1971) had to rely on breeding records collected by Howell in 1917. Gilbert critiques Howell's data as unreliable, and further rejects Diamond's study on the grounds that only six out of the nine islands (a substantial majority!) showed sufficiently high turnover rates. In general, Gilbert's criticism of all 25 studies purporting to support island biogeography theory relies on the following inference: if either a constant level of species richness or high turnover rates are not *decisively* shown to exist, then the study in question fails to provide any support for the equilibrium theory. Gilbert cites Karl Popper as the inspiration for this decision rule. Since the equilibrium theory has survived only one legitimate attempt at falsification, he concludes that the theory has little or no scientific credibility.

Of course, philosophers of science have long recognized that Popperian falsificationism is deeply flawed—I shall not review the various objections to it here (Putnam 1974; Salmon 1981; see especially Cooper 2003: 137–147 for a discussion of falsificationism in ecology). Instead of asking whether island biogeography theory been subject to adequate attempts at falsification, an ecologist should ask: what is the likelihood that this theory is true given the available evidence and the existing alternative explanations? In his review, Gilbert describes several experiments that *partially* support island biogeography theory. Some studies record colonization rates in accordance with MacArthur and Wilson's projections, many others support the species/area rule, a handful of others suggest that extinction rates are proportional to an island's size. Instead of rejecting each of these studies for failing to decisively test the theory, Gilbert might have interpreted them as each providing at least partial support. Gilbert also fails to offer any alternatives to the MacArthur–Wilson model that accord as well or better with the available data. Without an alternative hypothesis, island biogeography stands as the best *available* explanation for the dynamics underlying the species/area relation.

The final step in Margules et al.'s objection involves another faulty inference, from the claim that the theory lacks adequate *scientific* support to the conclusion that it cannot serve as a basis for *conservation* policy. This move flatly rejects one of the core principles on which conservation biology was founded. Recall Soulé's argument that a relaxation of epistemic standards is necessary in order to attain conservation goals within a reasonable time frame. Given the impending biodiversity crisis, he argued, conservationists must base their policy guidelines on the best *available* ecological theories. Diamond (1984) similarly characterizes island biogeography theory as a "blind man's cane" that guides conservationists in roughly the right direction when detailed ecological data are unavailable. Margules et al. fail to appreciate the distinction between a theory that is scientifically well confirmed, and one that is sufficiently accurate to serve as a basis for conservation guidelines. Instead, they conclude their article by insisting that, "it is imperative that *all possible factors* are taken into consideration when [conservation] decisions are made" (1982, 126). Likewise, Simberloff concludes his 1988 article with the suggestion that "[a]n army of unemployed or underemployed ecologists is available to conduct the requisite

Table 1 Types of breeding habitat and the numbers of amphibian species dependant on each occurring in two randomly chosen 500 ha plots in Amazonia, adapted from Zimmerman and Bierregaard (1986)

Habitat type	No. of species	Plot 1	Plot 2
Large stream	3	Present	Absent
Stream	6	Present	Present
Small permissive pool	7	Present	Present
Permissive flood pool	8	Present	Absent
Terrestrial	6	Present	Present
Unknown	8	?	?
Totals	38	30	19

Averaging across the two sample plots suggests that suitable breeding habitats for approximately 24.5 of the 30 known amphibian species (82%) would have been conserved within a randomly selected 500 ha plot

research, which is simply straightforward population and community ecology” (1988, 501). Yet, he fails to consider how such an army will be mobilized or where the necessary resources will come from.

The impracticality of these suggestions is made vivid by a study conducted by Zimmerman and Bierregaard (1986). Ironically, these authors portray their results as a decisive critique of the IBT guidelines. The study compared the viability of two competing strategies for conserving amphibians in the Amazon basin: one drawing exclusively on the species/area rule, the other employing a detailed autoecological study of amphibian breeding requirements. The species/area curve estimated that a minimum of 500 ha would conserve 90% of the 38 frog species surveyed. However, the ecological study revealed that several of those species required specific breeding habitats which, due to their patchy distribution, might not fall within a single 500 ha reserve. Zimmerman and Bierregaard support this claim by surveying the breeding habitats contained in two randomly chosen 500 ha plots. Although Plot 1 contained adequate breeding habitats for all 30 of the species whose breeding requirements could be determined, the second survey contained breeding sites for only 19 of them (Table 1). Based on this survey Zimmerman and Bierregaard conclude that a randomly chosen 500-ha reserve would have most likely fallen below the 90% mark. They add that a network of sites based on habitat requirements could conserve all 38 species with only 100 carefully chosen hectares.¹

Although Zimmerman and Bierregaard do not provide this calculation, averaging across the two plots suggest that 24.5 of the 30 known species (82%) would have found adequate breeding sites in a randomly chosen 500 ha plot. This number is only slightly lower than the 90% estimate derived from the species/area curve. More to the point, these authors mention in passing that their ecological survey required *3 years* of continuous, labor-intensive field work (even then, the breeding requirements of eight species could not be determined). By contrast, a rapid species inventory supplying enough data to calculate a species/area estimate could have been obtained in a fraction of that time (Hayden 2007). Zimmerman and Bierregaard fail to consider the relative *costs* of these two conservation strategies when comparing them, concluding instead that:

¹ However, later in their article Zimmerman and Bierregaard qualify this statement considerably, noting that many frog species do not reside close to their preferred breeding habitats. So even though a 100-ha reserve might conserve adequate breeding grounds for all 38 species, they claim, a 500-ha reserve might be required to conserve both breeding and non-breeding locations.

Our results and those of other empirical studies... lead us to conclude that calculation of reserve sizes based on species-area data can never be more than inspired guessing... If the impressive brain power and effort used in repeated vain attempts to extract conservation strategy from biogeographic theory were instead devoted to autoecological research, how much better would conservation be served? (1986: 141)

The authors' own data suggest an answer: approximately 8% better, and at an astronomically greater cost.

Objection 2: The species/area rule is not a law of nature

It is perhaps an unfortunate oversight that, in their enthusiasm for the species/area rule and its implications for conservation biology, some advocates portrayed this generalization as a law of nature (e.g. Schoener 1976). Strict natural laws of the sort found in the physical sciences are sometimes characterized as exceptionless generalizations. This understanding of natural laws apparently carried over to ecology, opening the door for critics like Simberloff to argue that the status of the species/area rule is in question because, "some species do not conform to [its] predictions and other variables (such as habitat) may be more important than area [in determining species richness]" (1988: 497).

Of course, the fact that the species/area rule admits of some exceptions does not undermine its significance for conservation biology. There are plenty of generalizations in the "inexact" sciences (like biology) that admit of exceptions, but which are of significant explanatory and predictive value. Nor does Simberloff's point about habitat heterogeneity undermine the predictive accuracy of the species/area rule. To understand why this is so, it is helpful to distinguish two different interpretations of this "law". According to one interpretation, area is regarded as the driving cause of species richness: holding everything else fixed, increasing the area of a region tends to increase the number of species it supports. This causal interpretation of the species/area rule is difficult to establish empirically, because rarely in nature do differentially sized regions differ in area alone. It is much more often the case that as area increases, habitat heterogeneity increases along with it. Habitat heterogeneity is also widely recognized as a driving cause of species richness (Rosenzweig 1995; Nilsson et al. 1988). Thus, according to a second "permissive" interpretation of the species/area rule, area is a reliable proxy for habitat heterogeneity which in turn is the driving cause of species richness. It should be clear that Simberloff's objection applies only to the causal interpretation, not to the more permissive reading. That is, if habitat heterogeneity is tightly correlated with area, then the fact that habitat is "more important" than area in determining species richness (as Simberloff argues) does not threaten the predictive accuracy of the species/area rule. Simberloff's objection misses its mark.

But then why not abandon the species/area rule altogether and rely just on habitat heterogeneity to estimate species richness? In some instances where habitats are clearly defined and easily recorded, this strategy might recommend itself. However, in most cases individuating habitat types is a difficult and laborious task. Part of the problem is that habitat boundaries are determined by the species who occupy them. As the species composition of a region changes over time, the number of habitats will vary accordingly. From a conservation standpoint, where speed and ease of measurement are important considerations, using area as a proxy for habitat heterogeneity is generally the preferred strategy.

What sorts of considerations would argue against the permissive reading of the species/area law? In a further attempt to discredit this generalization, Simberloff mentions several

stochastic factors that are potentially more significant than either area or habitat heterogeneity in determining species richness. For instance, he claims that diseases and introduced predators tend to spread more rapidly in large continuous regions or in reserves connected by corridors than from one isolated reserve to another. Furthermore, natural disasters like fires or cyclones will have more concentrated affects on a single large area than on a collection of widely dispersed reserves. If such stochastic factors are indeed prevalent, then species/area rule does not reliably predict species richness because, in actuality, all things are never equal.

In responding to this objection one might take a page out of Gilbert's book and ask: what is the empirical evidence that stochastic factors are the "greater cause" of species richness? Simberloff's suggestion that geographic isolation acts as a natural barrier to the spread of disease and introduced predators is based on a single example, and an imperfect one at that. The introduction of invasive predators to the Seychelles islands resulted in the extinction of only 2 out of 14 species of endemic land birds. Simberloff suggests that extinction on these islands would have been more pervasive had they been interconnected by corridors. His only basis for this claim however is that on some of the smaller and more remote islands, where predators were not introduced, several bird species managed to avoid extinction. An obvious problem with this example is that it is largely hypothetical. Simberloff assumes that corridors would have promoted the spread of invasive predators, but this need not be the case. As other ecologists have noted, when a novel predator is introduced to an area prey species will often relocate to less accessible regions. The existence of corridors can facilitate this process, whereas a prey species trapped on an isolated island might be left without an escape route. So perhaps extinction rates would have been even *lower* on the Seychelles if corridors had been in place. A slightly different consideration applies to the spread of disease. It is generally accepted that fracturing a single population into several isolated sub-groups leads to increased homozygosity and a loss of genetic variation. The more homozygous a population, the more vulnerable it is to disease. So, although geographic barriers might guard against the spread of disease in the short term, the inevitable loss of genetic variation contributes to their vulnerability over the long run. The only way to guarantee the protection of a populations from the spread of disease is to isolate them entirely them from neighboring regions, and this is rarely if ever possible.

Perhaps the strongest argument in favor of stochastic factors influencing species richness concerns the threat of natural disasters, like cyclones or fire, that wipe out entire communities in a single blow. A species that is spread out over a large expanse of isolated refugia is less likely to be eliminated by these processes than one that is concentrated in a single area, even if the region is fairly large. However, the influence of such events on species richness depends on their frequency. If fires or cyclones are common in a region, then it might be wise for conservationists to hedge their bets over a range of small isolated refuges. But if stochastic events are infrequent, as they are in many parts of the world, their influence on species richness is negligible. Generally speaking, except in cases where stochastic events are common (which might few and far apart) stochastic factors can be regarded as provisos to the species/area rule: for the most part they probably do not qualify as primary causes of species richness.

Objection 3: Terrestrial reserves are disanalogous to islands

Presenting their readers with a map of Southern Wisconsin between 1831 and 1950, Macarthur and Wilson (1967) illustrated how natural woodland habitats became

increasingly fragmented over this period. They noted that the remaining woodland patches bore a distinct resemblance to islands located in a “sea” of agricultural and urban development. Assuming that most of the species inhabiting these “islands” cannot survive in the intervening regions (either because the habitat is unsuitable or because they are actively eradicated to make way for human expansion), these authors suggested that fragmented terrestrial habitats fall within the scope of island biogeography theory.

However, numerous critics have rejected this analogy. In particular, Margules et al. (1982) argued that developed landscapes are typically more hospitable to terrestrial species than seascapes. Drawing on a survey of 311 species of plants found on limestone pavements in Great Britain, these authors note that only one species—a type of fern—was largely dependent on the pavement habitat. The remaining 310 were scattered both among and within pavements. Margules et al. concluded that a conservation policy based on island biogeography theory would, in this case, have resulted in an inefficient expenditure of funds. Saving a single large pavement (or any single large habitat) is usually more costly than conserving a few small ones. If most of the same species found on “islands” are generally capable of occupying intervening regions, then the preservation of large continuous reserves is a waste of limited conservation resources.

This objection suffers from at least two conceptual confusions. Firstly, Margules et al. are unclear about what qualifies as an inhospitable terrestrial habitat. In the case of true islands, intervening ocean expanses usually cannot sustain migrating species for even a brief period of time: either the migrant reaches terra firma or it perishes. In the case of developed landscapes this process can be more protracted. A migrant that lands between terrestrial refugia might survive for a short period, perhaps even years, before being poisoned by a farmer or flattened under a developer’s backhoe. Clearly, the hospitability of a terrestrial landscape must be evaluated over the long term. Snapshot surveys of species distributions, of the sort Margules et al. cite, do not provide an accurate picture of the long term ecological dynamics of a region. By failing to consider the survivorship of plant species over the long run, these authors potentially misrepresent the hospitability of mid-island habitats. Secondly, these critics are insufficiently precise about what constitutes an island. Suppose that the 310 plant species mentioned in this study are in fact capable of surviving indefinitely between limestone pavements. It would therefore follow that limestone pavements *are not islands* as far as the theory of island biogeography is concerned. The general point here is that, theoretically speaking, islands are individuated by the habitat requirements of the species occupying them, not by geographic features per se. Rosenzweig makes this notion explicit: “an island is a self contained region whose species originate entirely by immigration from outside the region” (1995: 211). He explains that a region is “self contained” if it supports positive population sizes of a given species or community over an extended time period. Islands are distinguished from habitat “sinks” and “mainland sources” on similar grounds. A region qualifies as a sink if it cannot sustain positive population sizes over the long run. A region qualifies as a mainland source if its species originate entirely by speciation within the region. As Rosenzweig notes, these definitions describe idealized endpoints at opposite ends of a continuum. Perhaps no terrestrial bioregion qualifies as a perfect island or mainland source for all of the species inhabiting it. However, using these definitions it is possible to construct realistic models based on the proportion of immigrants occupying relatively self contained bioregions (Rosenzweig 1995). The important thing to note is that whether some region counts as an island, a sink, or a mainland source cannot be determined simply by eyeballing the landscape. Habitat requirements of individual species must be taken into account.

Yet, these considerations potentially cut both ways. One might argue that this gelatinized definition of “island” robs the notion of its practical import. The problem is that habitat requirements can vary considerably among species. Thus, what constitutes an island for one type of plant might qualify as a sink for another species or as a mainland source for a third. On this view, the biogeographer is potentially committed to a landscape containing as many islands as there are individual species. The complaint is that such a multidimensional landscape leaves the conservationist with no clear directive when it comes to designing terrestrial reserves.

However, one must be careful not to overstate this objection. The utility of the island concept depends partly on the degree to which species’ habitat requirements overlap in nature. The fact that many species depend on the same basic resources, engage in mutualistic interactions, parasitize one another and specialize in their diets guarantees a considerable amount of overlap in their habitat requirements. However, even if islands do not overlap perfectly (which seems likely) it does not follow that the conservationist will be left without direction. Generally speaking, any conservation effort must begin with a clearly defined goal. No realistic strategy for reserve design can hope to conserve all species. Conservationists must focus their efforts on a subset of the species inhabiting a given region, and this reduces the range of habitats under consideration to a manageable number. Once a particular species or species assemblage has been identified as a conservation target, island biogeography theory can provide the framework for identifying the relevant islands, sinks and sources for the biological entities of interest.

Objection 4: Island biogeography theory focuses exclusively on species richness

The suggestion that islands can be defined in relation to the habitat requirements of particular species or species complexes marks a slight departure from MacArthur and Wilson’s original formulation of the theory. Initially, the IBT guidelines aimed exclusively at maximizing species richness. No mention was made of how to reconcile those guidelines with competing conservation objectives, such as the maximization of genetic diversity or the conservation of some rare or cherished species. Some authors view this oversight as a serious strike against the theory’s relevance to conservation biology. As Margules et al. argue:

There can be a variety of conservation aims, and these may not necessarily complement one another. If species richness is favored and others such as rarity and representativeness given less importance, overall, many species and habitats will be lost and attainable maximum genetic diversity consequently lowered (1982: 117).

This objection raises the thorny question of how to define “biodiversity”. If biodiversity is equated with some other property besides species richness (such as genetic diversity or degree of endemism), then there is no guarantee that the IBT guidelines satisfy the conservation biologists’ goal of preserving the maximum amount of biodiversity. But setting competing definitions of biodiversity aside, let us grant for argument’s sake that there are legitimate conservation goals on which island biogeography theory offers little or no direction. This fact does not require conservation biologists to exclude island biogeography theory from their toolbox. Conservationists are often interested in maximizing species richness, and on those occasions the IBT guidelines provide a useful framework. Although critics like Simberloff lamented the over-zealous application of the IBT guidelines, the tunnel-vision of a few policy makers is surely no a fault of the guidelines themselves.

Why were the IBT guidelines abandoned?

Generally speaking, it is surprising that the IBT guidelines were so thoroughly abandoned in light of such weak and inconclusive objections. Why, given the impracticality of the alternative autoecological approach, were the IBT guidelines abandoned? Wouldn't a more reasonable strategy have been to apply these guidelines cautiously, modifying them in light of further empirical evidence, or substituting them with autoecological when possible? The closing paragraphs of Simberloff's 1988 paper suggest an explanation. An uncomfortable implication of the IBT guidelines is that some reserves will be deemed too small or isolated to justify the expenditure of limited conservation resources. This "triage" approach to conservation management has long been a controversial issue in the field. It is an outcome that Simberloff appears to have been particularly uneasy with. He describes with some hostility an example in Israel where the IBT guidelines provoked the abandonment of few small reserves, and concludes that there are no hopeless cases, only expensive ones. We can surmise that his rejection of the IBT guidelines was at least partially motivated by his repugnance for the triage approach. However, had Simberloff foreseen the implications that his critique would have on the future direction of conservation biology, he might have presented it less forcefully. As I shall now argue, the conservation heuristics that emerged in place of the IBT guidelines are much less well grounded in ecological science than Simberloff might have hoped for.

How ecologically viable are place prioritization algorithms?

In 1988, Margules, Nicholls and Pressey formulated one of the first place prioritization algorithms for designing conservation reserve networks. This strategy would become refined over subsequent years, and is now lauded as a significant advance in the field of conservation biology (Justus and Sarkar 2002; Sarkar 2005). Place prioritization algorithms aim to preserve the maximum amount of biodiversity within the minimum required area (Margules et al. 1988). A defining feature of these algorithms is the iterative application of a decision rule over an entire network of candidate reserve sites, resulting in a ranking of each site's relative *conservation value*. For example, starting with a given reserve (R1) containing a particular set of species (S1), the algorithm evaluates the conservation value of the next candidate reserve (R2) according to the proportion of its species (S2) not already preserved in R1. If S1 and S2 complement one another, then R2 is assigned a high conservation value; if S1 and S2 overlap to a large degree, then the value of R2 is low. The algorithm halts either when all candidate reserves have been ranked, or when some conservation target has been reached (for example, when 10% of all species thought to inhabit a region are protected). The algorithm just described employs complementarity as the sole criterion for evaluating reserves. Other algorithms apply alternative criteria for ranking reserves, like species richness or rarity. But these algorithms are less popular and will not be considered here. Nor shall I address challenging questions of how to choose surrogate species when estimating the species composition of a region (Sarkar 2005).

It is fairly easy to understand why place prioritization algorithms have become popular. One practical benefit is that they allow conservation managers to operate within a restricted land budget. Managers can also incorporate non-biological considerations into the decision process, for example, by excluding economically or politically unfeasible areas from the list of candidate reserves. These algorithms also place no lower limit on reserve number or size. So no matter how dismal the circumstances a conservation manager has to work with,

place prioritization algorithms provide a decision-making strategy. However, despite these pragmatic advantages, there are at least four reasons for thinking that reserve networks designed by these algorithms are ecologically unsound.

Firstly, with their emphasis on efficiency, complementarity-based algorithms are biased in favor of selecting small, potentially isolated reserves containing relatively low species abundances. Such a configuration has negative implications for population viability, promoting inbreeding depression and the loss of genetic variation due to drift. The fact that these considerations have been overlooked in the adoption of complementarity based algorithms is a testament to the influence of critics like Simberloff, Margules and others. Simberloff and Cox admitted that, “inbreeding depression has been demonstrated in small populations... and must be considered a possible threat”. However,” they add, “different species appear to tolerate inbreeding to different degrees,” therefore avoiding this phenomenon should not be a priority for conservationists (1987: 65). The problem with this argument is that it confuses the exceptions with the rule: in the majority of cases a reduction in population size will result in increased mating among relatives, causing the expression of harmful recessive alleles. Exceptions occur occasionally when a population has persisted in low numbers for an extended number of generations, or when a population undergoes a slow decline in size allowing harmful recessives to be weeded out gradually. However, it is safe to assume that most natural populations will not fall into either of these two categories. Human encroachment into natural habitats has been rapid. Most populations will not be afforded sufficient time to adapt to low population sizes, and the effect of inbreeding depression on these populations could be significant. Simberloff (1988) further acknowledges that lowered genetic diversity due to drift can limit a population’s ability to evolve. When the environment suddenly changes, a genetically homogeneous population can find itself at an evolutionary dead end. However, the only suggestion he offers for offsetting the effects of drift and inbreeding depression is (unsurprisingly) exceedingly impractical: he advocates the manual transplanting of individual organisms among disconnected reserves – the same strategy used by zookeepers. Surely it would be easier and cheaper to design reserves that promote gene flow in the first place!

The complementarity heuristic also ignores the species/area rule. Advocates of complementarity sometimes mention in passing that the “SLOSS” debate (Single Large or Several Small) remains unresolved, and then proceed to apply the heuristics as if it was neutral on this issue (Sarkar 2005). In principle, it is not a logical necessity that networks of small isolated reserves will have higher complementarity values than single large ones. In practice, however, large continuous areas are bound to contain a higher degree of species overlap than a patchwork of disconnected sites designed to maximize complementarity. Therefore, in practice complementarity-based algorithms are biased in favor of networks of several small reserves. The species/area rule and island biogeography theory predict that such fragmented reserves will contain lower overall species richness and higher extinction rates than single large reserves. Given that the standard objections to these ecological principles are far from conclusive, prudence would suggest more moderate enthusiasm for the complementarity approach.

Margules et al. (1988) appear to acknowledge these shortcomings by suggesting ways to accommodate ecological considerations into place prioritization algorithms:

Another approach might be to attempt to minimise the possibility of local extinction by asking for the largest population of each species, assuming data on abundance are available. If re-colonisation following local extinction proves to be a significant

factor in maintaining diversity in island like reserve networks, then proximity could be built in as a constraint” (1988: 73).

However, this qualification merely side-steps the issue of how to design a reserve network when these two values—complementarity vs. high population sizes—are at odds. Other place prioritization algorithms attempt to strike a balance between complementarity and other ecological considerations (e.g., by estimating minimum viable population sizes within complementary reserves). It would be misleading to categorize these efforts as an alternative to ecologically motivated conservation guidelines. These mixed models are better understood as a return to ecological theory, not as a flight from it.

A third reason for doubting the ecological viability of complementarity-based algorithms is that they overlook the habitat requirements of particular species. Zimmerman and Bierregaard’s study on Amazonian frogs illustrates one the dangers in this approach. As these authors discovered, many frog species spend the majority of their time in spots not conducive to breeding. A complementarity approach might prioritize areas containing high levels of frog diversity, but inadvertently exclude suitable breeding habitats where these animals are rarely found. Although island biogeography theory does not take particular habitat requirements into account, its preference for large continuous land reserves errs on the side of caution.

A final shortcoming of the complementarity approach is that it is sensitive to “apparent novelties” or species that appear rare in a region but occur in large numbers outside the area being investigated. In many cases a species will appear novel because it is at the edge of its natural distribution. However, as Rodriguez and Gaston (2002) note, organisms living at the edge of their natural distribution are often at a higher risk of extinction than ones living closer to the geographic center of their home range (usually there is an ecological reason why the species’ distribution tapers off at a given point). Therefore, complementarity-based algorithms have a tendency to prioritize reserve sites containing apparently novel species with a higher than average extinction risk. Once again, this strategy does not contribute to a population’s long term viability.

Generally speaking, complementarity-based algorithms promote species diversity over a network of reserves *in the short term only*. Political and economic considerations are likely to influence the ways that these algorithms are applied, resulting in the selection of several small reserve sites containing non-overlapping species. Ecological considerations like the threat of inbreeding depression, genetic drift, the species/area rule and specific habitat requirements, and heightened extinction risk at species’ boundaries suggest that such small isolated populations are not stable over the long term. The widespread popularity of these algorithms is therefore somewhat alarming.

Conclusion

Conservation biology was founded on the hope that ecological science could supply adequate and easily applicable guidelines for preserving the earth’s remaining biodiversity. Theoretical developments in population genetics and island biogeography theory offered important insights into how biological reserves should be designed to best achieve this goal. The founding fathers of conservation biology recognized that these theories were scientifically controversial. However, they offered a pragmatic argument for the relaxation of epistemic standards in conservation contexts: with the looming biodiversity crisis, conservation decisions could not wait for ecology to mature as a science and these principles were the best it currently offered.

Although ecologically-motivated conservation guidelines enjoyed an initial surge in popularity, they were rapidly abandoned in light of objections put forward by academic ecologists and conservation biologists. Using the example of island biogeography theory, I have argued that this flight from ecology was premature. In particular, the four leading objections to island biogeography theory fail to undermine its significance for conservation. The first objection, that island biogeography theory lacks adequate empirical support, presupposes a flawed model of hypothesis confirmation and further ignores Soulé's pragmatic argument for a relaxation of epistemic standards. Moreover, the objection does not apply to conservation guidelines that follow from the species/area rule alone. The second objection that the species/area rule is flawed because it is not a strict law of nature is simply a red herring. Likewise, the claim that habitat heterogeneity is a better predictor of species richness than area is true, but does not undermine the use of area as a proxy for species richness. The species/area "law" is undermined only if stochastic factors regularly overwhelm the influence of habitat heterogeneity on species richness. Suggestions to this effect are typically based on a few poorly chosen examples and/or a reliance on hypothetical considerations. The third objection that terrestrial reserves are disanalogous to islands often relies on blurry definitions of key theoretical terms. Islands are to be defined in relation to the habitat requirements of particular species or species complexes, and population sinks must be determined by taking the long term ecological dynamics of a region into account. Worst of all, the objection that island biogeography theory is inadequate because it offers no strategy for maximizing genetic diversity or preserving particular species merely shifts the normative goalposts. The maximization of species richness remains *one* important aim of conservation biology: island biogeography theory provides perhaps the best available strategy for achieving this goal, especially under limited resources or severe time constraints.

It is ironic that authors like Margules et al. (1982) would denounce island biogeography theory on the grounds that it is empirically unsubstantiated, only to recommend just a few years later an even *less* ecologically well supported alternative in its place (Margules et al. 1988). Complementarity-based place prioritization algorithms facilitate the decision making process in the short term at the potential cost of placing species at greater risk of extinction in the long run. In practice, these algorithms are biased in favor of selecting networks of small reserves with non-overlapping species. This configuration threatens to promote inbreeding depression and drift, it contravenes the rule that large interconnected areas tend to support more diverse and healthier populations than small isolated ones, it ignores habitat considerations, and it favors populations at the edges of their natural distribution where extinction rates are relatively high. Thus, insofar as conservation biology has abandoned island biogeographic and population genetic principles in favor of complementarity-based algorithms, the field has not progressed toward its ultimate aim of conserving the maximum possible biodiversity in the long run.

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