LETTER

Species interactions constrain geographic range expansion over evolutionary time

Alex L. Pigot* and　Joseph A. Tobias

Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK

*Correspondence:
E-mail: alex.pigot@zoo.ox.ac.uk*

Abstract

Whether biotic interactions limit geographic ranges has long been controversial, and traditional analyses of static distribution patterns have made little progress towards resolving this debate. Here, we use a novel phylogenetic approach to test whether biotic interactions constrain the transition to secondary sympatry following speciation. Applying this temporal framework to a diverse clade of passerine birds (Furnariidae), we reject models of geographic range overlap limited purely by dispersal or environmental constraints, and instead show that rates of secondary sympatry are positively associated with both the phylogenetic and morphological distance between species. Thus, transition rates to sympatry increase with time since divergence and accelerate as the ecological differences between species accumulate. Taken together, these results provide strong empirical evidence that biotic interactions – and primarily ecological competition – limit species distributions across large spatial and temporal scales. They also offer phylogenetic and trait-based metrics by which these interactions can be incorporated into ecological forecasting models.

Keywords

Biotic interactions, competitive exclusion, dispersal, geographical range limits, secondary sympatry, traits.

Ecology Letters (2013) **16**: 330–338

INTRODUCTION

The role of biotic interactions in regulating species distributions continues to polarise opinion, particularly in the case of competition for ecological resources (Sexton *et al.* 2009; Wiens 2011). On the one hand, striking examples of ecological release on oceanic islands, and of the abrupt replacement of ecologically similar species across smooth environmental gradients, imply that competition is a pervasive force limiting abundance and distribution (MacArthur 1972; Diamond 1975; Price & Kirkpatrick 2009). On the other hand, species ranges often appear largely individualistic at regional scales (Connor & Bowers 1987; Davis & Shaw 2001; Ricklefs 2011), such that demonstrating the role of competitive exclusion has been notoriously difficult (Connor & Simberloff 1979; Colwell & Winkler 1984). Even in those cases where regional patterns are consistent with competition, they take the form of complementarity (i.e. 'checker-boards') rather than constraints on range limits (e.g. Gotelli *et al.* 2010). Moreover, empirical research has repeatedly highlighted strong associations between range limits and aspects of the physical environment, such as temperature or precipitation (Sexton *et al.* 2009). These findings have led to the widespread perception that environmental determinism and biogeographical history overwhelm any influence of species interactions at large spatial scales (Shmida & Wilson 1985; Pearson & Dawson 2003; Cavender-Bares *et al.* 2009; Peterson *et al.* 2011; Wiens 2011), and that contiguous (i.e. parapatric) distributions mainly reflect autoecological differences rather than competition (Case *et al.* 2005; Sexton *et al.* 2009).

Resolving these conflicting viewpoints remains an important priority for theoretical and applied ecology. Competitive exclusion – often described in terms of 'niche incumbency' – forms the foundation for theories of adaptive radiation and equilibrium models of diversity, in which species interactions limit diversification via their effects on geographic range expansions (Rosenzweig 1975). The

same concept also has major implications for ecological forecasting, as it has the potential to radically alter predicted range shifts in response to environmental change (Araújo & Luoto 2007). In both cases, much depends on understanding how species interact across large spatial and temporal scales, and the extent to which these interactions can be predicted by species traits.

Previous attempts to identify the spatial signal of biotic interactions have generally relied on simple null models comparing whether static patterns of co-occurrence differ from those expected if species are distributed independently in space (e.g. Bowers & Brown 1982; Letcher *et al.* 1994; Gotelli *et al.* 2010). The results are often difficult to interpret, particularly at larger biogeographical scales where the role of evolutionary history – including speciation, extinction and long-distance dispersal – may greatly influence species distributions (Shmida & Wilson 1985; Ricklefs 2004). Thus, the pattern of closely related species inhabiting mutually exclusive ranges is consistent with competitive exclusion, but could also simply reflect the signature of allopatric speciation coupled with insufficient time for dispersal back into sympatry (Mayr 1942). Conversely, even if species now overlap extensively, this may be uninformative about whether competition limited range expansion in the past. Incorporating trait differences into analyses based on static patterns is also problematical (Davies *et al.* 2007): greater ecological divergence amongst sympatric vs. allopatric lineages may be interpreted as evidence for competitive sorting via constraints on range expansion, but an almost identical pattern could arise due to character displacement, whereby biotic interactions drive ecological trait divergence in sympatry (Pfennig & Pfennig 2010).

An alternative approach has been to use controlled or 'natural' experiments, including human introductions, to test the factors regulating species co-occurrence in a given system. This approach tends to show that the likelihood of species survival is greatest for lineages that are more phylogenetically, and presumably ecologically,

distinct from members of the resident community (Fargione *et al.* 2003; Schaefer *et al.* 2011; Violle *et al.* 2011). For instance, Moulton & Pimm (1987) showed that birds successfully introduced to Hawaii had bills, which were more different from native species already present than were those of other introduced species which failed to establish populations. While these studies provide tantalising evidence that competition can limit range expansion, their relevance to wider biogeographical patterns is unclear. In particular, they tell us little about the importance of species interactions relative to other factors, including dispersal and environmental constraints.

Given the difficulty of making inferences based on static geographical or ecological patterns, or extrapolating from experimental data, an obvious next step is to explore the potential of phylogenetic models for testing theories about range limits over evolutionary time. However, while molecular data have been used to calculate the relationship between the extent (Davies *et al.* 2007; Martin *et al.* 2010) and timing of range overlap (Weir & Price 2011) following speciation, we are not aware of any attempts to test alternative processes in an explicitly temporal framework. Here, we address this issue by developing a conceptual model for the dynamics of geographic range overlap, and then applying this approach to test the mechanisms limiting species co-occurrence in a diverse avian clade.

An evolutionary model of species co-occurrence

Most new lineages arise in geographical isolation (allopatry), and thus geographic range expansion is required to produce spatial overlap, i.e. secondary sympatry (Mayr 1942). Different range-limiting processes are predicted to influence the timing of secondary sympatry between sister lineages (those most closely related to each other). First, range expansions may arise from chance dispersal events or the combined outcome of many independent factors. Under this random model, the probability of attaining sympatry is equal across species and constant with time since divergence (Fig. 1a) (MacArthur 1972). Thus, the timing of sympatry will vary stochastically, but the rate of secondary sympatry will be constant,
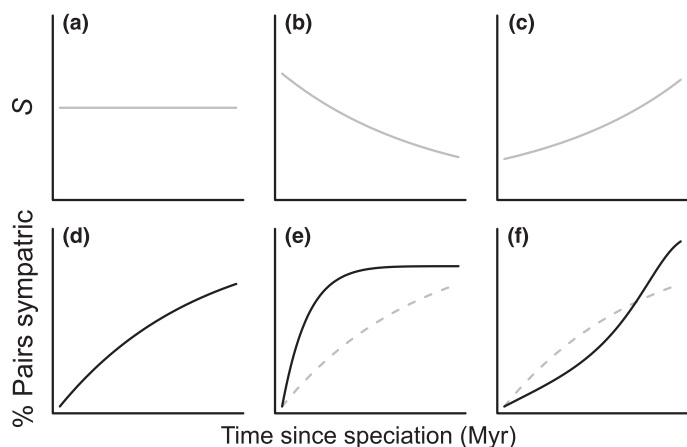
i.e. a constant proportion of sister pairs will become sympatric per unit of time after speciation (Fig. 1d).

In contrast, if differences in dispersal limitation or environmental filtering regulate range expansions, then rates of secondary sympatry should vary predictably across lineages. Species that are either weak dispersers or separated by impermeable barriers should have slower rates of secondary sympatry than more vagile organisms (MacArthur 1972; Case *et al.* 2005). Equally, species adapted to divergent environments are more likely to remain spatially isolated than those adapted to the same environmental conditions, particularly where habitats are disjunct rather than intermingled on a geographical scale (Southwood & Kennedy 1983). We refer to these macrohabitat or spatial components of niche divergence as the 'β-niche'. When viewed across species, both these scenarios should lead to the appearance of declining rates of secondary sympatry with time since speciation (MacArthur 1972; Southwood & Kennedy 1983; Fig. 1b). Compared with the null model, secondary sympatry is expected to initially accumulate rapidly (i.e. amongst strong dispersers and species with conserved β-niches), but then slow down as the continued build-up of sympatry occurs amongst lineages with increasingly slower rates (i.e. weak dispersers and those with divergent β-niches; Fig. 1e).

The hypothesis that range overlap is primarily limited by biotic interactions generates a contrasting set of predictions. Interactions precluding co-occurrence should be strongest amongst recently formed species and then weaken over time as ecological niches diverge (Elton 1946; Cavender-Bares *et al.* 2009; Violle *et al.* 2011). Rates of secondary sympatry would therefore be expected to increase with time since speciation (Fig. 1c), perhaps leading to a characteristic sigmoid curve as the percentage of sympatric pairs first rises slowly but then accelerates, before reaching an asymptote (Fig. 1f).

Increasing rates of secondary sympatry with time since speciation may be produced by at least three different forms of biotic interaction. According to the most frequent interpretation, delayed coexistence indicates that ecological competition is strongest between close relatives – often termed the 'competition-relatedness' hypothesis (Cahill *et al.* 2008). However, the same pattern may be caused by phylogenetically conserved pathogens or parasites (Ricklefs 2010), or incomplete reproductive isolation (Gröning & Hochkirch 2008), both of which would theoretically lead to mutually exclusive geographic ranges amongst closely related lineages.

Few studies have attempted to disentangle these alternative processes, but the relationship between rates of sympatry and the extent of divergence in key ecological traits linked to resource use – i.e. the 'α-niche' – may be informative. Specifically, a positive association between rates of secondary sympatry and the extent of α-niche divergence suggests a role for competition, particularly in older clades where the dominant mode of speciation involves divergence in mating signals rather than ecological traits, i.e. 'nonadaptive radiations' (Rundell & Price 2009). Conversely, rates of secondary sympatry may be unrelated to divergence in the α-niche if range limits are primarily set by shared natural enemies or reproductive interference. Note that divergence in the β-niche is potentially less informative because species partitioning by habitat (i.e. mosaic sympatry), may reduce contact between individuals, and thus also the risk of hybridisation and pathogen transfer.

Here, we develop models to apply this conceptual framework to phylogenetic data. Then, as a case study, we use our method to examine the role of biotic interactions in limiting geographic range expansion across a large radiation of passerine birds, the Furnariidae (ovenbirds and woodcreepers). Birds offer an ideal study system

Figure 1 Conceptual model for the evolution of geographic range overlap showing rates of secondary sympatry (S) against time since speciation under (a) the null model of constant and equal rates, (b) when overlap is regulated by species dispersal constraints or environmental filtering, and (c) overlap is constrained by biotic interactions (e.g. competition); (d-f) black curves show the corresponding accumulation in the percentage of sympatric pairs with time since speciation. Grey dashed lines in (e, f) show the accumulation of sympatry under the null model.

because the predominance of allopatric (or parapatric) speciation (Phillimore *et al.* 2008) allows us to unambiguously interpret sympatry as the result of post-speciation range expansion. The furnariid clade is especially suited to our analysis because it is an ancient, highly diverse radiation, with 293 species on the same continental landmass (South and Central America) exhibiting both remarkable sympatric diversity (Fig. 2a) and striking cases of range exclusion between closely related lineages (Fig. 2b). Across the entire furnariid clade, pairs of sister species occupy the full spectrum of stages in the speciation process from allopatry, to secondary contact or parapatry and finally to complete sympatry (Fig. 2b–d). Furthermore, all furnariid species are predominantly insectivorous, and this narrow feeding specialisation enables variation in α-niches to be quantified using relatively simple ecomorphological traits (e.g. bill size and shape).

Using estimates of divergence times and current patterns of geographic range overlap between sister species, we ask the following questions: (1) do rates of secondary sympatry increase or decrease with time since speciation, (2) does the time taken to achieve sympatry vary with the extent of divergence in the α-niche and (3) do the dynamics of secondary sympatry depend on divergence in the β-niche? We predict that if biotic interactions are important in limiting range overlap, then rates of secondary sympatry will increase with time since speciation and with the extent of α-niche divergence. In contrast, for species with divergent β-niches, we expect the signature of biotic interactions on range overlap to be weak or absent. Our results confirm both these predictions, and provide evidence that competition mediates the geographic exclusion of species for millions of years following speciation.

MATERIALS AND METHODS

Evolutionary age and sympatry

We estimated rates of secondary sympatry using the ages and current geographical relationships of sister lineages. We defined sympa-

try as co-occurrence within the same geographical area, but not necessarily the same habitat (Mayr 1942). Sister species pairs ($n = 94$) and their estimated divergence times were extracted from a recently published molecular phylogeny (Derryberry *et al.* 2011) (Table S1; see Appendix S1 in Supporting Information). Species pairs were then assigned as allopatric or sympatric using breeding range polygons, with modifications according to recent literature (Table S1; Appendix S1). Although the degree of overlap between species varied, confirmed sympatric pairs typically overlapped by > 20% of the smaller species range (Fig. S1).

Quantifying α- and β-niche divergence

We quantified α-niche divergence between sisters using five morphological traits closely related to resource use and foraging strategies in birds: bill length, bill width, bill depth, tarsus length and wing length (Schoener 1965; Grant 1968; Miles & Ricklefs 1984). Trait measurements were taken by Derryberry *et al.* (2011), and data for an average of 4.8 specimens per species (Table S1) were downloaded from MorphoBank (http://morphobank.org/permalink/?P513). Distances between species average position in morphological space were described using phylogenetic Principal Components (PC) analysis (Revell 2009) following log-transformation of individual trait values. We calculated both the distance between sister species along each PC axis, and the Euclidian distance across all axes combined. We performed two sets of analyses, one based on all morphological traits and the other restricted to bill dimensions.

To quantify divergence in species' β-niches, we used published information on macrohabitat affinities and elevational range limits, representing two major environmental axes of diversification (Table S1; Appendix S1). Sister species were assigned as having conserved β-niches if their elevational ranges coincided and they shared at least one of their primary habitat types. While α-niche divergence leads to clear predictions for the intensity of species interactions, the effects of β-niche divergence are more complicated, either favouring or
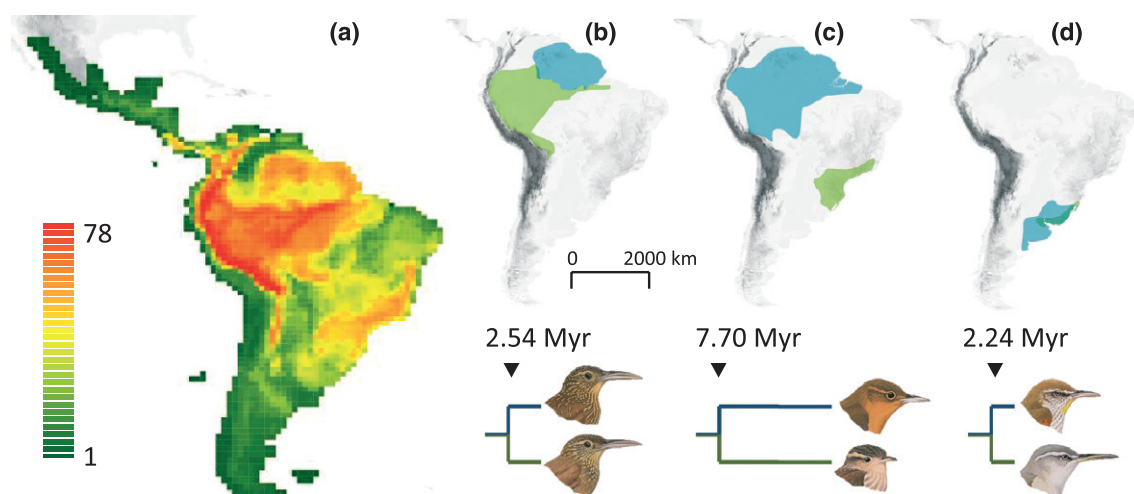

Figure 2 (a) Geographical variation in furnariid α-diversity across the Neotropics and (b–d) examples of sister species pairs showing contrasting geographical, phylogenetic and morphological scenarios: (b) young, morphologically similar sisters occurring in allopatry (upper: *Xiphorynchus pardalotus*; lower: *X. ocellatus*), (c) old and morphologically distinct sisters occurring in geographically isolated regions (*Philydor pyrrhodes*; *Heliobletus contaminatus*), and (d) young, but ecologically divergent sisters occurring in sympatry (*Cranioleuca sulphurifera*; *Limnoctites rectirostris*). The *Xiphorhynchus* species come into contact around the headwaters of the Rio Negro. Illustrations are reproduced and adapted from Handbook of the Birds of the World with the permission of Lynx Edicions.

inhibiting co-occurrence depending on the spatial arrangement of habitats. We therefore controlled for β-niche divergence by estimating rates of secondary sympatry, both across all species and only those sisters with conserved β-niches (too few species pairs [$n = 15$] were available to estimate rates for species with divergent β-niches).

Quantifying geographical isolation

Allopatric lineages vary in their degree of spatial separation, from species with abutting distributions (Fig. 2b) to those occupying disjunct ranges separated by broad barriers (Fig. 2c). The potential for biotic interactions to limit range expansion is expected to be strongest for lineages occurring in close geographical proximity. We therefore calculated the shortest great circle distance between geographic ranges, assigning sympatric species and those with abutting (parapatric) distributions a distance of zero (Table S1). Following Bowers & Brown (1982), we restricted our analyses of α-niche divergence to sister pairs separated by gaps of < 250 km. We note that our results were unaltered when distance cut-offs were either more stringent (125 km) or relaxed (500 km, 1000 km; Tables S2 and S4).

Statistical analysis

Given the distribution of sister species ages and current geographic states, we used maximum likelihood to fit continuous multistate Markov models and estimate the rate at which species pairs transition from allopatry to sympatry (S) per million years (Myr). We assume that all sister species are allopatric at population divergence and that transition from allopatry to sympatry is an irreversible process. Although it is possible to relax this assumption by permitting reversion to allopatry, we found no support for this more complex model in any analysis (Table S5; Appendix S1).

In our simplest (Constant-Rate) model, we assume that S is constant with time (t) since divergence ($t = 0$) and equal across species pairs. Under this approach, waiting times to sympatry are exponentially distributed, with the mean waiting time W, equal to $1/S$. We used the Constant-Rate model to provide an estimate of the overall rate of secondary sympatry. To test whether species interactions delay the attainment of sympatry, we examined the time dependency in S using a non-homogeneous Markov model in which S can increase or decrease with t. In this alternative (Rate-Switch) model, an initial constant rate ($S1$) following speciation switches to a different rate ($S2$) at time ts, also estimated from the data (Fig. S2; Appendix S1). A switch in rates over time may be predicted by a burst of morphological change or by constant rates, but with a threshold (i.e. limiting similarity) of minimum ecological divergence between co-occurring species (Uyeda *et al.* 2011). We tested whether there was evidence for significant time dependency in the rate of secondary sympatry by comparing the fit of the Constant-Rate model to the Rate-Switch model using likelihood ratio tests.

To ensure that our conclusions are robust to the method used to examine rate variation, we implemented an additional (Time-Variable) model in which S changes exponentially with t. Under this model, the transition rate at time t is given by

$$S_{(t)} = S_{(0)} \exp(bt),$$

where b is the rate of change in the transition rate and $S_{(0)}$ is transition rate at the time of speciation. A value of $b > 0$ indicates that the S increases with t, while a value of $b < 0$ indicates that S

decreases with t. When $b = 0$, S is constant and thus reduces to the Constant-Rate model. The Time-Variable model may fit best if the strength of species interactions declines gradually with time since speciation (Cahill *et al.* 2008).

Both species interactions and dispersal constraints can delay the attainment of sympatry and it may be possible to extend our models to separate these effects. Under the Rate-Switch model, the waiting time to sympatry following the break point ($W2$) should primarily capture the delay due to dispersal constraints because the influence of species interactions amongst long-diverged pairs is expected to be weak (Fig. 1). The difference between $W2$ and the average observed lag time (W, estimated under the Constant-Rate model) thus approximates the delay due to species interactions (Fig. S4; Appendix S1). We use this framework ($\Delta W = W - W2$) to provide a preliminary assessment of the relative contribution of dispersal and species interactions in determining the timing of sympatry in furnariids.

If species interactions, and in particular competition, prevent range expansion then we expect the frequency of range overlap to increase with the extent of α-niche divergence. However, both the cumulative probability of attaining sympatry and the extent of α-niche divergence between sisters are expected to increase with time since speciation, potentially leading to a spurious association between sympatry and α-niche divergence. We account for this in our analyses by modelling how α-niche divergence influences the rate of transition from allopatry to sympatry, rather than the probability of sympatry *per se*. Specifically, we fit a proportional-intensities (Trait-Dependent) model, in which the morphological difference between sister species (z) was included as a covariate on S (Appendix S1). Under this model, the transition rate for sister species pair j at time t is given by

$$S_{(jt)} = S_{(0)} \exp(\beta_S^T) Z_{jt}.$$

We used likelihood ratio tests to compare support for the Trait-Dependent model to a Constant-Rate model, in which rates of secondary sympatry are independent of α-niche divergence.

RESULTS

Waiting times to secondary sympatry

Across furnariids, sister species predominantly occur in allopatry, with relatively few (19/94; 20.2%) in sympatry. These sympatric lineages are on average substantially older (4.32 Myr) than those occurring in allopatry (2.66 Myr). The low frequency and old age of sympatric sisters implies that species tend to remain in allopatry for long periods following speciation. Confirming this, we estimate that the transition rate from allopatry to sympatry (S) is extremely protracted ($S = 0.069$/Myr [95% CI: 0.044, 0.108]), equating to an average waiting time to sympatry of 14.52 Myr (95% CI: 9.23, 22.85) (Table 1).

The majority of furnariid sister pairs (94%) have conserved β-niches, indicating that most speciation occurs within the same macrohabitats (Fig. 3a). When we restricted our analysis to this subset, waiting times to secondary sympatry were reduced, but remained extremely long [$W = 11.59$ Myr (95% CI: 7.25, 18.51)] (Table 1). This slight reduction may arise because divergent habitats tend to be spatially disjunct, reducing the likelihood of secondary contact between species.

Table 1 Models of secondary sympatry specifying constant or time varying rates across Furnariidae

Data		Constant Rate				Rate Switch							Time Variable			
	n	S	W	AIC	$S1$	$W1$	$S2$	$W2$	TS	AIC	P	S_0	b	AIC	P
All pairs	94	0.07 (0.04,0.11)	14.52 (9.23,22.86)	83.5	0.06 (0.03,0.11)	16.16 (8.92,29.28)	0.1 (0.03,0.36)	9.58 (2.75,33.33)	4.6	85.1	0.6	0.05 (0.02,0.13)	0.08 (−0.16,0.32)	85.1	0.5
β-niche Conserved	79	0.09 (0.05,0.14)	11.58 (7.25,18.5)	68.2	0.06 (0.03,0.12)	16.35 (8.58,31.17)	0.33 (0.12,0.9)	3.03 (1.11,8.26)	4.6	66.1	0.04	0.04 (0.01,0.1)	0.31 (0.06,0.56)	65.4	0.03

Rates and waiting times (95% CI) estimated across all sister pairs ('All pairs') and across those occupying the same β-niche ('β-niche conserved'). n = number of pairs; S = rate of secondary sympatry per sister pair per million years (Myr); W = expected waiting time to secondary sympatry per sister pair per million years (Myr); $S1$, $S2$, $W1$ and $W2$ = rates and waiting times estimated under the Rate-Switch model before and after the breakpoint (TS) respectively; b = rate of change in transition rate with time since divergence estimated under the Time-Variable model; P = significance from likelihood ratio tests comparing the Rate-Switch and Time-Variable models to a Constant-Rate model respectively.

The temporal dynamics of coexistence

Across all species pairs we found that a null model assuming a constant rate of secondary sympatry could not be rejected (Table 1; Fig. 3b). However, when we accounted for divergence in species β-niches, we found support for a model in which S does vary significantly with t (Fig. 3c–d; Table 1). In the Rate-Switch model, the best-fit break point occurs 4.6 Myr following speciation, whereupon an initially low rate of secondary sympatry [$S1 = 0.061$ (95% CI: 0.032, 0.117)] increases to a significantly higher rate [$S2 = 0.33$ (95% CI: 0.121, 0.90)] (Fig. 3b; Table 1). Although the timing of the rate shift is uncertain (Fig. S3), the increase in rates corresponds to a dramatic difference in the waiting times to secondary sympatry prior to [$W1 = 16.35$ Myr (95% CI: 8.58, 31.17)] and after [$W2 = 3.03$ Myr (95% CI: 1.11, 8.26)] the break point (Table 1). These results suggest that while dispersal constraints have delayed sympatry by *c.* 3 Myr, the corresponding delay due to species interactions (ΔW) is *c.* 8.6 Myr (Fig. S4; Appendix S1).

We detected a similar increase in S with t using the Time-Variable model, showing that our results are robust to the way variation in rates is modelled (Fig. 3d; Table 1). The difference in support between the Time-Variable and Rate-Switch models was small (Table 1), and so we cannot yet discriminate precisely how the intensity of species interactions declines with t. As expected, evidence for time dependency in rates of secondary sympatry was strongest amongst species occurring in close geographical proximity where the potential for interaction is greatest (Fig. S3; Table S2). We note, however, that these significant relationships were present regardless of the distances over which species were compared (Fig. S3; Table S2).

α-niche-dependent rates of secondary sympatry

A null model with rates of secondary sympatry equal across all lineages could not be rejected (Table 2). However, when we refined our analysis to those sisters with conserved β-niches ($n = 61$), we found that S was significantly positively associated with α-niche divergence (Table 2). This effect was detected despite the reduced sample size, and thus statistical power. The reduction in waiting times to sympatry amongst sisters that had diverged more rapidly in niche space (Fig. 4) was primarily driven by divergence along the first PC axis, which provides an overall measure of beak size (Fig. 4; Tables S6 and S7). Distances between species along the remaining PC axes, which describe variation in beak shape (Tables S6 and S7), were also positively associated with rates of secondary sympatry, but these relationships were not significant (Table 2). The results were very similar when α-niche divergence was quantified using all morphological traits or only bill dimensions (Table 2). Finally, we note that while the effects of α-niche divergence in limiting S were strongest amongst species occurring in close proximity, these relationships remained significant regardless of geographical distance (Table S4).

DISCUSSION

Using a phylogenetic approach to explore temporal patterns of geographic range overlap in furnariids, we have shown that the dynamics of range expansion cannot simply be explained by limits to dispersal or environmental filtering. Instead, our results are consistent with a model in which biotic interactions play a key role in limiting range overlap amongst recently diverged species. Evidence of

Table 2 Trait-dependent models of secondary sympatry fitted to observed α-niche divergence (z) across species pairs

Variable	Proportional change	P	$S_{(z\,=\,\min(z))}$	$W_{(z\,=\,\min(z))}$	$S_{(z\,=\,\max(z))}$	$W_{(z\,=\,\max(z))}$
Bill.PC1	2.82 (0.38,5.32)	0.01	0.06 (0.14,0.03)	15.72 (7.1,34.81)	1.03 (6.74,0.16)	0.97 (0.15,6.35)
Bill.PC2	3.37 (−3.16,10.35)	0.19	0.09 (0.2,0.04)	11.35 (5.02,25.68)	2.42 (884.12,0.01)	0.41 (0,150.48)
Bill.PC3	0.49 (−1.4,2.42)	0.62	0.11 (0.23,0.05)	9.49 (4.27,21.08)	0.17 (0.66,0.04)	5.79 (1.51,22.27)
Bill. Euclidian	4.15 (0.28,8.18)	0.01	0.06 (0.14,0.02)	17.43 (7.17,42.34)	3.36 (76.17,0.15)	0.3 (0.01,6.74)
Morph.PC1	2.51 (0.06,5.01)	0.02	0.07 (0.15,0.03)	14.48 (6.61,31.7)	0.82 (5.44,0.12)	1.22 (0.18,8.09)
Morph.PC2	2.93 (−2.94,9.16)	0.2	0.09 (0.2,0.04)	10.99 (5.06,23.89)	1.64 (326.42,0.01)	0.61 (0,121.74)
Morph.PC3	1.06 (−0.63,2.79)	0.24	0.09 (0.19,0.04)	10.93 (5.35,22.32)	0.26 (0.92,0.08)	3.79 (1.08,13.28)
Morph.PC4	−0.17 (−1.92,1.62)	0.85	0.13 (0.27,0.06)	7.66 (3.65,16.08)	0.11 (0.4,0.03)	9.05 (2.47,33.13)
Morph.PC5	1.56 (−1.29,4.48)	0.26	0.09 (0.19,0.04)	11.11 (5.13,24.07)	0.42 (4.17,0.04)	2.37 (0.24,23.41)
Morph.Euclidian	3.91 (0.15,7.81)	0.02	0.06 (0.14,0.02)	17.34 (7.02,42.8)	2.66 (53.15,0.13)	0.38 (0.02,7.5)

To aid comparison, values of z were standardised from 0 (minimum divergence) to 100 (maximum divergence). Proportional change indicates the percentage change in S per 1% increase in z. S and W = expected rates and waiting times to secondary sympatry, respectively, corresponding to the minimum ($z = 0$) and maximum ($z = 100$) α-niche divergence. Except for Morph.PC4, greater α-niche divergence results in shorter W. P = significance from a likelihood ratio test comparing the Trait-Dependent and Constant-Rate model. Models were fitted to all sister pairs with conserved β-niches and whose ranges occurred within a distance of 250 km ($n = 61$).
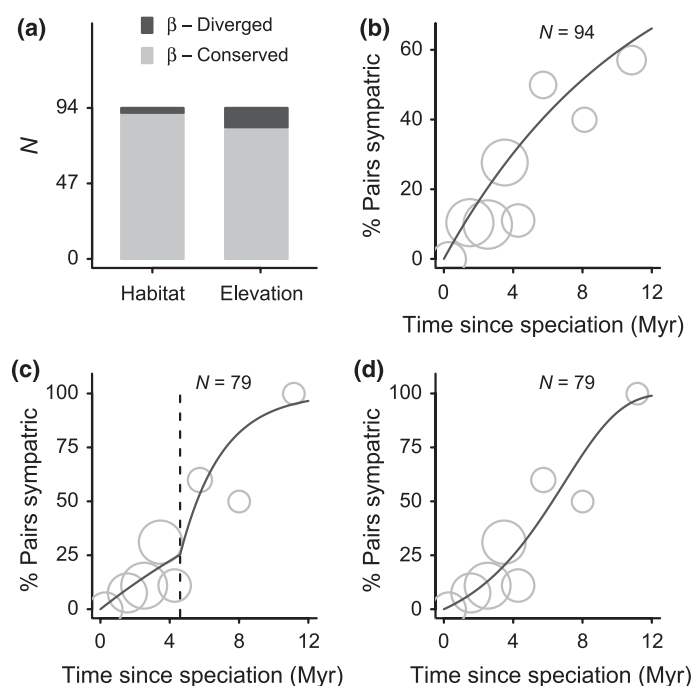

Figure 3 (a) Number (N) of sister species pairs with conserved and diverged β-niches for habitat and elevation range, and (b–d) accumulation of secondary sympatry (%) with time since speciation (Myr) across (b) all pairs and (c–d) those with conserved β-niches. Solid line shows sympatry accumulation predicted by the (b) Constant-Rate, (c) Rate-Switch and (d) Time-Variable models. Dashed line in (c) shows the estimated rate switch ($ts = 4.6$ Myr) (see Fig. S2). Circles indicate percentage of sympatric pairs within 1-Myr time intervals against average species age. Circle size is proportional to the number of pairs in each time interval (minimum = 4 sister pairs). Time intervals containing < 4 sisters were grouped with the preceding time interval.

this process varies with ecology, being most prominent when pairs of lineages are ecologically similar and much weaker when they are ecologically divergent.

Across Furnariidae as a whole, rates of secondary sympatry conform to a null model of random range expansion in which the build-up of sympatric diversity occurs at a constant rate. However, when we accounted for environmental filtering by restricting the analysis to species pairs with conserved β-niches, we found that the

tempo of range expansions leading to secondary sympatry has not been constant. Rather, the transition is initially slow and then accelerates with increasing time since speciation. This pattern is opposite to that expected if range overlap was determined primarily by opportunities for dispersal, but consistent with a model in which biotic interactions limit range overlap amongst recently diverged lineages (Fig. 1c, f). Taken together, these findings indicate that constraints on range overlap weaken over time as the ecological differences between species accumulate, and – importantly – that this process is hard to detect at large scales because seemingly stochastic patterns (Fig. 1a, d) arise from the opposing effects of environmental filtering and biotic interactions.

A possible alternative explanation is that rates of secondary sympatry have declined over the period sampled by our sister species, perhaps due to the formation of a major geographical barrier to dispersal (Fig. S2). However, given the ecological heterogeneity and geographical scale of the furnariid radiation (Derryberry *et al.* 2011), it is unlikely that a single biogeographical event has governed the spatial dynamics of all species in concert (Appendix S1). Moreover,
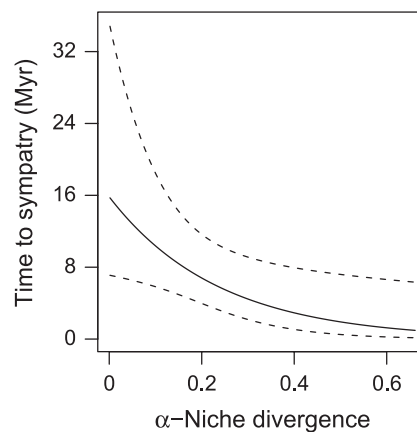

Figure 4 The effect of α-niche divergence on the waiting times to secondary sympatry (Myr). Times to secondary sympatry as a function of α-niche divergence were estimated from a Trait-Dependent model with distance along bill PC1 included as a covariate on the transition rate (Table 2). Models were fitted to all sister pairs with conserved β-niches and whose ranges occurred < 250 km apart ($n = 61$).

the acceleration we detect is relative to divergence events that vary in their timing, making it much less likely that our results can be explained by biogeographical history. Rather, the most parsimonious explanation for an accelerating build-up of sympatry as species age increases is the general trend of ecological divergence with time since speciation (Uyeda *et al.* 2011).

Although we reject a model based purely on dispersal limitation, low rates of dispersal almost certainly contribute to the slow build-up of sympatry in furnariids. The majority of furnariid species occupy ecological niches associated with reduced dispersal (e.g. many are specialist insectivores with lifelong territory defence) and the major Neotropical barriers that initiated geographical isolation (e.g. Andean mountain ranges, Amazonian rivers) persist long after speciation (Salisbury *et al.* 2012). A potential advantage of our models is that they allow us to assess the relative contributions of dispersal limitation and biotic interactions in regulating range expansion. While these estimates must be viewed as preliminary, they suggest that constraints on dispersal may delay the attainment of sympatry by *c.* 3 Myr, whereas the average observed waiting time to sympatry is far longer (̃ 12 Myr; Fig. S4; see Appendix S1 for details of analysis). Thus, biotic interactions appear to be a key factor delaying secondary sympatry following speciation.

Evidence for this is further strengthened by our analysis of ecomorphological traits. Species pairs with divergent bill shape and/or body size attain sympatry at an earlier age than those with more similar trait values. This makes sense as these traits are closely tied to variation in resource use and foraging strategy (the α-niche), and their overdispersion amongst locally co-occurring species has long been a classic example of trait-mediated coexistence (Schoener 1965; Grant 1968). Given strong interspecific aggression and territoriality in furnariids, the most obvious explanation for patterns of geographic exclusion between related lineages is therefore competition for ecological resources, including space (Cody 1974).

An alternative hypothesis is that range overlap amongst recently diverged species could be limited by reproductive interference, whereby species incur fitness costs associated with sexual, rather than ecological, interactions (Gröning & Hochkirch 2008; Weir & Price 2011). Reproductive interference is expected to be strongest amongst species with similar mating signals, potentially leading to delayed coexistence. However, this seems unlikely to provide an adequate explanation for the patterns we detect because numerous pairs of ecologically similar furnariids (e.g. *Automolus infuscatus* and *A. paraensis*, *Xiphorhynchus spixii* and *X. elegans*) remain parapatric in distribution despite being relatively old with widely divergent plumage signals or songs (and hence almost certainly reproductively isolated). Thus, our finding that rates of secondary sympatry are mediated by divergence in the α-niche suggests that the main constraint to coexistence in furnariids is ecological.

A third explanation is that constraints on range overlap are not driven by direct species interactions, but indirectly via shared parasites or pathogens (Ricklefs 2010). This hypothesis is controversial because it implies that species diversification and community assembly are uncoupled from the processes of niche filling and resource competition. If such a mechanism does operate, it might be expected to be strongest in tropical continental systems (e.g. Furnariidae), where the diversity and virulence of pathogens is greatest. However, while we cannot rule out the influence of phylogenetically conserved 'shared enemies', the consistent associations we find between rates of secondary sympatry and divergence in ecomorphological traits suggest that

direct interactions between ecological competitors are the primary limits to range expansion in the furnariid clade.

Our analyses also provide new insights into the long-standing question of whether ecomorphological trait differences amongst co-occurring species arise predominantly through ecological (e.g. species sorting) or evolutionary (e.g. character displacement) processes (Pfennig & Pfennig 2010). Specifically, while character displacement may contribute to an association between sympatry and α-niche divergence, it cannot explain the initial lag we detect in range overlap following speciation, which must be caused by a sorting mechanism. Moreover, in numerous cases of range overlap between young but ecologically divergent species (e.g. Fig. 2d), ecomorphological traits appear to be equally divergent in sympatry and allopatry. This indicates that our results are not simply a reflection of character displacement in sympatry, and that species sorting is a critical factor mediating geographic range expansion.

By highlighting the role of competition in structuring biogeographical patterns, our findings contrast with those of numerous previous studies where convincing evidence for strong species interactions over regional scales has been lacking. In part, our findings may reflect the greater power of combined phylogenetic and trait-based models of secondary sympatry to isolate the signal of species interactions compared with traditional approaches based on static distribution patterns (e.g. Letcher *et al.* 1994; Ricklefs 2011). This seems especially likely given that we have shown how a combination of competition and habitat filtering can produce the impression of neutral or random patterns if temporal dynamics are not taken into account. We also suspect that there may be real differences in the importance of competition across taxonomic groups, and note that most previous studies have focused on systems such as plants (e.g. Cahill *et al.* 2008) or microbes (e.g. Violle *et al.* 2011) where competitive interactions may have weaker effects on spatial exclusion. The niche incumbency framework seems more relevant to vertebrates. Tropical bird communities, for example, are characterised by old lineages and saturated niches (Weir & Price 2011), coupled with interspecific aggression and intense competition via year-round territoriality (Connor & Bowers 1987; Tobias *et al.* 2011).

Taken together, our results challenge the widespread view that biotic interactions have a weak influence on large-scale geographic distributions (Shmida & Wilson 1985; Pearson & Dawson 2003; Cavender-Bares *et al.* 2009; Peterson *et al.* 2011; Wiens 2011). They also run counter to the expectation of neutral models of species diversity, in which range overlap is explained simply by dispersal limitation and is unrelated to ecological divergence (Bell 2005). Instead, we provide compelling support for the idea that, at least in vertebrates, geographic range expansions are regulated by interspecific interactions, and primarily ecological competition. This evidence for niche incumbency in limiting species co-occurrence across biogeographical scales suggests that as niche space is filled, range expansions will become increasingly inhibited, thus slowing the build-up of regional diversity (Rosenzweig 1975; Rundell & Price 2009). Future work could extend our modelling framework to explicitly test these hypotheses by examining how rates of range expansion have changed over deeper timescales and in response to alternative range-limiting mechanisms (e.g. reproductive interference and/or shared natural enemies).

A corollary of our findings is that ecological competition is likely to constrain future shifts in geographic distributions in response to

environmental change, perhaps exacerbating contractions in range size and declines in diversity (Urban *et al.* 2012). In effect, patterns of range overlap in furnariids suggest that the standard assumption of ecological forecasting models – i.e. that species interactions have a negligible effect on geographic ranges (Pearson & Dawson 2003) – is invalid. Our analyses thus add weight to the increasing number of studies calling for biotic interactions to be incorporated into the next generation of species distribution models (Araújo & Luoto 2007; Lavergne *et al.* 2010; Kissling *et al.* 2011). Moreover, by quantifying the probability of range overlap over time in relation to phylogenetic and ecological trait differences between species, our approach offers a suite of novel metrics by which this may be achieved. We conclude that the transition to sympatry is an important conceptual bridge, not only linking theories of regional diversification with those of local community assembly, but potentially providing a framework for understanding and predicting the impacts of environmental change.

AUTHORSHIP

ALP and JAT developed conceptual framework and devised analytical approach, ALP and JAT collected data, ALP performed analyses, ALP and JAT wrote the manuscript.

REFERENCES

Araújo, M.B. & Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecol. Biogeogr.*, 16, 743–753.

Bell, G. (2005). The co-distribution of species in relation to the neutral theory of community ecology. *Ecology*, 86, 1757–1770.

Bowers, M.A. & Brown, J.H. (1982). Body size and coexistence in desert rodents - chance or community structure. *Ecology*, 63, 391–400.

Cahill, J.F., Kembel, S.W., Lamb, E.G. & Keddy, P.A. (2008). Does phylogenetic relatedness influence the strength of competition among vascular plants?. *Perspect. Plant Ecol.*, 10, 41–50.

Case, T.J., Holt, R.D., McPeek, M.A. & Keitt, T.H. (2005). The community context of species' borders: ecological and evolutionary perspectives. *Oikos*, 108, 28–46.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009). The merging of community ecology and phylogenetic biology. *Ecol. Lett.*, 12, 693–715.

Cody, M.L. (1974). *Competition and the Structure of Bird Communities*. Princeton University Press, Princeton.

Colwell, R.K. & Winkler, D.W. (1984). A null model for null models in biogeography In: *Ecological Communities: Conceptual Issues and the Evidence* (eds. Strong, D.L., Simberloff, D., Abele, L.G. & Thistle, A.B.). Princeton University Press, Princeton, pp. 1–603.

Connor, E.F. & Bowers, M.A. (1987). The spatial consequences of interspecific competition. *Ann. Zool. Fenn.*, 24, 213–226.

Connor, E.F. & Simberloff, D. (1979). The assembly of species communities - chance or competition?. *Ecology*, 60, 1132–1140.

Davies, T.J., Meiri, S., Barraclough, T.G. & Gittleman, J.L. (2007). Species co-existence and character divergence across carnivores. *Ecol. Lett.*, 10, 146–152.

Davis, M.B. & Shaw, R.G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, 292, 673–679.

Derryberry, E.P., Claramunt, S., Derryberry, G., Chesser, R.T., Cracraft, J., Aleixo, A. *et al.* (2011). Lineage diversification and morphological evolution in a large-scale continental radiation: the Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution*, 65, 2973–2986.

Diamond, J.M. (1975). Assembly of species communities. In: *Ecology and Evolution of Communities* (eds. Cody, M.L. & Diamond, J.M.). Harvard University Press, Cambridge.

Elton, C.S. (1946). Competition and the structure of ecological communities. *J. Anim. Ecol.*, 15, 54–68.

Fargione, J., Brown, C.S. & Tilman, D. (2003). Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl. Acad. Sci. U.S.A.*, 100, 8916–8920.

Gotelli, N.J., Graves, G.R. & Rahbek, C. (2010). Macroecological signals of species interactions in the Danish avifauna. *Proc. Natl. Acad. Sci. U.S.A.*, 107, 5030–5035.

Grant, P.R. (1968). Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Syst. Zool.*, 17, 319–333.

Gröning, J. & Hochkirch, A. (2008). Reproductive interference between animal species. *Q. Rev. Biol.*, 83, 257–282.

Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G.J. *et al.* (2011). Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *J. Biogeogr.*, 39, 2163–2178.

Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010). Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annu. Rev. Ecol. Syst.*, 41, 321–350.

Letcher, A.J., Purvis, A., Nee, S. & Harvey, P.H. (1994). Patterns of overlap in the geographic ranges of Palearctic and British mammals. *J. Anim. Ecol.*, 63, 871–879.

MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distributions of Species*. Harper and Row, New York.

Martin, P.R., Montgomerie, R. & Lougheed, S.C. (2010). Rapid sympatry explains greater color pattern divergence in high latitude birds. *Evolution*, 64, 336–347.

Mayr, E. (1942). *Systematics and the origin of species*. Columbia University Press, New York.

Miles, D.B. & Ricklefs, R.E. (1984). The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology*, 65, 1629–1640.

Moulton, M.P. & Pimm, S.L. (1987). Morphological assortment in introduced Hawaiian passerines. *Evol. Ecol.*, 1, 113–124.

Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?. *Global Ecol. Biogeogr.*, 12, 361–371.

Peterson, A.T., Soberon, J., Pearson, R.G., Anderson, R.P., Martinez-Meyer, E., Nakamura, M. *et al.* (2011). *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton.

Pfennig, D.W. & Pfennig, K.S. (2010). Character displacement and the origins of diversity. *Am. Nat.*, 176, S26–S44.

Phillimore, A.B., Orme, C.D.L., Thomas, G.H., Blackburn, T.M., Bennett, P.M., Gaston, K.J. *et al.* (2008). Sympatric speciation in birds is rare: insights from range data and simulations. *Am. Nat.*, 171, 646–657.

Price, T.D. & Kirkpatrick, M. (2009). Evolutionarily stable range limits set by interspecific competition. *Proc. Biol. Sci.*, 276, 1429–1434.

Revell, L.J. (2009). Size-correction and principal components for interspecific comparative studies. *Evolution*, 63, 3258–3268.

Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.*, 7, 1–15.

Ricklefs, R.E. (2010). Host-pathogen coevolution, secondary sympatry and species diversification. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 365, 1139–1147.

Ricklefs, R.E. (2011). Applying a regional community concept to forest birds of eastern North America. *Proc. Natl. Acad. Sci. U.S.A.*, 108, 2300–2305.

Rosenzweig, M.L. (1975). On continental steady states of species diversity. In: *The Ecology and Evolution of Communities* (eds. Cody, M. & Diamond, J.M.). Harvard University Press, Harvard.

Rundell, R.J. & Price, T.D. (2009). Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends Ecol. Evol.*, 24, 394–399.

Salisbury, C.L., Seddon, N., Cooney, C.R. & Tobias, J.A. (2012). The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. *Ecol. Lett.*, 15, 847–855.

Schaefer, H., Hardy, O.J., Silva, L., Barraclough, T.G. & Savolainen, V. (2011). Testing Darwin's naturalization hypothesis in the Azores. *Ecol. Lett.*, 14, 389–396.

Schoener, T.W. (1965). The evolution of bill size differences among sympatric congeneric species of birds. *Evolution*, 19, 189–213.

Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009). Evolution and ecology of species range limits. *Annu. Rev. Ecol. Evol. Syst.*, 40, 415–436.

Shmida, A. & Wilson, M.V. (1985). Biological determinants of species-diversity. *J. Biogeogr.*, 12, 1–20.

Southwood, T.R.E. & Kennedy, C.E.J. (1983). Trees as islands. *Oikos*, 41, 359–371.

Tobias, J.A., Gamarra-Toledo, V., Garcia-Olaechea, D., Pulgarin, P.C. & Seddon, N. (2011). Year-round resource defence and the evolution of male and female song in suboscine birds: social armaments are mutual ornaments. *J. Evol. Biol.*, 24, 2118–2138.

Urban, M.C., Tewksbury, J.J. & Sheldon, K.S. (2012). On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proc. Biol. Sci.*, 279, 2072–2080.

Uyeda, J.C., Hansen, T.F., Arnold, S.J. & Pienaar, J. (2011). The million-year wait for macroevolutionary bursts. *Proc. Natl. Acad. Sci. U.S.A.*, 108, 15908–15913.

Violle, C., Nemergut, D.R., Pu, Z.C. & Jiang, L. (2011). Phylogenetic limiting similarity and competitive exclusion. *Ecol. Lett.*, 14, 782–787.

Weir, J.T. & Price, T.D. (2011). Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient. *Am. Nat.*, 177, 462–469.

Wiens, J.J. (2011). The niche, biogeography and species interactions. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 366, 2336–2350.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).