

Hard and soft allopatry: physically and ecologically mediated modes of geographic speciation

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ABSTRACT

Aim Three common patterns have emerged in comparative phylogeographic analyses at many barriers: (1) a potential geographic pseudocongruence of lineage divergences; (2) a disconnect between the inference of temporally clustered, relatively recent timing for observed speciation events, and dates spanning a broader, apparently random time-scale; and (3) an apparent prevalence of speciation with recent or continuing gene flow. It is unclear if there is a unifying explanation for these phenomena. We argue that the interaction between geographic barriers to dispersal and ecological limits on the distribution of species can explain these patterns. We suggest that these patterns can be explained by the presence of a continuum between two underlying processes, here termed 'hard' and 'soft' allopatric divergence, which result from the interplay between organismal ecology and the physioecological nature of geographic barriers.

Location Examples from North America.

Methods We examine comparative phylogeographic divergences in 18 groups of terrestrial vertebrates at two major biogeographic features in North America – the Mississippi River Embayment and the Cochise Filter Barrier – to test predictions made by this hypothesis.

Results We find support for the two distinct processes of hard and soft allopatry, and note several examples exhibiting characteristics of both. Hard allopatry is caused by physical barriers promoting divergence as a function of consistent geographic isolation. Soft allopatry is caused by ecological processes that isolate populations geographically in allopatric refugia through niche conservatism, or across ecological transition zones through niche divergence, but which may be periodic or inconsistent through time.

Main conclusions Viewing geographic speciation as a continuum between hard and soft allopatry can explain all three patterns as a consequence of the physical and ecological mechanisms that isolate populations, and provides an alternative perspective on the impact of ecological factors and physical barriers on lineage formation.

Keywords

Biogeography, genetic divergence, geographic barrier, lineage formation, niche conservatism, niche divergence, North America, phylogeography, speciation, vertebrates.

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INTRODUCTION

Of the primary modes of speciation, lineage divergence in allopatry is widely recognized to be one of the most common

(Diamond, 1977; Futuyma, 1998; Coyne & Orr, 2004). Allopatric divergence is typically ascribed to the presence of geographic barriers dividing populations, through either vicariance or trans-barrier dispersal. This separation is a

commonly assumed first step in promoting speciation (Coyne & Orr, 2004). All barriers ultimately represent regions of unsuitable ecological conditions for a species, which reduce dispersal (Lomolino *et al.*, 2006) and affect range limits (Kirkpatrick & Barton, 1997). However, the means by which this occurs appear to lie on a continuum between physically and ecologically mediated disruption of the range of a species, through processes that here we term 'hard' and 'soft' allopatric divergence. Aspects of these patterns and their differential impacts on speciation have been noted by several previous researchers (e.g. Fransen, 2002), who refer to 'climatic' (Gee, 2004) and 'physical' (Steeves *et al.*, 2005) barriers affecting dispersal.

'Soft' allopatry (ecological disruption) refers to an intrinsic organismal response to large-scale ecological variation promoting allopatric separation, via the fragmentation of a single population into areas divided by ecologically, but not physically, unsuitable habitat. This geographic separation of populations may occur as a result of either niche conservatism, as populations track geographically separated patches of optimal habitat [e.g. the refugial speciation model of Moritz *et al.* (2000); see also Haffer (1969), Wiens (2004) and Waltari *et al.* (2007)], or niche divergence, as populations adapt to new niches in different geographic areas [e.g. the gradient speciation model of Moritz *et al.* (2000); see also Gee (2004)]. Thus, populations are isolated by the geographically divergent effects of ecological conditions experienced by individuals in different regions, and by their impacts on the range limits and distribution of the species (e.g. Kirkpatrick & Barton, 1997; Knowles, 2001a; Gee, 2004; Wiens & Graham, 2005).

In this case, the 'barrier' is defined geographically by a shift in environmental conditions where ecologically suitable habitat ends. This type of barrier can occur in the absence of any substantial physiographic transition or other geological feature such as a river or mountain range impeding dispersal (e.g. Costa *et al.*, 2008). Thus, the effect of the barrier arises from the intrinsic response of species to range-wide environmental variation, rather than to local physiographic features. This type of barrier may be geographically fluid and subject to change on short time-scales (e.g. Carstens & Knowles, 2007; McGuire *et al.*, 2007), owing to the cyclical nature and potential rapidity of ecological changes. These processes have also been referred to as 'soft vicariance', and have been found to be important drivers of speciation, particularly for marine organisms (e.g. Fransen, 2002; Hickerson & Meyer, 2008).

In contrast, 'hard' allopatry (physical disruption) refers to extrinsic factors that determine the range limits of a species, where dispersal between potentially favourable habitats is limited by a discrete topological, geological, or physiographic feature, such as a river, isthmus, or mountain range (e.g. the riverine barrier speciation model of Moritz *et al.*, 2000; Soltis *et al.*, 2006). In the case of physical inhibition, where dispersal is limited by a discrete geographic feature (e.g. Burbrink *et al.*, 2000; Steeves *et al.*, 2005), the effects of climate on the distribution of the broader population may be immaterial (but see Jackson & Ausin, 2009). Isolation is instead caused by the

localized reduction of dispersal at a single point in the range of the species, owing to ecological conditions that are intrinsic to the barrier, rather than by the environmental conditions experienced by the populations. These barriers are less likely to be subject to large changes on short time-scales (e.g. relative to the existence of a species; Lemmon *et al.*, 2007; Burbrink *et al.*, 2008).

It is important to note that, regardless of the effect of a barrier, all barriers are dependent on the interaction between species-specific ecological preferences and the environmental nature of the barrier. Thus, ecologically and physically mediated modes of allopatric divergence are opposite ends of a continuum, rather than a strict dichotomy, as we discuss below. As these two processes are also not mutually exclusive, intermediate patterns may be observed in a region where a barrier promoting 'hard' allopatry occurs periodically, such as varying sea levels isolating and subsequently re-connecting adjacent land areas (e.g. Glor *et al.*, 2004; Leaché *et al.*, 2007). However, many observed lineage divergences appear to lie towards the ends of the spectrum when comparing phylogeographic patterns in multiple species at the same barrier. Thus, the degree to which the processes are differentiated can be distinguished in a comparative context using three primary criteria (Fig. 1).

First, is the barrier a single geographic feature that represents a physical impediment to dispersal (e.g. the Isthmus of Panama; the Mississippi River) or simply a general region associated with lineage divergence (e.g. Madrean sky islands)? Hard allopatric divergence will be localized to and defined geographically by specific physical features, while soft allopatric divergence will occur in regions that are subject to climatic oscillations or exhibit local ecological gradients. Thus, comparative analyses should show strong geographic concordance among taxa subject to hard allopatry, whereas lineages separated by soft allopatric divergence should not show such strict spatial congruence, owing to species-specific differences in the location of the limits of the species ecological niches.

Second, are lineages geographically congruent at a barrier with limited dispersal, or do they only share a general location and overlap broadly? Sky island divergences may occur in the same mountain range (e.g. Knowles, 2001b), but not necessarily on the same mountains, whereas divergences at the Isthmus of Panama are necessarily geographically congruent, and dispersal across the barrier is rare (e.g. Bowen *et al.*, 2001; Steeves *et al.*, 2005). Patterns of trans-barrier dispersal between 'hard' allopatric populations should reveal little to no mixing, whereas in the most extreme cases of 'soft' allopatry, sampling near the barrier might yield equivalent numbers of individuals from either lineage.

Finally, is the temporal distribution of divergences at a barrier clustered or random with respect to time? If lineage formation was promoted by processes such as isolation in refugia during Pleistocene glacial cycles in sky islands (e.g. Knowles, 2001b; Shepard & Burbrink, 2008) or environmental changes such as Pliocene aridification of North American deserts (e.g. Riddle & Hafner, 2006), then divergence times in

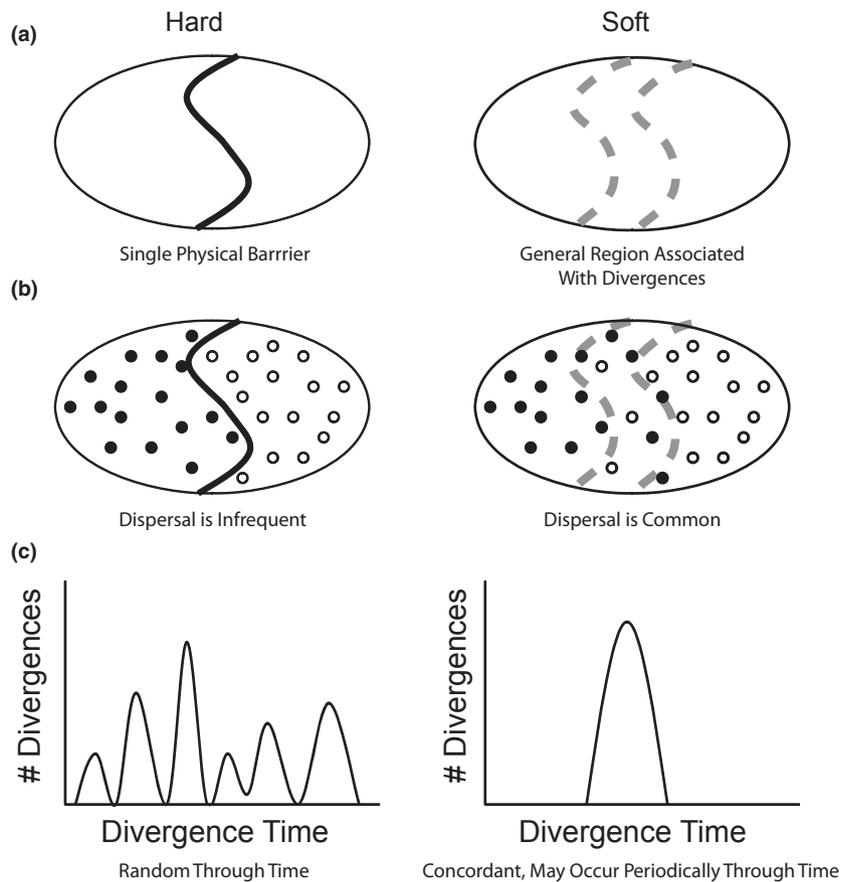


Figure 1 Illustration of the predictions for phylogeographic patterns arising from mechanisms of hard and soft allopatric divergence through niche conservatism and divergence: (a) barrier specificity, (b) trans-barrier dispersal, (c) temporal concordance.

those taxa should be centred around those periods of glacial activity or climatic shift. For ancient and putatively constant barriers such as the Mississippi River (Cushing *et al.*, 1964), lineage formation is dependent only on the formation of populations on opposite sides of the river. Thus, divergences in multiple unrelated taxa should be distributed randomly in time, dependent only on the time of colonization for each organism. For hard allopatric divergences, the impact of climatic cycles will probably serve only to strengthen an existing physical barrier (e.g. Jackson & Ausin, 2009).

Here we present comparative phylogeographic analyses illustrating allopatric divergences at the two ends of the hard–soft allopatric divergence continuum. The results from a number of phylogeographic studies indicate that these processes affecting hard and soft allopatric divergence are both important in promoting speciation, yielding the disparate patterns recently observed in comparative phylogeography.

MATERIALS AND METHODS

For this study, we chose two examples of comparative speciation events at different single ‘barriers’, one of which exhibits patterns indicative of isolation through soft allopatric divergence during recent glacial cycle-induced climatic shifts [the Cochise Filter Barrier (CFB) at the Western Continental Divide (WCD) in North America; see Riddle & Hafner

(2006)], and another that putatively represents hard allopatric divergence via dispersal throughout the Neogene [the Mississippi River Embayment (MRE) in central North America; see Soltis *et al.* (2006)]. Note that soft allopatric divergence could also occur through other processes such as isolation by distance (e.g. Palumbi, 1994), but for brevity we present two terrestrial examples, putatively representing dispersal (MRE) and vicariance (CFB).

The MRE has long been noted as a major geographic feature in North American biogeography, and has been implicated in lineage divergence in organisms ranging from gymnosperms to rodents to snakes (see Soltis *et al.*, 2006; Lemmon *et al.*, 2007). As the river dates to the Cretaceous period (Cushing *et al.*, 1964), any divergences in terrestrial taxa are likely to be the result of trans-barrier dispersal rather than vicariance. The CFB also has been implicated in numerous phylogeographic divergences (Morafka, 1977; Castoe *et al.*, 2007; Leaché & Mulcahy, 2007; Pyron & Burbrink, 2009a). Divergence is typically hypothesized to be related to the uplift of the Colorado Plateau, widespread aridification of the desert south-west during the late Pliocene and early Pleistocene, and subsequent Pleistocene glaciopluvial cycles isolating the Sonoran and Chihuahuan desert provinces (see Riddle & Hafner, 2006). We restricted our comparisons to organisms likely to exhibit similar responses to these barriers, namely terrestrial vertebrates. We identified 18 phylogeographic or

phylogenetic studies that had phylogeographic lineages localized to the MRE (9 examples) or CFB (9 examples), primarily based on mitochondrial DNA (mtDNA) (Table 1).

For each study, we obtained the geographic locations of the individual samples, either from the publication or upon request from the authors. When information was provided by the authors, we recorded estimated divergence times between clades separated at the barriers. We also noted, if given, both the hypothesized geological time period and the hypothesized causal mechanism (e.g. glacial refugial dynamics, etc.) implicated for lineage formation at the barriers. Finally, we performed binomial probability tests to assess whether or not the frequency of trans-barrier dispersal was consistent with a null model of random interchange. Each species examined exhibits at least one break across the barrier with which it is associated (i.e. at least two lineages, one on either side). We were thus able to pinpoint trans-barrier dispersals, namely individuals from a given lineage found on the 'opposite' side of the barrier (e.g. an individual from the 'western' lineage on the east side of the barrier).

For each species with more than two samples near the barrier, we counted the number of individuals from each lineage that were found on the opposite side (e.g. an individual from the 'Eastern' lineage on the west side of the barrier, or vice versa). All individuals found on the opposite side of a barrier from that expected, given their lineage, were counted as independent dispersals. While this assumption may be violated if multiple individuals are the offspring of a single ancestral colonizer, we use this more conservative assumption, given no *a priori* data on the relatedness of individual dispersals.

We calculated the probability of observing the empirical number of dispersals out of the total number of samples, summed across species, based on a hypothetical dispersal probability of 50% [P (Dispersal/Total Samples) = 0.50]. Binomial probabilities were calculated by hand. We defined proximity to the barrier for the MRE as samples occurring in states bordering the Mississippi in the region of the MRE (i.e. Louisiana, Arkansas, south-eastern Missouri, southern Illinois, south-western Kentucky, western Tennessee and Mississippi). For the CFB, we counted samples as proximal to the barrier if

Table 1 Comparative North American phylogeographic divergences of terrestrial vertebrates exhibiting patterns of hard and soft allopatric divergence.

Taxon ^(Reference)	Order: Family	Age (range) (Ma)	#D	#N	Time period	Putative cause
Cochise Filter Barrier						
<i>Peromyscus eremicus</i> ¹	Rodentia: Cricetidae	0.7	3	8	Pleistocene (Plt.)	Glaciopluvial refugia
<i>Crotalus atrox</i> ²	Squamata: Viperidae	1.36 (0.9–1.5)	8	13	Pleistocene	Glaciopluvial refugia
<i>Lampropeltis getula</i> ³	Squamata: Colubridae	2.16 (1.11–3.44)	11	26	Pliocene/Pleistocene	Glaciopluvial refugia
<i>Gambelia wislizenii</i> ⁴	Squamata: Crotaphytidae	–	0	3	Pliocene/Pleistocene	Gulf of California Embayment
<i>Hypsiglena torquata</i> ⁵	Squamata: Colubridae	–	7	17	–	–
<i>Callispsa</i> sp. ⁶	Galliformes: Odontophoridae	1–4.1	–	–	Pliocene/Pleistocene	–
<i>Sceloporus magister</i> ⁷	Squamata: Phrynosomatidae	2.41 (0.40–4.59)	0	8	Pliocene/Pleistocene	–
<i>Kinosternon</i> sp. ⁸	Testudines: Kinosternidae	–	–	–	Late Miocene/Pliocene	Madrean Uplift/ Glaciopluvial refugia
<i>Bufo punctatus</i> ⁹	Anura: Bufonidae	–	3	25	Late Miocene/Pliocene	Madrean Uplift/Plt. secondary contact
Mississippi River Embayment						
<i>Eumeces fasciatus</i> ¹⁰	Squamata: Scincidae	0.83–3.8	4	25	Pliocene/Pleistocene	Mississippi River/glacial refugia
<i>Sceloporus undulatus</i> ¹¹	Squamata: Phrynosomatidae	–	–	–	–	Mississippi River
<i>Kinosternon subrubrum</i> ¹²	Testudines: Kinosternidae	–	0	24	–	–
<i>Acris blanchardi/crepitans</i> ¹³	Anura: Hylidae	–	2	8	–	Mississippi River
<i>Lampropeltis getula</i> ³	Squamata: Colubridae	4.91 (2.63–7.32)	1	18	Late Miocene/Pliocene	Mississippi River
<i>Pseudacris nigrata</i> ¹⁴	Anura: Hylidae	4.97 (3.50–6.72)	–	–	Late Miocene/Pliocene	Mississippi River Embayment
<i>Acris gryllus/crepitans</i> ¹⁵	Anura: Hylidae	–	0	6	–	–
<i>Coluber constrictor</i> ¹⁶	Squamata: Colubridae	6.09 (3.2–9.6)	0	70	Late Miocene/Pliocene	Mississippi River Embayment
<i>Pantherophis obsoletus</i> ¹⁷	Squamata: Colubridae	7.90 (5.80–10.20) ¹⁸	3	22	Miocene	Mississippi River

The columns '#D' and '#N' represent the number of trans-barrier dispersals and number of samples proximal to the barrier, respectively.

Dashes indicate inadequate or no data. References: ¹Riddle *et al.* (2000); ²Castoe *et al.* (2007); ³Pyron & Burbrink (2009a); ⁴Orange *et al.* (1999); ⁵Mulcahy (2008); ⁶Zink & Blackwell (1998); ⁷Leaché & Mulcahy (2007); ⁸Serb *et al.* (2001); ⁹Jaeger *et al.* (2005); ¹⁰Howes *et al.* (2006); ¹¹Leaché & Reeder (2002); ¹²Walker *et al.* (1998); ¹³Gamble *et al.* (2008); ¹⁴Lemmon *et al.* (2007); ¹⁵Gamble *et al.* (2008); ¹⁶Burbrink *et al.* (2008); ¹⁷Burbrink *et al.* (2000); ¹⁸dates from Pyron & Burbrink (2009b).

they occurred within ~200 km of the WCD in the Deming Plains area of south-eastern Arizona and south-western New Mexico (see Riddle & Hafner, 2006). In both cases, we counted all dispersals, regardless of distance from the barrier. We counted the total number of trials as the number of samples in the proximity of the barrier plus the total number of dispersals.

RESULTS

The distinction between hard and soft allopatric divergence operating in these two examples can be seen in light of the three criteria mentioned above (Table 1; Figs 1 and 2). In the MRE, the river itself appears to present a geographic barrier to dispersal between lineages (Table 1; Fig. 2). Out of 173 samples near the river (i.e. states bordering the river in the MRE) in nine studies, only 10 individuals were found to represent trans-barrier dispersals (Fig. 2), an observed dispersal probability of 0.057. The binomial probability test significantly rejects a hypothesis of random dispersal ($P < 1 \times 10^{-5}$). While some individuals appear to represent trans-barrier dispersals of significant distance (e.g. *Plestiodon* in Texas; Howes *et al.*, 2006), there appear to be no areas of broad sympatry between lineages distributed east and west of the river, suggesting that dispersal is rare and strongly inhibited by the river itself. This is the case despite results that suggest that, at least for some taxa (e.g. *Lampropeltis getula*), broad areas east and west of the river are ecologically suitable for both lineages (Pyron & Burbrink, 2009a). Finally, divergences at the river range in age from ~2.3 Ma to ~8 Ma, with no apparent temporal concordance among the taxa (Table 1).

In contrast, despite the fact that the CFB is nominally associated with the WCD in New Mexico (e.g. Castoe *et al.*, 2007), no specific feature can be identified as an actual barrier to organismal dispersal in the region. For the purposes of identifying trans-barrier dispersal, we nominally refer to the WCD as the 'barrier'. Lineages that exhibit divergences across the CFB overlap broadly in south-eastern Arizona and south-western New Mexico, and exhibit little geographic congruence around the WCD (Fig. 2). Note that the CFB is only the narrow gap between the Rocky Mountains and the Sierra Madre Oriental; lineage overlap on the Colorado Plateau is typically recent secondary contact (see Jaeger *et al.*, 2005; Riddle & Hafner, 2006) and is not necessarily related to divergence at the CFB (Fig. 2). In several taxa, concordance of ecological niche and/or recent allopatric refugia has been documented across the CFB (Waltari *et al.*, 2007; Pyron & Burbrink, 2009a). Out of ~100 samples within the region, 32 are found on the opposite side of the WCD to the main distribution of their lineage (Table 1), with the majority being east-to-west dispersals (Fig. 2). The data reject the hypothesis of random (i.e. 50%) trans-barrier dispersal ($P = 0.0002$), but cannot reject a moderately high (33%) dispersal probability ($P = 0.456$). This suggests that dispersal across the WCD is a relatively common phenomenon, probably owing to the ecological suitability of trans-barrier habitats (Fig. 2; Pyron & Burbrink, 2009a). Most striking, however, is the apparent temporal concordance of most of the divergences with the Pliocene/Pleistocene boundary ~2.6 Ma and the aridification of south-western North America (Table 1).

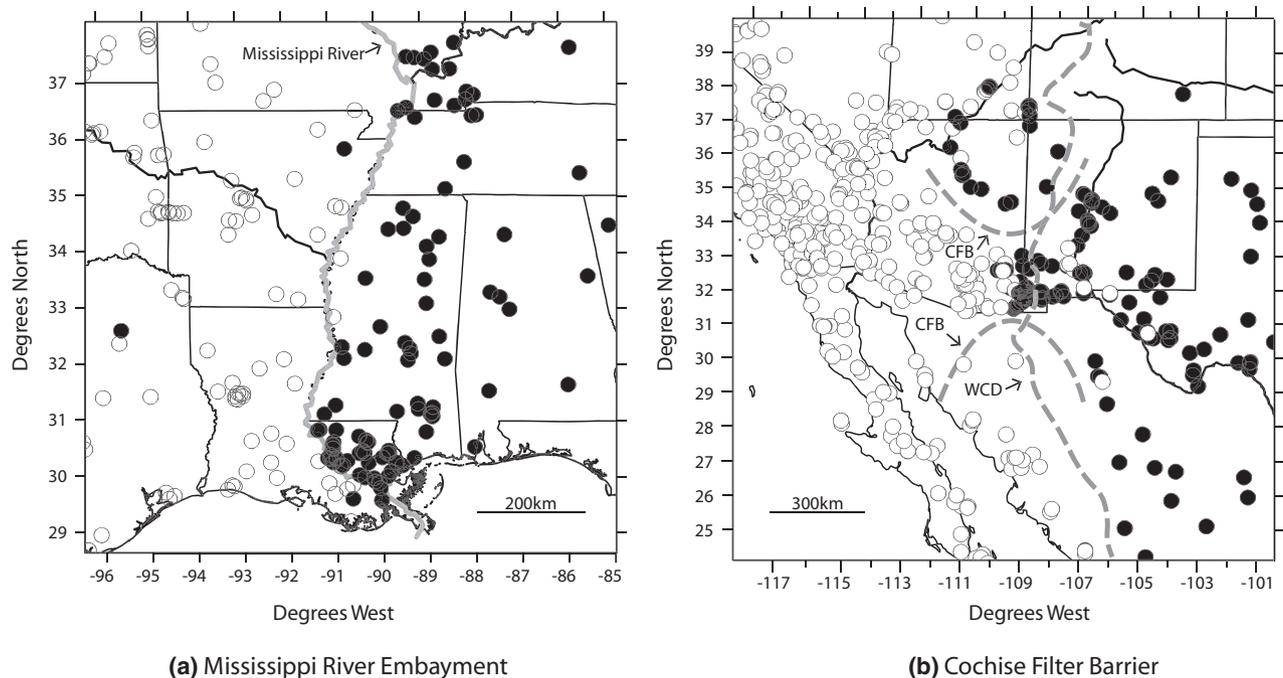


Figure 2 Geographic distribution of 13 lineage divergences of terrestrial vertebrates at the Mississippi River Embayment (MRE) (6) and Cochise Filter Barrier (CFB) (7). The locations of the Mississippi River, the CFB and the Western Continental Divide (WCD) are indicated in grey. Open circles represent 'western' lineages, while closed circles represent 'eastern' lineages.

The outcomes of the assessments by the three criteria (specificity of the barrier, distribution of the lineages, and temporal concordance of divergences) are not completely consistent in these examples. For instance, the frog *Pseudacris fouquettei* appears to have established populations east of the Mississippi, despite the *Pseudacris fouquettei/nigrita* divergence having putatively occurred at the MRE (Lemmon *et al.*, 2007). In addition, the snake *Coluber constrictor* and the skink *Plestiodon fasciatus* appear to disperse more easily across the northerly portions of the Mississippi River drainage (Howes *et al.*, 2006; Burbrink *et al.*, 2008). However, the temporal and geographic patterns exhibited by lineages divergent across these barriers display clear signals of physically versus ecologically mediated allopatric lineage formation.

DISCUSSION

The characterization of hard and soft allopatric divergence has three important implications for understanding historical biogeography and the processes that drive speciation. First, hard and soft allopatric divergence can predict the degree of geographic concordance in comparative phylogeographic studies, explaining the possible geographic pseudocongruence observed as a result of soft ecological barriers (i.e. Soltis *et al.*, 2006). Note that here we are using 'pseudocongruence' in the second, atemporal sense of Soltis *et al.* (2006), referring to apparently spatially congruent distributions of taxa that give the appearance of a single pattern, while actually representing multiple independent patterns. However, in the sense of Cunningham & Collins (1994), 'pseudocongruence' refers to congruent spatial patterns with different temporal and biogeographic origins (see Donoghue & Moore, 2003), which would apply to hard allopatric divergences.

Second, the difference between hard and soft allopatric divergence can explain the prevalence of speciation with gene flow (i.e. Niemiller *et al.*, 2008; Nosil, 2008), which depends on the permeability of barriers, and may be commonly associated with soft allopatric divergence, such as between the rat snake species, genus *Pantherophis* (Gibbs *et al.*, 2006). Particularly in regions where formerly disjunct populations have come back into contact, gene flow may be an expected pattern between recently diverged taxa (e.g. Gee, 2004; Niemiller *et al.*, 2008). This appears to be the case for numerous taxa distributed across the CFB (e.g. Leaché & Mulcahy, 2007; Fig. 2).

Third, the temporal differentiation expected between hard and soft allopatric divergence events can explain the apparent dichotomy between the inference of wide-scale recent Pleistocene speciation (e.g. Avise & Walker, 1998; Johnson & Cicero, 2004; Lovette, 2005; Peterson & Nyári, 2008) and the more dispersed timing of divergences stretching further back in time (i.e. Klicka & Zink, 1997; Feldman & Spicer, 2006; Pyron & Burbrink, 2009a,b). Widespread speciation temporally concordant with Pleistocene glacial cycles (e.g. Avise & Walker, 1998) is likely to be indicative of soft allopatric divergence through niche conservatism, while more temporally dispersed divergences across a broader time-scale are likely to be

attributable to hard allopatric divergence at ancient physical barriers. Note, however, that the old/young dichotomy is specific to the barriers examined here, whereas random versus clustered at any given time period is the general pattern expected for soft versus hard allopatry (Fig. 1).

Even a casual glance at many comparative phylogeographic divergences at barriers such as the MRE and CFB raises several questions. Why are so many species divergent at the CFB when in reality there is not actually a 'barrier' there? In contrast, why are many of the lineages separated at the CFB likely to exhibit dispersal across the WCD? Finally, why are divergences at the CFB relatively recent and temporally concordant, while divergences at the MRE appear to occur across a long period of time? Lineage formation at the MRE appears to be related solely to the physical isolation of populations by the river itself, dependent only on the establishment of populations on either side, and not to be the result of temporal or ecological influences.

In contrast, divergences at the CFB do not appear to have been caused by a specific geographic feature, but by the isolation of populations into climatic refugia on either side of the continental divide during the Pliocene aridification and subsequent Pleistocene glacial cycles. This illustrates the potentially ephemeral nature of soft allopatry, as more strongly desert-adapted taxa are likely to have been forced into refugia separated by the Sierra Madre Occidental (e.g. Jaeger *et al.*, 2005), a process potentially involving hard allopatry. In contrast, other species may persist across the CFB for longer periods and be more sensitive to ecological variation. This highlights the importance of considering not only the niche of organisms, but also the interplay between the ecology of species and the environment in which they occur (e.g. Holt, 2009), and the timing of these interactions (e.g. Donoghue & Moore, 2003).

Integrative examinations of comparative phylogeography yield slightly more ambiguous patterns of concordance than a simple hard/soft allopatry dichotomy might imply, which is to be expected given the complex nature of historical biogeography and lineage formation (Avise, 2000; Zink, 2002; de Queiroz, 2005; Devitt, 2006; Feldman & Spicer, 2006; Lomolino *et al.*, 2006; Riddle & Hafner, 2006). Thus, while a strict dichotomy between hard and soft allopatric divergence does not result in perfect congruence across taxa, the underlying mechanisms still predict major differences in the biogeographic nature of recent speciation events. Understanding the action of barriers as a continuum between these two processes dependent on the ecological characteristics of organisms highlights the variable effects of these features in reducing dispersal and promoting divergence.

For instance, riverine barriers may not promote hard allopatric divergence in amphibians or other aquatic or semi-aquatic taxa (e.g. Zamudio & Savage, 2003; Austin *et al.*, 2004; Guhier & Burbrink, 2008). Furthermore, organisms with high dispersal ability, such as large terrestrial carnivores, may be less susceptible to either process on local scales (e.g. Wooding & Ward, 1997; Culver *et al.*, 2000). Finally, allopatric divergence may occur at physical barriers with a potentially

cyclical nature, such as on islands or in coastal regions with fluctuating sea levels. Such cases may result in intermediate patterns between hard and soft allopatric divergence, with temporally and geographically congruent divergence at a physical barrier that subsequently eroded, allowing secondary contact owing to ecological changes (e.g. Glor *et al.*, 2004; de Bruyn *et al.*, 2005; Pauly *et al.*, 2007; Woodruff & Turner, 2009).

General exceptions to the patterns presented above based on the major criteria proposed for hard versus soft allopatry may also exist. For example, a number of hard allopatric divergences may be contemporaneous and/or recent if the geographic barrier represents a relatively young vicariant event, such as the separation of marine taxa as a result of the uplift of the Isthmus of Panama ~3 Ma (see Lessios, 2008), although subsequent divergences would not be expected to be clustered. Moreover, more ancient climatic cycles (e.g. Miocene/Pliocene) may have resulted in soft allopatric divergences that are temporally congruent, but at a deeper time-scale (e.g. Carstens *et al.*, 2005; Steele *et al.*, 2005). These hypotheses may be further tested using coalescent methods for groups with population-level sampling at barriers, either for assessing the temporal congruence of divergence (e.g. Leaché *et al.*, 2007; Hickerson & Meyer, 2008; Carnaval *et al.*, 2009), investigating historical demographic patterns related to glacial refugial dynamics (Fontanella *et al.*, 2008; Guiher & Burbrink, 2008), or for assessing lineage divergence at barriers obscured by incomplete lineage sorting and/or recent migration (Knowles, 2001a, b; Carstens & Knowles, 2007; Shepard & Burbrink, 2008).

These patterns are also not specific to the two barriers examined here. Additional evidence for soft allopatric divergence, both recent and relatively ancient (e.g. early Pliocene), is also found in numerous temperate terrestrial and marine taxa (e.g. Xiang *et al.*, 2000; Knowles, 2001b; Wares, 2001; Carstens *et al.*, 2005; Steele *et al.*, 2005; Kozak & Wiens, 2006). Processes related to soft allopatric divergence have also long

been implicated in refugial speciation dynamics in the Neotropics (e.g. Haffer, 1969; Peterson & Nyári, 2008; Carnaval *et al.*, 2009). Furthermore, patterns indicative of hard allopatric divergence are found at numerous other physical barriers world-wide (e.g. Bowen *et al.*, 2001; Brown *et al.*, 2002; Steeves *et al.*, 2005; Lessios, 2008; Hird & Sullivan, 2009). In addition, intermediate patterns of cyclically occurring physical barriers are observed in regions where sea-level fluctuations may periodically isolate geographic regions (e.g. Glor *et al.*, 2004; Riginos, 2005; Leaché *et al.*, 2007). We hypothesize that divergences at a number of major biogeographic features world-wide exhibit evidence of hard and soft allopatry, as well as of intermediate processes (Table 2). However, the detailed phylogeographic data necessary to assess such hypotheses are still deficient in many areas of the world for barriers that are likely to exhibit these patterns, such as Patagonia, New Guinea, Madagascar and east Africa (Beheregaray, 2008).

Based on the results presented here, we suggest that allopatric lineage divergence at the primary phylogeographic level can be understood as a continuum between two contrasting modes of geographic isolation: physically mediated ('hard') and ecologically mediated ('soft') allopatry. Aspects of this distinction have been noted by previous researchers (e.g. Gee, 2004; Steeves *et al.*, 2005; Lomolino *et al.*, 2006). Soft allopatric divergence is defined by an intrinsic organismal response to varying ecological conditions, which fix the range limits of populations relative to a barrier representing unsuitable habitat. In contrast, hard allopatry is defined as the subdivision of a continuous range by a discrete physiographic feature that limits dispersal locally owing to extrinsic ecological factors unique to the barrier.

This view of allopatric speciation does not stand in contrast to traditional understandings of allopatric divergence; rather, it attempts to distill the abiotic forces that influence lineage formation at barriers into their primary components, to

Table 2 Examples of major regions of biogeographic divergence potentially related to processes of hard and soft allopatry.

Barrier	Cause(s)	Taxa	References
Hard allopatry			
Isthmus of Panama	Uplift severing marine habitats	Numerous	Lessios (2008)
Atlas Mountains	Mountains dividing desert habitats	Lizards	Brown <i>et al.</i> (2002)
South Pacific Archipelagos	Isolation following dispersal	Lizards, Birds	Adler <i>et al.</i> (1995)
Galapagos Islands	Isolation following dispersal	Numerous	Parent <i>et al.</i> (2008)
Soft allopatry			
Amazonia	Refugial formation during climate change	Birds, Frogs	Haffer (1969); Carnaval <i>et al.</i> (2009)
Apalachee Formation	Refugial formation during climate change	Numerous	Soltis <i>et al.</i> (2006); Pyron & Burbrink (2009a)
Southern Europe	Refugial formation during climate change	Numerous	Weiss & Ferrand (2007)
Isthmus of Tehuantepec	Conservatism limiting trans-barrier dispersal	Numerous	Peterson <i>et al.</i> (1999)
Intermediate			
Peninsular Baja California	Periodic mid-peninsular inundation	Numerous	Riginos (2005); Leaché <i>et al.</i> (2007)
Indonesian Archipelago	Periodic connection of islands	Mammals	Esselstyn <i>et al.</i> (2009)
Strait of Gibraltar	Isolation, reconnection and aquatic dispersal	Numerous	Cosson <i>et al.</i> (2005); Barata <i>et al.</i> (2008)

Patterns of comparative speciation at these barriers appear to be concordant with processes of hard and soft allopatry. However, numerous, potentially conflicting hypotheses have been proposed for some of these regions (see, for instance, Moritz *et al.*, 2000).

illustrate more clearly how the ecology of organisms and the environment interact to promote speciation. Future studies should consider these alternative biogeographic scenarios in light of the functional aspects of the geographic features influencing lineage formation. Most importantly, phylogeographic studies should be conducted with an eye towards the potential comparative value of the data, including GIS-based locality information, molecular divergence time estimates, and hypotheses about causal agents of divergence. This will allow for the construction of broadly integrative biogeographic frameworks across space and time for multiple taxa, leading to a fuller understanding of the underlying mechanisms of diversity across landscapes.

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