MECHANISMS OF PLANT COMPETITON

Plant competition, temporal niches and implications for productivity and adaptability to climate change in water-limited environments

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Summary

1. We review plant competition in water-limited environments with focus on temporal niche dynamics and examine implications for diversity–productivity relationships and the response of ecosystem productivity to changes in water availability. The main theses under examination are that (i) plant functional types (PFTs) have distinct resource pulse use and coexist through mechanism of temporal resource use complementarity; and (ii) species of same PFT (functionally redundant species) coexist through distinct recruitment niches.

2. In water-limited systems, opportunities for plant resource uptake and growth fluctuate through time, dependent on precipitation patterns. Species differ in the sensitivities of germination, seedling mortality and adult productivity to pulses of water availability, and this generates opportunity for temporal niche diversification. We illustrate this in two case studies.

3. Case study I. Savannas: This is an example of niche separation between two distinct plant functional types (PFTs), trees and grasses. Several models suggest that the two PFTs have complementary resource pulse use, which regulates their abundances, but other models suggest that tree abundance is regulated by the narrow recruitment niche of trees. Overly restrictive recruitment niches can cause a mismatch between resource availability, PFT composition and ecosystem productivity.

4. Case study II. The tropical dry forest: Here, we examine niche separation between closely related species of same PFT. These species commonly have distinct temporal recruitment niches based on differences in seed and seedling traits. A diversification of recruitment niches may be necessary for sympatric speciation and has the effect of broadening of the recruitment 'portfolio' of a phylogenetic lineage and PFT.

5. Synthesis: Functional diversity, characterized by differences in adult resource use, optimizes ecosystem function in a pulsed resource environment only if PFT abundances are regulated by adult resource use. Regulation through recruitment niches tends to uncouple plant productivity from resource availability. However, we hypothesize that a diversification of recruitment niches within PFTs may help alleviate recruitment limitations and help communities attain a PFT composition that optimizes resource use and permits adaptation to climate change.

Key-words: climate change, diversity–productivity relationship, relative nonlinearity, resource pulse, savanna, storage effect, tropical dry forest, water use efficiency

Introduction

The availability of liquid water in terrestrial ecosystems is the primary factor limiting the growth of land plants (Rosenzweig 1968; Chapin, Matson & Vitousek 2012).

Where water limitations are strongest, in arid and semi-arid environments, plants grow only during those parts of the year in which water availability meets some minimum level. At other times, plants are able to do little more than minimize losses. Integrating these intermittent and year-to-year highly variable processes of plant growth, reproduction and death into one coherent theory of community

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and ecosystem function has been a major challenge to ecologists, and opinions remain divided on the role that competition and stable coexistence through niche diversification plays in communities strongly limited by water (Grime 1979; Fowler 1986; Chesson & Huntly 1997; Goldberg & Novoplansky 1997; Brooker 2006).

An increase in water limitation has elicited significant expectations of ecological pattern change in ecosystems. These are (i) species become less competitive and more stress resilient (Grime 1979); (ii) competitive interactions decline while facilitative interactions increase (Bertness & Callaway 1994); (iii) density-independent effects on plant fitness become stronger, while density-dependent effects become weaker (Huston & McBride 2002); and (iv) because species must pass through increasingly narrower environmental filters, species trait diversification declines in general (Kleidon & Mooney 2000). These expectations paint a picture of plant resource niches becoming more similar and potentially less stabilizing (more neutral) in water-limited environments, implying that, within the deterministic limits of species tolerance to a climate regime, community dynamics are essentially driven by the random effects of weather and disturbance.

Nonetheless, we are of the view that water limitations do not in fact change the rules of evolutionary and ecological games. This is not to say that water limitations are unimportant. On the contrary, fluctuations in plant-available water are ubiquitous in the vast majority of terrestrial environments, key to community structure and a major engine of terrestrial plant diversification (Beerling & Woodward 1997; Vaten & Bergmann 2012). In the following pages, we review mechanisms and population dynamic consequences of niche differentiation involving the use of water, and examine the hypothesis that, on a fundamental level, they correspond to temporal niches, stabilized through typically high variability in precipitation.

Our second goal is to ask 'so what'? Is there anything in this approach that helps us address some of the prominent ecological issues of our time: What is the relationship between biodiversity and productivity and how will communities respond to climate change?

Under classic niche concepts, coexistence, productivity and adaptability to change are closely interrelated. According to niche theory, species vary in the use of multiple resources, including materials, space, time and light energy in plants. Stable coexistence is the result of no species being able to pre-empt resource to levels that are intolerable for any other species in the community (MacArthur & Levins 1967), which assures the persistence all species, barring random extinction at very low population size. Furthermore, theoretical models predict that communities self-organize in manners that tend to maximize resource use and ecosystem productivity (Tilman 1999). The most productive species in a given resource regime are expected to become most abundant, but any resources they leave over are utilized by other, differently specialized species, for example shade tolerant herbaceous species growing in the shade of trees. On this basis, the productivity advantage of more diverse communities is understood to be caused by (i) an abundance distribution skewed towards the most efficient users of limiting resources (the 'sampling' effect) and (ii) by resource use complementarity among species assuring that resources are maximally exploited (the 'complementarity' effect; Loreau 2000). The same principles dictate that diverse communities can adapt to change; competitive interactions will assure that the most efficient resource users under any resource regime rise to the top of the abundance ranking.

Below we examine the strength of these ideas in the context of competition under water limitation and involving temporal niches. It is not our purpose to examine to what extent plants are limited by or compete for water versus nutrients (Hooper & Johnson 1999), rather, we focus on the fact that the uptake of water, nutrients and CO_2 for growth are tightly coupled and highly variable over time. We also do not rule out that species may additionally differ in the uptake ratios for various resources and that this may create additional opportunities for stable coexistence (Tilman 1982).

In contrast to spatial niches or niches based on the differential use of multiple resources, the exploration of temporal niches in the context of ecosystem function have been limited (Doak *et al.* 1998; Yachi & Loreau 1999; Norberg *et al.* 2001; Chesson, Pacala & Neuhauser 2002). In one context, temporal niches have been evoked to explain the stable coexistence of 'functionally redundant' species in communities (Loreau 2004). These are species that are nearly identical in the ecosystem interactions and belong to the same plant functional type (PFT). Their presumed function is to provide insurance of uninterrupted ecosystem function in the face of risk to individual species (Walker 1992; Naeem 1998). By filling in for one another, redundant species are thought to stabilize ecosystem function, so long as species differ in sensitivity to environmental or biotic factors that cause populations to fluctuate (Hector *et al.* 2010). Below we suggest that this scenario is most likely realized when species are closely related but have evolved distinct temporal recruitment niches. In another context, temporal niches have been associated with species' rates of primary production varying asynchronously over time (Yachi & Loreau 1999). In this scenario, a diversity of species with distinct temporal niches do more than just substitute for one another but can raise average ecosystem-wide productivity over time. We suggest that this scenario corresponds to mature adults using water pulses in distinct ways.

We evaluate these postulates with the help of two case examples, one focusing on the interactions between two PFTs, trees and grasses in savannas, the other on interactions between members of the same PFT; congeneric tree species coexisting in a tropical biodiversity hotspot. We start with a general review of plant–water interactions and the kind of traits involved in diversifying the use of fluctuating resources.

Two-phase resource dynamics and temporal resource niches

Goldberg & Novoplansky (1997) coined the term 'two-phase resource dynamics' to describe fluctuations between phases of resource abundance and paucity, usually at an annual scale. During the 'pulse phase' water is in sufficient abundance to allow water and nutrient uptake, carbon accumulation, growth and competition. In the 'interpulse phase', resource uptake ceases, and plants tend to lose live biomass by respiration, abscission, consumption or death. The model is closely related to the pulse–reserve paradigm at the ecosystem level, with pulse periods causing brief periods of production into ecosystem stores that then rapidly decay, except for well-protected biomass that persists and allows plants to respond to the next pulse phase level (Noy-Meir 1973).

Resource fluctuations of this magnitude make it necessary for species to concentrate growth and reproduction into the pulse phase, and devise mechanisms for preserving gains in plant or population size during the interpulse phase. Different types of plants will handle the transitions from one mode to the other in different ways and at different times (Noy-Meir 1973). For example, ephemerals concentrate primary production in the wettest phase of the pulse period and survive interpulse periods as seeds. Woody perennials generally maintain primary production for longer, using the tail end of the resource pulse to a greater extent and survive interpulse periods in vegetative form. Thus, one form of temporal niche separation in water-limited environments is produced by plants being photosynthetically active at different times and by differing in the rates of resource uptake as a function of water availability during those times (Ogle & Reynolds 2004).

For species with substantial differences in morphology, anatomy and physiology, that is for different PFTs, differences in the timing of resource uptake are probably inevitable because of a number of trade-offs. Traits that maximize resource uptake under some conditions, often limit resource uptake at other times (Givnish 1986; Smith, Monson & Anderson 1996; Schwinning & Ehleringer 2001; Schwinning et al. 2004). For example, shallow roots, a low root/shoot ratio, high maximal leaf conductance, are some of the traits that facilitate rapid water uptake and high rates of photosynthesis during the peak pulse phase when soil near the surface is frequently saturated with water. But these traits often constrain the ability to express other traits (e.g. deeper roots, cavitation-resistant xylem, osmoregulation, low leaf conductance at full stomatal closure) that allow growth under lower soil water potentials and when most remaining water is stored deeper in the soil.

Plants do not start life as fully-fledged adult phenotypes, however, and there are other dimensions of water use differentiation that are apparent only when considering the entirety of the life cycle. Species differ greatly in the degree or type of seed dormancy, requirements for breaking dormancy and for initiating germination, which together determine when and in what numbers seedlings appear on the scene (Brown & Venable 1986; Humphrey & Schupp 1999; Bowers, Turner & Burgess 2004; Adler & Levine 2007). Early seedling development also takes very different routes for different species, notably in patterns of root growth, storage allocation and hydraulic architecture, which affect early survivorship odds (Canham et al. 1999; Padilla, Miranda & Pugnaire 2007; Padilla & Pugnaire 2007; Kursar et al. 2009; Leon et al. 2011). In general, trade-offs between maximal growth rate and tolerance to stressful conditions in seedlings are well documented across climate zones from tropical forests (Poorter & Markesteijn 2008) to deserts (Pake & Venable 1995; Angert et al. 2007; Kimball et al. 2010) and temperate forests (Beckage, Lavine & Clark 2005).

The same traits that govern responses to a single pulse–interpulse cycle also make species differentially sensitive to interannual variation in pulse intensity, length or consistency. The well-studied population dynamics of Sonoran winter annuals provide a good example. Germination in these winter annuals is differentially sensitive to temperature, so that some species consistently peak earlier in the year than others (Adondakis & Venable 2004). 'Early' species are characterized by high water use efficiency (WUE) and low relative growth rate (RGR), thought to be an adaptation to growing conditions more limited by temperature than by water (Huxman et al. 2008), and reversely for 'late' species. These differences in physiology translate into differential sensitivity to year types, such that 'early' species achieve relatively higher fitness in years with small rainfall events and colder temperature until late in the season, while 'late' species respond more positively to years with large rainfall events (Kimball et al. 2012).

Random, interannual rainfall variability, affecting the onset, length or intensity of the rainy season is inherent to all water-limited ecosystems (Loik et al. 2004), but there is also variability on longer than annual time-scales that may be of additional significance to plant fitness and the characterization of temporal niches. In many tropical and subtropical regions, interannual rainfall variability has a quasi-periodic component, the El Niño-Southern Oscillation (ENSO) with a return time of 2–7 years (Collins et al. 2010). Quasi-periodicity implies temporal autocorrelation in weather patterns, such that an exceptionally wet year has a higher probability of being followed by another wet year, but can also change rapidly from one extreme regime to another (Stechmann & Neeln 2011). This can amplify environmental effects on plants. For example, the cumulative effects of two drought years in a row are harder on plants than when drought years are separated by average years (Martiny, Richard & Camberlin 2005). Conversely, two exceptionally wet years can produce recruitment spikes in species that otherwise rarely recruit through the combination of high seed production in the first year and high emergence in the second, or high emergence followed by high survivorship over 2 years (Allen et al. 2008; Rossi et al. 2012). A wet year following

an exceptionally dry year will often reduce predation pressure on plants, because consumer numbers will be low (Williamson & Ickes 2002; Yang *et al.* 2010), but a dry year following an exceptionally wet year can have negative effects by increasing fire probability and intensity due to fuel accumulation in the previous year (Brown & Wu 2005; Ghermandi *et al.* 2010).

El Niño-Southern Oscillation return times and amplitudes are themselves variable and may fluctuate on centennial time-scales, possibly related to global temperature trends. On this time-scale, the waxing and waning of community components can be observed, presumably linked to species' abilities to utilize strong ENSO patterns (Donders *et al.* 2005; Lim & Fujiki 2011), and it is possible that for some long-lived, slow-growing community components, this is the relevant time-scale for observing population regulation. It is still a matter of debate whether anthropogenic climate change will accentuate or dampen ENSO anomalies (Nicholls 2008; Collins *et al.* 2010), but it is widely expected that pattern change in precipitation will be at least as important to communities as shifts in average temperature or precipitation (Knapp *et al.* 2008; McCluney *et al.* 2012). A ubiquity of temporal niche dynamics in water-limited ecosystems explains why this would be.

Nonetheless, it is not widely accepted that water-limited systems are governed by temporal niches. One of the most common misconceptions about water-limited environments is that, because of the brevity of competitive interactions, the harshness of the interpulse period, and the typically low plant densities, interplant competition is less important for community dynamics than purely environmental effects on vital rates (Kikvidze & Brooker 2010). A related argument is that, because population fluctuations are often positively correlated over time, distinct temporal niches do not therefore exist (Houlahan *et al.* 2007). The confusion over this issue should have been laid to rest by Fowler (1986), Chesson & Huntly (1997) and Kelly & Bowler (2002), among many others. However, the persistence of these views suggests a lingering disconnect between perception and the relatively unimposing conditions that have to be met to support the case for competition and temporal niches, namely that all plant species have resource-mediated density limits and that species are differentially sensitive to resource fluctuations.

So where does perception go wrong? Lack of water imposes fundamental, physiological limits on plant photosynthesis and cellular survival; therefore, all plant species gain from stronger pulse periods and suffer losses during drought. Relevant to the niche concept is not whether growth is correlated, but whether all species are equally favoured by wet years and equally reduced by dry years, and this possibility is exceedingly unlikely given the differences in pulse use and life histories discussed above. This implies that despite strong positive covariance between species' individual or population growth, species remain differentially sensitive to patterns of moisture fluctuation and therefore have distinct niches.

Second, the life cycle phase most vulnerable in general and arguably most sensitive to competition, is the seedling stage. But this stage is also the least observable, because it is often brief, irregular and/or cryptic. Most seedlings may indeed be killed by density-independent agents, such as pathogens, herbivores or desiccation (Augspurger & Kelly 1984; Goldberg & Turner 1986), but this is not relevant to the question of competition. Relevant is whether the few seedlings that do make it into adulthood, succeed in doing so due to the absence of certain types of neighbours (those with most similar niches) at a critical life stage. Proximity to other plants, seedlings or adults, most often reduce seedling growth and survivorship, either directly or by apparent competition (Fowler 1986). In some circumstances, proximity to an adult perennial can also promote growth and survivorship (facilitation; Brooker 2008). However, for effects to remain net positive over an individual's lifetime, nursed and nurse plant must have distinct plant functional characteristics to minimize competitive interactions (Liancourt & Tielborger 2011; Verdu, Gomez-Aparicio & Valiente-Banuet 2012). This special relationship between some species does not exclude negative interactions an individual will also have with other species. Thus, competition may not be the only possible kind of plant–plant interaction, but it is indeed ubiquitous.

Last, the time-scales relevant to the processes that regulate population interactions in water-limited environments are much longer than the typical length of an experiment or observation. The fact that decadal observations are required to examine population regulation even in short-lived plants such as desert annuals suggests that the relevant observation period for long-lived perennials could be in the hundreds of years (Fernandez-Illescas & Rodriguez-Iturbe 2003; Angert *et al.* 2009; Moustakas *et al.* 2009).

These misconceptions are noteworthy, because they have important connotations for the future of water-limited ecosystems under climate change. As the following case examples will illustrate, how plants interact, particularly whether communities and ecosystems are regulated by processes at recruitment or mediated by interactions between resources and mature adults all have bearing on diversity–productivity relationships and adaptability to climate change.

Case study I: competition between trees and grasses in savannas

The scientific literature on savanna ecology is vast, but there are several excellent reviews of which we make extensive use here (Scholes & Archer 1997; House *et al.* 2003; Sankaran, Ratnam & Hanan 2004; Sankaran *et al.* 2005; Bond 2008). Resolving the 'savanna conundrum', as it has been described (House *et al.* 2003), is not our goal, but the continuing, lively discussion surrounding savanna dynamics provides an excellent perspective on how difficult it can be to identify stabilizing niche processes in natural

communities in spite of much that is known about individual species or PFTs.

Competitive effects of grasses on trees, both on seedlings and adults, as well as competitive effects of trees on grasses have been confirmed in experiments, although the details vary greatly with climate, soil and the species characteristics of the trees and grasses involved (Scholes & Archer 1997). Opinions about which mechanisms are responsible for maintaining the tree/grass balance of savannas are equally diverse but can be divided into three sorts of models (Sankaran, Ratnam & Hanan 2004): (i) those that assume complementary resource use; (ii) those that assume complementary resource use but allow a role for disturbance (grazing, browsing, fire) to shift the competitive balance; and (iii) patch models with fluctuating rates of colonization. There is also a hypothesis rejecting any form of stable coexistence between trees and grasses and looks upon savannas as transient communities on their way to becoming either stable grasslands or woodlands, but are frequently interrupted in their successional trajectory (House *et al.* 2003; Sankaran, Ratnam & Hanan 2004). This model is considered least likely by many savanna experts (e.g. Scholes & Archer 1997), as it is hard to explain why, without density regulation, ecosystems should not eventually converge on a climax state, since even a long and frequently interrupted process of succession should eventually be completed.

A good example of a model with resource niche complementarity is Walter's (1971) two-layer hypothesis, the first mechanistic savanna model. Walter interpreted natural savannas as stable associations of grasses and trees maintained by complementary use of water. Grasses, in the model, are superior competitors for water stored in the top layers of the soil, due to their higher root density and more pronounced growth response to water, but only trees have access to water stored in deeper soil layers. Thus, by proposing a mechanism that restricts the pulse use of each species, the two-layer hypothesis explains not only why trees and grasses can stably coexist, but also temporal and geographical correlations between annual precipitation and vegetation trends: Stronger pulses or winter rainy season with deeper water infiltration favour trees; smaller pulses or summer rainy season that do not result in subsurface recharge favour grasses (Walter 1971; Ogle & Reynolds 2004; Sankaran *et al.* 2005; Notaro 2008). Other models stress different kinds of resource use complementarities, for example between light capture (trees superior) and capture of soil resources (grasses superior; Scheiter & Higgins 2007), or between resource capture in the early (trees) and mid pulse phase (grasses) based on differences in leaf phenology (Westoby 1980).

The model of Scheiter & Higgins (2007) is one of deterministic coexistence, analogous to the Lotka Volterra competition model, and does not require spatial or temporal variation to facilitate coexistence. The models of Walter (1971) and Westoby (1980) are temporal niche models.

Although Walter's two-layer model is often referred to as an example of a spatial (vertical) niche model, it is truly a temporal niche model because of the fundamental relationship between infiltration depth and precipitation patterns. All three models assume that savanna dynamics are regulated through the interactions and trait characteristics of mature trees and grasses.

Two general kinds of temporal coexistence mechanisms have been described by Chesson (1994). One is called 'relative nonlinearity of competition' and is based on complementarity in species' rates of resource uptake as a function of resource availability (specifically, the functions that describe growth as a function of resource availability must have different shapes). This general coexistence mechanism may be the best fit for the verbal models of Walter (1971) and Westoby (1980), since it explains how coexistence can be accomplished through differences in the sensitivity of resource uptake to resource levels in persistent community members, i.e. mature adults. However, fairly specific criteria must be met for this model to deliver stable coexistence (Chesson 2000), and to our knowledge, whether trees and grasses meet these criteria has not been tested.

A criticism of purely resource use–oriented models is that they predict a monotonic relationship between average annual precipitation and average tree cover, whereas in reality, only maximal tree cover appears to be bounded by climate, while actual tree cover varies widely within those bounds (Fig. 1; Sankaran *et al.* 2005). The discrepancy is most often attributed to fire and/or herbivory, which affect tree recruitment selectively. Thus, another class of savanna models attributes the stable coexistence of grasses and trees to recruitment processes (Bond & Keeley 2005). Patch models fall into this category, in which recruits compete for patch possession (Higgins,
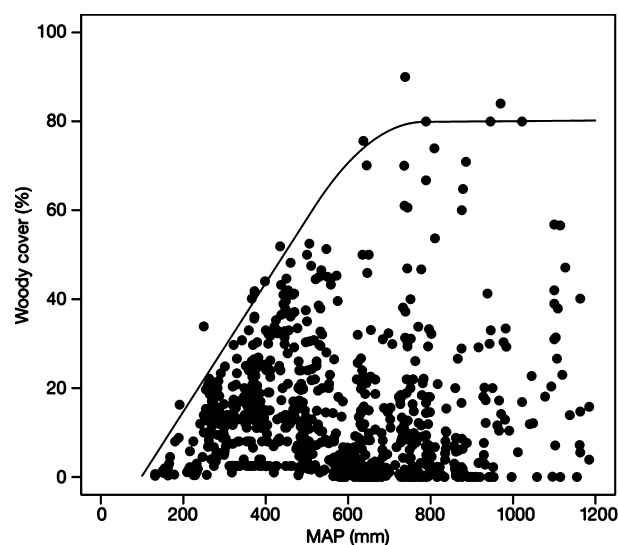

Fig. 1. Woody cover of African savannas as a function of mean annual precipitation (MAP). Data are from 854 sites across Africa. From Sankaran *et al.* (2005).

Bond & Trollope 2000; Fernandez-Illescas & Rodriguez-Iturbe 2003; Moustakas *et al.* 2009). For example, in the model by Fernandez-Illescas & Rodriguez-Iturbe (2003), soil moisture fluctuations switch competitive hierarchies between grass and tree colonizers. In the model by Higgins, Bond & Trollope (2000), tree recruitment success varies with rainfall amount and fire intensity, and the joint effect of water and fire on recruitment is amplified by the fact that good conditions for seedling growth rarely coincide with low fire intensity, because high rainfall stimulates grass growth, which in turn increases fire intensity.

These 'demographic bottleneck' models fall into the other category of temporal coexistence mechanism, the 'storage effect' (Chesson & Huntly 1997). Coexistence is stabilized through distinct recruitment niches and the existence of long-lived, relatively insensitive adults. Importantly, these types of models do not require complementary resource use by adults to enable stable coexistence. In fact, adult pulse use patterns could be identical or vary independently of the recruitment niche. It has not been lost on savanna experts that the control of community dynamics by recruitment processes has the potential generate a mismatch between climate and vegetation (Bond & Keeley 2005).

The presence of savanna biomes where climatically there should be forests is often attributed to the special characteristics of C_4 grasslands, which evolved relatively recently (3-8 million years ago), coinciding with the rise of fire as a regular occurrence. Fire is thought to have prompted the expansion of C_4 grasslands into forests and was then followed by the evolution of fire tolerance in both savanna trees and grasses (Scheiter *et al.* 2012). But one has to wonder if there is a more general dynamic brought to light by the savanna example, one in which ecosystem function is regulated by differences among recruits more so than differences in the resource use of adults.

Quite generally, the storage effect mechanism has the potential to uncouple ecosystem productivity from climate drivers. Ecosystem productivity is governed by the joint resource use of adult community members, but adult densities and species composition is governed by recruitment, which depends only in part on adult productivity through seed production, and to another part on independent climate effects on seed germination and seedling survivorship.

Thus, when the effects of climate on seedling competition begin to outweigh the effects of climate on adult growth and seed yield, diversity-productivity relationships become somewhat uncertain.

For species that have weak differentiation in adult function, recruitment niches and the storage effect are among the few mechanisms that can deliver stable coexistence. This suggests a special role for the storage effect in speciation, since no two species are more alike than those that have recently diverged. This is the topic of our next case example.

Case study 2: competition between congeneric trees in tropical dry forests (TDF)

Tropical forests are communities of such extraordinarily high diversity that it is hard to imagine that each tree species has a distinct resource niche. There has been debate as to whether functional redundancy really exists (Loreau 2004), but if we find it at all, we would find it among closely related tree species of the tropical forest biome. Even world-wide, 30% of woody plant species diversity is due to the co-occurrence of congeners, with tropical forests having 50% or more of their species in congeneric pairs or groups (Kelly *et al.* 2001; Kelly & Bowler 2005). Although species within ancient, deeply divergent genera may notably differ (Beltran, Valiente-Banuet & Verdu 2012), on the whole, genera describe monophyletic groups and are expected to be similar simply as a function of the gradualism of Darwinian evolution (Darwin 1859; Felsenstein 1982, 1985; Harvey & Mace 1982; Losos 2008; Jablonski & Finarelli 2009a, 2009b).

If temporal recruitment niches exist, they should make themselves be known in anti-correlated population growth. The population dynamics of trees can be inferred from analysis of age or size structure. For example, after discounting for annual mortality across size classes, an over-abundance of trees in the *i*'th age class suggests the existence of a particularly strong recruitment cohort *i* years ago. An application of this analysis to co-occurring species pairs in a TDF in Mexico showed that that most closely related congeners have anti-correlated population fluctuations, that is, whenever one species had a strong recruitment interval, the other had a weak one, and *vice versa* (Fig. 2; Kelly & Bowler 2002). This finding is all the more
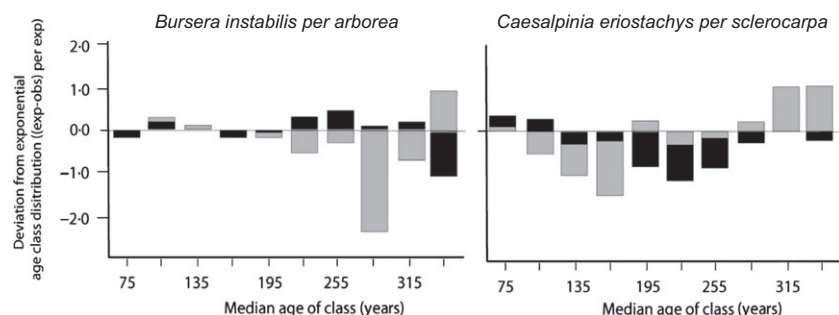

Fig. 2. Deviations from expected exponential age class distribution. Grey bars represent the rarer of the two species (*B. arborea* and *C. sclerocarpa*). Adapted from Kelly & Bowler (2002).

significant since, because of the very high species diversity in this forest, average competitive interactions between any two species must be very weak. Contrary to neutral theory, which hypothesizes that all forest trees are competitively equivalent (Hubbell 2005), this and subsequent analyses of the fractional abundance of species pairs demonstrate that most closely related congeners do not have random competitive relationships; on average, they compete more strongly with each other than with any other tree species in the forest (Kelly *et al.* 2008, 2010).

These findings support the hypothesis that functionally redundant species substitute for each other on the basis of temporal niches and the storage effect model of coexistence, but do not explain how the mechanism works biologically.

There is no compelling evidence that congeneric trees have asynchronous fluctuation in seed production, on the contrary, interannual fluctuation in reproduction in forest trees is notably correlated across years (Kelly 1994; Kelly & Sork 2002). Therefore, seed and seedling traits must be considered for explaining anti-correlated recruitment. The common trade-off between potential growth rate and stress tolerance in seedlings (Poorter & Markesteijn 2008) is expected to enhance asynchronous recruitment fluctuations, as follows: The faster-growing species will grow particularly well in 'good' years, which sets up a size advantage against more-tolerant species that germinated in the same year. In 'average' years, the faster-growing species rarely survives, but the more-tolerant species does and gains size. In the first few years, seedlings are often too small and widely spaced to influence each other's growth rates. Therefore, actual competitive interactions probably occur between surviving saplings many years after establishment and even before the canopy opens to allow one sapling to ascent into the class of overstory trees. Any size advantage obtained up to that point, either by unequal initial growth rate and asymmetric competition for light (Schwinning & Weiner 1998) or simply by late arrival will work to select the ultimate winner of the canopy gap. Thus, faster-growing species recruit more often after emerging in a 'good' year and more-tolerant species more often after emerging in an average year. All else being equal, this dynamic would lead to the expectation that the faster-growing species is less abundant than the more-tolerant species (Kelly & Bowler 2002, 2005).

Nevertheless, it is remarkable that alternating recruitment between congeners is observable at all. It implies an especially high potential for competitive interaction ('focused competition'; Kelly & Bowler 2005), the nature of which is not well known, but is likely to be related to the overall similarity between congeneric species. Seedlings of closely related species may simply be more likely to meet in space and time and when they do, have the same friends and enemies. In distantly related species, other differences between species may frequently overwhelm differences in seedling growth and tolerance. But among species that respond so similarly to a multitude of variable biotic and abiotic factors, a difference along just one axis of specialization has great potential to result in nonrandom recruitment patterns.

The differentiation of recruitment niches among coexisting congeners is an exceedingly common pattern in nature, not specific to any one type of environment (e.g. Vander Kloet & Hill 2000; Wright *et al.* 2000; Liu, Liu & Guan 2008; Kelly *et al.* 2010; Loera, Sosa & Ickert-Bond 2012). As we argued above, this is not coincidental, given the scarcity of other niche mechanisms available to very similar species. But how do such differences evolve? Analysis of species distributions in the Mexican TDF suggests a general mechanism through which the growth/tolerance trade-off in recruitment can evolve in sympatry.

The Mexican TDF has a highly folded topography, with lower elevations being drier and hotter. Phylogenetic analysis has shown that congeners that persist in the harsher, lower end of an elevation gradient are evolutionarily more derived (Williams & Kelly 2013), consistent with the classic ecological expectation that species require more specialized functions to cope with harsher conditions (e.g. Woodward & Diament 1991; Kleidon & Mooney 2000). Thus, species appear to have radiated out from more benign into more stressful recruitment niches. Only this direction of radiation would relax competition by parent on daughter species through escape in time, simultaneously providing the opportunity to also spread out in space (Kelly *et al.* 2013). Directional speciation towards increased tolerance has been suggested for other adaptive radiations (Wright 1999; Onofri *et al.* 2007; Tebbich, Sterelny & Teschke 2010) and is also consistent with the geological development of the Mexican TDF from more mesic origins (Becerra 2005).

This pattern is significant in the context of ecosystem function, since it suggests an evolutionary tendency within lineages to overcome the recruitment limitations of a specific plant functional type in its native environment. It should result in an increase in adult cover and move lineages closer to filling the ecological potential of the shared adult phenotype. It is not unreasonable to think that similar processes may have been at work during the evolution of fire tolerance within lineages of forest trees (Simon *et al.* 2009). What may have begun as temporal recruitment niche separation based on the length of fire-free intervals, could have eventually allowed the more-tolerant species to spread out of wet forests or their ecotones into tropical grasslands.

Based on these considerations, communities with a high degree of functional redundancy should have greater buffering capacity for environmental variation, and potentially greater resilience to climate change since its recruitment portfolio would contain both faster-growing and more-tolerant species. While this has been the stated expectation in the part of the literature that examines diversity–productivity relationships (e.g. Loreau 2000), this adds an evolutionary mechanism, at least in the context of sympatric speciation. However, in communities where
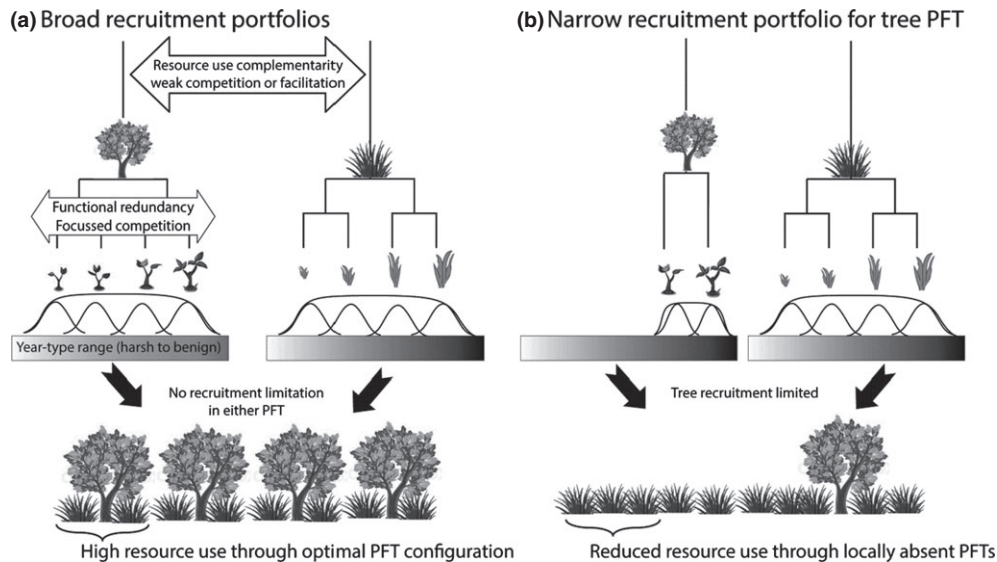
Fig. 3. Illustration of the separate roles of adult function and seedling sensitivity on ecosystem function. Shown are two plant functional types (PFTs), each represented by several functionally redundant, closely related species. We depict deep-rooted tree and shallow-rooted grass PFTs, but this choice is arbitrary, any two PFTs with complementary resource use could take their places (e.g. N-fixers and nonfixers; shade and sun plants, evergreen and drought-deciduous perennials). PFTs have quasi-identical adult phenotypes, which govern resource use efficiencies, interactions with other PFTs, and all other aspects of ecosystem function. By the assumption of resource use complementarity, close spatial associations of different PFTs optimize ecosystem productivity by increasing resource use. Locally reduced PFT diversity reduces ecosystem productivity by letting some resource get away unused (e.g. deeply infiltrated water, light). Functionally redundant species differ from one another in sensitivity to year type at the seedling stage, which affects the relative recruitment potential of germination cohorts; this is symbolized by the bell-shaped curves. The broader curves enveloping the individual bell-shaped curves represent the collective recruitment potentials of PFTs across year types. In panel (a), each PFT has the potential to recruit over a broad range of year types and ecosystem-wide resource use is optimized. In panel (b), the narrow recruitment portfolio of the tree-PFT generates a recruitment bottleneck and reduces tree abundance; available resources are thereby underutilized and ecosystem function is reduced.

functional redundancy is the result of allopatric speciation and secondary sympatry, or convergent evolution in distantly related lineages, there is no a priori expectation of a specific kind of niche structure. In such cases, recruitment variability may often be random, with each functionally redundant species responding idiosyncratically to environmental variation. Without compensatory dynamics enhanced by focused competition in recruitment, we would expect the ecosystem services provided by the PFT not to be particularly well buffered against environmental variation or pre-adapted for climate change, except through the statistical effects of increasing the size of a random sample (Doak *et al.* 1998).

Conclusion and synthesis

Evolution has produced numerous distinct strategies for coping with the conflicting goals of maximizing pulse-growth and interpulse survival, reflected in the traits of adults, seeds and seedlings. These strategies for growth, reproduction and survival generally exclude any one species from pre-empting all ecological opportunities for water and nutrient uptake, resulting in the realization of distinct temporal niches; a great many involve differences in water and nutrient uptake over time.

Temporal niches affect communities in the same way as any other kind of niche; they afford protection from competitive effects for species at low density, so that when and where an individual is infringed upon by a neighbour, at low density, the neighbour will be likely to belong to a different species, have slightly (or greatly) divergent resource needs, and thus exert less competitive suppression than a conspecific would. The difference to other kinds of niches is that they are generally much harder to observe. Temporal niche dynamics imply that competitive interactions fluctuate over time, and in highly water-limited environments, the relevant density-dependent processes may play out during brief as well as sporadic episodes of recruitment, but affect community composition for decades or longer. It is therefore not surprising that the snapshot approach to measuring competitive interactions may leave the impression of weak or neutral competition (e.g. Lamb, Cahill & Dale 2006; Cahill *et al.* 2008; Burns & Strauss 2011, 2012) but see (Daehler 2003).

In rare circumstances, temporal niche dynamics can be inferred from the age structure of populations, as the example from the Mexican TDF illustrated, or from direct long-term observation, as was possible for Sonoran Desert annuals (Kimball *et al.* 2012). In many cases, we will have to continue relying on models and, unfortunately, ad hoc assumptions about regulatory niche processes (Sankaran *et al.* 2005).

In our view, the most essential unresolved question is the extent to which community composition and dynamics

are governed by the characteristics of juvenile or adult stages. Either one, acting alone, is capable of producing stable coexistence according to theory. For temporal niches to be realized by differences in adult phenotype, species must have fairly substantial differences in pulse use (Chesson 2000). It is not farfetched to imagine two PFTs as different as grasses and trees being different enough to meet the fairly stringent criterion of 'relative nonlinearity' of resource use, but almost by definition, this is, much less likely for species within the same PFT, that is, for species with similar overall strategies of water use. For such species, recruitment alternating through time provides another mechanism for stable coexistence.

However, we cannot exclude that juvenile traits and storage dynamics also dominate the population dynamics of contrasting PFTs, as the savanna example suggests. This generates fundamental uncertainty for linking functional diversity to productivity, since it seems that nothing disallows a less productive species having a stronger recruitment niche. An obvious example is the invasion of less productive exotic species into more productive communities attributed to 'propagule pressure' (e.g. Levine *et al.* 2003; Simberloff 2009).

Uncertainty in the relationships between diversity and productivity imposed by different coexistence mechanisms has also been noted by Mouquet, Moore & Loreau (2002) in the context of a model with spatial heterogeneity. In their model, productivity was linked to the spatial sorting of habitat specialists into their habitat of maximal productivity. Coexistence enabled through site variability and lottery competition for empty sites increased the probability of a mismatch between species and habitat, thus lowering overall productivity. In some ways, the distinction we have made here between niche dimensions that concern the resource use of adults and those that concern the recruitment potential of seedlings is related to the differentiation between response and effect traits in PFT classification (Lavorel *et al.* 2007). Response traits govern how populations respond to disturbance and climate change – this is linked to recruitment – while effect traits govern species' contributions to ecosystem function – linked to adult resource use. Hooper *et al.* (2005) observed that response and effect traits may or may not be correlated with one another, creating significant uncertainties for the prediction of climate–vegetation interactions, and this essentially corresponds to our conclusion.

Taking the longer view, evolutionary processes might reduce this uncertainty. Our second case example suggested an evolutionary tendency to overcome recruitment limitations by speciation without concomitant change in adult function. This evolutionary response suggests a mechanism for what is called 'niche conservatism' (Ackerly 2003; Losos 2008): speciation without change in adult function. This process generates functional redundancy and builds a diverse recruitment portfolio. The long-term effect of this evolutionary dynamic should be the removal of overly restrictive recruitment limitations and ultimately

a better match between the environment, functional diversity and primary production at the ecosystem scale. The origin of fire tolerant savanna trees from intolerant forest trees is an apt example of the general principle (Simon *et al.* 2009).

The conceptual framework developed in the preceding pages is summarized in Fig. 3. We have described PFTs as groups of species – often more closely related to each other than to other community members – that contribute to ecosystem function in a complementary manner. This complementarity is a form of niche separation, which reduces competitive interactions and allows stable coexistence among PFTs. Niche diversification based on adult traits and functions are only one aspect of each species' niche, which is shared among functionally redundant species. Species within PFTs are unlikely to coexist through resource-mediated mechanisms, and we suggest that temporal recruitment niches, evolved to separate species along environmental stress axes, are often the key to their stable coexistence. Niche diversification based on seed and seedling traits is therefore the other aspect of each species' niche, one that enables coexistence among species with nearly identical adult function.

The more similar the adults, the more strongly species compete. This focused competition ensures strongly linked, compensatory dynamics, such that poor recruitment in one species facilitates higher recruitment in another. This dynamic steadies PFT abundances and ecosystem function. Therefore, lack of evolved redundancy within PFTs, or secondary species loss, can reduce PFT abundances below their ecological potentials by limiting recruitment (Chesson, Pacala & Neuhauser 2002), with negative consequences for ecosystem function.

Adaptive radiations, which produce functional redundancy, often coincide with shifts in climate regime (Becerra 2005; Warren *et al.* 2011; Scheiter *et al.* 2012). Within plant lineages that profit from climate change, species with ancestral traits do not become extinct, but persist locally or regionally and thus contribute to the maintenance of biodiversity. This builds capacity for buffering against the effects of climate variability within the normal range, as well as resilience against climatic regime shifts, provided that the new regime is not entirely novel. Thus, the key to climate change resilience lies in the capacity of ecosystems to retain species not optimally adapted to present climatic averages, but secure within the community through the stabilizing effects of temporal niche dynamics.

The Milankovitch cycles of the past 2·6 million years, which drove earth in and out of glacial maxima, exemplify the kind of regime shift to which earth's patterns of diversity may be well adapted. However, the projected global changes of the present era will take us into a novel regime (Williams, Jackson & Kutzbacht 2007). Ecosystems of the future are therefore likely to go through a period of maladaptation and reduced productivity, in part because recruitment portfolios may be out of tune with the new range and character of environmental variability (Chapin

et al. 1997; Williams & Jackson 2007). The investigation of evolutionary change in temporal recruitment niches is therefore an important agenda in the spectrum of climate change research.

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