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Extinction debt: origins, developments, and applications of a biogeographical trope

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Abstract: The concept of the extinction debt has two components: a direct timelag between an environmental perturbation and the consequent extinction of a species and the idea that among species going extinct the strong competitors/weak colonizers go extinct first. Although the term was first used in 1994 in the context of metapopulation models, its roots go back to general systems theory and the theory of island biogeography. It has been qualified and elaborated since 1994, mostly in terms of the effects of spatial pattern on the outcomes. The strongest critiques of the concept emphasize that the direct trade-off between competition and colonization abilities is not simple. The original application was to remnant habitat patches, but it could be applied to spatially heterogeneous habitats that are subject to climate change or invasive species. As a guide to conservation practice, extinction debt remains a general cautionary principle rather than a specific prescription, but the raising of awareness is nevertheless significant.

Key words: biodiversity, fragmentation, metapopulation, model, timelag.

I Introduction

Extinction debt is 'time-delayed but deterministic extinction' (Tilman *et al.*, 1994: 65) and is a phrase used to indicate that, following the creation of remnants by surrounding habitat destruction, some species on the remnant are doomed to eventual extinction, even if it occurs after multiple generations. This time delay is significant for assessment of changes in ecological communities, but Tilman *et al.* (1994) went further and reported that the order of time-delayed extinction would be directly in the order of competitive dominance. The basic ideas behind the time delay, the issue of competition versus colonization abilities in the order of extinction, and the elaboration and critiques of the extinction debt model will be reviewed, and its potential applications in three areas of global change will be discussed.

While Forman and Godron (1986: 89) recognized the time-delay for extinction in remnant habitat, they and other early workers used the systems term 'relaxation'. The temporal pattern by which a system changes from one equilibrium condition to another, including dynamic equilibria and even non-equilibrium conditions, is the relaxation path.

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For extinction debt, the shape of the path and the total time to reach the new equilibrium make up this path. Chorley and Kennedy (1971) explained that the rate of relaxation through time, describing the shape of the path, is determined by two factors: (1) the distance between the equilibria before and after the change (eg, as seen in a large versus small remnant); and (2) the ratio of perturbation force to resistance force (eg, in comparing the growth rates and lifespans of invasive and native species). They noted (for beach geomorphology) that changes in relations among variables during the relaxation period and feedbacks among these variables can make the study of relaxation difficult. Relaxation was specifically used as a systems term in work related to the extinction debt model by Diamond (1972), and others have used similar ideas for decades, mostly linked to island biogeography (eg, Brown, 1971; Simpson, 1974; Lomolino *et al*., 1989; Patterson, 1990; McDonald and Brown, 1992; Wiersma and Nudds, 2001; Golinski and Boecklen, 2006).

Other work in ecological modelling refers to 'transient dynamics' to capture the importance of relaxation in a more general way. In the models most closely related to the extinction debt literature, the general significance of transient dynamics was recognized (Hanski, 1994; Hastings and Higgins, 1994). Here I will focus on the more limited scope of extinction debt and – what was really new in Tilman *et al*. (1994) – the aspect of competitor versus colonizer dynamics.

II Origins

Following on from *The theory of island biogeography* (*TIB*) with Ed Wilson five years earlier (MacArthur and Wilson, 1967), MacArthur (1972) produced a slim volume that summarized many of his ideas about the relations between geography and ecological processes in the structuring of communities. Following on from the fundamental idea in *TIB* that an equilibrium number of species is maintained by balancing the inputs of immigration and the outputs of extinction, he noted that reaching this equilibrium can take time. In MacArthur's (1972) Figure 5-20 (see Figure 1) he theorized that a new island that appeared in an ocean with no organisms would add species asymptotically to the theoretical equilibrium. He also considered so-called land bridge islands, which had formerly been part of the mainland and were cut off by rising sea levels. Such islands, before cut-off, would have the same species density as a mainland area of the same size. After cut-off, the island would lose species asymptotically to the same theoretical equilibrium.

This and other aspects of *TIB* were presaged by Munroe (1948) – see Brown and Lomolino (1989) and Lomolino and Davis (1997). MacArthur (1972) did not elaborate on the nature of the dynamics between time 0 and the time at which equilibrium was reached in either case. The importance of the interval was recognized in island biogeography (eg, Brown, 1971) and cited in relation to conservation of tropical forest remnants (eg, Diamond, 1972) but without direct consideration of the pathway to eventual extinction.

The identification of superior competitors was at least augured in early work on land bridge islands as well. Reasoning from post-Pleistocene land bridge islands of the New Guinea archipelago, but with reference to shorter relaxation periods elsewhere, Diamond *et al*. (1976: 1028) suggested that isolated refuges would 'lose the sedentary species of mature habitats that are most threatened by human activities, and retain the rapidly dispersing successional and edge species'.

The elaboration of the significance of island biogeography to conservation ecology took a number of turns in the 1970s when it was brought to bear on the problem of designating remnant patches of habitat as nature reserves surrounded by areas of

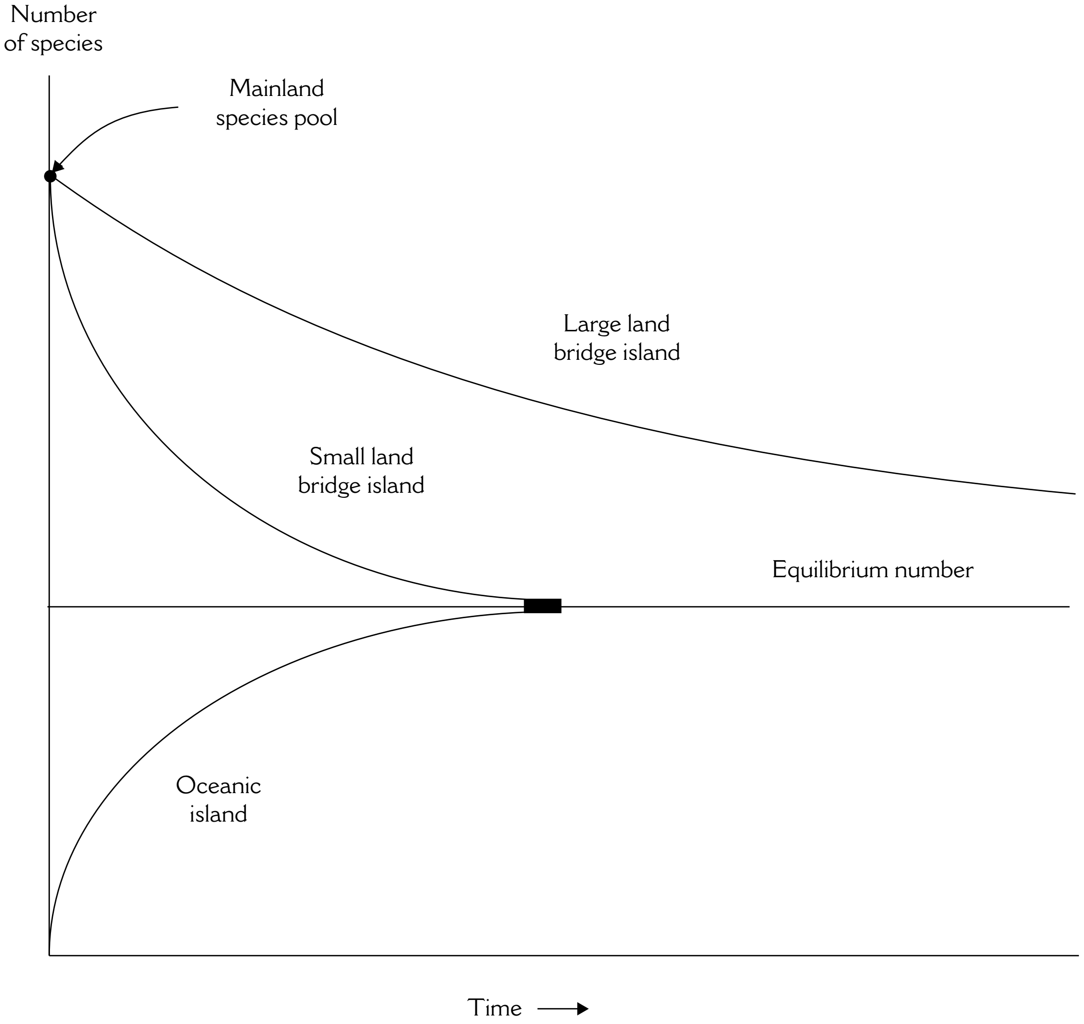

Figure 1 MacArthur (1972) used this figure to illustrate that land bridge and newly created oceanic islands would take time to reach the equilibrium number of species expected in the theory of island biogeography
Source: MacArthur (1972: Figure 5-20).

disturbance or habitat destruction (eg, Terborgh, 1975). However, the 1980s saw a replacement of island biogeography rhetoric with that of metapopulations (Hanski and Simberloff, 1997, who clearly recognized the connections in making the comparison), even reconsidering the SLOSS debate *per se* (Ovaskainen, 2002). Thus by the early 1990s work on metapopulation dynamics had little or no reference to island biogeography, even though some workers were important in both stories (eg, May, 1975; 1994).

Metapopulation ecology focused on isolated remnants of habitat following surrounding habitat destruction and did not recognize the significance of MacArthur's ideas on land bridge islands; although many recognized the debt to island biogeography and noted that MacArthur and Wilson (1967) began with a specific case of forest habitat destruction and remnants from Curtis (1956).

III Development

1 Basics

Working on multispecies metapopulation modelling with competitive attributes, Nee and May (1992) specifically noted that there was a decline in species richness on remaining patches in their model following the removal of other patches. This basic modelling result was an important step because it presented a quantitative model of superior and inferior competitors in a spatially varying environment. They showed that even for homogeneous patches the removal of some could increase the relative importance of an inferior competitor by lessening the viability, even to the point of extinction, of the superior competitor. Notably they concluded by citing the increasing interest in remnants while referring to MacArthur and Wilson (1967) and Levins (1969).

As introduced above, the significance of the relaxation time of patches or remnants following surrounding habitat destruction was articulated by Tilman *et al*. (1994). This fundamental idea of the extinction debt is in no way different from the point made by MacArthur (1972) for land bridge islands. The more specific original contribution by Tilman *et al*. (1994) was that for a group of species that differed in their competitive and colonizing abilities – specifically in an ordered trade-off – the order of extinction was in the order of competitive ability or inverse of the order of colonizing ability (Figure 2). While a glib 'weeds do well with disturbance' might capture this result, its contribution of articulating in a clear model that it happened in the remnants, not in the areas disturbed *per se*, was stronger than the brief verbalization of Diamond *et al*. (1976). The rhetorical contribution went beyond the ecology, however. The term 'extinction debt' is catchy, it grabs attention, and it communicates the important point about timelags in a way that MacArthur (1972) apparently did not recognize and certainly did not communicate in referring to land bridge islands.

Tilman *et al*. (1997) made a further elaboration (more details are given in Lehman and Tilman, 1997, and Tilman and Lehman, 1997). They developed their analytical model and built a simulation in order to examine spatially explicit patterns of remnants. This effort found that the basic conclusions of the earlier model – that the superior competitors/poor colonizers go extinct first following habitat destruction – were robust across a number of variations in the model. One of the most important considerations was to what extent the results applied to abundant versus rare species; superior competitors went extinct early whether they were common or not. Temporal variations of whether the habitat destruction occurred acutely or progressively, continuous or periodic reproduction, and whether the competitive displacement itself had a timelag did not change the outcome. Among the spatial questions, dispersal distances, the spatial pattern of the habitat destruction and its extent (the latter two can also be phrased as the aggregation and size of the remnants) also had the same qualitative outcome: extinction occurs in the order of competitive ability/reverse order of colonizing ability. Of course they noted that these factors altered the quantitative outcomes, ie, the relaxation path, but they did not analyse all possibilities in detail (eg, does the eventual equilibrium diversity or the steepness of the relaxation path depend in the distribution of the commonness or rarity of species as they are arranged on the trade-off continuum?).

Their conservation message was 'the species most susceptible to deterministic extinction, whether abundant or rare in pristine habitat, would be those with the poorest dispersal relative to mortality'. They only

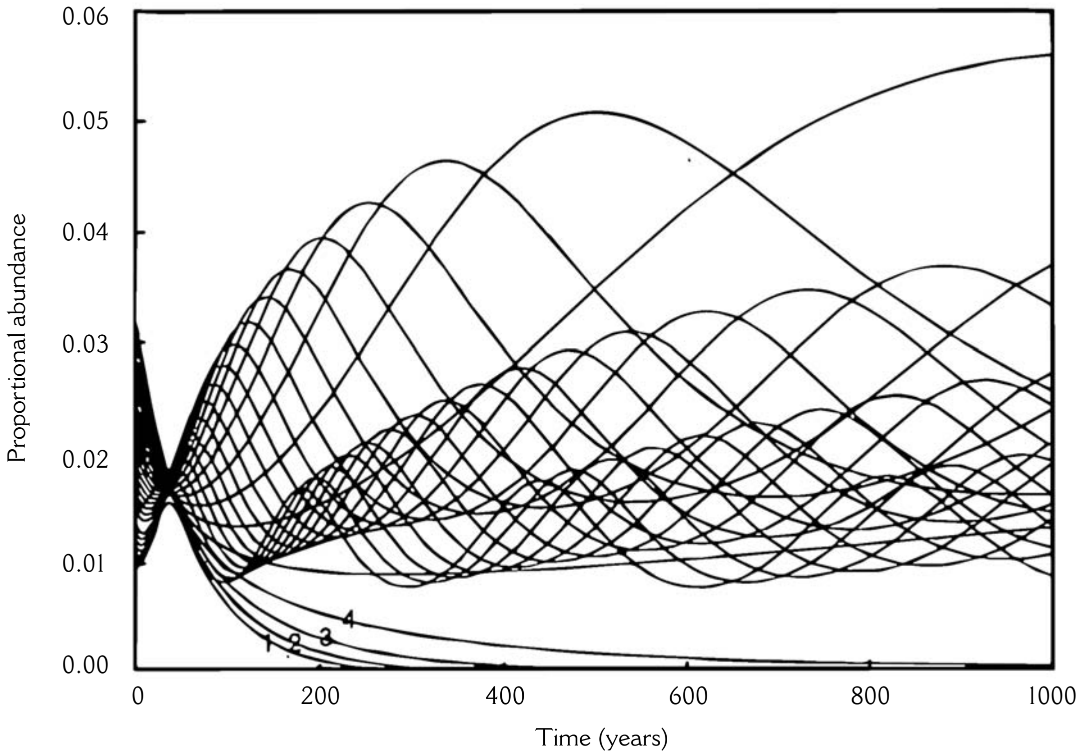

Figure 2 In the original extinction debt model the superior competitor goes extinct first after >200 years, followed by the second, third and fourth best competitors over *c.* 1000 years, comprising the extinction debt for this model system
Source: From Tilman and Lehman (1997) but essentially a better reproduction of a figure in Tilman *et al.* (1994).

scratched the surface of the question about how much habitat can be destroyed before losing species. Classic metapopulation models show a threshold effect for single species occupying a number of sites. Tilman *et al.* (1997) concluded that for the pattern of extinction among multiple species the amount of habitat that could be destroyed before extinction began at all was variable with assumptions but could be small. They further noted that spatial pattern does matter, and that clumping into larger remnants provides a degree of protection to these otherwise doomed species – extinction does not set in until a larger amount of habitat is lost.

2 *Caveats and elaborations*

Given that the extinction debt was based on simple models and simulations, it is no surprise that Tilman *et al.* (1994; 1997) added caveats to the conservation implications of their work. Foremost was the warning that the assumptions of the basic model, notably the direct trade-off between quantified competitive and colonizing traits, needed to be examined for real species. Second, they emphasized the restricted implications of the endogenous processes in the model without regard for exogenous forces such as climate change.

One of the early elaborations of the extinction debt model addressed the assumption of a strict trade-off between traits for successful competition (the most fundamental is by definition: that competitors replace colonizers, period) and colonization. Banks (1997) examined the 1994 model by creating a scatter of trade-off relations instead of a linear 1:1 trade. Thus he had species that were both above and below the diagonal in a competition:colonization graph. In this approach, not even in a pristine environment would all species coexist, which is unfortunate for interpreting the model since a general assumption is that pristine environments have the species that they have (cf. Morozov and Li, 2008). But, moving past that point, he found that further species losses were linear with increasing habitat destruction instead of showing a non-linear response where extinctions started to increase after ~40% habitat loss is exceeded. The important point here is that a loose trade-off means that some species are closer to extinction and that losses could occur with minor loss of habitat.

Another potential elaboration compares the competition-colonization model with an entirely different explanation for the potential coexistence of species before habitat destruction. Pacala and Rees (1998) added niche differentiation, in which the superior colonizers would not be excluded from resource-rich sites by the superior competitors, at least not immediately. To some extent the changes made are similar to the addition of a lag in competitive effect that Tilman *et al*. (1997) included in their extension, but phrased or presented in a way that better informs theory. They found that the degree of recruitment limitation (which could be in either fecundity or dispersal) is the best indicator of extinction risk. Neither addresses spatially differentiated niches wherein two superior competitors could occupy different areas/niches and compete not with each other but with a single colonizer/generalist. Another biological elaboration is the inclusion of age structure in the populations for determination of reproduction and mortality risk. Johnson (2000) outlined its importance. Further, Mikkelson (1993) found that the collapse of a trophic web takes time in fragmented habitats, and Wennergren *et al*. (1995), citing the existence of an extinction debt, found that increased extinctions occurred when predators were added to a herbivore model.

The most extensive elaborations of the extinction debt model are in the area of spatial representation. These were preceded by spatial models using cellular automata (Dytham, 1994; 1995a; 1995b) to follow the aspatial model of Nee and May (1992). Dytham (1994) first limited colonization to the eight neighbours of any occupied patch. Although the general result holds, the amount of habitat at which the superior colonizer becomes more abundant than the superior competitor shifts so that small changes are not so important. This view does not address the overall decline in abundance of the superior competitor relative to its abundance in undisturbed habitat, wherein the initial conditions give it 25 times more cells than the superior colonizer. Moilanen and Hanski (1995) used a different formulation of spatial relations that included distance-dependent migration, patch aggregation, and variation in patch size (areas of contiguous habitat) by using an incidence function model (IFM; sensu Hanski, 1994). They argued that their representation was more realistic than Dytham's (1994) cellular automaton. They found that a larger minimum number of patches is needed to support a population. In terms of colonizers and competitors, their results were qualitatively similar to those of Nee and May (1992) but they found that adding colonization from a dependable source or even increasing patch aggregation reduced the risk for the competitor relative to the colonizer. Bulman *et al*. (2007) using an IFM reported a 100-year course of extinction debt payout.

Of these efforts to elaborate on the model of Nee and May (1992), only Dytham (1995a) mentions Tilman *et al*. (1994) and that in passing. More detailed analyses of spatial patterns followed. Hanski and Ovaskainen (2000) showed that aggregation in landscape patterns reduced extinctions, which was further reinforced in analytical models (Ovaskainen and Hanski, 2001; Ovaskainen *et al*., 2002). Yu and Wilson (2001), limiting competitive displacement to a seedling stage in a hypothetical forest, were able to show that trade-offs need not be along a competitive gradient alone, and that trade-offs between fecundity and dispersal could affect dynamics given variations in patch density. Higgins and Cain (2002) found that direct simulation of more realistic species interactions, with distance-decay dispersal limitations and spatial patterning, eliminated the extinction of the superior competitors. While referring to Tilman *et al*. (1994 and/or 1997) these spatial elaborations were mostly focused on the general metapopulation model better exemplified by Nee and May (1992). In terms of the extinction debt idea, they reported on the long-term outcome, not on the relaxation path, and found more or less the same result *vis-à-vis* competitors and colonists in terms of landscape: that spatially explicit process (dispersal) and pattern (habitat and non-habitat) matter and tend to reduce the extinction of the superior competitors.

Further spatial elaborations were directly aimed at the extinction debt version and came from Tilman's coworkers at the University of Minnesota (Klausmeier, 1998; Neuhauser, 1998). Klausmeier (1998) addressed the distance to which offspring disperse, which had been treated as unlimited in Tilman *et al*. (1994; 1997). While Dytham (1994) did likewise, limiting dispersal to immediate neighbours, Klausmeier (1998) examined a range of distances in an analytical (as opposed to simulation) model with space represented by a one-dimensional line. Most notably he found that extinction was more likely with longer dispersal distances and that a population could be sustained on small areas of habitat. His results were reported with several caveats because the actual spatial representation of extant habitat and destroyed habitat may not be realistic. Neuhauser (1998) examined the patterns created by habitat destruction. Although Tilman *et al*. (1997) had also examined the extremes of a single large block and maximally dispersed cells, she added middle-range aggregations of different pattern. In her results, particular patterns that allow short-range dispersal along corridors but with isolation of habitats so that long-range dispersal often falls on non-habitat can sustain the better competitor after extinction of the superior colonizer.

Malanson (2002a) used similarly direct simulations with a focus on Tilman *et al*. (1997) to explore the dynamics of relaxation *per se*. With considerably less elegance than in most of the metapopulation models but more comparable to Dytham's (1994; 1995a; 1995b) work, he followed the abundance of five hypothetical species through time, in which habitat destruction occurred during the simulation. He set the trade-off between competition and colonization for fecundity and dispersal similar to earlier examples but then forced all species to coexist at near equal levels of cell occupancy prior to habitat destruction – unlike earlier work. He created landscapes that varied in the aggregation of habitat destruction and remnants using the approach common in landscape ecology rather than that used in the analytic methods but with similar resulting patterns. By focusing on the trajectories of species abundance through time following habitat destruction he found that the slope of these relaxation paths was similar for different amounts of habitat destruction, but that the declines in abundance were greatest for initial stages of habitat destruction (eg, from 90 to 80% habitat) and relatively small declines thereafter (eg, going from 20 to 10% habitat) for the superior competitor – but the opposite for the superior colonizer. These trends, rather than a clear threshold in the middle, were unexpected in light of percolation theory. They also have implications of cumulative effects. Changes in spatial aggregation across a range of fractal dimensions showed, as expected, that more aggregated remnant habitat decreased the losses for the competitor and increased the losses of the colonizer but the changes across the increments did not have a clear pattern.

Malanson (2002b) ran this same model but on landscapes where the habitat was not binary but varied in quality continuously (0–1) and this fraction was used as a multiplier of fecundity and mortality. A landscape with a mean quality of 0.5 was assumed to be equivalent to one that had 50% habitat (within which the multiplier is effectively 1). The general effects of the extinction debt model hold: superior competitors are most affected by habitat loss of quality – but there a decrease in quality has an even greater impact than the equivalent loss of habitat cells and the difference increases with habitat loss. Also, the spatial pattern overall matters less in the continuous than binary landscapes (where everywhere is potentially habitable) and so the importance of aggregation is less and variance in habitat quality decreases extinctions. Further along this line, Malanson *et al*. (2007) examined such trajectories in the case where habitat destruction (eg, forest cutting) was acute and was followed by succession. By including the dynamics of the 'matrix' in addition to the remnants, they found that they could be tied to changes in landscape pattern as the sequence of colonizer to competitor became a temporal sequence of dominance alternating with periods of turnover. Korner and Jeltsch (2008) elaborated a similar model with a focus on plant functional types with similar results regarding extinction debt. Wang and Malanson (2008) reported that aspects of landscape pattern maintained hyperdynamism (sensu Laurance, 2002) long after initial fragmentation.

Among all the spatial elaborations, one can see that both the process, dispersal, and the pattern, patch or landscape configuration, matter. This point is nicely illustrated by Hanski and Ovaskainen (2002) who found that in systems that were near the metapopulation threshold, below which long-term maintenance of a species fails and which is determined by both the dispersal of the species and the configuration of habitat, extinction debt times are likely to be long and thus possibly difficult to incorporate in conservation plans.

IV Applications

Extinction debt, with its heritage in relaxation paths, has a number of potential applications, but as theory will need empirical support. Three areas in which we might expect time-lags but eventual extinction are in habitat destruction (the usual application), climate change, and invasive species. As it happens, these are the three most important aspects of current global-scale biological change on Earth.

1 Habitat destruction and fragmentation

The division of habitat into smaller contiguous pieces isolated by a 'matrix' of non-habitat is seen as the leading cause of species extinctions and endangerment (Vitousek *et al*., 1997). The initial destruction kills most of the organisms not resident in the remnants and this initial loss depends uniquely on the specific locations of the destruction. As noted, it is the remnant habitat that is the focus of most study and of extinction debt modelling in particular, and all of the developments mentioned above are aimed at this phenomenon as the creation of extinction debt. Land use change *per se* is the broad phenomenon. It is driven by changes in population, including migration, technology and consumption (Meyer and Turner, 1992).

We have the ability to examine the dynamics of remnants because there are so many, but a strict experimental control is often impossible because of unknowable initial conditions. The studies of Laurance in the Brazilian Amazon are some of the best, and he specifically cites Tilman *et al*. (1994)

in developing his thinking on hyperdynamism (Laurance, 2002). We can also consider ex post facto experiments where we have inadvertently created remnants. Studies on Barro Colorado Island in the Panama Canal were among the first to refer to land bridge island extinctions (eg, Willis, 1974) and others have cited the extinction debt model in term of the timelag or persistent non-equilibrium conditions that are encountered there (Pearman, 2002; Laube and Zotz, 2007).

Other flooding that creates islands demonstrates the importance of initial conditions. Terborgh *et al*. (2001) reported that the creation of land bridge islands by the flooding of a reservoir in Venezuela created unique assemblages based on chance distributions at the time the reservoir rose. Although not addressing extinction debt *per se*, the post land bridge dynamics of these islands (eg, Terborgh *et al*., 2006) indicate that the initial conditions of remnants need to be included when moving between the general and the specific.

Land-use changes that trade off amount of remnant habitat for overall habitat quality, as in the species-friendly farming arena (Green *et al*., 2005), may also benefit from extinction debt concepts. A more spatially explicit view of remnants in a matrix of human land use would better capture what it means to be land sparing.

Additional studies have examined habitat destruction and remnants in terms of the extinction debt model or at least a timelag. Brooks *et al*. (1999) and Helm *et al*. (2006) reported slow responses to fragmentation for bird and plant species, respectively. Ellis and Coppins (2007) found that an extinction debt for epiphytes in remnant Scottish woodlands; with local extinctions greater for both rare and specialist species – on both sides of Tilman *et al*.'s (1994; 1997) conclusions. More detailed explanation of the processes underlying the relaxation path need to separate out the various impacts of restricted population size, reduced immigration, trophic structure, and edge effects.

2 Climate change

The importance of relaxation paths for ecological response to climate change has also been proposed, primarily for vascular plant species. Davis (1989) considered the lag in species geographical response to climate change that could occur due to limits on dispersal. In this case species would not be able to move fast enough to keep up with a geographically shifting niche. It is the difference between the realized and fundamental niche, as well explained by Jackson and Overpeck (2000) for climate change, that could lead to an extinction debt *per se*. In the simplest case, if the climate conditions change so that species cannot reproduce locally, the extinction path will be determined by the remaining lifespans of the individuals. A more complicated case arises if the climate changes so that the conditions change from those of a species' realized niche but remain within its fundamental niche; it will not go extinct in that location unless or until the factors that limited it to its realized niche come into play. If it is competition with other species that created the limitation, the species will continue to exist until the arrival of those competitors. If the competitors do not go globally extinct before they can disperse to this location, they will eventually arrive and displace the species that had existed here. Thus that original species was doomed to eventual extinction but with a timelag following climate change. In this case the overall diversity of the area does not decrease because the environmental change did not set necessarily set a new equilibrium number of species as theorised in *TIB*; instead the change drives toward a new community composition that may have more, fewer, or the same number – but some of those originally in place will become locally extinct. If these species have *not* been able to move into areas in which the climate has created conditions within which they will find a realized niche, they can become globally extinct – and then a global extinction debt will have been created and paid. Whereas Jackson and Overpeck provided a good explanation of the general concepts, Malanson *et al*. (1992) illustrated some of the effects by using simulations in which the realized niche was replaced by fundamental niche conditions on one side of a species climatic gradient. Following reasoning from Darwin (1859) to Keddy (1989), he maintained the climatic constraint where the climate was less productive but removed it, so that competition was the only constraint, where the climate would be more productive (eg, in warmer *and* wetter conditions for many species). This assumption led to longer timelags and less local extinction, reducing the extinction debt.

3 *Invasions*

The changes in conditions created by the introduction of new species to an area can also create an extinction debt. In *TIB* terms, temporally constrained introductions would raise the number of species above the equilibrium, and thus the location would respond as would an area of habitat that had become isolated. If the introductions are continuous and the change is that new species are being introduced constantly, then in *TIB* terms the immigration rate will have increased and the number of species at equilibrium will increase and a drop in local diversity is not guaranteed. Arguments that local diversity can be increased by introductions are thus in accord with *TIB*. But we should want to look at the identities of species locally and consider diversity globally.

The continuous introduction of species will not only raise the equilibrium number of species in a place (in *TIB* the immigration rate per number of species is higher so it would be the same as changing from a far to a near island in any *TIB* representation), which pushes the intersection with the extinction rate further to the right on above the axis of number of species, S, in *TIB*, but also raises this point higher on the vertical axis of rates, which tells us that the turnover rate should be higher. If turnover means that globally distributed species are replacing local ones, it is possible that some local extinctions are global extinctions. *TIB* is a bit weak as a basis for argument here because it does not really address endemic species, but we would not have to work hard to reason from their discussion (MacArthur and Wilson, 1967: 173–74) to see where endemic species are threatened by higher turnover rates.

Rosenzweig (1995) developed a larger logic derived in large part from *TIB*. For the process of plate tectonics, he calculated that the subdivision of the Earth into multiple continents will increase its diversity 'a little' (p. 282): >33%. If we imagine that intercontinental species introductions are similar to rejoining continents, then we would conclude that there would be a loss of species. Rosenzweig (1995) examines an example case of mammal exchanges following the joining of North and South America and reported that the loss of families was 12 of 50 for North America. This is not the whole story. These 12 were replaced by families from South America and at this level the family diversity of both continents had a symmetrical exchange and did not change (Marshall *et al*., 1982). For mammalian genera, however, North America has seen a slight rise while South America saw more than a doubling. But this was after evolution produced new genera, and in the mean time extinctions did occur. Following the joining of the continents, which is conceptually similar to species introductions between them, native North American and South American mammalian genera dropped by ~25% – over the course of 2 million years. That is some payout period!

If we continuously introduce species among continents up to the point where the continents function as Pangaea then in the intermediate term some species should eliminate others. As of now it seems that extinctions are not keeping pace with introductions (Stohlgren *et al*., 2008), but potentially creating a global extinction debt. Once that is paid there may be interest due in terms of eventual further speciation, but this is uncertain at best.

V Policy and management implications

While the extinction debt tells a cautionary tale, is it a theory that can guide management? Calculation of an extinction debt has been used at least to suggest policy (eg, Cowlishaw, 1999; Hanski, 2000), but does it describe real ecological processes and patterns? Loehle and Li (1996) pointed out important limitations in which the extinction debt and order of extinction do or do not hold for different assumptions of the spatial nature of the disturbances. The strongest general critique is that of McCarthy *et al.* (1997). Their critique is aimed at Tilman *et al.*'s (1994) presentation, and some of their criticisms are rebutted indirectly by Tilman *et al.* (1997), but it is still a good starting point for a review of problems. First, they noted that the assumption that there was a trade-off between competitive and dispersal abilities is questionable. While there may be some generality to the assumption within taxa, it must be questioned for individual application. Second, the spatial and temporal characteristics of fragmentation were limited in Tilman *et al.* (1994). The number and sizes of patches need to be treated independently in metapopulation models or, perhaps better, represented explicitly in less elegant simulations. McCarthy *et al.* (1997) bring field evidence to bear. In examining cases with some order of dominance of species for five birds, four small mammals and one vascular plant, they reported that extinction or direction of change in abundance was not predicted by the extinction debt model. Furthermore, there are indications that rare species are more likely to become extinct. This critique seems somewhat selective in its examples, and some of the argument applies to the effects of habitat destruction *per se*, not to what happens in remnants: any extinction debt explanation related to the dominance hierarchy is meant to apply only to species extant in remnants following surrounding habitat loss. Still, an overarching point of McCarthy *et al.* (1997) is that rare species, which are not usually competitively dominant, are still threatened with extinction, and this point is supported by extensions in extinction debt modelling, at least those where demographic stochasticity is included during the relaxation period. This point was emphasized in model results.

Following the critique of McCarthy *et al.* (1997), others have identified specific cases where the extinction debt result relative to competitors versus colonizers would not hold. Some address Tilman *et al.* (1994; 1997) directly, others in passing. Many of these find that the specifics of species and their history and geography preclude the general assumptions of the extinction debt model (eg, Lindenmayer *et al.*, 1999; Gonzalez, 2000; Gutierrrez *et al.*, 2001; Jakobsson and Eriksson, 2003). In general, it may take more time to identify extinction debts than we have yet to observe (Vellend *et al.*, 2006; Stohlgren *et al.*, 2008).

The caveats raised by conservation ecologists concerned with specific field cases are largely aimed at the conclusions of extinction debt models relative to the threat faced by competitive dominants versus those faced by rare species. The existence and importance of a timelag, the basic point of which extinction debt reminds us, is not disputed. The management and conservation implications of the two ideas need to be separated.

The finding of the extinction debt model, that competitive dominants go extinct first in the conditions modelled, has largely held up in subsequent refinements of the model. The criticism is that it depends on the trade-off between competitive ability and dispersal ability. If this assumption cannot be sustained, then the application of the model is suspect at the least. How to establish competitive abilities is an open ecological question. Regarding rare species, the models predictions that they can thrive depend on the assumptions that they do have dispersal capability and that they compete for the same resources or locations of habitat as the competitors, so that they can expand into places from which the competitors die out. Here multiple niche axes represented in a spatially explicit simulation might better elucidate the range of possible outcomes.

The point about timelags is important for policy and management. While not new in 1994, its reiteration and development has been valuable. An important part of recognizing that we may not see impacts immediately is that we may not be able to distinguish impacts of multiple disturbances or stresses that have their own relaxation paths. For example, it may be difficult to distinguish the cause of a present extinction that might be a payoff of an extinction debt created by fragmentation initiated a century ago or climate change beginning with the end of the Little Ice Age and continuing in current global warming or the arrival of invasives. In the policy and management arena this is a double whammy:

> whammy n. 1 The evil eye. Pop. by Al Capp, cartoonist, who created 'Eagle Eye Fleegle,' a character who could put people into a trance by looking at them; his stare with one eye is called the 'whammy,' but in emergencies he uses both eyes, ie, the 'double whammy.' From comic strip 'Li'l Abner.' (*Random House historical dictionary of American slang*)

In policy and management we are potentially entranced into inaction if we cannot differentiate among two or more (thus double) causes. The overlapping of extinction debts from multiple sources is a likely source of this problem, and the identification of which species lost are more likely to be due to any specific cause may not be subject to generalization.

VI Conclusion

If, in looking at remnants, timelag is seen as having significance for conservation practice, then we can acknowledge MacArthur (1972) for identifying the fundamental issue. We should also recognize, first, Nee and May (1992), and perhaps the work on metapopulations in general, as opening a pathway for modelling; and, second, Tilman *et al*. (1994), for raising consciousness through articulating, with apt choice of words, a clear and striking model that jolted people with the counterintuitive finding of a greater threat to some competitively dominant species and a lesser threat to some rare species.

By identifying the future extinctions as a debt incurred by present habitat destruction that must be paid off in the future, Tilman *et al*. (1994) sparked renewed interest in the temporal trajectories of remnants. Given that the fundamental nature of the extinction debt was recognized prior to its coinage by Tilman *et al*. (1994), it is notable that the use of a powerful trope accelerated this field of study. As of this writing, this will be the 528th citation of Tilman *et al*. (1994) as recorded by ISI Web of Knowledge (http://portal.isiknowledge.com/portal.cgi) – not extreme but respectable. Although the idea of the extinction debt is based in island biogeography and so its elaborations and insights apply primarily in cases of remnant patches resulting from habitat destruction, the recognition of timelags or relaxation times is fundamental to a larger systems orientation. A broader base allows us to extend the idea to other ecological dynamics and other concerns in conservation ecology where the threat is in underestimating or misunderstanding cumulative impacts. The quantitative transient dynamics and their species-specific consequences for real places is, however, still an open area for research. Even with all the attention garnered by Tilman *et al*. (1994), extinction debt accounting and payments are uncertain.

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