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8

Temporal niches, ecosystem function and climate change

8.1 INTRODUCTION

This chapter differs from the main current of this volume – the identification and quantification of coexistence mechanisms associated with temporal niche dynamics – in exploring the ramifications of these processes for ecosystem ecology. The intimate link between niches and ecosystem function has long been recognised, at least in the general sense that more species, representing a greater diversity of 'life-styles', make more complete use of available resources and thus achieve higher levels of productivity (e.g. Preston 1948, Odum 1953, MacArthur 1955, May 1975). This broadly stated principle has been unpacked in numerous models that are more specific, for example in resource-ratio niche theory (Tilman 1982) and various forms of spatial niche theories (Loreau 1998). However, the role of temporal niches in the ecosystem context is somewhat less well developed, but critical to understanding ecological responses to climate change.

Two main features characterise worldwide, anthropogenic climate change: a general warming trend that is strongest at low latitudes and weakest at high latitudes, and complex changes in precipitation patterns, currently predicted to include reductions in precipitation at the poleward fringe of the subtropical dry belt at midlatitudes (IPCC 2007, Scheff and Frierson 2012). Both temperature and precipitation shifts, as well as their interactions, have the potential to alter environmental heterogeneity. For example, the onset of spring/summer growing seasons could be advanced (Menzel *et al.* 2006) and the frequency and amplitude of extreme hydrological events such as drought

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and flooding increased (Huntington 2006). Both temperature trends and precipitation variability are important factors in structuring temporal niches, for example by functioning as triggers of life-history events (Kelly *et al.*, this volume, Venable and Kimball, this volume) or by controlling competitive interactions through their effects on primary production (Haxeltine and Prentice 1996). Simultaneous changes in seasonal temperature and precipitation patterns may have complex effects on populations and their interactions. Predicting such effects, and their feedbacks on climate, is one of the premiere challenges of earth system science and, in our opinion, cannot be adequately tackled without a more complete understanding of temporal niche dynamics and its role in ecosystem function.

At the most basic level, ecosystem function is measured in terms of primary productivity, the sum total of the productivity contributed by all plants present. For convenience, ecologists often group plant species into 'plant functional types' that are *alike* in their interactions with the ecosystem and as a group markedly *different* from other functional types (Figure 8.1). Classification schemes vary widely (Box 1996, Lavorel *et al.* 2007) but in general they involve structural and physiological distinctions that determine their participation in material cycles (e.g. capacity for nitrogen fixation, rooting depth, woodiness) and in energy flows (e.g. albedo, surface roughness) (Westoby and Wright 2006). Species belonging to different plant functional types are assumed to have more complementary ecosystem functions and less overlap in habitat and resource requirements. Species that are very similar in structure and physiology are called functionally redundant and assumed to be largely interchangeable in terms of their ecosystem functions (Figure 8.1; Walker 1992, Naeem 1998, Yachi and Loreau 1999).

Even though this conceptual framework does not specifically address how species richness is maintained, it is natural to assume that plant functional types coexist because they have little niche overlap and weak, if any, competitive interactions, or may even interact facilitatively (Dawson 1993, Schwinning and Parsons 1996, Chapin *et al.* 1998, Cardinale *et al.* 2002, Hooper *et al.* 2005). For example, deep-rooted shrubs may provide a good microhabitat for perennial grasses. By extension, competition between functionally redundant species can be expected to be stronger than, on average, with random community members, but differences in sensitivity to environmental factors variable in space and time (precipitation patterns, soil type, aspect, etc.) could provide opportunities for stable coexistence (Loreau 2000).

In this framework, ecosystem productivity and adaptability to climate change depends in part on direct effects of climate on plant

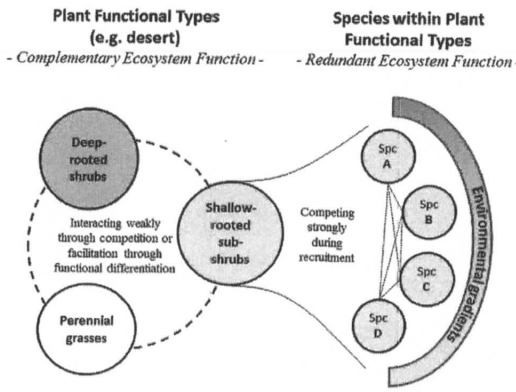

Figure 8.1 The presumed roles of complementarity and redundancy in ecosystem function. Left: Plant functional types, differentiated by numerous structural and physiological traits, giving them broad niche separation and complementarity in ecosystem function. Right: Functionally redundant species within a functional type, differentiated primarily by their sensitivities to environmental conditions, with high potential for competitive interactions. Functional richness is expected to elevate average ecosystem performance through synergistic interactions; redundancy is expected to reduce variance of ecosystem function in the face of environmental heterogeneity (= insurance function).

function – for example, aridification is relatively more adverse to the productivity of deeper-rooted species due to less deep infiltration – and in part on the environmental niche structure of redundant species, about which much less is known as a rule. Does a functional type with many species operate at a consistently higher level of primary production? Does it occupy a wider range of environmental niches? Can richness in redundant species buffer more efficiently against species loss or climate change? In sections 8.2–8.4, we attempt to address these questions from the viewpoint of community theory and the evolutionary origins of temporal niche structure.

8.2 PLANT FUNCTIONAL TYPES, REDUNDANCY AND PRODUCTIVITY

Agricultural experiments have long ago shown that crop mixtures can overyield, that is, produce more biomass, when intermixed than when grown separately on the same land (Vandermeer 1992). If carefully selected, mixtures can even produce more biomass per land area than any monoculture of the component species. This has been called

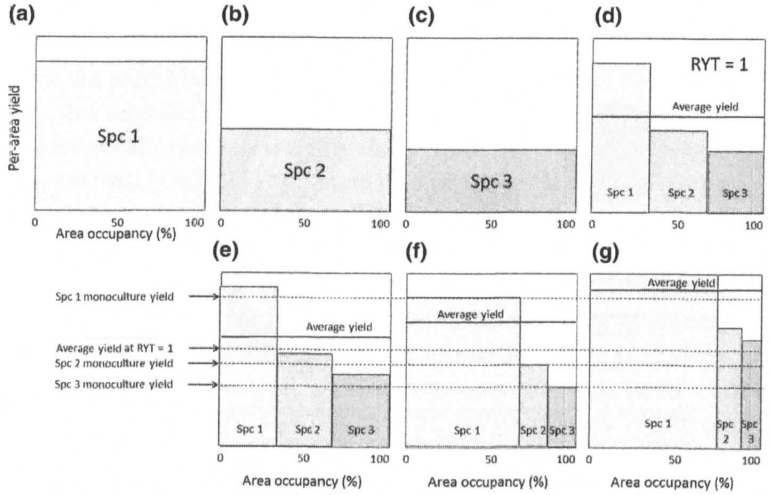

Figure 8.2 Overyielding. To quantify overyielding, the yield of polycultures is compared to the mean and maximal yields of the component species' monocultures. (a–c) Monoculture yields for three species. (d) Polyculture yield corresponding to Relative Yield Total = 1, in which area-based species yields are exactly as in the monocultures. (e) Non-transgressive overyielding through the complementarity effect. In this example, all three species yield more per area than in monoculture. (f) Non-transgressive overyielding through the selection effect. Here, the most productive species 1 increased area occupancy, while area-specific yields stayed the same. (g) Transgressive overyielding achieved through complementarity and selection effects.

transgressive overyielding, while *non-transgressive overyielding* is the term used when crop mixtures yield more than the average yield of monocultures, but no more than the highest yielding monoculture.

Theoretically, polycultures can overyield in two distinct ways (Loreau 2000; Figure 8.2). One or more species could increase yield-per-unit-cover (or per seed sown), so that species' yield reductions due to sharing space with other species is less than proportional to their reduction in cover or density (Tilman 1999). Overyielding through this mechanism has been called the 'complementarity effect' and is consistent with the idea that species have distinct resource needs, so when they are grown together they capture a greater fraction of the available resource per unit land. However, the complementarity effect does not necessarily result in transgressive overyielding if species have large differences in monoculture yields, because the negative effect of reducing the cover of the most productive species weighs against the

positive effect of increasing individual yields-per-unit-cover. The second way in which polycultures can overyield is through the selection effect, which depends on the more productive species becoming dominant. This effect does not require synergistic relationships between species, only that species that are more productive competitively displace those that are less productive. While the selection effect was originally seen as evidence against the hypothesis of a productivity-enhancing effect of species richness (Huston 1997, Wardle 1999, Schwartz *et al.* 2000), it is now interpreted as a relevant mechanism through which ecosystems increase productivity in nature (Hector *et al.* 2002).

A second presumed benefit of species richness is the reduction of variance in ecosystem function in the presence of environmental variability. There are two ways to think about this 'insurance' function of biodiversity (Yachi and Loreau 1999). One way is in the sense of a 'portfolio effect': if species in a community have a component of independent yield variation, the variance around the community's average performance should decrease with the number of species simply as a consequence of statistical averaging (Doak *et al.* 1998). At the same time, the mean performance of the mixture could be above, below or the same as the average across monocultures, depending on species selection vis á vis the frequency of environmental conditions favouring them. The other way is in terms of 'compensatory dynamics' (Tilman 1996), in which better-adapted species grab resource opportunities vacated by less-well-adapted species. At the very least, this would provide even more stability of ecosystem function. But if some species fail where others succeed for ecologically significant reasons – e.g. because they have different environmental optima – a community of functionally redundant species could also regularly achieve higher average productivity, as long as species increase under conditions in which they are more productive and vice versa.

Which of these effects have actually been observed in experiments? The following is a brief summary for terrestrial ecosystems (mostly grassland experiments) derived from meta-analyses and informal syntheses (Hooper *et al.* 2005, Balvanera *et al.* 2006, Cardinale *et al.* 2006, 2007, 2011, Isbell *et al.* 2009, Zhang *et al.* 2012):

1. The great majority of mixtures overyield, but transgressive overyielding is uncommon;
2. Productivity responds more strongly to functional diversity than to species richness;
3. Mixtures overyield in part because they contain the most productive species, indicative of a 'selection effect';

4. In addition, there are positive effects of having multiple species in the community; indicative of a 'complementarity effect';
5. The magnitude of the complementarity effect and the degree of overyielding increases with the length of the biodiversity experiment or its spatial scale;
6. Mixtures that are more diverse are more stable over time and more resilient to some (e.g. nutrient stress, invasions) but not all types of perturbation (e.g. temperature stress, drought).

In general, these patterns suggest that plant species tend to have large differences in area–yield not easily overcome by complementary resource use and so transgressive overyielding is not the norm. In addition, the establishment of a maximally productive community takes time, presumably involving a slow process of sorting of species with respect to each other and environmental heterogeneity in space and time (Mouquet *et al.* 2002, Hillebrand *et al.* 2008, Zhang *et al.* 2012). Apart from a positive effect of including legumes, which, through symbiotic nitrogen fixation, enrich soil fertility and therefore the productivity of most other species (Fornara and Tilman 2009, Hooper *et al.* 2012), there is little further clarification of the ecological and biological mechanisms responsible for producing diversity effects on ecosystem function. The strong focus on grassland ecosystems in biodiversity experiments may limit the mechanisms available for complementary resource use, since herbaceous species are relatively restricted in morphological and physiological differentiation, e.g. compared to plants in forest communities (Zhang *et al.* 2012).

It is also noteworthy that experimental grassland communities appear to be poorly buffered against environmental factors most directly related to climate change – temperature and water. Since temperature and water are two of the most fundamental constraints on terrestrial plant photosynthesis, this is not a surprise, but raises questions about the generality of conclusions drawn from this system regarding the effects of species richness in climate change adaptation.

8.3 THEORETICAL EXPECTATIONS

Many authors have found it useful to explore heuristic models to determine the theoretical underpinnings of diversity–productivity relationships (Doak *et al.* 1998, Loreau 1998, 2004, Tilman 1999, Yachi and

Loreau 1999, 2007, Norberg *et al.* 2001, Mouquet *et al.* 2002, Loreau *et al.* 2003, Beckage and Gross 2006, Marquard *et al.* 2009). Here, we examine the properties of two very general types of models representing interactions between species with distinct functional niches, which do not require environmental heterogeneity to coexist, and between species that are functionally identical and coexist because of differential sensitivity to fluctuating environmental conditions.

Arguably, the quintessential model of coexistence between species with distinct resource niches is the Lotka–Volterra competition model. It requires neither temporal nor spatial variation for coexistence, and can be unpacked into more mechanistic consumer–resource models with two different kinds of resources (for two species) that are required in different proportions by each species (MacArthur and Levins 1967, Tilman 1982). For the purpose of illustration, we use the Lotka–Volterra model with explicit mortality terms:

$$\frac{dN_1}{N_1 dt} = r_1 N_1 \left(1 - \frac{\alpha_1 N_1 + \beta_1 N_2}{K_1}\right) - d_1 N_1 \tag{8.1a}$$

$$\frac{dN_2}{N_2 dt} = r_2 N_2 \left(1 - \frac{\alpha_2 N_2 + \beta_2 N_1}{K_2}\right) - d_2 N_2, \tag{8.1b}$$

where the r_i are the maximal growth rates of species, K_i the carrying capacities, d_i the per capita mortality rates, α_i the intraspecific competition coefficients and β_i the interspecific competition coefficients. For species to be in equilibrium, their rates of growth (the first terms in the equations) must equal their rates of mortality (the second terms), and the absolute magnitudes of both rates are adequate measures of productivity, or the ecosystem carbon and nutrient flux required to maintain the population at a given density. Thus, the total productivity or ecosystem flux F required for maintaining any combination of standing biomass for the two species is

$$F = d_1 N_1 + d_2 N_2. \tag{8.2}$$

In Figure 8.3, we superimposed contour lines for F-values onto the classic zero-growth isocline representation of two-species interaction models, so that ecosystem fluxes associated with monocultures can be readily compared with those for stable equilibria. Fixing values for d_1 and d_2, we varied the remaining parameters to generate a set of case examples.

Figure 8.3a shows that both non-transgressive and transgressive overyielding is possible under stable coexistence between competitors.

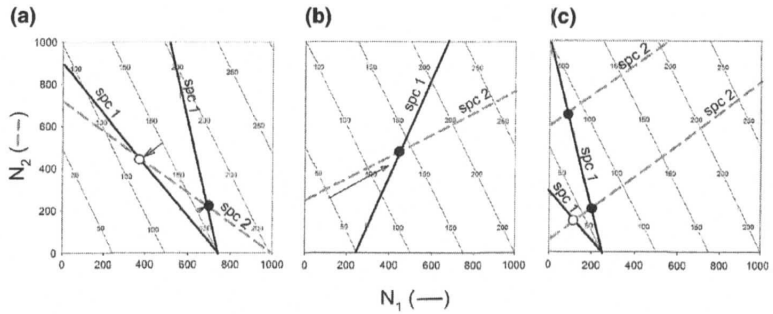

Figure 8.3 Coexistence and productivity in the Lotka–Volterra model. Shown are zero-growth isoclines (thick) and contour lines (fine) that indicate the total productivity required to maintain any combination of standing biomass (i.e. $F = d_1N_1 + d_2N_2$). Shown are only cases of stable coexistence. Transgressive overyielding at equilibrium is indicated by solid symbols, non-transgressive overyielding by open symbols. **(a)** Competition. By assumption, the productivity of species 1 in monoculture is higher than that of species 2. Depending on the slope of the species 1 isocline relative to the slope of the productivity contour lines, stable mixtures either transgressively or non-transgressively overyield. **(b)** Mutualism. A stable mixture of mutualists always has higher productivity than either monoculture. **(c)** Exploitation. If the exploited species (here, species 1) in monoculture, has higher productivity than species 2 in monoculture, stable mixtures either transgressively or non-transgressively overyield, depending on the slope of the species 1 isocline. If the exploiting species 2 has higher productivity in monoculture, stable mixtures necessarily transgressively overyield.

Transgressive overyielding happens if the slope of the higher-yielding species' isocline is steeper than the slope of the contour lines for ecosystem flux, mathematically:

$$\frac{\beta_1}{\alpha_1} < \frac{d_2}{d_1}. \tag{8.3}$$

Thus, transgressive overyielding does not occur when interspecific relative to the intraspecific competitive effect on species 1 is greater than the mortality rate of species 2 relative to species 1. Suppose that species 1 has the higher mortality rate, so that it must assimilate more resources to maintain a unit of standing biomass. It is then easy to see that a relatively steep reduction of its standing biomass by adding the competitor can only lower the combined resource uptake of the mixture. Biologically, this violates no known tradeoffs; it only requires that a faster growing species can be strongly competitively suppressed by a slower growing species.

By changing the sign of the competition coefficients, the Lotka–Volterra model can also express mutualistic (+,+) and exploitative (+,−) relationships between two species. Mutualistic interactions between primary consumers can arise if both species make the environment more benign for the other species, for example, one species may produce a more favourable microenvironment for the other species, while the other species may enhance soil fertility. Interactions between primary consumers can be exploitative if one species makes more resource available (e.g. a nitrogen-fixing legume), while the other species only competes for mutually limiting resources (Schwinning and Parsons 1996).

A stable mutualism always transgressively overyields (Figure 8.3b). This is a direct consequence of the premise that both species increase standing biomass in the presence of the other species. An exploitative interaction either transgressively or non-transgressively overyields (Figure 8.3c). If the exploited species (1) has the higher yield in monoculture, then, as in the case of competition, the isocline slope relative to the contour line slope determines the degree of overyielding. If, on the other hand, the exploiting species (2) has higher monoculture yield, an equilibrium exists only if the species 1 isocline is steeper than the contour lines, and the mixture necessarily transgressively overyields.

Thus we can conclude quite generally that linear interactions between coexisting species in a constant environment, if the productivity of the mixture is a linear combination of species' standing biomass, always overyield. All types of species interactions (e.g. (−,−), (+,+), (+,−)) can produce transgressive overyielding, but only mutualistic interactions (+,+) must transgressively overyield.

Different results obtain for nonlinear interactions. For example, Loreau (2004) observed that stable mixtures of competing species could underyield in a generalised Lotka–Volterra competition model with concave-up isoclines. Strong interference competition can produce this effect by lowering resource-use efficiencies in both competitors, as has been observed for two *Drosophila* species (Gilpin and Justice 1972). This may be an unlikely case for plants, however, since plants tend to become more efficient, not less efficient, under resource scarcity or competition.

We now turn to the lottery model (Chesson and Warner 1981, Chesson *et al.* 2001) to represent the interactions of functionally redundant species that do not vary in resource requirements, only in sensitivity to environmental fluctuations. A fundamental assumption

of the lottery model with coexistence through the storage effect is that populations divide into at least two distinct life-history classes, of which one engages in high stakes lottery competition (e.g. seedlings) and the others are relatively persistent stages for surviving seedlings (e.g. perennial adults). Mathematically, the model is

$$\sum_{j=1}^{k}\beta_j(t)n_j(t) > 0:$$

$$n_i(t+1) = n_i(t)*(1-d_i) + \sum_{j=1}^{k} d_j n_j(t) * \frac{c_i(t)\beta_i(t)n_i(t)}{\sum_{j=1}^{k} c_j(t)\beta_j(t)n_j(t)} \quad (8.4a)$$

$$\sum_{j=1}^{k}\beta_j(t)n_j(t) = 0 : n_i(t+1) = n_i(t) * (1-d_i)\,, \quad (8.4b)$$

where k is the number of suitable sites (occupied or empty) for members of the community, n_i is the proportion of adults of species i relative to k, d_i is the per capita death rate of adults, β_i is the per capita seed production and c_i is a parameter that expresses temporal variation in competitiveness between seedlings of different species (Chesson and Warner 1981, Chesson *et al.* 2001). Equation (8.4a) expresses what happens in a year when at least one species recruits. The first term describes the number of plants that survive from one year to the next and the second term adds the number of new recruits, as determined by lottery competition for open sites. Equation (8.4b) expresses what happens in years when no species recruits. By expressing community dynamics in terms of proportions relative to the number of suitable sites, the model allows for potentially large variation in total site number (or establishment opportunities) from year to year, as may be the case in highly water-limited environments. However, establishment opportunities are equally available for all species. Thus, absolute establishment success of species may be highly correlated over time, and variation between species comparatively small, but for coexistence via temporal niches, only the independently variable fraction of establishment fluctuations matters.

An arbitrarily large number of species can stably coexist under this model, if each species has positive average growth rate at low density. Furthermore, species with average fitness differences can coexist if the stabilising effect generated by a lessening of intraspecific competition at low density is sufficiently strong (Chesson 1994).

In keeping with the definition used previously, we define the ecosystem function of this community as the matter flux required to grow and maintain adults, and in this case, to grow seeds as well. Since this is a model for functionally redundant species, we assume that species are identical in all metabolic costs for seed production and growth and

maintenance of adults, and have the same mortality rates. We ignore the productivity of all seedlings unsuccessful in recruitment. Setting k constant, the long-term average annual ecosystem flux of the community is

$$F = C_{adult}\, d\overline{\sum_{J=1}^{k} n_J(t)} + C_{seed}\overline{\sum_{J=1}^{k} n_J(t)\beta_J(t)}\,, \quad (8.5)$$

where C_{adult} and C_{seed} are the average annual per capita metabolic costs associated with adult growth and maintenance, and with seed production, respectively. Here we set both cost parameters to unity and scale β so that the average cost of community-wide seed production is equivalent to the cost of maintaining full site occupancy by adults. The relative annual cost of seed production versus the growth and maintenance of adults of course varies between groups of species, although in most plants appreciable growth versus reproduction tradeoffs suggest that neither cost is negligibly small (Obeso 2002, Herben *et al.* 2012).

We consider three variations of the lottery model. For models 1 and 2, we assume that every year is a recruitment year (so new recruits immediately occupy vacated sites), as in the original model proposed by Chesson and Warner (1981). With adult numbers constant, variation in ecosystem function is caused only by varying seed production. However, seed production need not vary at all between species for stable coexistence to occur (i.e. all variation could be in c_i; Equation (8.4a)). Thus, one possible outcome for communities coexisting through temporal niche separation is that species richness has no effect on community productivity. In the following analysis, we assume the opposite extreme: that all recruitment variation stems from differences in seed production.

In model 1, year types arrive at random, so that species cannot take over in the community by being consistently favoured over several reproductive cycles. In model 2, environmental conditions remain constant for several reproductive cycles before they switch to a random, new regime. Model 3 is a version of the lottery model examined by Chesson *et al.* (2001), in which each species requires a different year type for recruitment. A consequence of this assumption is that communities with fewer species recruit less often than those with more species, and total adult densities decline with species numbers. Parameter values for the three models are shown in Table 8.1, and the relationships between species richness and yield under the different models are shown in Figure 8.4.

In model 1, more species-rich mixtures overyield on average, but no mixture transgressively overyields, and some mixtures, if they are composed of the lower-yielding species, underyield (Figure 8.4a). Since year types arrive in random order, years of maximal per capita

Table 8.1 *Parameter settings for the lottery models in Figure 8.3. Shown are seed production values (β_i) for five species across 5-year types. Mortality rate is* $d = 0.1$ *unless otherwise specified and the competition parameter* $c_i = 1$ *for all species across all simulations. All year types have equal probability.*

	Models 1 and 2					Model 3				
Year type	Sp 1	Sp 2	Sp 3	Sp 4	Sp 5	Sp 1	Sp 2	Sp 3	Sp 4	Sp 5
1	1.13	0.68	0.45	0.23	2.25	0	0	0	0	4.28
2	2.25	1.13	0.68	0.45	1.13	5.63	0	0	0	0
3	1.13	2.25	1.13	0.68	0.45	0	5.41	0	0	0
4	0.68	1.13	2.25	1.13	0.23	0	0	4.95	0	0
5	0.45	0.23	0.45	2.25	0.23	0	0	0	4.73	0
Mean	1.13	1.08	0.99	0.95	0.86	1.13	1.08	0.99	0.95	0.86

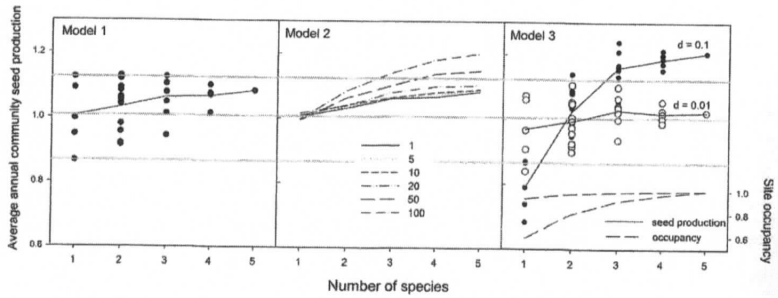

Figure 8.4 Biodiversity–productivity relationships in three lottery models. In models 1 and 2, all sites are always occupied and differences in productivity are solely due to differences in seed production. In model 1, year types arrive randomly; in model 2, year types repeat 1–100 times as indicated in the legend. In model 3, all species have a specific year type in which only they reproduce and results are shown for $d = 0.1$ (solid symbols) and $d = 0.01$ (open symbols). In model 3, site occupancy can be < 1 and is indicated by the broken lines. All panels show as grey lines the minimal, average and maximal seed production of monocultures at full patch occupancy. A mixture underyields if it yields below the average, overyields non-transgressively if it yields above the average but below the monoculture maximum, and overyields transgressively if it yields above the monoculture maximum.

reproduction are just as likely to arrive when a species is at high as when it is at low frequency. Thus, the contribution of any species to average seed yield just depends on its average frequency, and since species that are fitter on average achieve higher frequencies, species mixtures tend to yield more than the average of monocultures. Thus,

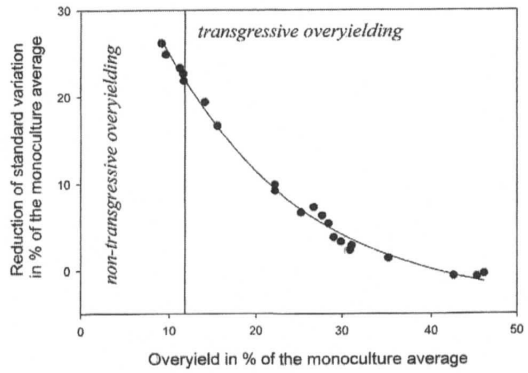

Figure 8.5 Transgressive overyielding at the cost of increased seed yield variability. Values are shown for model 2 with all five species and year-type repeat values between 1 (top left) and 350 (bottom right). Above the overyield percentage of 11.8%, the mixture yields more than the highest yielding monoculture.

overyielding is caused by the selection effect, and depends on the magnitude of fitness differences among species.

Model 2 does exhibit transgressive overyielding because species favoured by the environment have time to spread in the community, so that over time, high per capita seed yields are positively correlated with higher than average adult frequencies across species. However, immediately after an environmental regime shift, in the process of switching dominance from one species to another, the community is poorly adapted to the environment and underyields. The degree of overyielding and the magnitude of variance reduction are therefore negatively correlated in model 2 (Figure 8.5); a higher degree of overyielding occurs at the cost of higher temporal yield variance. The exact relationship depends on the time a community takes to switch dominance between species relative to the frequency of regime shift. For example, the existence of stable refugia could help recovery by limiting how rare a species can get, and large fitness differences between species under any stable regime (as in model 3) help the currently favoured species to rapidly displace all other species.

Transgressive overyielding also occurs in model 3, which exhibits an especially high degree of sensitivity to species numbers if adults have low survivorship. This is because diversity affects not only average per capita seed production, but also total adult densities. However, if adult mortality is low, in other words if adults are long-lived compared to average recruitment rates, the model behaves similarly to model 1, since most sites remain occupied at all times.

Thus, both transgressive and non-transgressive overyielding is possible, but not necessary in groups of functionally redundant species with distinct temporal niches. Contrary to what is sometimes expressed in the literature (Loreau 2000, Gonzalez and Loreau 2009, Hector *et al.* 2010), temporal niches may have no effect on ecosystem productivity or stability, if niche dynamics play out entirely through germination and seedling dynamics. This is assuming, of course, that seedling dynamics have negligible effects on ecosystem fluxes, as would be the case for long-lived species with adults that have a much larger combined biomass than seedlings, for example forest trees. Furthermore, groups of functionally redundant species could have highly variable production as a whole, but if these are caused by shared environmental responses, they cannot be buffered by temporal niches.

If temporal niche dynamics have a component that does correlate with adult performance, for example through seed production, non-transgressive overyielding can occur and only requires that species have average fitness differences and that species with higher fitness on average are more frequent on average. Transgressive overyielding, while possible, requires more stringent conditions. In species that are not recruitment-limited, transgressive overyielding can only occur if environmental variation has intermittent periods of relative stability that last through several reproductive cycles, so that the currently fittest species can spread. On the time scales of experiments, we might observe transgressive overyielding in annuals or biennials responding differentially to El Niño Southern Oscillation (ENSO) cycles. In tree populations, we would need centennial time scales to see this, making direct observation unlikely, but long-term cycles of population fluctuation in temporal niche partners found by Kelly and Bowler (2002) are consistent with this. Conversely, if adult densities are recruitment-limited, transgressive overyielding can occur if each species occupies a distinct specialised recruitment niche and therefore has partially additive effects on total adult abundance. Desert winter annuals may be a good example for this case, but at the same time, suggesting that the contribution of such ephemeral species groups to overall ecosystem productivity could be small.

Clearly, it matters whether adults or juveniles are driving niche dynamics. By definition, functional niches, which involve adult phenotypes and distinct resource use by adults, will necessarily leave imprints on ecosystem function and response to climate. For temporal storage effect niches driven by seed and seedling traits, the ecosystem effects are not so obvious. However, as a start, we can look at how

different recruitment niches are associated with the evolution of distinct environmental sensitivities.

8.4 EVOLUTION OF FUNCTIONAL REDUNDANCY

As a fundamental consequence of the gradualist nature of Darwinian evolution, closely related species are, by and large, highly similar (Darwin 1859). With similar resource requirements, consumers and climate sensitivities, closely related species are integrated into the material and energy flows of ecosystems in similar ways, so that redundancy in ecosystem function is often generated by close relatives (Woodward and Kelly 1997). Furthermore, increasing evidence indicates that the line between functional redundancy and complementarity is drawn generally at the genus level (Kelly *et al.* 2008, Queenborough *et al.* 2009, Kelly *et al.* 2010, Burns and Strauss 2011). It is therefore of interest that congeneric species comprise on average 30% of woody communities worldwide (Figure 4 in Kelly and Bowler 2005). In the widespread distribution around this average, the hyper-diversity of tropical forests produces both higher percentages and much higher numbers of co-occurring congeners (e.g. México: 86 of 191 spp.; Panama: 121 of 220 spp.), signifying considerable potential redundancy in ecosystem function and services. We suggest that coexisting congeners are often the product of sympatric/parapatric speciation enabled by temporal niche dynamics, with implications for the action of redundancy in ecosystem function.

There is a developing consensus that sympatric and parapatric speciation predominate in biodiversity hotspots, although the prevalence of specific paths to speciation may differ with geography (Couvreur *et al.* 2011, Warren *et al.* 2011, Keller and Seehausen 2012, Hughes *et al.* 2013). Sympatric speciation requires environmental heterogeneity and genetic variability, with opportunities for genotypes of differing sensitivity to this environmental heterogeneity to become reproductively isolated while maintaining coexistence (Dieckmann and Doebeli 1999). This contrasts with allopatric speciation, produced when a physical barrier of distance or geography disrupts gene flow between two subpopulations, with subsequent adaptive divergence (Mayr 1942). Divergence in sensitivity is not an essential outcome of physical separation, but can evolve secondarily by coevolutionary character displacement when reproductively independent sister species are geographically reunited (Schluter 2001).

The same sort of differential sensitivity to the environment that can allow sympatric speciation also supports temporal niche dynamics,

but temporal dynamics alone do not lead to sympatric speciation. An additional requirement is that differential sensitivity be linked to a mechanism of reproductive isolation (Doebeli and Dieckmann 2003). For example, anti-correlated seed production between years could stabilise the coexistence of two species, but would not promote sympatric speciation unless flower production is also anti-correlated to prevent gene flow between different sensitivity types. However, flowering in forest trees is notably correlated across years (Kelly 1994), for a number of good reasons (e.g. Iwasa *et al.* this volume, Satake *et al.* this volume), making this an unlikely route for reproductive isolation. On the other hand, within-year differences in the timing of reproduction, correlated with resource-use differences, have been shown to support sympatric speciation (Savolainen *et al.* 2006, Rymer *et al.* 2010). The necessary conditions for sympatric speciation have been more tightly connected to resource use in the tropical tree genus *Bursera*, where the association of ecological sensitivity and reproductive isolation is evident in the potentially pleiotropic control of environmental response traits (germination and vegetative bud-break) and flowering period, which in turn are reflected in local distribution patterns (Kelly *et al.* this volume).

Irrespective of the mechanism for reproductive isolation, the evolution of functional redundancy rests fundamentally on the divergence of seed/seedling niches, without concomitant change in adult ecology. The evolutionary record suggests a flexibility in seedling traits that exceeds that of adult traits. While the latter are very closely tied into phylogenetic groups and the majority of functionally relevant traits, seedling characters are not (Wright *et al.* 2000). In addition, we commonly see distinct recruitment traits, involving such factors as seed size, dispersal syndromes, and germination requirements, in groups of coexisting congeneric species (e.g. *Vaccinium* in Newfoundland tundra, Vander Kloet and Hill 2000; *Acacia* in Australian eucalypt forests, Brown *et al.* 2003; *Ephedra* in North America, Loera *et al.* 2012). Taken together, these lines of evidence signify that different seedling types can produce similar adults.

Combining the larger pattern of clade development documented in Williams and Kelly (unpublished manuscript) with the model of speciation in Kelly *et al.* (this volume) builds a picture of the physical directionality of evolutionary change. In the tropical dry forest of México, gradient analysis shows a proliferation of lineages of increasingly derived species from more to less benign conditions both locally and across the landscape (Williams and Kelly 2013, Williams and Kelly unpublished manuscript). In Kelly *et al.*'s speciation model, sympatric speciation into distinct temporal niches occurs most readily by way of a sensitive parent species giving rise to a more resistant daughter species. This occurs because recruits of the sensitive type are unable to survive harsh years, but the resistant type is not physiologically excluded from years that are more benign. Therefore, the resistant type has competition-free intervals in which it can grow from a low number but the competitive type does not. The directional selection on tolerance that leads to speciation also leads to greater resistance in the daughter species, supporting year-type specialisation and continued sympatry, but also allowing the daughter species to expand into new, harsher habitats.

Kelly *et al.*'s (this volume) model, together with the distributional data from México dry forest, thus point to a specific chain of events in the process of speciation from temporal dynamics. That is, when a new, more tolerant species first arises, it owns a fundamental recruitment niche that overlaps with the parent species', but also includes conditions that are harsher than the parent can withstand. The *realised* recruitment niche of this new species is likely to be narrower than that of its parent, however, due to the greater competitive ability of the parent in most of its fundamental niche. Persistent exclusion of the daughter species from more benign conditions may lead eventually to further evolutionary separation and specialisation to the conditions of the realised niche, but the extent to which this leads to a narrower fundamental niche is an open question (Grime 1994).

In the larger context of climate change at the scale of glaciation cycles and tectonic uplift, this model meshes well with the frequently observed pattern of increased speciation rates coinciding with increased aridity (Axelrod 1972, Axelrod and Raven 1985, Becerra 2005, Hampe and Petit 2005, Valente *et al.* 2010, Metcalf and Nash 2012). A turn to more arid conditions would provide more exclusive habitat for incipient species and accelerate the establishment of secure population sizes. Patterns of current distributions in North American *Ephedra* are consistent with this scenario of climate-responsive radiation in the context of temporal niches (Loera *et al.* 2012), as are a number of genera from México dry forest (*Bursera, Caesalpinia, Lonchocarpus* and *Croton;* Williams and Kelly unpublished manuscript) and African rainforest (*Isolona* and *Monodora*; Couvreur *et al.* 2011). Within these groups of congeners, extant sister species predominantly share the same climate bracket, with overlapping or nested distributions across the same landscape, but distinct habitat preferences or dispersal syndromes. At the

next deepest node, pairs have less overlap, or are parapatric with each other, but in all cases, the general direction of adaptive radiation is from conditions that are less arid to those that are more arid.

Thus, the feasibility of stable, temporal niches at the micro-evolutionary scale sets in motion a cascade of evolutionary dynamics that can result in the accumulation of functional redundancy within a climate zone. More than just explaining the evolutionary origin of functional redundancy, this model predicts consequences for the presumed insurance function of redundancy in the context of species loss and modern climate change. First, lineages that have evolved in this way are expected to increase environmental competence with each additional species and, as a group, should have a greater capacity for maintaining ecological function under climate change than lineages prevented from adaptive radiation. That said, an alternative to speciation is the evolution of exceptional phenotypic plasticity or genetic diversity (e.g. *Arabidopsis thaliana*; Lasky *et al.* 2012). Nonetheless, insurmountable functional tradeoffs and inescapable hybridisation may constrain niche opportunities for most species. Second, species that evolved recently in sympatry are more likely to have largely overlapping fundamental niches, and thereby the greatest capacity to substitute for one another in space and time, should one species become extinct. Last, in older lineages, species loss has asymmetrical consequences on ecosystem function: the loss of the more derived, more tolerant species is expected to reduce the environmental competence of the lineage more than the loss of less derived, more competitive species. Thus, the conversion of natural forest into plantations of species composed of the most productive of congeners may come at the price of reduced climate adaptation.

8.5 CONCLUSIONS

The framework for the role of niche dynamics in ecosystem function and climate response presented here consists of a hierarchical structure involving two factors. First are functional niches, expressed in the traits of adult phenotypes and exhibiting a high degree of phylogenetic signal (Blomberg 2003, Losos 2008a, b). Second are recruitment niches, needed for the stable coexistence of functionally redundant, closely related species and supported by the greater responsiveness of seed and seedling traits to environmental variability (Figure 8.1). Our purpose has been to examine the implications of this framework for ecosystem productivity, stability, sensitivity to species loss and climate adaptation.

More succinctly, what is the role of functional redundancy in natural communities?

For the system of redundancy we have outlined here, we perceive no necessary or immediate impact on ecosystem productivity. Instead, we suggest that temporal niche processes have provided long-term functional stability through generating species that as a group inhabit a wider range of recruitment niches for a given plant functional trait (PFT). Rather than subdividing the ancestral niche, which could potentially increase the extinction risk to individual species, we suggest that speciation supported by temporal processes expands out from the ancestral recruitment niche based on novel or new combinations of reproductive traits. Published geographical distributions of a number of genera support this inference (cited above).

This mechanism of speciation could also support the persistence of ecosystem function in the face of contemporary climate change, at least for as long as fundamental functions of the adult phenotype remain viable. A broad portfolio of recruitment niches cannot rescue a group of species if it no longer has a viable adult phenotype, but it may decrease the chance that an entire PFT becomes locally extinct for failure to recruit. A broad recruitment portfolio may also increase the chance of successful geographical range shift, as some sympatrically evolved recruitment syndromes may be well suited for long-distance dispersal and establishment in novel terrain. Not all functionally redundant species would be expected to persist or to migrate successfully under contemporary climate change, least so species with the most highly specialised recruitment niches. However, our point is that directional evolution towards increased tolerance and generalism within a clade heightens the chance of that clade enduring climate change. This may in fact provide some explanation as to why supergenera exist and contribute disproportionally to redundancy in ecosystems. A genus that is genetically or ecologically predisposed to respond to temporal environmental variation by sympatric speciation may experience both an accelerated speciation rate and reduced extinction risk under climate change.

We believe the evolutionary process of temporal dynamics and congeneric proliferation to be widespread and important but, patently, not all plant genera have undergone this sort of adaptive radiation. Similarly, not all plant supergenera need to have arisen from temporal niche processes. The primary issue is that we have outlined a coexistence and speciation process that generates testable predictions of large-scale species distributions and local-scale ecology with direct relevance to ongoing and future ecosystem function.

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