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What temporal processes in trees tell us about competition, community structure and speciation

3.1 INTRODUCTION

This chapter reviews evidence concerning the vital role that temporal dynamics can have in the ecology of trees and other long-lived species in the assembly and maintenance of natural communities. The research synthesised here was stimulated by a desire to determine the action of temporal dynamics in nature, and its implications for the nature of competition, community structure and assembly on multiple scales and across a range of climatic conditions. For the most part, the results discussed concern tropical forests, but we think they provide strong support for a more general view that can be applied across biomes. Finally, we ask if there may be a potential role for temporal dynamics in speciation, in light of what we have learned from the tropical trees.

A field programme begun in the late '90s in the tropical dry forest of México was consciously designed to study the coexistence of closely related species in a very speciose community, but the role of temporal dynamics had not been suspected and its finding was serendipitous. With centuries-long lifespans, decades-long juvenile stages and low population turnover rates, trees are problematic candidates for demographic analyses, either observational or experimental. Unless instant death is involved, the particular hurdle with trees, as with any long-lived organism, is directly connecting any specific response in the early

life of the individual with the long-term individual persistence or character of the standing population. However, trees differ from many long-lived organisms in carrying their history in their structure at both the individual and population levels. Thus, a tree population itself documents individual success over the history of the population (Parker *et al.* 1997, Cole *et al.* 2011). The distribution of a population with regard to physical conditions, size and age structure and relative to other woody species all contain information on the ecology and inter-actions of species (e.g. Veblen 1989, 1992, Villalba and Veblen 1998, Kelly *et al.* 2001) and it was the age structure of populations that revealed the action of temporal dynamics at Chamela Biological Station.

Although not exclusively so, the majority of studies that we discuss in this chapter have focused on forest trees in the tropics, in the interest of acquiring sample sizes sufficient to generalise our infer-ences. A substantial number of these studies examine the relationships between congeneric species forming terminal dichotomies in the phylo-genetic tree of the examined communities. This design utilises the a priori similarity of close relatedness unbiased by pre-existing ecological expectations. In this way, we have been able to identify a general role of similarity in determining species interaction and community assembly. Congeneric comparison is also an analysis that has been well explored as a natural 'all else being equal' comparison of independent contrasts, strengthening the inference that an observed pattern of difference between taxa is attributable to the target factor (Felsenstein 1985, Harvey and Pagel 1991, Harvey 1996).

Congener comparisons also suggest evolutionary processes, and we present results and theory on temporal niche dynamics as a route for speciation, and a potential source of plant 'supergenera'. At the land-scape level, supergenera comprise a small proportion of genera present, but a disproportionate amount of standing mature individuals (Williams and Kelly 2013). From the patterns of change seen across a gradient of temperature and rainfall, we can better understand direc-tional evolutionary change resulting from ecological pressures, and the response of the community to environmental variation.

Finally, we discuss the ramifications of these results. In this, we touch upon the differences and similarities between temporal processes for congeneric and non-congeneric temporal niche partners. We also consider the problem of assessing competitive relationships in light of the effects and increasingly apparent ubiquity of both temporal and spatial storage dynamics in which competitive interaction is condition dependent rather than definitive. Intermingled congeneric species

form a significant proportion of woody communities worldwide (Gentry 1991, Kelly and Bowler 2005); in itself, this number represents a significant proportion of species potentially able to support temporal dynamics, but temporal dynamics may also occur between unrelated species, making its potential impact on ecological process of even greater significance (Mason 2005, Ellis 2007, Chesson *et al.* this volume, Adler this volume, Fowler this volume, Ellis *et al.* unpublished manuscript.)

3.2 POPULATIONS AND COMMUNITIES

Population structure

For mature trees, growth and mortality at any one point in time will vary only gradually in a regular manner across size classes (Johnson and Frier 1989, Hara *et al.* 1991). Thus, if adult mortality rates were the only determinant of age structure in mature trees then the age distribution of adult trees of each species should be exponential and related meas-ures should show smooth curves, with regular transitions from one age class to the next when a population is represented as sequential age classes. Substantial deviations from this simple expectation are observed among the species resident at Chamela (Figure 3.1). The most likely causes for deviations are effects taking place prior to an individual reaching the canopy, in particular as variation either in seedling/sapling mortality or in availability of propagules. If recruitment to the adult stage were cut off for a number of years, the result would be an expo-nential punctuated with gaps. To infer other than recruitment depres-sion would require assuming that at any one time, size-dependent growth or mortality of mature trees is low in one size class, high in the next largest size class, low again in the following size class, etc. Such a pattern of 'pick-and-choose' growth and death rates directly contradicts what is well known and documented about size-dependent patterns of vital rates of mature trees. Consistent with this explanation, a summary of a 32-year-long study of a single species (Connell and Green 2000) showed that seedling cohort size, i.e. recruitment, could predict the relative frequency of the corresponding adult size class.

The premise that such variability in recruitment over time may allow species to coexist produces an expectation of a specific relation-ship between age classes of those coexisting species: a short-term loss in one species offsets gain in the other(s) in the dynamic, and a long-term stability of numbers at any one site. From this, the rarer of the
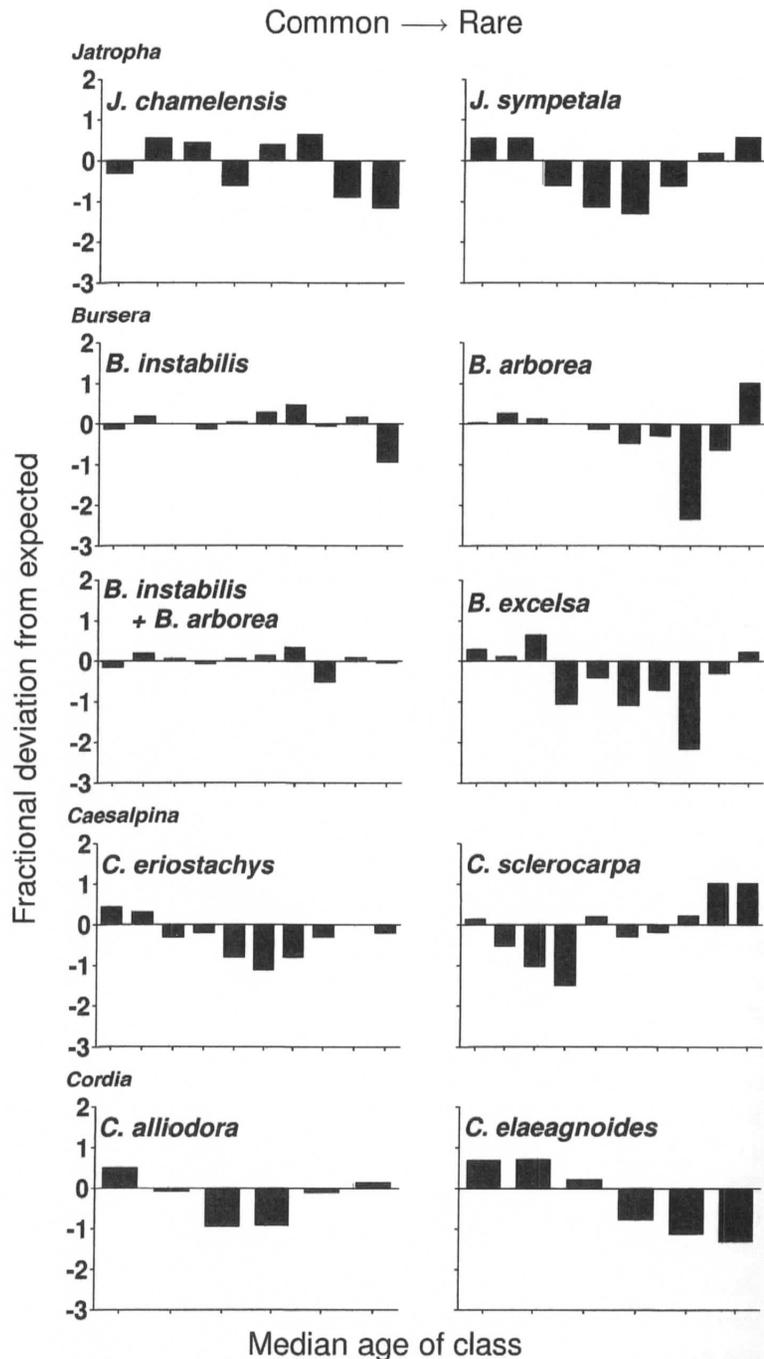
Figure 3.1 Fractional deviation of age classes from an expected exponential distribution. The deviations were calculated as (Expected − Observed)/ Expected. Comparisons (contrasts) were made within, not between rows of

interacting taxa should show greater deviation than the commoner taxon does in the transition from one age class to the next: trading off approximately the same number of individuals would produce a greater fractional change in the less abundant species. Applying a quantitative model of a temporal dynamic to this interaction also generates a testable prediction at the population level that the rarer species will be the more competitive/more responsive to environmental variation, and the commoner species will be the more tolerant/less responsive to environmental variation (Kelly and Bowler 2002).

Support for these expectations was found in the highly diverse ecosystem of the tropical dry forest of México. At Chamela Biological Station in the western state of Jalisco, the high percentage of congeneric tree species offers sufficiently large sample sizes to allow statistical tests of long-term growth rate and fractional deviations in the age structure of coexisting congeners. In all pairwise comparisons between most-closely related congeners, the less abundant of these interdigitated species pairs showed greater fractional variation in age structure, and greater competitiveness than the more common ($p = 0.00096$, Figure 3.1; Kelly and Bowler 2002).

Of existing models postulating coexistence of competitors, only temporal niche dynamics (storage theory) explains these patterns. Models predicating coexistence through resource 'patchiness' and effective escape from competition (Nee and May 1992, Pacala and Tilman 1994) offer no expectations of any regular difference in the community in age profiles for more and less abundant competitors, nor does the assumption of coexistence through chance immigration (Hubbell 2001). As a third possibility, disturbance theory addresses population fluctuations in competing species by raising the expectation of in-phase pulses, but offers no predictions of relative differences

Caption for figure 3.1 (cont.) taxa representing pairs of taxa more closely related to one another than to any other taxon in the figure (i.e. forming terminal dichotomies in the phylogeny of the community). Each bar represents a 30-year interval. Field growth measures of *Bursera instabilis* indicate that individuals of less than 3 cm dbh, the assumed minimum dbh for canopy individuals in this study, could be greater than 30 years old, necessitating the use of the 60–90-year class as the smallest age class for the two contrasts using this genus. For all other genera, age classes begin at 30–60 years. At Chamela Biological Station, *Jatropha sympetala* had been known historically as *J. standleyi*, and has been displayed in previous studies as such (Pirie *et al.* 2000, Kelly *et al.* 2001, Kelly and Bowler 2002, Buckley and Kelly 2003). E. J. Lott has recently corrected this identification.

between species in the degree of those fluctuations (Hutchinson 1959, Connell 1978). However, neither nearest neighbour tests of patch-based recruitment (Veblen 1989, Kelly and Bowler 2005) nor simultaneity of fluctuations reveal significant patterns for any of the paired comparisons. Instead, the pattern of deviations in Figure 3.1 suggests antiphase fluctuations, an observation in line with storage dynamics in the absence of temporal variation in the number of sites.

Focused interactions and relative abundance

The consistent success of the preceding studies in identifying pattern suggests that the focused, paired structure used to compare closely related species may also reflect the character of the actual temporal process. Although diffuse competition is mathematically reasonable, to support the relationships illustrated above, diffuse competition requires that the competitive ability of each of the species involved have a very tight relationship with the long-term average competitive ability of the forest as a whole: biological fine-tuning. If this fine-tuning does take place in nature, to support the observed relative differences in growth rate and degree of fluctuation, the diffuse model developed to examine this question predicts a simple linear correlation between relative abundance and degree of variation in population structure across species, and no such relationship occurs in the data (Kelly and Bowler 2005).

This inference of focused competition invokes a robust body of ecological theory. General resource partitioning theory posits an underlying structure of niches in which particular species excel at exploiting particular resources (MacArthur 1957, Preston 1962a, b, Armstrong and McGehee 1980, Sugihara 1980, Nee *et al.* 1991, Sugihara *et al.* 2003). In such a niche-structured dynamic, abundance of any one species is directly affected primarily by the abundance of only one to a very few highly similar species. In this way, competition affects community composition through regulating population size and persistence of the species within a focused competitive interaction.

We therefore asked whether focused, pairwise interactions of the kind envisaged by Sugihara and indicated in our earlier work are prevalent and forceful enough in forest trees to be of significance at the level of the community. In particular, in the Sugihara model of sequential breakage (Sugihara 1980, Sugihara *et al.* 2003) each bifurcation of an ecological niche dendrogram has a probability distribution for resource

allocation, taken to be reflected in the relative numbers of the two taxa involved. This splitting function is the distribution of the fractional abundance in a pair, r, defined as

$$n_{commoner} / (n_{commoner} + n_{rarer}), \tag{3.1}$$

where $n_{commoner}$ is the number of individuals of the more common member of the pair and n_{rarer} of the less common. This splitting function contains the signature of focused competition when the pairs are chosen from ecological bifurcations. In contrast, if there is no niche structure (i.e. species are interchangeable or 'neutral', as proposed in Hubbell (2001)) then composing pairs according to any meaningful biological algorithm should yield a distribution of fractional abundance indistinguishable from that of pairs chosen at random from the community.

Tests of these ideas were performed for two biome types: the tropical dry forest of Chamela Biological Station, the site of the previously described studies on temporal niche dynamics; and the tropical moist forest of Barro Colorado Island (BCI), Panama, the original stimulus for the development of the idea of neutrality (Hubbell and Foster 1986). For both sites, pairs were identified through membership in terminal dichotomies in their respective community-level phylogenetic trees, and were segregated into two groups: (i) pairs where both species are members of the same genus (congeneric pairs) and (ii) pairs where species do not have congeners within the data set but whose nearest relatives are members of the same family or order (non-congeneric pairs). The distribution of abundances in congeneric pairs was different from that of pairs selected at random from the community for both Chamela and BCI. For the Chamela assay, the distribution of abundances of non-congeneric pairs was not statistically different from randomly selected pairs (Kelly *et al.* 2008); for the BCI data, the distribution of non-congener fractional abundances was significantly different from random in the fifth of five regular censuses, but not in the first four (Table 3.1; Kelly *et al.* 2010).

These observations are consistent with Sugihara's niche apportionment model, but not with the assumption upon which neutral theory is based, that individuals within a community are effectively equivalent. The same studies examined the possibility that the observed distribution of congeneric pairs might conform either to that expected from species interchangeability (rather than neutrality) within congener pairs, or to competitive exclusion (Figure 3.2; Kelly and Bowler

Table 3.1 *Fractional abundance distributions at BCI for each census year.*
Species were paired according to their occurrence as terminal dichotomies in
the fully resolved molecular phylogeny of tree species in the 50-ha plot on
Barro Colorado Island, Panama; population was determined as the number
of individuals greater than the size at first flowering time for that species as
determined by Robin Foster (potentially more accurate maximum
likelihood estimates have been calculated, but only for a small subset of species
and individuals within the larger census area (Wright et al. 2005); the
Foster assessments were made by a single individual for all species, and were
thus assumed to have more consistent error over the greater range of species).
The figures here show the probabilities that the distribution of BCI
congener and non-congener pairs (34 and 21, respectively) was significantly
different from a random draw of the full species complement.

	Year of census				
	1985	1990	1995	2000	2005
Congeneric species pairs	0.01	0.039	0.03	0.01	0.024
Non-congeneric species pairs	> 0.25	> 0.14	> 0.25	> 0.25	> 0.25

2009a, Kelly *et al.* 2010). Neither hypothesis was consistent with the observed distribution of paired congeneric species at either site.

Applying maximum likelihood methods, the observed distributions of congeneric fractional abundances have been fitted by the temporal niche model of differential sensitivity between niche partners (Figure 3.3; Kelly and Bowler 2009a, Kelly *et al.* 2010). For either site, stable coexistence through the focused competition of differential sensitivity dynamics is possible over a wide range of environmental fluctuation frequencies, but still consistent with local and regional climate records (Bullock 1986, Ayala 2007). In these distributions, the single assumption was made that the competitive advantage of one species over another will not be immensely greater than it needs to be to coexist successfully with its competitor. Thus, species are unlikely to be at the upper end of the fractional abundance distribution because it takes only a small competitive advantage for the more sensitive, rarer species to increase its population size rapidly. Because it takes an inordinate competitive advantage for the more sensitive species to maintain a population size close to that of its less sensitive niche partner, species are unlikely to be at the lower end of the distribution. The ranges of 'permissible' environmental frequencies also allow the possibility that the fraction of good times
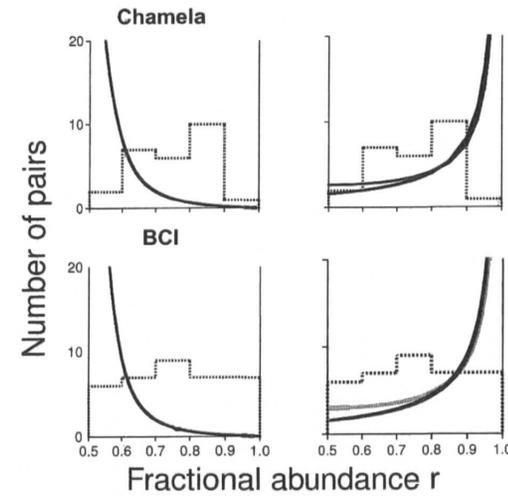
Figure 3.2 Expected fractional abundance distributions under neutrality and competitive exclusion within congeneric pairs at Chamela (top) and BCI (bottom). In all panels, the dashed line represents the distribution of fractional abundances at the site in question. The panels on the left side of the figure show the fractional abundance distribution expected for two species coexisting with equal probability of occupying each of N sites (an approximation of neutrality) rather than interacting with one another. The panels on the right side of the figure show the fractional abundance distributions expected for one species being driven out by an invasive congener (competitive exclusion). Calculations are based on the assumption of pairs being sampled at random times during exclusion. The black line corresponds to a large competitive advantage for the invader, the grey line to a minor advantage. The data for congeneric species (histogram in each part) could not with any significant probability be drawn from the distributions illustrated. Figure after Kelly and Bowler (2009a) and Kelly *et al.* (2010).

may differ among genera: some species may more readily and thus more frequently experience 'bad' conditions than others, and still be able to maintain stable coexistence through a temporal differential sensitivity dynamic.

Conformity of the congener fractional abundance distributions to the temporal niche models for both Chamela and BCI offers evidence that temporal niche dynamics, as a major component of community assembly, are not restricted to a single biome or species type. A more recent simulation study of temporal dynamics at BCI suggests that temporal dynamics may be frequent there in non-congeneric species as well (Usinowicz *et al.* 2012).
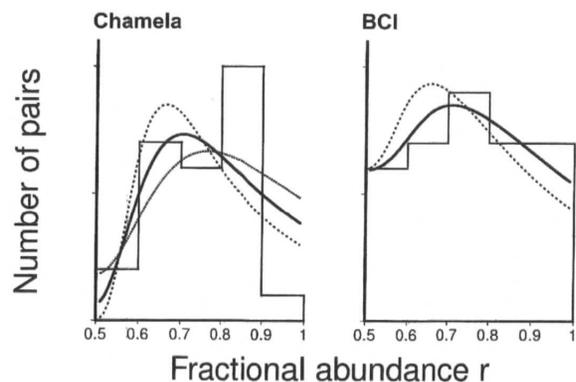
Figure 3.3 Comparison of the data with the model: histogram of fractional abundance data and superimposed [maximum likelihood] fitted distributions. Curves show expected values of *r* for differing frequencies of environmental fluctuation *f* overlaid on the histogram representation of the data from Kelly *et al.* (2008). Chamela: The best fit overall is $f = 0.7$ (solid black curve); the cases $f = 0.6$ (dashed black curve), 0.9 (solid grey curve) are essentially one standard deviation removed from the best value. BCI: The best fit overall is $f = 0.9$ (solid black curve). Figure after Kelly and Bowler (2009a) and Kelly *et al* (2010).

The differences in the projected frequency of good years, *f*, at BCI and Chamela (0.9 at BCI versus 0.7 at Chamela) fall within quite broad standard deviations making any conjecture tentative, but are not inconsistent with documented ecological differences between the two forests. In this regard, the greater water availability in the tropical moist forest at BCI (average 2612 mm rain/year; http://www.sil.si.edu/smithsoniancontributions/EarthSciences) than the tropical dry forest of Chamela (average 731 mm rain/year; http://www.ibiologia.unam.mx/ebchamela, Bullock 1988) and generally less extreme dry season at BCI relative to that of Chamela could have consequences on several levels. It could, for example, directly lower the competitive difference achievable between niche partners and thereby increase the number of high resource years required for persistence (see expression of relationship between *a* and *f* in next section). Alternatively, due to the propensity for faster growing plants to be more attractive to herbivores (Kelly and Hanley 2005, Mayrose *et al.* 2011, Hanley this volume), good years may be made less good for the more sensitive species by the higher pest and pathogen loads expected at BCI as a result of the greater water availability relative to Chamela (McCluney *et al.* 2012). Finally, the higher pest and pathogen level at BCI, with its inevitable cycling, could drive the temporal dynamic directly (Chesson and Kuang 2008, Kelly and Bowler 2009b).

The differential sensitivity of temporal niche dynamics provides a mechanism capable of generating the distribution of congeneric fractional abundances seen in Figure 3.2, which is also of the sort described in the hierarchical niche apportionment model of Sugihara (1980, Sugihara *et al.* 2003), for which temporal dynamics may provide a mechanism. Although the hierarchical niche dendrogram of Sugihara *et al.* (2003) is not phylogenetic, the similarity and interactions of congeners may be a signal of its presence. The possibility of interactions nesting within genera in the hierarchical manner described by Sugihara is suggested by available data. In Kelly *et al.* (2001), three rather than two congeners co-occurred as interdigitated populations in two genera (*Bursera* and *Caesalpinia*), and data were collected on all three. In both genera, the less common the species, the greater the level of temporal deviations from a smooth curve.

There are two major inferences to be drawn from the information contained in fractional abundances. First, interaction between species as a function of relatedness is strongest at the congeneric level (see also Jablonski and Finarelli 2009). There is no evidence for any relationship between relatedness and interaction above that level of similarity in the Chamela data with non-congeneric comparisons all at the family level; for the BCI data, the mix of family and order level pairs could not be discriminated from a random distribution. More recently, a similar finding of significant interaction signal restricted to the level of congeners was reported for a group of coastal scrub species (Burns and Strauss 2011). These patterns are not particularly surprising: competitive interaction depends on similarity, as does the taxonomic categorisation of species within genera. However, one implication of this result is that inference of competitive interaction from pattern in phylogenetic structure is not reliable above the level of genus. This does not mean that competitive interaction cannot occur between species more distantly related than congeners (e.g. Brooks 2000, Mayfield and Levine 2010); rather, above the level of congeners, inference of interaction rather than niche differentiation is not reliable. The possibility of nested interactions above the level of most similar pairs is a part of the previously cited work by Sugihara *et al.* (2003), and some of the data presented in section 3.5 and in Kelly and Bowler (2005) are consistent with such a nested structure, although still restricted to congeneric taxa.

A second insight of fundamental ecological process rests upon the distinctive failure of neutral theory to account for the observed patterns of structure or fractional abundance at any point. It has been suggested that coexisting congeners are a grouping most likely to support neutrality (Leibold and McPeek 2006), but the fractional abundance comparison described here is antithetical to neutral dynamics, as are the multiple lines of evidence for focused competition. Furthermore, it is becoming

increasingly evident that highly deterministic ecological processes are equally able to produce the previously supposed signature of neutrality (Hubbell 2001), the lognormal species abundance distribution (Pueyo 2006, Pueyo *et al.* 2007, Kelly *et al.* 2011, Bowler and Kelly 2012).

3.3 RECRUITMENT, COMPETITION AND THE ENVIRONMENT

When do temporal storage dynamics occur?

Storage dynamics can occur when there is covariance between competition and the environment (Warner and Chesson 1985). A clear statement in itself, its translation into patterns in nature or experimental results may not always be transparent, in particular with regard to assessing a competitive relationship between species. In essence, if environmental fluctuations can promote coexistence of species that would otherwise suffer competitive exclusion, then there must be covariance between competition and the environment. If competition were indifferent to environmental fluctuations, then the fluctuations could not promote coexistence.

However, there is some advantage in defining competition anyway, in the context of the lottery model for two competing species. The competition is for sites – places with resources for one adult. Let there be x_1 adults (reproductives) of species 1 and x_2 of species 2. These individuals take a fixed number of sites and the problem is the division between them; we might as well define x_1 and x_2 as fractions. Individuals of species i die at a rate δx_i; let both species have a common per capita death rate δ. New sites become available at a rate $\delta(x_1 + x_2)$ and these are up for grabs. Suppose the probability of species 1 successfully germinating a seed (from a seed rain proportional to the number of adults present), in the absence of either intraspecific or interspecific competition, is given by a_1x_1. Then our first guess at writing equations for the coupled population dynamics of the two species would be

$$\frac{dx_1}{dt} = -\delta x_1 + \delta(x_1 + x_2)a_1x_1 \qquad \frac{dx_2}{dt} = -\delta x_2 + \delta(x_1 + x_2)a_2x_2. \quad (3.2)$$

The nature of the problem is that populations cannot grow without limit and that to the extent that any dead adult is instantly replaced by an adult of the same or the other species, the sum of the two populations is a constant. This is achieved by multiplying the recruitment term in each equation by the competitive factor

$$\frac{1}{a_1x_1 + a_2x_2} \qquad (3.3)$$

so as to obtain the equations

$$\frac{dx_1}{dt} = -\delta x_1 + \frac{\delta(x_1 + x_2)a_1x_1}{a_1x_1 + a_2x_2} \qquad \frac{dx_2}{dt} = -\delta x_2 + \frac{\delta(x_1 + x_2)a_2x_2}{a_1x_1 + a_2x_2}. \qquad (3.4)$$

The recruitment terms now contain the effects of both intraspecific and interspecific competition, through the same factor. It is of course the values of the a parameters that fluctuate with the environment, and they are per capita recruitment rates per site in the absence of competition. In principle, one could measure them over the decade(s) it takes to mature an adult; certainly, it seems sensible to measure something like this for a year or two with test seedlings a healthy distance from seedlings of the same age as their own or the other species. Most seedlings die and with maturity taking a decade or more, the important thing will be when a sapling of one or the other species becomes sufficiently demanding on resources that no new seedling can do other than die in the larger individual's presence – seedling survival probability goes from vanishingly small to zero.

It is well accepted (or 'easily shown') that for species 1 to grow from a small population then $a_1 > a_2$ and conversely that for species 2 to grow from a small population then $a_2 > a_1$ (Pimentel *et al.* 1965, Pielou 1977, Turelli 1981). For coexistence to be possible, the ratio a_1/a_2 must fluctuate in response to environmental changes such as humidity level by sufficient amounts over suitable periods. The ratio goes up and down as humidity goes up and down – the interspecific competitive ratio covaries with the level of environmental humidity. In this context, we have essentially a precise definition of the meaning of covariance between competition and the environment.

Things may be less clear-cut in a seedbank model for densely packed annuals. In the seedbank model worked out in Kelly and Bowler (2009b), the condition was imposed that the sum of the populations of adults remained constant from year to year. The recruitment term for adults y was written as

$$y_i \propto a_iE_ix_i, \qquad (3.5)$$

where x_i is the number of seeds of species i in the seedbank, E_i is their germination fraction and a_i is a probability that a germinating seed produces an adult plant in the absence of competition. In the herbivore model, we envisaged herbivores attacking the seedlings but

there are many possible variants. The coefficient of x_i was factored so that different aspects could be allocated to environmental fluctuations.

With annuals, it may be that competition is not adequately represented in terms of the y_i above. Therefore in the seedbank model of Kelly *et al.* (2005, 2006), the adults y_i (for fractional populations) produced in one season from x_i seeds is written

$$y_i = \frac{\alpha_i \beta_i E_i x_i}{\sum_j \alpha_j \beta_j E_j x_j}. \tag{3.6}$$

The idea is that the *a* parameters represent the survival probability that is affected by environmental fluctuations and were originally defined as measurable in the absence of competition. However, within a season all seedlings that are going to become adults, and the majority that are not, are all growing together and one species might indeed overshadow the other and so modify the survival probabilities, although it need not. It seemed convenient to separate out the isolated survival probability from the survival probability in the hurly-burly, and to this end, the β parameters were introduced. It would also be possible to use these parameters to contain explicitly the cost to a plant of manufacturing herbicide for models of genetically modified herbivore resistance (Bowler *et al.* this volume), but the separation alphabetically then begins to become a bit arbitrary.

For seedbank models, again a competitive ratio can be defined. It is the thing we have called an a^* parameter (Kelly *et al.* 2005, 2006, Kelly and Bowler 2009a, b), and it is this that must covary with the environmental conditions (like herbivore density), so that more of one species survives at high herbivore densities and more of the other at low herbivore densities.

Seeds, seedlings and competition

In the first half of this section, *a* is described as the *population*-level advantage of species 1 over species 2, calculated as the number of individuals of species 1 that make it to adulthood versus the number that do so of species 2 in the absence of competition. For annual plants, this relationship between species can be demonstrated observationally over time as relative abundance in a given year type, or experimentally as a treatment- or condition-dependent population response (e.g. Rice and Menke 1985, Pake and Venable 1995, 1996, Angert *et al.* 2009, Venable and Kimball this volume). Direct observation of covariance between competition and the environment is more problematic in perennial species, where population turnover is in the accretion of individual successes over long periods. While initial conditions will inevitably be important to seedling survival, it is to be expected that over the decade(s) long recruitment period, the particular sequence of year types will on occasion be an important factor in successful recruitment, and thereby able to obscure the critical character of any single year type.

In the original model of Kelly and Bowler (2002) it was assumed that in a fraction *f* of years, conditions are good and that in the complementary fraction $1-f$ environmental fluctuations prevent any recruitment on the part of species 1 (the more sensitive) but that in good years species 1 has a recruitment advantage *a* over species 2. Implemented in the lottery-model equations the fraction x_1 of species 1 is

$$x_1 = \frac{f - 1/a}{1 - 1/a}. \tag{3.7}$$

Within the model, the maximum possible value of x_1 is the fraction of good years *f*. Working from the fractional abundances reported in Kelly *et al.* (2008), Kelly and Bowler (2009a) found that in the relatively harsh conditions of Chamela, *f* varies around 0.7 and *a* varies around 2.0 (Figure 3.3), and that species 1 is the rarer niche partner, with x_1 varying around 0.4. From this, we have built an expectation of the relative fraction of the shared spatial niche occupied by species 1, against which can be compared the behavioural (competitive) differences that affect coexistence.

As a measure of population-level differences, *a* will have some relationship with individual growth rate, which is, after all, a signal of resource acquisition capacity and can be the advantage itself (Tilman 1988). A specific example of the latter is that of more rapidly growing through the period of seedling vulnerability to pathogens (Augspurger and Kelly 1984), but there are a number of threats to seedlings for which greater size is an advantage (e.g. Puertolas *et al.* 2003, Villar-Salvador *et al.* 2012). To determine the condition-dependent competitive effects necessary to create covariance between competition and the environment in this context, experiments, manipulations and observations need to determine the *relative* individual response of niche partners under differing conditions. This has been done for six species (three pairs) in the tree genus *Bursera*, a prominent taxon of the tropical deciduous forest of coastal México (Becerra 2005) that was previously implicated in differential sensitivity temporal dynamics (Kelly *et al.* 2001, Kelly and Bowler 2002, 2005, 2009a).

The genus *Bursera* is thought to have originated in México (Rzedowski 1978), paralleling the development of tropical dry forest (Becerra 2005). *Bursera* has over 80 species in the tropical dry forests of México, a number of which are of economic or cultural importance (Hernández-Apolinar *et al.* 2006, Mabberley 2008). Significant populations of six *Bursera* species, including one documented only recently (*B.* sp. *nova*) are found at Chamela. At Chamela, these six species form three pairs of most-closely related congeners as determined by the molecular phylogenies of Becerra (2003) and De-Nova *et al.* (2012), and distinctive floral and morphological characters of *B.* sp. *nova* according to Toledo (1982).

The six species occur in intermingled populations, but with each pair having its own distinctive pattern within the system of ridge tops, canyon shoulders and slopes that characterises the topology of the region. In the tropical dry forest, interannual (or longer term) variation in water availability is a major factor in plant response (Bullock and Solís-Magallanes 1990, Bullock *et al.* 1995) and the gradient of *Bursera* distribution follows a gradient of water availability and humidity. Conditions grow consistently drier with increasing elevation on the local scale (Segura *et al.* 2003), and decreasing species diversity and canopy density reflect this change (Kelly, unpublished data). Figure 3.4 shows proportional differences in distribution of species pairs among the three distinct components of the local canyon system; this differential distribution of pairs results in each pair being most numerous in a specific section of the habitat: *B. instabilis/B. arborea* in the more humid slope areas, *B. excelsa/B. heteresthes* along the more-exposed shoulders of the canyons and *B. fagaroides/B* sp. *nova* on the flat, dry ridge tops.

In early 2007, seeds of all six species were collected from trees naturally occurring within the limits of the 1600-ha Chamela reserve, and planted individually into 0.5 litre plastic grow-bags containing well-mixed local soil. The seeded bags were arranged within a growing shed open on two sides, with screens on the remaining two sides and roof. Beginning at the inception of the rainy season in mid-July of that year, the bags were watered with non-chlorinated water and from that point forward the soil in the bags was not allowed to dry out. Germination was recorded daily, and in early October, aboveground growth of all resulting seedlings was measured. Concurrent with the measurement of pot-grown seedlings, 30 seedlings of each of the six target species were collected from the field and similarly measured. Supplementary watering of the potted seedlings continued until mid-November of that year. In 2008, the supplementary watering regime
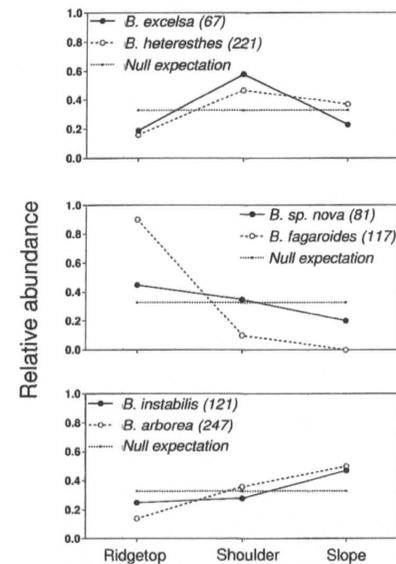
Figure 3.4 Relative distributions of species pairs within the 10-ha study area. In June 2008, all six target species were exhaustively censused over the study area; reproductive status and diameter at base were recorded for all individuals. Shown here are data including all individuals larger than the minimum size of reproduction occurring in the three principal habitat types within the sampled area.

was reinstituted in May, with consequent vegetative budburst and leaf development assessed on a regular basis.

The primary result of this experiment was that degree of difference in growth for niche partners in the field is significantly smaller than that under the well-watered regime in the growing shed (Table 3.2), signifying covariance between competition and the environment (*sensu* Chesson and Huntly 1997). This difference in relative growth rate is an indicator of competitive advantage, much like the parameter *a* defined earlier; a faster growing seedling is vulnerable to the habitat for a shorter period and more likely to reach a stage at which it can pre-empt a site. Under well-watered greenhouse conditions, the rarer species showed two to three times the aboveground final volume of the common species. It could be useful to determine how this difference relates to the maximum competitive advantage (probability of establishment) of 2–3 assigned to the more sensitive species in the model of Kelly and Bowler (2009a).

Comparing the six *Bursera* species as three pairs of most-closely related congeners, it is evident that an important component of the

Table 3.2 **Comparison of species traits**. *The rarer species, i.e. that predicted to be the more competitive in a pair, is highlighted in bold for all three pairs. Germination and budburst responses were modelled with accelerated failure time analyses, with Akaike Information Criterion (AIC) showing a Weibull distribution as the best model for germination and a logistic distribution for budburst. Coefficients describe the time-to-event (hence acceleration) for each species, relative to a baseline (here taken to be* Bursera arborea*). More negative coefficients mean quicker responses. The phylogenetic tree of the species group follows the molecular phylogenies of (Becerra 2003, De-Nova* et al. *2012) and is shown in the left-most column. Branch lengths in the figure do not represent branch lengths calculated from base-pair change of neutral gene sequences (see Williams and Kelly 2013 for a discussion on the use of such branch lengths in ecological inference). B. sp.* nova *is designated within the* fagaroides *clade based principally on floral morphology but fruit, seed and cotyledon morphology are all consistent with this designation.*

Phylogeny	Species	Abundance (mature trees)	Germination response coefficient	Leaf budburst response coefficient	Growth ($mm^3\ d^{-1}$) field/ +water
	B. excelsa	67	−0.046	−0.127	5.9 / 12.8
	B. heteresthes	225	0.148	0.384	3.1 / 4.2
	B. instabilis	164	−0.141	−1.658	3.2 / 21.1
	B. arborea	287	0	0	3.0 / 9.1
	B. sp. nova	81	0.030	−1.658	2.2 / 9.5
	B. fagaroides	111	0.366	0.020	1.5 / 4.8

growth/survival tradeoff is timing. In all pairs the rarer species more quickly released leaf buds from dormancy in the second year of growth and germinated sooner than did the more common species (Figure 3.5; Table 3.2). Both of these responses have the capacity to contribute to greater early growth in their respective seasons (Augspurger 2008, Firn *et al.* 2010), and even calculating growth as a per day response, there is a correspondence between germination date and first season growth. However, the looseness of the relationship between germination date and growth suggests the possibility of innate growth rate differences independent of the advantages of early germination and budburst. Overall, the characterisation of a growth/tolerance tradeoff is robust: the chance that the direction of difference should be as predicted for all three pairs is significant for either two or three.

(a)

(b)
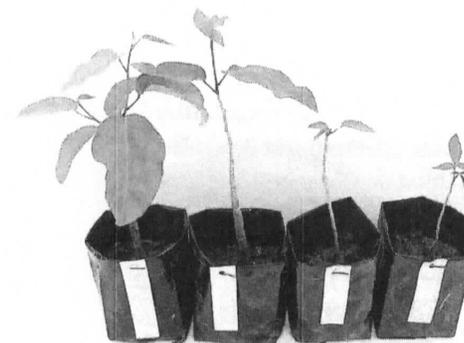
(c)
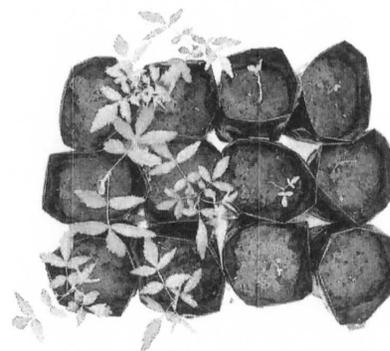
Figure 3.5 Differential budburst in congeneric pairs of *Bursera*. All plants were grown in well-mixed and sieved local soil in 0.5 litre bags. The photographs illustrate the difference between sensitive/resistant

ecologically independent responses ($p = 0.016$ for two traits and 0.002 for three; Siegal and Castellan 1988). None of the responses revealed significant correlation with relative abundance when species were treated independently (i.e. without accounting for their phylogenetic relationships; *p*-values from 0.46 to 0.89; regarding competitive ability and community structure, see also Fraser and Keddy (2005)).

Finally, the observed responses characterise the tradeoff as beyond a simple greater and lesser growth capacity; early germination, early bud-break and faster growth all involve or are correlated with risk. Both early germination and bud-break entail greater exposure of small and vulnerable life stages to the less reliable rains of the early wet season in this habitat, and the greater size that early response can achieve may leave a seedling more visible and less protected from macro-herbivores (Rafferty *et al.* 2010). In effect, the conditions describe disruptive selection ecologically dividing early- from late-responding species.

3.4 SPECIATION

Sympatric speciation via temporal dynamics?

It has been suggested that temporal dynamics, because of its capacity to support population growth from low levels, may also support sympatric speciation (Chesson and Huntly 1997, Kelly and Bowler 2002). However, effective ecological speciation also requires reinforcement, a connection between the ecological factor and reproductive isolation (Dieckmann and Doebeli 1999, Via 2002, Bolnick and Fitzpatrick 2007, Givnish 2010, Hopkins and Rausher 2012). In this section, we will first examine whether the alternating recruitment of temporal dynamics might achieve that end. Second, we present evidence that the differential sensitivity that allows the stable coexistence of temporal dynamics also affects the divergence of

Caption for figure 3.5 (cont.) congeneric pairs in budburst and subsequent early season growth; sample-level differences are in Table 3.2. **(a)** The two plants on the left are *B. excelsa* (sensitive); the two on the right are *B. heteresthes* (resistant). **(b)** The two plants on the left are *B. instabilis* (sensitive); the two on the right are *B. arborea* (resistant). **(c)** The six plants on the left are *B. sp. nova* (sensitive); the six plants on the right are *B. fagaroides* (resistant). Differences in budburst were such that for all three pairs, budburst had occurred in all sensitive individuals of the paired species before leaf buds on any individuals of the resistant species began to reveal developing green tissue.

floral phenology in temporal niche partners, potentially fulfilling the requirement of sympatric speciation for reinforcement.

What is going on in temporal dynamics can be explained accurately without going into mathematical detail. In the Kelly and Bowler (2002) lottery model for closely related forest trees, two competing species can coexist in dynamical equilibrium over a significant range of parameters because of differing responses to environmental fluctuations. In that model, species 2 is not affected by environmental fluctuations as badly as species 1; during good conditions species 1 has a competitive advantage over species 2 denoted by a parameter a^* greater than 1 (typically maybe 2 or 3; compare with growth rates in Table 3.1). In bad times (perhaps a third of seasons) species 1 cannot recruit at all and so species 2 always wins the lottery. Either of the species can grow from a very low level, and so if one were an emergent new variety, speciation could apparently take place. Hence, such a temporal dynamic seems a likely way of getting sympatric speciation.

We modified the equations for the two species to include a hybrid with diploid rules for making seeds (see discussion of the diploid model by Bowler *et al.* (this volume)). The most important feature is that species 1 can pollinate species 2 and species 2 can pollinate species 1. A stamen can only be pollinated once. This has two effects: (1) if species 1 and 2 are in a stable dynamical equilibrium, there is a steady input of hybrid (species 3) seeds. If some proportion of these grows to mature adults, there will always be hybrids present in the community. (2) If pollen from species 2 floods the stamens of species 1, the terms of the lottery competition are changed and the conditions for dynamical equilibrium are altered. This makes it difficult or impossible for the population of species 1 in particular to grow from an arbitrary low level. We return to this after setting out the model in more detail.

Suppose we have a dynamic equilibrium. The relative rate at which species 1 fertilises species 1 will be x_1x_1 and the rate at which 2 fertilises 2 will be x_2x_2. The rate at which hybrid seeds are formed is on the same scale, $e_{12}x_1x_2 + e_{21}x_2x_1$, where the coefficients e_{12}, e_{21} are not necessarily the same. If these coefficients are ~0.1, then very roughly about 10% of the seeds produced each season will be hybrid. The smaller the hybridisation coefficients are, the smaller the proportion of hybrid seeds produced.

There is another factor important for determining the proportion of adult hybrids and that is the probability of a hybrid seed being successful in producing an adult. As with species 1 we scale to the success of species 2; for species 1 we have the competitive advantage

Table 3.3 **Equilibrium population fractions**. *Here we have assumed that conditions were good 66% of the time, that species 1 had an advantage of 3 (over species 2) during good times and that both crossbreeding coefficients for 1 with 2 were 0.05. The 1–3 and 2–3 crossbreeding coefficients were both taken as 0.1 but are less important, it seems. Under good conditions the hybrid, species 3, has an advantage over species 2 of a_3^* (good) and under bad conditions of a_3^* (bad). Advantages less than 1 are disadvantageous. x_i is the fraction of species i in the population and shown here is the expected fraction of each type under the specified relationships between species 2 and the hybrid species 3.*

a_3^* (good)	a_3^* (bad)	x_1	x_2	x_3
1.5	0.5	~ 0.45	~ 0.45	~ 0.08
1.0	0.0	~ 0.49	~ 0.49	~ 0.02

of species 1 over species 2, a_1^*, with a value of 2 or 3 in good times and 0 in bad times. For species 3 we introduce a_3^*, which will also have different values in good and bad times; the smaller the average value, the smaller the fraction of hybrids in equilibrium. Table 3.3 gives the results of two calculations made by iterating the full set of equations.

There are many parameters, but it can be concluded at this point that it is possible to have a stable equilibrium and drive the hybrid population as low as wanted by reducing ever further the hybridisation coefficients. Values as low as 0.05 might just be reached by the species 1 and 2 flowering at different times, so that there is not much 1 pollen around when 2 can be fertilised (and vice versa). As an example, distributions of flowers over time were assumed to be normal and pollination was assumed to take place very quickly on the flowering timescale. From this, hybridisation at the level of 0.05 would result if the peaks of the two normal distributions were separated by 3.4 standard deviations. The other possibility is that the pollen of species 2 is in some way incompatible with the stamens of species 1, but we do not consider that here.

We now return to the question of competitive pollination. At least within this very simple model, competitive pollination has the effect of making it impossible for species 1 (the one that does well in good times and cannot recruit in bad times) to grow from an arbitrarily low level. The level above which the population of species 1 will grow to the stable equilibrium depends on the value of the coefficient for pollination of 1 by 2; very roughly, a coefficient of 0.05 implies that species 1 will

not grow if started below 0.05 of the total population. The same is not true for species 2 being swamped by species 1. The reason is that in the original simple model there are periods (bad times) during which species 1 cannot recruit at all, and species 2 has no competition. However, if recruitment for species 1 is not completely wiped out in bad times, there is competition. If speciation proceeds by the local appearance of a mutation, then a mutation in species 1 that generates species 2 would probably suffer less from pollen swamping than a mutation of species 2 that generates species 1. Even so, a local mutation is likely to be suppressed by pollination competition, even if the problem of starting with a male tree and a female tree carrying the same mutation could be overcome.

If the closely related species do not have any serious level of hybrids, that could be due to assortative mating resulting from differing flowering times (Fox 2003, Weis 2005, Devaux and Lande 2009). Such assortative mating can lead to a broad distribution of genotypes splitting into two major types as a result of the extreme ends of the distribution responding differently to environmental conditions, with some difference in fitness linked to time of flowering. The nearest to it within the confines of our simple model is to suppose that initially there is a population whose broad distribution of genotypes can be represented by fairly equal populations of species 1, species 2 and the hybrid. Initially they happily cross-pollinate and no variety has any fitness advantage.

The dynamical equations then simply leave the proportions of each where they started out (perhaps 0.25, 0.25, 0.5). Strictly speaking this is a three-variety neutrality and for strictly separate varieties stochastic drift would eventually lead to dominance either of one or of two – it seems unlikely that this proxy for a broad distribution of genotypes can be anywhere near a good representation.

Now change the environment. Changes might be spatial only or temporal only or of course both. Spatially, if species 2 is disadvantaged relative to 1 all the time, then species 1 will take over, and the original broad distribution of genotypes will be replaced by a subset of those genotypes from one end or the other of the spectrum of trait expression. Similarly, if species 1 is disadvantaged relative to species 2, then species 2 will take over. Either thing could happen because of geological or climatic change. In that case, spatial separation of the two varieties 1 and 2 would occur and if the robustness trait were linked to flowering phenology, then two new species could emerge from the original, distinguished by elevation perhaps.

If the environment changed on a purely temporal basis, with species 1 recruiting much better than species 2 in good years but

with higher mortality relative to the more robust species 2 in bad years then, again provided the flowering phenology trait were linked to the robustness characteristic, the hybrid would be depressed and a new equilibrium reached on a timescale of perhaps 10 mean tree lifetimes (calculated by starting from the broad band end and suddenly switching on the fluctuating climate pattern.) The hybrid level would be determined by just how low the hybridisation coefficient became. This would seem to fill the definition of sympatric speciation.

In conclusion, we have cast a harsh light on the idea of sympatric speciation being possible simply through either of two species being able to grow from a low level. On the other hand, a broad distribution of genotypes can split because of climate change and this response might be because of spatial variation or temporal variation. In either case, a link between robustness and flowering phenology is required.

Differential sensitivity and floral phenology

We propose that this necessary link between robustness and floral phenology is innate to the differential sensitivity of storage dynamics observed between congeneric species, either through the common control of timing among seasonal plant behaviours (Brachi *et al.* 2010, Yanez-Espinosa *et al.* 2010, Huff and Zilberman 2012), or working through the greater resource availability that sensitivity is expected to impart. Figure 3.6 shows that, as with germination and vegetative budburst, the more competitive species 1 is also the first to flower in all three congeneric pairs. Change in multiple responses because of a single, controlling change in a regulatory function has the potential to affect response to seasonality while at the same time supporting the observed tolerance–sensitivity tradeoff. For example, selection for the enhanced growth that can be gained with early leaf-out in deciduous forests (Augspurger 2008, Lopez *et al.* 2008) would also bring more rapid germination and early flowering as part of a package. At the same time, early germination exposes vulnerable, newly emerging seedlings to the riskier conditions of season changeover. Together, this common change in the character of scheduling would produce a bimodal selective regime of higher risk and greater payoff versus lower payoff but less risk in the context of interannual variation in rainfall in the tropical deciduous forest or late freezes in temperate forests.

The differences in the timing of flowering in *Bursera* are such that there exists a period during which the bulk of the floral crop of one niche partner is unavailable to the pollinators of the other.
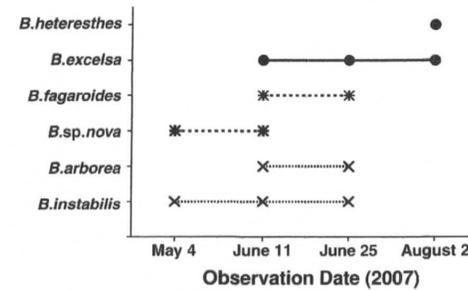
Figure 3.6 *Bursera* flowering phenology. Within all three pairs, the species with the more sensitive seedlings (greater speed of germination, higher growth rate and earlier second year budburst; see Table 3.2) is also the first species to begin flowering. *Bursera* flowering phenology follows a general schedule of an initial large burst of simultaneously open flowers lasting ~1–2 weeks, followed immediately by fruit expansion to approximately final size. Filling of the previously enlarged fruit is initiated in late September and early October, with staggered fruit maturity beginning at some point after the end of the rainy season in mid to late December.

Bursera species seem well able to hybridise (Weeks and Simpson 2004), and *Bursera* at Chamela have a number of common pollinators (P. Lopera Blair, unpublished data). In consequence, the inferred functionality of the observed floral asynchrony existing at Chamela is supported by the general lack of evident hybrids within the exhaustively censused study area.

While we believe this to be a viable and possibly general route for *in-situ* (sympatric) ecological speciation, a general link between flowering phenology and the timing of other vital rates such as germination and budburst would also facilitate the effectiveness of allopatric speciation. A link between ecological and phenological change would maintain reproductive isolation between populations when community assemblages and physical isolation are interrupted by Milankovitch-scale environmental fluctuations (Davis 1986, Schluter 2001).

One proposed criterion of sympatric speciation is that of co-occurrence of sister species (Coyne and Orr 2004). In an early molecular phylogeny of *Bursera*, only one of the Chamela pairs (*B. instabilis/B. arborea*) sorted out as sister species (Becerra 2003). However, Bolnick and Fitzpatrick (2007) point out that current distributions of species can give either false negatives or false positives regarding mode of speciation because of subsequent speciation and the plastic character of distributions.

In the previous part of this section, we concluded that the direction of speciation from a temporal dynamic is more likely to generate a

more tolerant rather than more sensitive form relative to the parent species. In the following section, examination of changing community structure along a landscape-level gradient of temperature and water reveals distributions of congeneric groups across a number of lineages consistent with this conclusion.

3.5 LANDSCAPE-LEVEL PATTERNS

Fractional abundance and coexistence across an elevation gradient

Among pairs of closely related congeneric species that coexist as intermingled adults at Chamela, recruitment appears to be more strongly affected by environmental fluctuations in the rarer of the two species than in the more common. In every case, the rarer species shows evidence of compensating for this by recruitment advantage when conditions are favourable (Kelly and Bowler 2002, 2005). The lowland coastal site of the original community-based studies, Chamela Biological Station, has the lowest rainfall and highest temperature in the deciduous dry forest that stretches down the Pacific Coast of México from Jalisco to Oaxaca; the major geological uplift from the coastal areas of this region is also accompanied by lower temperatures and greater rainfall (Williams *et al.* 2010, Williams and Kelly 2013). If the lottery model of temporal dynamics is applicable at all elevations in this extensive forest, the more sensitive species of a pair must become more dominant as elevation increases from the coastal lowlands. This can be accommodated within the lottery model, as follows.

In the original model (Section 3.3) the fraction x_1 of species 1 is

$$x_1 = \frac{f - 1/a}{1 - 1/a}. \tag{3.8}$$

Under the harsh conditions of Chamela, Kelly and Bowler (2009a) found that $f \approx 0.7$ and $a \approx 2.0$. Under these conditions, species 1 is the rarer, with $x_1 \approx 0.4$. At higher elevations, species 1 would become commoner if either the fraction of good years f grows or the competitive advantage of species 1 over species 2 grows. Note, however, that the maximum possible value of x_1 is the fraction of good years f.

Suppose we assume that f is in fact high, and we vary the competitive advantage of species 1, so that a decreases as we go to lower elevations. Figure 3.7 shows that if f is sufficiently high to have species 1 overwhelmingly dominant at the most favourable elevations, it remains the commoner until its competitive advantage in good times is $a \approx 1.1$ and it
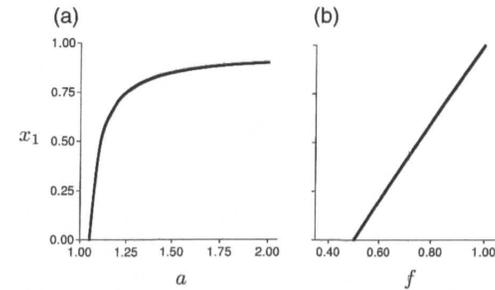
Figure 3.7 Factors affecting the proportion of the sensitive species, x_1, in the original temporal storage model of Kelly and Bowler (2002). **(a)** The effect of changing relative competitive ability of the sensitive species during high resource years, a^+; the frequency of good years, f, is held constant at 0.095. **(b)** The relative competitive ability of the more sensitive species (a^+) is held constant at 2.0 while f, the relative frequency of high resource years, is allowed to vary.

goes extinct for only a marginally smaller advantage. Roughly speaking, it is either dominant or it is not present. This is not impossible but it is implausible, being inconsistent with the pattern at Chamela of the faster growing species being associated with the lower population size.

There is another way to have species 1 dominant, even overwhelmingly so, in the balmy uplands, while being the rarer species close to sea level, as seen by Williams and Kelly (2013). Take the advantage parameter, a, as fixed and vary the fraction of good years, f. At higher elevations, f can be equal to 1 and decrease as we go downhill. This relationship is shown in Figure 3.7.

This is reasonable enough, in that species 1 is as dominant as desired at high elevations and has become the rarer as the fraction of good years f drops with descending altitude to a value of about 0.7. We would suppose that is about Chamela altitude. The uncomfortable thing about it is that the fraction of good years decreases at lower elevations (in Figure 3.7 the advantage factor is independent of elevation at a value of 2). If the advantage factor a grew with increasing harshness, then the fraction x_1 would drop less rapidly with f.

There is in fact a way of varying x_1 over the full range from 1 at high elevations to values typical of Chamela without varying either the fraction of good years f or the advantage of species 1 over species 2 during good years. In the original model, it was supposed that during bad years species 1 could not recruit at all, so that the advantage parameter in bad years is zero. If this assumption is relaxed so that in bad years species 1 is
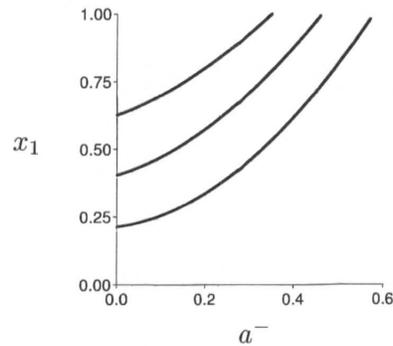
Figure 3.8 Changing relative abundance in the complex lottery model. The complex lottery model is applied to examine variation in proportional abundance of the more sensitive species 1 (x_1) as a response to variation in the negative impact of bad years on the more sensitive species (a^-). This response is placed in the context of specified frequency of good years, f, and the relative competitive advantage of species 1 over the tolerant species 2 during good years, a^+; top curve: $f = 0.7$, $a^+ = 5$; centre curve: $f = 0.7$, $a^+ = 2$; bottom curve: $f = 0.3$, $a^+ = 5$.

at a competitive disadvantage (that is, the parameter $a < 1$) then the full range is covered for f considerably less than 1. In this development of the original model, the analytic solution is more complicated than the solution for the original lottery model solved in Kelly and Bowler (2005).

The extended two-component lottery model has an analytic solution valid under the same conditions as the original. The model differs from the original only in that the more sensitive species is able to recruit during bad times. The fraction of good times is f and during these times, the more sensitive species has the advantage a^+ over the slow but steady species. In bad times, the advantage factor is a^- (less than 1). Then the population fraction x_1 of the sensitive species is

$$x_1 = \frac{(1 - a^-/a^+)f - (1/a^+ - a^-/a^+)}{(a^+ - 1)\{1/a^+ - a^-/a^+\}}.$$

$$(3.9)$$

Figure 3.8 serves as an illustration of this more complex model. These results show that it is perfectly possible to have the same time structure in environmental conditions at all elevations, maintain the Chamela results at Chamela elevations, and yet have the more sensitive species as dominant as desired at the highest (most benign) elevations, even though in hard times it is at a significant disadvantage relative to the more tolerant species.

Some mixture of these effects here treated individually could be constructed to match exactly output with observation, but the goal here is general agreement with expectations, with further development of the theory in a more appropriate treatment dedicated to it specifically. The essential point is that the time-structured lottery model can account for the more competitive of a pair of congeneric species being very dominant high up where the environment is less water stressed, and yet the rarer at sea level, the hottest and driest environment on a larger scale.

Observations

The first half of this section has described changes in the temporal niche dynamic to be expected from changes in the frequency f of good years. As f increases, the proportion of the more competitive (more sensitive, faster growing) niche partner should increase, eventually to the point that the more tolerant species is unable to sustain a population. One outcome of this could be a decreased number of interdigitated congeneric species as the environment becomes increasingly benign. This is a pattern that occurs within the local canyon system at Chamela: in the shadier, more humid lower reaches of canyons within the reserve, *Bursera* is represented principally by *B. instabilis* and *B. arborea*; in the more open conditions of the canyon shoulders, these two species are joined in force by *B. excelsa* and *B. heteresthes*, and on the exposed, low-statured forest of the hot, dry ridge tops (harsher on a local scale), *B. fagaroides* and *B.* sp. *nova* bring the numbers of *Bursera* species to six (Figure 3.4).

The above expectation from temporal niche dynamics of condition-dependent changes in the representation of species within genera is also manifest on the landscape scale. Here we draw on an existing study of tree community composition along a 600 m elevation gradient in the tropical deciduous forest of the Mexican state of Oaxaca (Williams *et al.* 2010). The study assayed 4300 woody individuals in 43 transects (100 individuals/transect) scattered over an area of approximately 1800 km^2. Transect sites were selected using criteria of similar aspect and stand type (undisturbed mature forest). Travelling up this elevation span, temperature decreases by 3°C and rainfall increases from ~1000 mm y^{-1} to ~3000 mm y^{-1} (Figure 3.9), significantly decreasing the level of evapotranspirational demand in this typically hot, dry biome type (Olson *et al.* 2001). This degree of change is also approximately that projected by climate change models for the region (Anonymous 2011).

Analyses show that the total number of species, genera and families did not change significantly across the elevation/environment
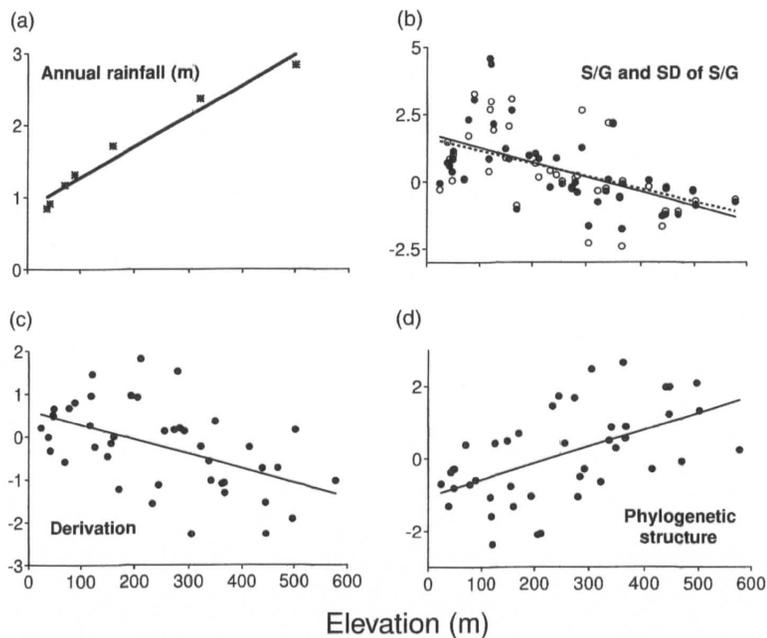
Figure 3.9 Oaxaca gradient analyses. Average annual rainfall relative to the elevation gradient (a) was calculated from raw data of seven weather stations occurring within the 1800-ha study area, and made available by WorldClim (Hijmans *et al.* 2005). Species per genus (S/G) and standard deviation (SD) of S/G (b; S/G = filled circles, SD of S/G = open circles) both showed significant negative relationships with elevation when tested independently (S/G: $p < 0.0001$, $r^2 = 0.33$; SD of S/G: $p = 0.0005$, $r^2 = 0.27$; S/G values shown are corrected for possible effect of sample size (Gotelli and Colwell 2001). When entered into a general linear model, S/G and SD of S/G together are able to account for all of the significant variation in the relationship between phylogenetic structure (d) and elevation (independent regression analysis shows elevation accounting for 30% of the variation in the commonly used measure of phylogenetic structure applied here (see text). Elevation accounts for 25% of the variation in the degree of species derivation among samples (c; derivation = species distance from community phylogeny base, summed across species in sample), but S/G accounts for all of that relationship, plus an additional independently significant 20% of variation among samples in species derivation ($p = 0.0011$).

gradient. However, the phylogenetic structure (NRI; Webb 2000) of the community did, in terms of the distribution of species among genera (S/G; Williams and Kelly 2013). In the relatively benign conditions at high elevation, species were quite evenly distributed among genera,

with only one or occasionally two species per genus. With the increasingly harsh environment at lower elevations, species became significantly more unequally distributed among genera. In these locations, most genera have only one species, with a few reaching four to five or as many as six congeners in a single transect. Furthermore, the changes in S/G and the standard deviation of S/G account for most or all of the response of phylogenetic structure to the elevation/environment gradient (Figure 3.9).

The documented changes are also consistent with the potential capacity of temporal dynamics to support speciation that is outlined in the previous section of this review. Lower elevation transects comprise significantly more derived species as, within clades, the average distance of species from the root of the phylogenetic tree becomes greater with decreasing elevation (Figure 3.9; Williams and Kelly unpublished manuscript). This is consistent with the classic ecological expectation that more benign habitats allow more inclusive species rosters and that species require more specialised functions to cope with harsher conditions (e.g. Woodward and Diament 1991, Kleidon and Mooney 2000). In the analyses of Williams and Kelly, the increase in degree of derivation is fully accounted for statistically by the changing distribution of species among the major genera (genera with ≥ 4 species) with elevation. Thus, the prediction of greater specialisation with greater environmental harshness is framed by a system of adaptive radiations within a subset of lineages (Losos 2010). The observed changes indicate multiple adaptive radiations from mesic to dry adapted species, a pattern consistent with the uplift event 5 million years ago that led to the transformation of a previously mesic habitat into the Mexican dry forest of today (Becerra 2005).

In conclusion, if the condition-dependent competition of temporal dynamics is responsible for the restriction of low elevation species to lower elevations, then these low elevation forests may serve as reservoirs of species redundancy. With the expected climate change effect of hotter, dryer conditions in this area (Anonymous 2011), species that do not currently exist at higher elevation may migrate upward to fill the niches vacated by less drought-adapted species as climate changes (Alexander *et al.* 2011, Schwinning *et al.* this volume). Therefore, maintaining dry forest diversity at low elevations may be especially critical in the face of climate change. This is especially important since these are also the areas currently most affected by commercial development. Evolutionarily, if low elevation forests are harbours for the multiple adaptive radiations that our evidence thus far suggests, then

they will also be reservoirs for unique genes and gene combinations, a second, but not secondary, reason for urgency in understanding and conserving these forests (Vane-Wright *et al.* 1991, Faith 1992, Magnuson-Ford *et al.* 2010).

3.6 LARGER CONTEXT AND DISCUSSION

Our attention so far has been on the action of temporal niche dynamics with regard to congeneric species, but temporal niche dynamics in perennials may also occur between unrelated species (see Adler this volume, Chesson *et al.* this volume). As a specific example for trees, working with coexisting populations of native *Fraxinus excelsior* (ash) and non-native *Acer pseudoplatanus* (sycamore) in the UK, Ellis *et al.* (unpublished) were able to use seedling age distributions combined with well-kept local weather records to link recruitment of each species to environmental factors (see also Mason 2005, Ellis 2007). Ellis *et al.* found that recent ash recruitment correlates with the sunny summers needed for seed production, and that best sycamore recruitment occurs in years where early spring rainfall supports seedling survival. The functionality of these correlations was shown by earlier experimental studies on seed and seedling ecology of the two species (Helliwell 1965, Dethioux 1970, Waters and Savill 1992, Tapper 1996, Binggeli and Blackstock 1999). The relationship between climate and first stage recruitment was then used to assess potential coexistence response to locally projected climate change; the analysis predicted that in future the dynamic might be expected to reverse, with the native ash favoured over the invading sycamore.

Each of these species is a large component of British woodland, and the specific findings show how an understanding of temporal dynamics might be useful for management purposes. However, this study illustrates a difference in the character of temporal dynamics in congeneric versus non-congeneric niche partners. The evolutionary source of temporal dynamics between congeneric species dictates that niche partners usually differentiate temporally along a single axis, with anticorrelation of effect: favouring one partner disfavours the other. Niche partners are more and less responsive to the stimulus, segregating out vital functions (germination, budburst) that expose the individual to disruptive risk/growth tradeoffs. In contrast, the ecological accident that produces non-congeneric niche partners is more likely to result in an uncorrelated, multi-axis regulation of the interaction, affecting different requirements or parts of the life cycles of each of the species involved.

Interannual variation in the timing and amount of rainfall is an important factor in temporal dynamics and tree coexistence, but certainly not the only one in either the tropical or the temperate zones (*contra* Penuelas *et al.* 2011). Temperature variation can affect successful recruitment through interaction with water availability, or through the direct action of cooling or freezing damage to seedlings or small plants. At any scale, warmer or cooler years will produce a different evapotranspirational environment even with the same schedule of water availability, thereby affecting the growth responses and mortality that support stable coexistence (Williams and Kelly 2013). As a primary rather than a companion factor, interannual variation in temperate zone spring warming schedules is also implicated in a risk/growth tradeoff, with seedling frost damage producing disruptive selection parallel to that of drought in more water-restricted environments (Kelly *et al.* 2003). Further evidence of temperature-based disruptive selection in trees can be found in Jump *et al.* (2006) and Augspurger (2008, 2009).

Pests and pathogens may also support temporal dynamics in trees. Damping off of tree seedlings is fairly ubiquitous and variable in space and time (Augspurger 1984, Augspurger and Kelly 1984, Packer and Clay 2000, 2003, Reinhart *et al.* 2003), with differential pathogenicity and susceptibility sufficient for the necessary resistant/non-resistant dynamic between competing tree species (Augspurger and Wilkinson 2007). Herbivores can support temporal dynamics in herbaceous plants (Hanley *et al.* 1995, 1996, Hanley and Sykes this volume), but folivory may be a less common factor in temporal dynamics between tree species. In the seedlings of many tree species, herbivore damage is very low (Eichhorn *et al.* 2006); sparsely dispersed tree seedlings, as they are for many tree species, will not represent an effective resource to the herbivore.

Nonetheless, herbivory on mature/large trees has notable interannual variation (Filip *et al.* 1995), and an asynchronous schedule of attack on congeners might be able to support a temporal dynamic through differentially disrupting seed set. In the tropical dry forest, folivores are sometimes able to fully denude mature trees. Although this is restricted to a subset of species (Kelly, pers. obs.), intense herbivory of this sort may be able to affect relative recruitment through limiting viable seed production. A pattern consistent with this may be found in Becerra (2007), in which at the very local scale congeners of *Bursera* are both more closely related and more divergent in their defence chemistry, than expected by chance. On the other hand, it may be that a temporal dynamic resulting from interannual variation in rain or temperature has allowed the development of divergent

defensive chemicals in co-occurring congeners. However, there is no reason that herbivory and variable climate cannot both play a role in ongoing species coexistence, and it would be surprising if they did not. A factor to consider in the development of such a dynamic is the reproductive isolation innate to the resistant/responsive dichotomy of tree species response to ambient conditions, a factor that would facilitate either allopatric or sympatric speciation. In so far as is currently known, chemical defence strategies of trees do not have any such innate capacity to simultaneously foster reproductive isolation (but see Agrawal *et al.* 2012 for a response to experimental escape from herbivory in an herbaceous species).

Finally, the action of temporal niche processes in species coexistence has general implications for assessing competition in trees and other long-lived species. Fundamental to this is the temporal process as it occurs in nature. Year-type specialisation at the seedling level means that interspecific competition for a site will not be between same age seedlings. The degree of asymmetry *sensu* Schwinning and Fox (1995) and Schwinning and Weiner (1998) and potential pre-emption of one seedling by the other will initially depend on the year type of the primary coloniser, and the sequence of subsequent years before a second, non-conspecific arrives; alternatively, the sequence of year types may switch the asymmetry between the competitors. Either way, the advantage of one species over the other is *condition dependent*, and the crucial measure to establish this is the comparison between the two species of the relative response of each to resource enhancement (or deprivation; section 3.3). Information of this sort can be used in simulation and vital rate models to project population-level change or stability relative to climate variables, as illustrated in several chapters in this volume).

The idea of condition-dependent advantage has a long history in ecology with regard to the divergent spatial distribution of species; the idea that it might also contribute to species coexistence through temporal dynamics is less well integrated into the ecological workbook. A consequence of this is that the components of such temporal dynamics – condition-dependent advantage, asymmetric competition, seedling dynamics and pre-emption – have not been incorporated effectively into many commonly used experimental techniques or statistical analyses aimed at understanding the determinants of coexistence or the lack of it (e.g. Armas *et al.* 2004, Cahill *et al.* 2008; for a counter-example see Daehler 2003). The central importance of this is that if temporal processes are not appropriately accounted for they are quite likely to be misidentified even when a major factor. Moreover, the presence of unidentified temporal processes may confound effects of non-temporal processes. Neither outcome is desirable – even if the world were not currently confronting rapid environmental change.

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