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Phylogeography: spanning the ecology-evolution continuum

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Synthesis of ecological and evolutionary concepts and tools has led to improved understanding of how diversification, dispersal, community assembly, long-term coexistence and extinction shape patterns of biological diversity. Phylogeography, with its focus on Quaternary interactions within and between populations, can help elucidate the processes acting between the evolutionary time-scales on which species arise and the ecological time-scales on which members of an assemblage interact with each other and their environment. Still, it has yet to be widely incorporated in that synthesis. Here, we highlight three areas where integration of phylogeography with ecological and evolutionary approaches can provide new insights into key questions. First, phylogeography can help clarify the roles of isolation, niche conservatism and environmental stability in generating patterns of alpha- and beta-diversity. Second, phylogeography can help isolate the effects of Quaternary dispersal limitation from other factors driving community assembly and spatial turnover. Third, phylogeography can help identify key processes leading to and resulting from extinction events, including the population dynamics of species range reduction and its effects on the strength and temporal flexibility of networks of species interactions. We conclude with an outlook on the data-gathering protocols necessary for this collaborative, interdisciplinary research agenda.

Ecology, evolution and phylogeography: state of the union

One of Avise et al.'s (1987) initial aspirations for phylogeography – described as the bridge between intra- and interspecific patterns – was to be able to seamlessly infer biogeographic histories from the population to the supra-specific level (Avise et al. 1987, Bermingham and Moritz 1998, Avise 2009). Over 25 yr of phylogeographic investigation have yielded hundreds of individual and comparative case studies which, together, provide invaluable insights into the roles of isolation and adaptation in diversification (Jordal et al. 2006, Cavender-Bares et al. 2011, Cooke et al. 2012, Moritz et al. 2012) and reveal the individualistic histories of ecologically similar species within the same habitat (Taberlet et al. 1998, Sullivan et al. 2000, Soltis et al. 2006, Bell et al. 2012, Marske et al. 2012). At the same time, studies uniting evolutionary patterns of diversification with ecological processes have yielded fresh insights into the generation and distribution of biological diversity (Herrera 1992, Ricklefs and Schluter 1993). This integration of disciplines has intensified with the availability of large ecological and phylogenetic datasets, shedding new light on classic questions such as the evolutionary factors controlling composition of

local species assemblages (Graham et al. 2009, Lessard et al. 2012a), large-scale patterns of species richness (Wiens et al. 2011, Condamine et al. 2012), or the susceptibility of whole clades to extinction under environmental change (Fritz et al. 2009, Thuiller et al. 2011). These combinations of ecological and evolutionary approaches have yet to take full advantage of phylogeographic data and methods, in spite of phylogeography's noted potential to contribute to such a synthesis (Bermingham and Moritz 1998, Diniz-Filho et al. 2008, Hickerson et al. 2010, Emerson et al. 2011). In this paper, we highlight how insights from comparative phylogeography can be incorporated with other ecological and evolutionary disciplines to explore the mechanisms driving diversification, dispersal, community assembly and extinction.

Links between phylogenetics and ecology are typically made at the species level or above, based on species' traits or patterns of overlap between species' distributions (Graham et al. 2009, Algar et al. 2011). However, these patterns are determined by processes associated with genetic diversification, species interactions, dispersal and extirpation at the population level (Hanski and Gilpin 1997, Thompson 2005, Ricklefs 2008, Vellend 2010; Fig. 1). Phylogeography is an important approach to investigating these intra-specific dynamics, with species replaced by haplotypes or lineages, allowing inference within a similar analytical framework but at a lower hierarchical level (Avise et al. 1987, Bermingham and Moritz 1998, Diniz-Filho et al. 2008). For example, phylogeographic exploration plays a recognized, vital role in studying speciation because of the opportunity to detect

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cryptic or incipient species (Camargo et al. 2010, Marshall et al. 2011). Scaled across a phylogeny or region, ignorance of this cryptic diversity can result in misleading conclusions about diversification rates (Etienne and Rosindell 2012) or the processes by which biological diversity is generated (Carine et al. 2012). Teasing apart the effects of historical contingency and contemporary environmental conditions is repeatedly highlighted as one of the greatest challenges facing ecological disciplines (Herrera 1992, Ricklefs 2004, Wiens and Donoghue 2004), and identifying the effects of Quaternary events has proven critical to understanding species' contemporary distributions (Haffer 1969, Hewitt 1996, Hortal et al. 2011). Phylogeography, which focuses on this period, is therefore an essential part of an integrative ecological toolkit (Fig. 1).

Phylogeography also stands to be significantly revitalized through integration with other disciplines. While an emphasis on hypothesis-testing, coalescent methods and statistical phylogeography have made the discipline more rigorous (Sullivan et al. 2000, Carstens et al. 2005, Hickerson et al. 2007, Lemey et al. 2009), phylogeography's reputation as a descriptive, ad hoc interpretation of phylogenetic trees has proven difficult to shake (Knowles and Maddison 2002, Peterson and Lieberman 2012). One popular response to this criticism has been to enlist species distribution models to independently confirm genetic patterns (Hugall et al. 2002, Carstens and Richards 2007, Lorenzen et al. 2011). As well as providing a much-needed dose of ecological realism, these recent advances in phylogeography have facilitated the estimation of increasingly detailed spatial histories for individual taxa (Knowles and Alvarado-Serrano 2010, Chan

et al. 2011). However, relatively few phylogeographic studies focus outward to look for patterns that transcend individual systems, likely due to the prevalence of idiosyncratic patterns among species within regions or the idiosyncratic availability of comparative phylogeographic data across regions and taxa (although see Martin and McKay 2004, Eckert et al. 2008, Pyron and Burbrink 2010). Being able to place these results within a broader ecological and biogeographic context would significantly help illuminate the underlying causes of idiosyncratic patterns among species, just as phylogeography can help tease apart the effects of historical versus contemporary processes on current patterns of biological diversity.

In this paper we highlight three areas where incorporation of phylogeographic data and tools can contribute to new understanding of the processes underlying the spatial and temporal patterns of diversity.

Diversification. Phylogeography can detect diverging lineages and facilitate examination of the complex roles of geography, isolation, niche conservatism, and environmental stability in generating patterns of biological diversity and endemism.

Dispersal. Phylogeography can weigh in on the complex process of community assembly by disentangling the role of Quaternary dispersal from other ecological and evolutionary drivers of beta-diversity patterns, and by clarifying the temporal cohesion of species assemblages.

Extinction. Phylogeography can clarify the relationship between range size, population size and genetic diversity for vulnerable species, and test the temporal flexibility of species interactions within ecological networks and the risk of cascade extinctions under environmental change.

It is not our intention to provide an exhaustive survey of the methods or literature for each topic, but to foster communication and collaboration between ecologists and phylogeographers by emphasizing current avenues of ecological and biogeographic research to which phylogeography can contribute. We conclude with a discussion on the data necessary to explore these themes.

Diversification, niche conservatism and geographic isolation

A unifying feature of macroevolution, macroecology, biogeography and its sub-discipline phylogeography is that they investigate the relationship between the history of a region and that of its species. This convergence of ecology and evolution stems from recognition that the uneven distribution of species diversity is the product of both contemporary and historical factors (Ricklefs and Schluter 1993, Mittelbach et al. 2007). While over 25 yr of phylogeographic data-gathering has resulted in numerous reviews and syntheses on particular regions, relatively few test for general patterns and processes across regions (although see Martin and McKay 2004, Eckert et al. 2008, Riginos et al. 2011). However, one advantage of linking phylogeography with other approaches may be gained not by focusing on the phylogeographic data itself, but by using phylogeography to target regions for other analyses. For example, Bermingham and Moritz (1998) highlighted phylogeography as an important tool for identifying evolutionarily independent regions for testing

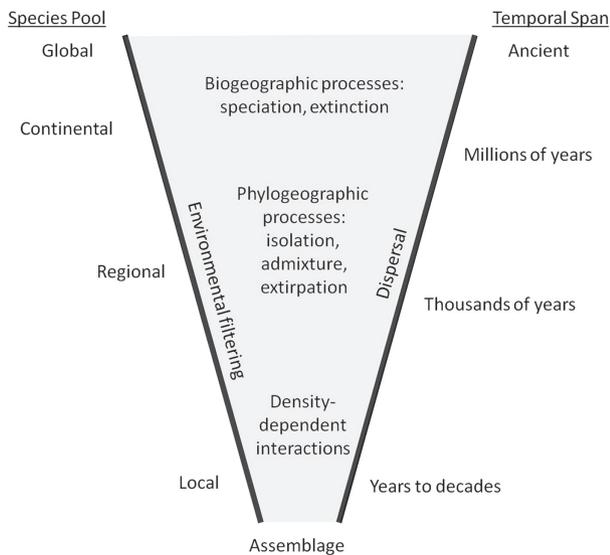


Figure 1. The ecology-evolution continuum can be viewed as a funnel of historical and contemporary processes through which species must pass to be retained within the species pool of a particular focal assemblage. The effects of biogeographic, phylogeographic and density-dependent processes are temporally and spatially nested, with environmental filtering and dispersal acting at different scales. Phylogeographic processes, which occur between biogeographic processes and density-dependent interactions, are often not considered in macroecology or community ecology but occupy a central position in the ecology-evolution continuum. Figure adapted from Cavender-Bares et al. (2009).

hypotheses about general processes. That is, systematically comparing historically similar or different regions (identified using phylogeography) might shed new light on the role of different modes of diversification, the processes driving spatial or evolutionary turnover, and their relative importance along a selection gradient (Bermingham and Moritz 1998).

Within this comparative mindset, phylogeographic break zones, or congruent regions of spatial turnover between phylogeographic lineages among co-distributed species, provide an ideal opportunity for examining allopatric diversification using nested comparisons between unrelated taxa sharing a break, phylogeographic break zones within regions, and regional break zone patterns between regions (Fig. 2). While many phylogeographic break zones are spatially consistent with contact points between populations expanding from glacial refugia, few are characterized by the simultaneous divergence which would indicate recent glacial cycles as the sole driver of lineage structure (Taberlet et al. 1998, S rsic et al. 2011, Bell et al. 2012, Fouquet et al. 2012). Lineage separation may also be maintained by contemporary environmental features, with populations from different refugia meeting in areas of less optimal current climate (Moritz et al. 2009), or with wandering contact/hybrid

zones getting caught on a shared contemporary environmental barrier (Dasmahapatra et al. 2010, Pyron and Burbrink 2010). Finally, phylogeographic break zones often coincide with continental 'suture' zones, or regions with extensive spatial turnover of species (Remington 1968), suggesting a lengthy time window for species generation in the same area (Avice et al. 1987, Taberlet et al. 1998, Rissler and Smith 2010). Thus, these regions have been repeatedly identified as 'hotspots' for observing the evolutionary process (Whinnett et al. 2005, Moritz et al. 2009, Rissler and Smith 2010, Hewitt 2011, April et al. 2013). Few studies explicitly compare phylogeographic break zones within or between regions to identify general characteristics about what drives diversification in these areas (but see Pyron and Burbrink 2010). However, a first step toward understanding the simultaneous generation of alpha- and beta-diversity at phylogeographic break zones is to quantify the regularity with which they correspond with suture zones (Swenson and Howard 2005, Rissler and Smith 2010) or a transition in contemporary environmental conditions (Moritz et al. 2009). Comparing these results across tropical versus temperate break zones or regions with different levels of historical instability might yield important insights into the longevity of evolutionary

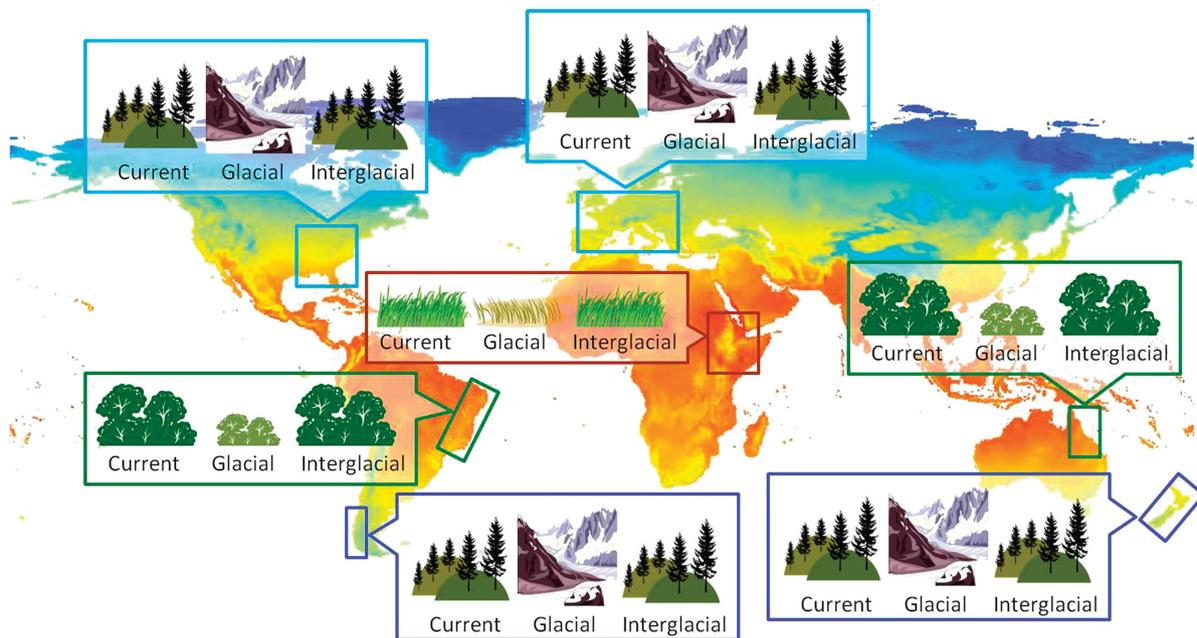


Figure 2. Comparing diversification patterns between species across phylogeographic break zones, between break zones within regions, and between regions can yield important insights into whether the processes underlying allopatric diversification and spatial turnover differ among climate zones or biogeographic regions. Seven regions with well-characterized phylogeographic break zones are indicated by colored boxes: southeastern North America (Soltis et al. 2006), central Europe (Taberlet et al. 1998), eastern Africa (Lorenzen et al. 2012), Australian wet tropics (Moritz et al. 2009), Brazilian Atlantic forest (Carnaval et al. 2009), Patagonia (S rsic et al. 2011) and New Zealand (Marske et al. 2012). Background map indicates mean annual temperature (Kriticos et al. 2012). Callout boxes for each zone indicate environmental changes associated with the Last Glacial Maximum. Box color indicates similarity of historical disturbance and contemporary environmental conditions between regions: Southern Hemisphere temperate forests (dark blue) are more similar to each other than to Northern Hemisphere temperate forests (light blue), but all four temperate forest systems are more similar to each other than they are to either tropical forests (green) or open savannahs (dark red). Phylogeographic break zones in regions with similar histories can be compared to identify how regularly breaks correspond with continental suture zones, physical barriers or transitions in environmental conditions, and the roles of biotic interactions, niche divergence or hybridization in maintaining lineage separation. Among regions with different biogeographic histories, such as between temperate and tropical regions or Southern versus Northern Hemispheres, diversification patterns across break zones may indicate important regional differences in the historical and contemporary environmental factors simultaneously promoting alpha- and beta-diversity.

hotspots, and provide opportunities to test various hypotheses about allopatric versus other modes of diversification in generating alpha- and beta-diversity (Fig. 2).

How present and past climates have influenced the distribution of alpha- and beta-diversity is likely one of the longest-investigated ecological enigmas (Wallace 1876, Whittaker 1960, Gentry 1988, Graham et al. 2006). One important hypothesis to emerge from this lengthy focus – which phylogeography can help to test – is phylogenetic niche conservatism, or the tendency of species to retain ancestral ecological attributes (Wiens and Graham 2005, see also Harvey and Pagel 1991). In practice, species are often considered to exhibit phylogenetic niche conservatism if they are more similar than expected by chance; although this definition does not mean they are ecologically equivalent (Warren et al. 2008), it does not necessarily conform to Losos' stricter definition, that they must be more similar than expected based on their phylogenetic relationship (Losos 2008). One of the first experimental tests for phylogenetic niche conservatism, which compared the geographic distributions of sister species, concluded that niche differentiation takes place over evolutionary, not ecological, time-scales, subsequent to allopatric speciation (Peterson et al. 1999). Since then, the concept has been applied to higher-level patterns, such as trait evolution and diversity gradients (Graham et al. 2009, Kozak and Wiens 2010). However, phylogenetic niche conservatism is often implicitly assumed among closely related species, and how to define and detect it is still subject to debate (Webb et al. 2002, Wiens and Graham 2005, Losos 2008). For example, tropical niche conservatism has been observed among genera and higher taxonomic levels in groups as diverse as birds, frogs and ants (Hawkins et al. 2006, Wiens et al. 2006, Lessard et al. 2012a), while at the other end of the taxonomic spectrum, phylogeographic lineages within species or between morphologically cryptic sister species can exhibit physiological or ecological differentiation (Cavender-Bares et al. 2011, Moritz et al. 2012, D'Amen et al. 2013). Given this dichotomy, testing for niche conservatism between phylogeographic lineages is an important indicator of the taxonomic and spatial scale of analysis at which phylogenetic niche conservatism may be a 'safe' assumption. Where niche divergence is detected between lineages, niche-related comparisons among species (e.g. phylogenetic trait dispersion) which attribute certain patterns to phylogenetic niche conservatism should be conducted only with great care, especially for fine-grained comparison of spatial niche parameters, such as climate variables. For course-grained comparisons at the species level and higher (e.g. tropical versus temperate niche conservatism), intra-specific niche differentiation does not negate the possibility of niche conservatism at higher taxonomic levels, although a definition of niche conservatism which acknowledges this variation should be used (Losos 2008).

Phylogeography can also provide important temporal context for inferring an acknowledged but difficult-to-model biogeographic process: the role of stochastic extinction in shaping species distributions and phylogenies. For example, pockets of high species endemism have long been attributed to Pleistocene climatic stability (Wardle 1963, Fjelds  and Lovett 1997, Graham et al. 2006), and Fjelds  et al. (1999) hypothesized that the distribution of endemic birds in the

Andes, where many species lack close relatives in adjacent mountains, was generated via a patchwork of climatically stable versus extinction prone areas (reviewed by Fjelds  et al. 2012). In the absence of fossil proxies, it is extremely difficult to directly test whether this endemism is connected to environmental stability and surrounding extinctions, or was generated via long-distance dispersal, another difficult-to-model process (Nathan 2006, Rabosky 2010). However, implicit within the stability hypothesis is the existence of climatically and geologically stable refugia across phylogeographic, as well as phylogenetic, time-scales (Hugall et al. 2002, Carnaval et al. 2009). Refugia stable enough to preserve narrow-range endemics should also accumulate comparative phylogeographic evidence of processes on multiple time-scales (Carnaval and Bates 2007, Bell et al. 2012, Marske et al. 2012), including deep intraspecific lineages in dispersal-limited species (Boyer et al. 2007, Marske et al. 2011, Fraser et al. 2012). While the temporal scale encompassed by phylogeographic lineages is likely shorter than that of the species whose histories they help to clarify, extinction of sister species leaves the focal endemics at the end of long branches, so divergence from their next nearest 'sister' species may significantly predate the events which generated extant biogeographic patterns. In contrast, less stable regions should provide comparative phylogeographic evidence for recent colonization (Hewitt 1996, 1999, Ilves et al. 2010) and may indicate long-distance dispersal routes used by some taxa (Fraser et al. 2012).

Dispersal, historical contingency and community assembly

The roles of dispersal, environmental filtering and biotic interactions in community assembly have been the focus of an intense debate spanning over three decades (Diamond 1975, Connor and Simberloff 1979, Sanderson et al. 2009, Collins et al. 2011). In spite of extensive development of new experimental, theoretical and null model approaches (Hairston et al. 1987, Gotelli and Graves 1996, Hanski and Gilpin 1997, Hubbell 2001, Thompson 2005, Gotelli et al. 2010), none of these has been able to resolve the problem of ecological contingency, or the unique, context-dependent circumstances by which communities are shaped (Lawton 1999), into any general rules. This problem is especially acute in regions where historical effects coincide with contemporary environmental gradients (Lawton 1999, Graves and Rahbek 2005, Vellend 2010, Chase and Myers 2011, Lessard et al. 2012b), necessitating a synthesis of ecological and evolutionary methods to identify community assembly processes operating at different spatial and temporal scales. While this synthesis is well underway, the evolutionary part has largely focused on processes acting at or above the species level (e.g. biogeography, trait conservatism or convergence; Webb et al. 2002, Cavender-Bares et al. 2009, Lessard et al. 2012b), leaving an inferential gap between the evolutionary time-scales on which species arise and the ecological time-scales on which members of an assemblage interact with each other and the environment. Integrating comparative phylogeography with cutting edge community ecology approaches may hold the key to identifying the processes which fill this temporal gap (Fig. 1).

Pleistocene climate fluctuation had a significant impact on the distributions of many mid- to high-latitude species (Hewitt 1999, 2000, Hortal et al. 2011), and some of what we call ecological contingency is likely a consequence of Quaternary range expansion, contraction and dispersal limitation. Phylogeography is an important avenue for investigating historical range dynamics, with phylogeographic breaks typically indicating historically isolated populations (although see Dasmahapatra et al. 2010, Waters 2011). Thus, shared phylogeographic break zones, particularly those which coincide with suture zones (see previous section), suggest natural limits to the species pool, or the list of 'available' species from which local assemblages are drawn, by indicating boundaries where lineages across several co-distributed species are excluded from those which could potentially occur in a community. Delineation of species pools can dramatically affect the outcome of community ecology studies (Graves and Gotelli 1983), particularly if the effects of regional- (biogeographic) and local-scale processes are confused (Gotelli and Graves 1996, Graves and Rahbek 2005, Graham and Fine 2008). Experimental manipulation of species pools, via implementing alternative species pool designations within a null model framework, has emerged as a powerful method for testing the effects of different processes on assemblage composition (Algar et al. 2011, Lessard et al. 2012a, b, Myers et al. 2013). Incorporating phylogeography-informed species pool hypotheses into community ecology studies will thus allow identification of the influence of Quaternary range dynamics on community composition, and variation in this influence among different climatic regions.

Another approach to detecting deterministic community assembly processes amid the black box of ecological contingency is to focus on the temporal cohesiveness of species pools through time (Zink 2002), since Pleistocene range shifts may have resulted in changes in the composition of coexisting species (Rowe et al. 2006, Stone et al. 2012). For example, shared glacial refugia but different histories of postglacial dispersal were detected for four New Zealand fungus beetles (Marske et al. 2012). These dynamics suggest similar responses to glaciation at the regional scale but stochastic differences in how species were sorted from regional species pools into local assemblages during postglacial colonization. Phylogenetic community ecology, which examines the evolutionary processes underlying community assembly (e.g. conservatism of heritable traits versus intensified competition among closely related species; Cavender-Bares et al. 2009), attempts to separate the results of these regional (e.g. environmental filtering) versus local (e.g. species interactions) processes on the composition of species assemblages. Whether community composition is maintained over evolutionary time-scales or reflects contemporary assembly processes is not directly addressed by phylogenetic community ecology methods. However, where phylogeographic data are available for most potential community members, species assemblages of historical refugia – the historical species pool for contemporary assemblages – could be identified, permitting serial estimation of phylogenetic community structure. Stable trait structure between historical and present-day communities would suggest that these 'evolutionary communities' reflect historical assembly processes, while a significant change in

trait structure would suggest that community composition reflects relatively recent assembly processes.

Phylogenetic community ecology compares the trait structure of species assemblages, quantifies the importance of regional versus local filters (e.g. biotic, abiotic, historical) on community trait structure, and infers the processes underlying these filters (Webb et al. 2002, Graham and Fine 2008, Cavender-Bares et al. 2009, Algar et al. 2011). Although numerous processes can result in phylogenetic clustering or evenness of species' traits (Cavender-Bares et al. 2009, Algar et al. 2011), phylogenetic community analyses often relate trait dispersion to inferences about the relative importance of environmental filtering versus competition (Mayfield and Levine 2010): under the first situation we expect assemblages to contain more close relatives than an assemblage drawn randomly from the phylogeny, while under the second we expect species to be more distantly related. There are two key issues with this approach which comparative phylogeography can help to clarify. First, the filtering/competition dichotomy is a relatively coarse association of pattern with process (Cavender-Bares et al. 2009, Mayfield and Levine 2010). However, many other drivers of phylogenetic patterns, such as renewed contact and sympatry between formerly allopatric lineages after the onset of reproductive isolation (Jordal et al. 2006) or strong selection gradients separating sister taxa (Cooke et al. 2012), are difficult to detect at the species level but can be readily examined using phylogeography. Second, if most speciation occurs allopatrically (Coyne and Orr 2004), we should expect recently-diverged sister-taxa to co-occur infrequently, regardless of potential competition (Johnson and Stinchcombe 2007). Returning to our phylogeographic break/suture zones, we might expect a gradient in phylogenetic trait dispersion, with a negative relationship between phylogenetic evenness and distance from the break zone, reflecting distance decay in the influence of the historical factors which created the zone (Fig. 3). While competition has been inferred to maintain phylogeographic/biogeographic breaks after the breakdown of environmental barriers (Waters 2011), competition itself is less likely to generate congruent genetic breaks among lineage or species pairs, as the genetic signature of colonization is difficult to overcome via subsequent competition (Taberlet et al. 1998, Waters et al. 2013).

Extinction, abundance and ecological interactions

Predicting the response of species diversity to ongoing climate change is critical to developing proactive conservation policies. However, two of the pervasive assumptions underlying the dynamics of climate-driven extinctions have been rarely explored at the temporal and geographical scales at which phylogeography operates. First, the relationship between species' abundance and their geographical distributions is one of the most studied ecological patterns (Brown 1984), and given that decreasing population and range sizes are assumed to increase extinction risk (Johnson 1999, Purvis et al. 2000, Payne and Finnegan 2007, Nogués-Bravo et al. 2010), has clear implications for conservation biology. Second, the disruption of key species interactions through

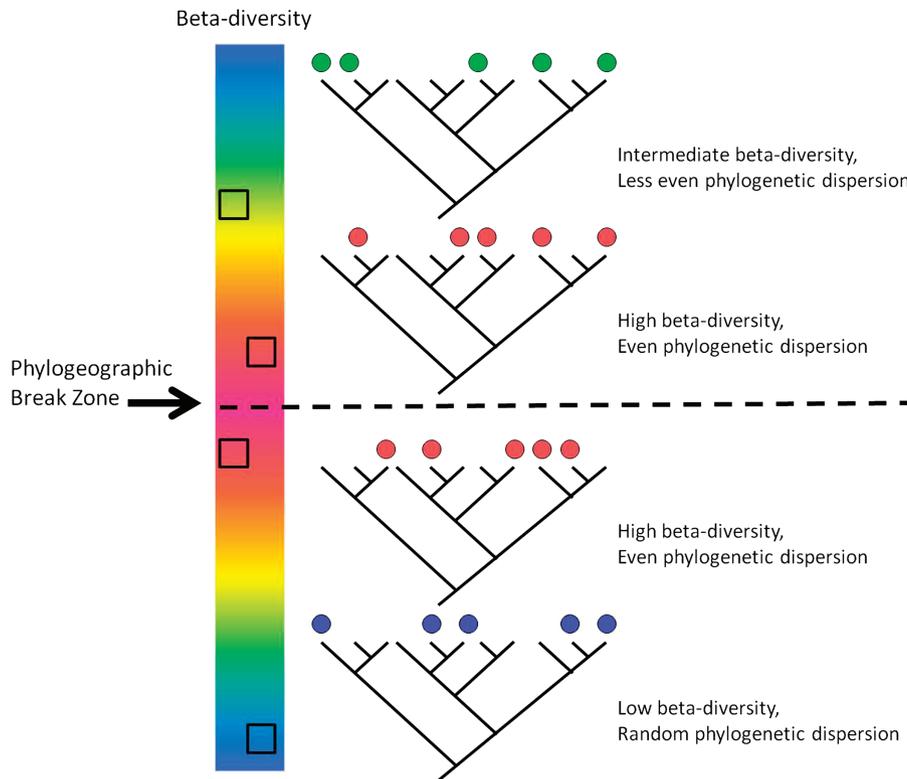


Figure 3. Regions encompassing phylogeographic break/suture zones include a gradient in beta-diversity which likely underlies a gradient in community phylogenetic dispersion, regardless of the presence or absence of competition between sister-taxa. To test for the influence of proximity to such zones on phylogenetic community structure, communities can be sampled along the beta-diversity gradient, ranging from high (red) beta-diversity at the phylogeographic break zone to low (blue) beta-diversity away from the zone. Four communities (black squares), each containing five species, are sampled along this gradient, and hypothesized phylogenetic dispersion of each community is shown. Communities closest to the break should show a pattern of phylogenetic evenness because of the presence of sister-taxa on either side. In the absence of strong environmental differences on either side of the break, communities will show increasingly random phylogenetic dispersion as distance from the break zone increases and its influence on local community assembly lessens. Such a relationship, if detected, would highlight the need for appropriate community ecology null hypotheses or species pool designs which control for the influence of phylogeographic break zone proximity on assemblage composition.

the extinction of one or a few species has been hypothesized to drive chains of co-extinctions on ecological time-scales (Diamond 1989, Olsen et al. 1991), but the extent to which species interactions are sustained across evolutionary time-scales, suggesting heightened sensitivity to cascade extinctions, has yet to be established. Exploring these key assumptions within a phylogeographic framework may yield vital insights into both the extinction process and the ramifications of extinction events on associated species.

The distribution–abundance relationship has been investigated from local to continental scales, within and across species, with a plethora of hypothesized drivers operating at different spatial scales, but consensus on the mechanisms linking population and range size remains elusive (reviewed by Borregaard and Rahbek 2010). Although intraspecific range–abundance dynamics have been assessed at decadal time-scales (Borregaard and Rahbek 2006), phylogeography provides an opportunity to characterize historical changes in population size across a species’ geographic range (Galbreath et al. 2009), including differentiating between natural and anthropogenic habitat fragmentation (Carnaval and Bates 2007). Ancient DNA phylogeography is particularly insightful for studying historical range dynamics because serial sampling permits a more accurate reconstruction of past

population dynamics than those based solely on contemporary samples (Ramakrishnan and Hadly 2009), including the power to detect population extinction (Dalén et al. 2005, Campos et al. 2010). For example, Lorenzen et al. (2011) integrated ancient DNA and species distribution models to assess the relative influence of climate change and human pressure on population trends and range size throughout the Late Quaternary (last ca 50 000 yr), and how these trends differed between extinct and extant megafauna herbivores across the Palearctic. Trends in effective population size across four of the six species mirrored the availability of suitable climate conditions, confirming a link between range size and abundance across the Late Quaternary. Ancient DNA phylogeography has, until recently, been restricted to short fragments of mitochondrial DNA (Paijmans et al. 2012) and has often relied upon relatively simplistic phylogenetic inference methods (Ramakrishnan and Hadly 2009), but the genomics era is revolutionizing the ancient DNA field by increasing the length and diversity of loci which can successfully be retrieved (Knapp and Hofreiter 2010, Paijmans et al. 2012), increasing the statistical power for testing hypotheses (Mourier et al. 2012). While ancient DNA – and serial coalescent estimation – are currently only feasible for a (growing) subset of species, steady improvement

in coalescent methods allows estimation of population trends from contemporary multi-locus DNA with increasing accuracy (Heled and Drummond 2008, Gill et al. 2012).

Whether species within a community respond to environmental changes in an individualistic or concerted manner is of utmost importance for understanding whether extinction pulses can drive cascade extinctions. While numerous analyses of fossil assemblages (Stewart 2008) and comparative phylogeography have revealed individualistic responses of co-occurring – but not necessarily interacting – species to Quaternary climate change, partially individualistic responses have also been detected among species with close-knit biotic interactions. For example, a monophagous beetle and its alpine host plant shared largely similar phylogeographic histories but utilized different Late Quaternary dispersal pathways (Borer et al. 2012), and even more distinct histories were identified between herbivorous gall wasps and their parasitoids, with significant host turnover detected during their postglacial invasion of Europe (Stone et al. 2012). These historical discrepancies among coevolved species reflect asymmetrical dependencies (Borer et al. 2012) or inherent evolutionary flexibility (Stone et al. 2012), rather than the ‘expected’ pattern of concerted demographic trends identified between tightly co-evolved Joshua trees and yucca moths (Smith et al. 2011). The ability of these biotic interactions to withstand disruption is an important factor determining species’ extinction risk in the face of climate change – an issue traditionally outside the scope of comparative phylogeography but which can be simulated using ecological network methods. Likewise, ecological networks can identify interacting species (Newman 2003, May 2006, Bascompte 2009), quantify whether network linkages are maintained or turn over between communities (Olesen and Jordano 2002, Ollerton and Cranmer 2002, Martín González et al. 2009, Dalsgaard et al. 2011), and simulate species’ exposure to extinction under network disturbance (Bascompte and Stouffer 2009, Kaiser-Bunbury et al. 2010); however, they reflect only contemporary interactions. Integrating comparative phylogeography and ecological network methods can help infer whether parallel population histories have allowed sustained interactions across recent evolutionary time-scales, suggesting heightened risk of cascade extinctions, or have been frequently disrupted throughout the Quaternary, suggesting greater network resilience following the loss of individual species.

Quantitative network approaches, which weight interactions based on their observed frequency, provide a more nuanced, and sometimes different, estimate of network stability and extinction risk than those based on qualitative approaches, in which all observed interactions are given the same importance (Kaiser-Bunbury et al. 2010). Quantitative networks thus highlight the most relevant subset of interacting species for comparative phylogeographic analyses – those with relatively tight-knit interactions – and the species most at risk of cascade extinctions – those with strong connections to a few other species. Comparative phylogeographic studies often focus on spatial congruence (e.g. refugia and dispersal routes) between species’ histories, but an important next step to testing network conservatism across evolutionary time-scales is to identify shared trends in population size through time among interacting species (Smith et al. 2011).

For example, if strong network connections are conserved throughout the Quaternary, we would expect to find a history of shared bottlenecks or population growth, in addition to spatially consistent phylogeographic scenarios, while weak connections are more likely to yield idiosyncratic scenarios (Fig. 4). Integrating ecological networks and comparative phylogeography, for networks ranging from a few close-knit species to complex food webs representing multiple trophic levels, will clarify the level of evolutionary independence between community members over both ecological and evolutionary timescales, and help infer the likelihood of cascade extinctions under ongoing climate change.

The way forward: data-gathering, collaboration and the ecology-evolution synthesis

Originally described as the link between population genetics and interspecific relationships (Avice et al. 1987), phylogeography has the conceptual potential to contribute well beyond providing detailed microevolutionary histories of individual species. Rather, by virtue of its focus on Quaternary interactions within and between populations, phylogeography provides the bridge between ecological and biogeographic time-scales. For a true synthesis of ecology and evolution, phylogeography is a necessary component of a diverse methodological toolbox. We have identified several opportunities, under the broad categories of diversification, dispersal, community assembly and extinction, in which phylogeographic inference can address the evolution of individual species to species assemblages, in conjunction with a wide variety of ecological and evolutionary data and methods.

One key difficulty for bringing phylogeography into a unified ecological and evolutionary framework is that phylogeographic data only exist for a subset of species for most systems: for example, comparative data for small to medium clades or representatives of different trophic levels within a forest community may be rapidly within reach, but covering all the breeding birds of South America would be a tremendous task. The challenge here is to design analyses which fit the available data, and most ideas presented above were conceived with these limitations in mind. In many cases the results of phylogeographic studies (such as phylogeographic breaks or environmental separation of geographic lineages) lead to new questions which can be directly tested without necessitating additional (genetic) data manipulation (Moritz et al. 2009, Rissler and Smith 2010, D’Amen et al. 2013) or can serve as the starting point for other phylogeographic analyses (Martin and McKay 2004, Alsos et al. 2012, Dawson 2012). In other cases, such as integrating phylogeography with phylogenetic community ecology, focused phylogeographic sampling of a few additional species from an already well-characterized system might open new opportunities to look at community evolution across phylogenetic scales (Fig. 5). However, questions which incorporate extensive ecological datasets, like the spatial and temporal cohesion of ecological networks, require thoughtful experimental design and a return to the field. Incorporating genetic sampling with other community monitoring strategies has already led to new insights into the historical and contemporary

Step 1: Quantitative ecological networks identify species with tightly-knit interactions across their geographic ranges.

Step 2. Statistical comparative phylogeographic methods test hypotheses about whether these species coexisted in the past.

Step 3. Where species' histories are spatially consistent, shared demographic trends indicate similar responses to past events.

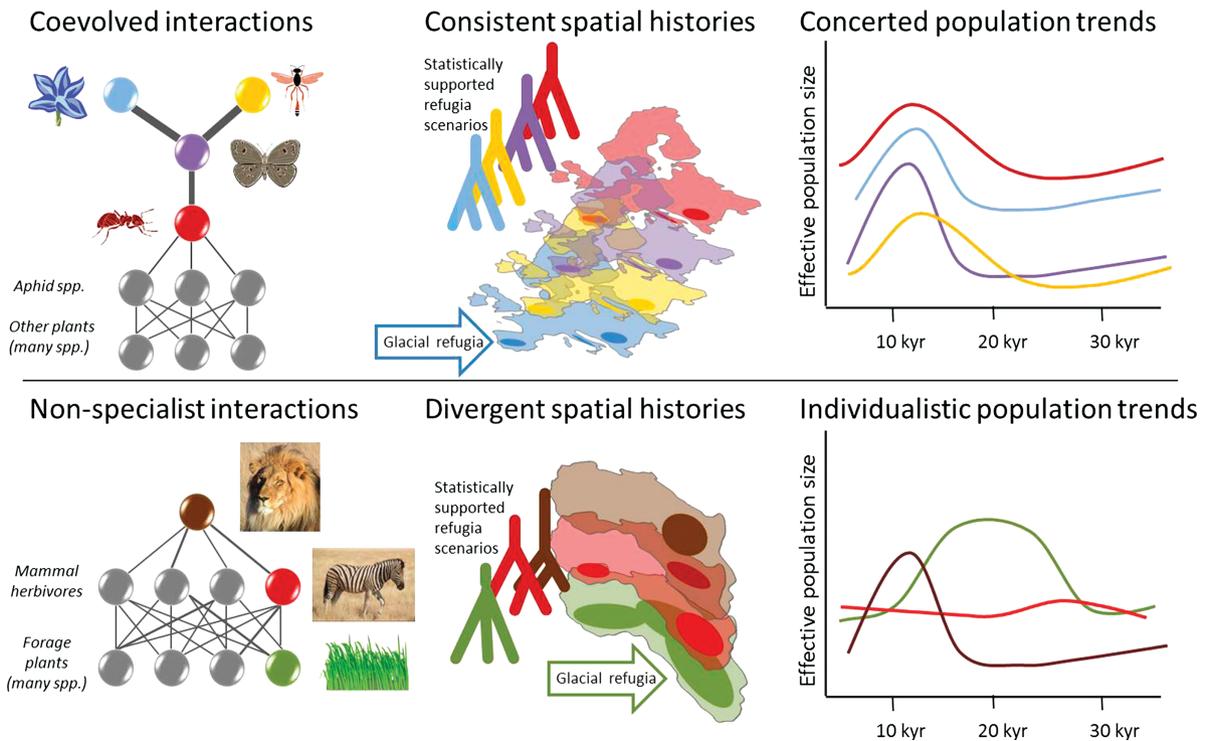


Figure 4. Phylogeographic sampling of ecological networks can clarify whether parallel population histories have fostered sustained interactions among species or whether interactions are frequently disrupted, yielding non-analog sets of interactions across the Quaternary. Strongly conserved interactions may indicate susceptibility to co-extinctions, while relatively recent connections may indicate the potential for new connections to be formed pending the extinction of an interaction partner.

The framework: first, quantitative ecological networks identify the strength of contemporary interactions among co-occurring species. Network perturbations, such as extinction of individual species, are simulated to detect the likelihood of cascade extinctions based on contemporary species interactions. However, contemporary network connections may not represent the full suite of connections available to a species, and so may not be temporally conserved. Second, comparative phylogeography of species linked by strong connections indicates whether these species could have co-occurred in the past, facilitating conservation of network links. Since this step has an explicit spatial component, fossil localities or species distribution models may be incorporated to fine-tune statistical phylogeographic hypotheses (sensu Richards et al. 2007). Third, demographic trends are estimated for species which co-occurred in the past using statistical phylogeography and coalescent-based modeling; species linked by strong connections likely experienced similar demographic changes, such as bottlenecks or range/population expansion.

Two multi-trophic networks illustrate this framework. In both examples, networks (left side) illustrate interactions (lines) among species (circles), of which a focal subset is shown in color. Line thickness indicates connection strength between species. For each colored species, hypothetical glacial refugia and demographic trends are indicated in the same color. (Please note that networks, refugia and demographic trends are illustrative only and may not reflect existing knowledge for some species.)

The upper example illustrates a mixture of strong and weak connections. European *Maculinea* butterflies oviposit on gentians, upon which the larvae feed. After reaching a certain size, the larvae move to the ground and are collected by ants, which the larvae 'trick' into carrying to the nest and caring for them as the ants' own brood. In the nest, butterfly larvae are parasitized by a wasp able to circumvent the ants' defenses. The ants receive no benefit from these interactions, but obtain resources elsewhere. Because of the strong connections between the butterfly, plant, ant and wasp, comparative phylogeography would likely reveal spatially consistent evolutionary histories and concerted demographic trends, suggesting that extinction of certain species may result in extinction of others.

The lower example illustrates a series of weak connections. African lions predate several ungulate species, including the zebra, which grazes on several species of savannah grass also grazed by the other ungulates. Because no species is strongly linked to any other, comparative phylogeography is unlikely to indicate spatially consistent evolutionary histories or concerted demographic trends, suggesting network flexibility in the face of perturbation. Lion and zebra photos courtesy of Kevin Pluck and Rui Ornelas, respectively.

factors behind community assembly, maintenance and turnover (Craft et al. 2010, Dexter et al. 2012) and the relationship between diversity at different levels of biological organization (Taberlet et al. 2012). Sampling along environmental gradients, in particular, can facilitate consideration of ecological processes across evolutionary time-scales, such as

the role of historical dispersal limitation versus adaptation on population structure or beta-diversity patterns (Confalonieri et al. 1998, Toju and Sota 2006, Zakharov and Hellman 2008, Cooke et al. 2012).

We avoid a blanket discussion of phylogeographic data quality, while acknowledging that published studies exhibit

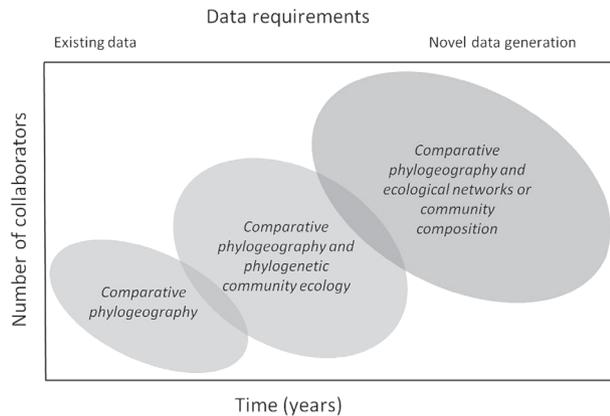


Figure 5. Matrix indicating the magnitude of experimental effort needed to integrate phylogeography into ecological studies of increasing experimental complexity, in terms of time, number of collaborators and extent of novel data generation required. Each oval indicates a range of interactions between these three factors for different synthesis projects: for example, a project using mostly comparative phylogeographic data (Martin and McKay 2004, Alsos et al. 2012) will take longer if these data have to be generated from scratch, but will take less time with the help of more collaborators. Combining phylogeographic data with ecological field studies (Craft et al. 2010, Dexter et al. 2012) will require more time than a project requiring comparative phylogeographic data alone, because of the multiple types of data required and the likelihood that it will have to be generated from scratch.

considerable variation in their support for proposed scenarios. In particular, mitochondrial DNA (mtDNA) alone is frequently insufficient for testing detailed hypotheses (Edwards and Beerli 2000, Singhal and Moritz 2012), although it often carries a stronger phylogeographic signal than nuclear DNA because of its smaller effective population size (Zink and Barrowclough 2008), and synthetic studies will likely rely heavily upon mitochondrial DNA for the next couple of years because of its widespread availability in public databases. On the other hand, Next-Generation Sequencing (NGS) holds great promise for efficient generation of multi-locus data, although large comparative NGS databases spanning taxa and geographic regions are still several years away. Three key challenges for NGS phylogeography are reducing the massive data output per individual to an informative subset of loci, sampling those loci across up to hundreds of individuals from non-model taxa, and obtaining markers suitable for coalescent-based analyses (Carstens et al. 2012, Lemmon and Lemmon 2012, McCormack et al. 2012, Lexer et al. 2013, O'Neill et al. 2013). As these challenges are overcome, up to hundreds of loci can be used to test phylogeographic scenarios (Carstens et al. 2012), vastly improving the temporal setting in which ecological processes can be inferred. Another key advance, as the distinction between model and non-model organisms continues to break down, will be the ability to associate neutral with non-neutral genetic variation (Lexer et al. 2013, McCormack et al. 2013). Incorporating this 'next generation biogeography' (Lexer et al. 2013) into a spatial ecology framework will provide unprecedented ability to understand the drivers behind the distribution of alpha- and beta-diversity.

To achieve the ideas proposed here, phylogeography should be implemented in concert with other evolutionary and ecological methods as part of an integrative, interdisciplinary research agenda. Some of the ideas presented above are possible in the short term, while others are beyond what single researchers can achieve (we do not propose that all ecologists become phylogeographers, and vice versa), and thus will require ambitious sampling design, significant financial investment and extensive collaboration (Fig. 5). Several researchers have called for large-scale experimental and observational studies capable of linking local processes with macroecological patterns and evolutionary history (Ricklefs and Schluter 1993, Nogués-Bravo and Rahbek 2011, Swenson 2011, Lessard et al. 2012b), and adding phylogeography to this toolbox will bring a spatial and temporal perspective not available from other methods. While this multi-scale, collaborative focus represents a departure from traditional practice and may pose new challenges (Nogués-Bravo and Rahbek 2011), such large collaborations are possible and can be productive (Taberlet et al. 2012). Incorporating phylogeography into a multifaceted ecological-evolutionary approach will yield more comprehensive understanding about the origins, organization and future fate of species diversity.

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