ENTOMOLOGICAL
SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Molecular Phylogenetics, Phylogenomics, and Phylogeography

The Phylogeographic Shortfall in Hexapods: A Lot of Leg Work Remaining

Jordan D. Satler,[1,5,] Bryan C. Carstens,[2] Ryan C. Garrick,[3,] and Anahí Espíndola[4,]

[1]Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA, [2]Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH 43210, USA, [3]Department of Biology, University of Mississippi, Oxford, MS 38677, USA, [4]Department of Entomology, University of Maryland, College Park, MD 20742, USA, and [5]Corresponding author, e-mail: jordansatler@gmail.com

Subject Editor: Patrick Mardulyn

Abstract

In the 21st century, phylogeography has experienced dramatic growth in the data and methods used by the field. Insect (more generally, hexapod) phylogeography has contributed to major advances and many of the influential papers included hexapods as model systems. In this literature review, we: (i) highlight recent phylogeographic work in hexapod systems, and (ii) identify broader trends and critical future steps in the field. We include a summary of useful methodological approaches and identify the methods used to approach different questions asked in phylogeographic studies. An updated summary of the applications that phylogeography has contributed to the field of entomology, including spatial studies, conservation, systematics, pest control, and invasive species, is included to highlight vital work in the field. Special attention is devoted to investigations which seek to use multi-species data to understand community ecological and evolutionary processes. Finally, we overview the main challenges, opportunities, and emerging areas, highlighting the "phylogeographic shortfall" that exists between the number of described hexapod species vs. the number of species that have been the focus of phylogeographic investigation.

Resumen

La filogeografía del siglo XXI demuestra un crecimiento fuerte y sostenido en la integración y expansión de fronteras en relación al uso de datos y desarrollos metodológicos. La filogeografía de insectos (y en forma más general, de hexápodos) ha contribuido a avances mayores de la disciplina, con varios trabajos filogeográficos fundamentales tratando modelos de hexápodos. Esta revisión de la literatura tiene dos objetivos: i) realzar y tratar estudios filogeográficos recientes en insectos y hexápodos y ii) evaluar sus resultados principales para así identificar tendencias generales y oportunidades futuras. Con el fin de asistir en la selección de métodos apropiados a aquellos interesados en estos estudios, comenzamos haciendo una revisión de los métodos filogeográficos existentes, presentando también una guía para asistir en su selección. Después de esta revisión metodológica, presentamos un resumen general de aplicaciones recientes en entomología, demostrando, entre otros, su importancia en áreas tales como estudios geoespaciales, conservación, sistemática, control de plagas y de especies invasoras. Siguiendo en esta línea, revisamos las contribuciones únicas de la filogeografía entomológica en estudios comparados, conectando ecología de comunidades con procesos evolutivos, siendo esta una de las áreas más activas y prometedoras de la filogeografía actual. Finalmente, discutimos los mayores desafíos, oportunidades y áreas emergentes de la filogeografía contemporánea, e identificamos el "déficit filogeográfico" existente entre la cantidad de especies de hexápodos descritas y aquellas que han recibido atención en estudios filogeográficos.

Key words: community phylogeography, comparative phylogeography, phylogeographic shortfall, spatial genetic structure, species delimitation

Phylogeography was created as a hybrid study area that connected historical demographic events to external or environmental factors that had shaped the spatial distribution of genetic diversity within and among populations over relatively deep timescales. Because insects can have close relationships with other species (e.g., specialized host development, specialized diets, etc.), these taxa became informative systems for studying how processes traditionally proposed as explaining diversification (e.g., spatial and topographic, abiotic, and biotic drivers) affect the early stages of speciation. Insect phylogeography has quantified the species-level processes that can generate macroevolutionary patterns (Tian et al. 2015, Bain et al. 2016, Barrios-Leal et al. 2019), and bridged the gap between micro- and macroevolution.

Phylogeographic studies in the 2020s may be superficially different from the pioneering work of Avise (1987), Hewitt (1999), and other early practitioners in the field, but the discipline remains an excellent bridge between population genetics and phylogenetics. As such, it is capable of merging ecological and evolutionary perspectives to bring new insight into spatial patterns of genetic (and by extension, phenotypic) diversity within a species. In this review, we highlight recent phylogeographic work in insect systems while using the authors' main findings to elucidate broader trends. After providing a general overview of current methods, we discuss several applications of phylogeography in entomology, present an overview of the new frontier of comparative and community phylogeography, and close by discussing some of the main knowledge gaps, opportunities, and needs in the field.

The Evolution of Phylogeography and Phylogeographic Methods

Phylogeographic investigations into insect systems are motivated by a range of factors. Many studies follow broader trends in the field by inferring the historical demography (e.g., Buckley et al. 2010) or spatial genetic structure (e.g., Finn et al. 2006) of the focal taxon. Others address more practical concerns, such as Tembrock et al.'s (2019) investigation into invasive demographic expansion in a noctuid moth. Regardless of their motivation, phylogeographic investigations of insect systems often include the use of (i) complex models of demographic history, (ii) hypothesis testing and model selection approaches, (iii) large geo-referenced genomic datasets, and (iv) the incorporation of nongenetic data.

Scientists have been interested in describing patterns of spatial genetic structure since it was possible to assay genotypes in natural systems (e.g., Hubby and Lewontin 1966; see Roderick 1996 for a review). However, phylogeography as a discipline started when scientists began to collect data from mitochondrial genomes and analyze these data using approaches that were borrowed from traditional phylogenetics and previously geared towards questions above the species-level (Box 1). One early goal was to bring an evolutionary and historical perspective to intraspecific investigations, largely based on allele phylogenies coupled with overlays of these alleles in geographic space (Avise et al. 1987). Modern data and inference methods enable researchers to make precise estimates of parameters of biological interest, including effective population size (Ne; e.g., Carling et al. 2007, Smith et al. 2011), gene flow (e.g., Martin et al. 2013), intrinsic rates of population expansion (e.g., Buckley et al. 2010), and population divergence times (e.g., Satler and Carstens 2017). While parameters such as these can be estimated using a variety of methods, approaches such as Approximate Bayesian Computation (ABC; Beaumont et al. 2002; also see Csilléry

Box 1

Referred to as "Not 'Just Another' Molecular Marker," mitochondrial DNA (mtDNA) was the workhorse of phylogeography early on in the field's inception (Avise et al. 1987). Although mtDNA has been useful for phylogeographic research, challenges associated with making inferences from single locus data spurred a transition to multilocus data sets (Edwards and Beerli 2000; Brito and Edwards 2009). With the advancement in sequencing technologies over the last couple of decades, the amount of data used in phylogeographic investigations has steadily grown (Garrick et al. 2015), enabling researchers to make more refined inferences of population genetic structure (Morales-Hojas et al. 2020) and more precise estimates of relevant parameters (Satler and Carstens 2017). Approaches like restriction site-associated DNA (RAD) sequencing (Baird et al. 2008) and double digest restriction site-associated DNA (ddRAD) sequencing (Peterson et al. 2012) allow researchers to generate sequence data (often short read, between 50 and 150 base pairs) and SNPs from thousands to hundreds of thousands of loci for phylogeographic inference (e.g., Hotaling et al. 2018). Importantly, these approaches do not require prior genomic information from the taxon of interest, which is often lacking in studies of non-model organisms. When genomic information is available, however, sequence capture approaches can be used (e.g., Faircloth et al. 2012; Lemmon et al. 2012). Researchers have used ultraconserved elements (UCE; Branstetter et al. 2017; Derkarabetian et al. 2019; Satler et al. 2019; Branstetter and Longino 2020; Gueuning et al. 2020), anchored hybrid enrichment (AHE; Hamilton et al. 2016), or other capture-probe based methods (e.g., Suchan et al. 2016, Wachi et al. 2017) to sequence hundreds to thousands of loci in parallel. These loci are usually longer than those generated with RAD sequencing, allowing researchers to use the full sequence data rather than primarily relying on SNPs. In particular, UCE loci have been identified across many insect groups (Faircloth et al. 2015; Faircloth 2017), providing available probe set information useful for generating markers for phylogeographic and phylogenetic studies of arthropods (reviewed in Zhang et al. 2019). In addition, researchers are also using whole-genome sequences from population-level sampling in model insect systems (e.g., Olazcuaga et al. 2020; Kapun et al. 2020). As sequencing costs continue to decrease, researchers in non-model systems will be increasingly likely to utilize entire genomes as the basis for phylogeographic investigations, which will enable better understanding of how natural selection influences the evolution of insect systems (e.g., Lindtke et al. 2017).

et al. 2010) or fastsimcoal2 (Excoffier et al. 2013) allow researchers to design custom statistical models of the historical demography in empirical systems of interest. These landscape- and species-specific models, informed by other data and preexisting hypotheses, allows for a great deal of creativity in the field (Fig. 1; Table 1).

Song et al. (2018) provide an example of the flexibility offered by modern phylogeographic analyses. They aimed to discover how the recent evolutionary history of the moth *Grapholita molesta*

Four questions to ask at the beginning of a phylogeography research project.

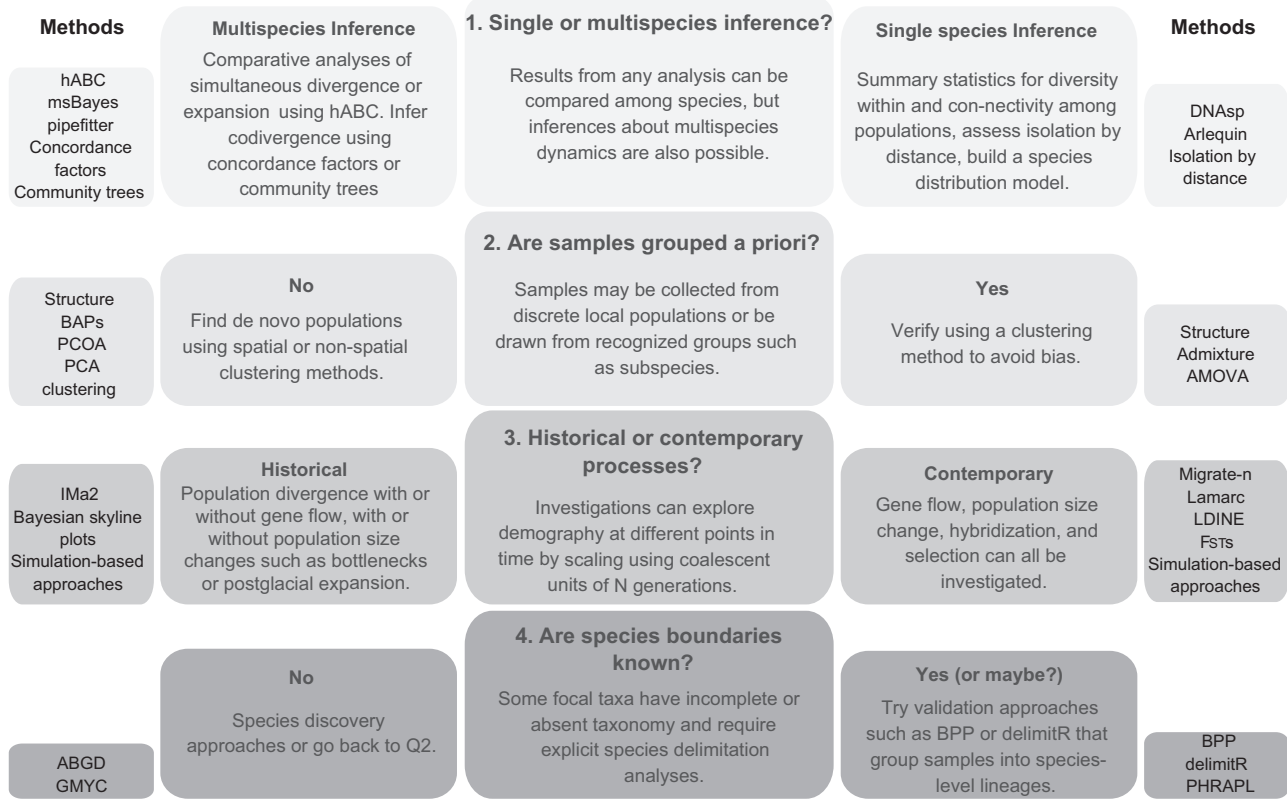| **Methods**	**Multispecies Inference**	**1. Single or multispecies inference?**	**Single species Inference**	**Methods**
hABC msBayes pipefitter Concordance factors Community trees	Comparative analyses of simultaneous divergence or expansion using hABC. Infer codivergence using concordance factors or community trees	Results from any analysis can be compared among species, but inferences about multispecies dynamics are also possible.	Summary statistics for diversity within and con-nectivity among populations, assess isolation by distance, build a species distribution model.	DNAsp Arlequin Isolation by distance
	No	**2. Are samples grouped a priori?**	**Yes**	
Structure BAPs PCOA PCA clustering	Find de novo populations using spatial or non-spatial clustering methods.	Samples may be collected from discrete local populations or be drawn from recognized groups such as subspecies.	Verify using a clustering method to avoid bias.	Structure Admixture AMOVA
	Historical	**3. Historical or contemporary processes?**	**Contemporary**	
IMa2 Bayesian skyline plots Simulation-based approaches	Population divergence with or without gene flow, with or without population size changes such as bottlenecks or postglacial expansion.	Investigations can explore demography at different points in time by scaling using coalescent units of N generations.	Gene flow, population size change, hybridization, and selection can all be investigated.	Migrate-n Lamarc LDINE F_{ST}s Simulation-based approaches
	No	**4. Are species boundaries known?**	**Yes (or maybe?)**	
ABGD GMYC	Species discovery approaches or go back to Q2.	Some focal taxa have incomplete or absent taxonomy and require explicit species delimitation analyses.	Try validation approaches such as BPP or delimitR that group samples into species-level lineages.	BPP delimitR PHRAPL

Fig. 1. Important questions to ask before starting a phylogeographic investigation. Shown in center boxes are four questions to consider at the beginning of an investigation. Adjacent boxes show potential answers to these questions, with the smaller edge boxes showing phylogeographic methods to consider.

had been influenced by Pleistocene glacial cycles in eastern Asia. To accomplish this, Song et al. (2018) adopted the useful strategy of conducting a series of exploratory analyses before estimating parameters using a custom scenario. They first estimated F_{ST} values and used a clustering method to determine that there were three genetic populations present in their sampling. After other analyses suggested that population sizes had remained relatively constant over time, Song et al. (2018) used ABC to evaluate several admixture scenarios before using IMa2 (Hey 2010) to generate estimates of the rates of gene flow (i.e., admixture rates) among populations. Ultimately, the authors incorporated multiple analytical methods ranging from descriptive statistics (i.e., F_{ST}'s) to simple correlational tests (i.e., isolation by distance) to complex demographic modeling using ABC and IMa2. Their approach recognizes that no single method is likely to be adequate, but the primary inferences derived from this research were dependent on parameter estimates made under a model of historical demography they determined to be appropriate to the *G. molesta* system.

While no single method can serve as the basis for all historical inferences, many phylogeographic investigations evaluate a specific hypothesis about the evolutionary history of the focal taxon. In such cases, researchers should avoid casual tests of hypotheses based on qualitative interpretations of statistics (e.g., F_{ST}'s are low) or parameters estimated under general models (e.g., phylogenetically-based divergence time estimates) in favor of the direct evaluation of statistical models of historical demography. Under a frequentist statistical framework, a formal hypothesis test can be conducted using parametric bootstrap simulation of data under a model of historical

demography that corresponds to the hypothesis being tested (e.g., Knowles 2000). Using a predetermined α-level of significance, this enables the researcher to either reject or fail to reject the null hypothesis. Parametric simulation-based hypothesis testing (e.g., Knowles and Maddison 2002) was an important transitional step between early phylogeographic investigations—which tended to be overly descriptive and subject to confirmation bias (see Carstens et al. 2009)—and modern model-based investigations.

Several flaws, however, are inherent to this approach. First, these tests rely on data simulated under parameters that are estimated from the empirical data, and, as such, hypothesis testing is sensitive to sampling and decisions about the type of data collected and the model used to estimate the parameters (see Koopman and Carstens 2010). Second, rejecting a hypothesis might enable researchers to rule out a particular historical scenario, but failing to reject a hypothesis does little to point researchers towards a model that might represent a better fit to the data. Researchers might test many different hypotheses to circumvent this issue, but the need for multiple comparison corrections may lead to false negative results, particularly because it is difficult to estimate statistical power and error rates for phylogeographic hypothesis testing (unlike hypothesis testing in experimental sciences). As a result of these difficulties, researchers have largely adopted model comparison or model selection approaches.

Like Song et al. (2018), many researchers use ABC to calculate the relative posterior probability of models of historical demography. Unlike hypothesis testing, which ideally tests a single model in order to avoid issues of significance threshold correction, ABC enables the relative posterior probability of any number of models

Table 1. Summary of some common research questions or goals in phylogeography, coupled with examples of associated analytical methods used to generate inferences that address them (also see Fig. 1)

Goal	Exemplar methods	Brief description	References
Species delimitation	GMYC	Fits a lineage through time plot to data to identify inflection point of rate change	Pons et al. (2006)
	ABGD	Distance based clustering algorithm	Puillandre et al. (2012)
	delimitR	Machine learning to identify demographic model of speciation	Smith and Carstens (2020)
	BPP	Reversible jump MCMC method	Yang and Rannala (2010)
	BFD/BFD*	Bayes factor delimitation of species tree	Grummer et al. (2014), Leaché et al. (2014)
	PHRAPL	Information theoretic approach based on gene tree distributions	Jackson et al. (2017)
Find *de novo* populations	BAPS	Spatial or nonspatial individual- or group-based clustering of codominant or haploid data	Corander et al. (2003)
	BARRIER	Finds locations with abrupt increases in genetic differentiation over short geographic distances	Manni et al. (2004)
	SAMOVA	Group-based spatial clustering that maximizes among-group genetic variance (F_{ct})	Dupanloup et al. (2002)
	STRUCTURE	Optimizes grouping of individuals to minimize departure from HWE and LE within "populations"	Pritchard et al. (2000)
	DAPC	PC reduction of individual-based genotype data with k-means test to find clusters, followed by DA	Jombart et al. (2010)
Diversity within populations	haplotypic diversity	Mean proportion of pairs of randomly selected haplotypes that are different from one another	Nei (1987)
	nucleotide diversity	Mean per-site number of nucleotide differences between pairs of randomly selected haplotypes	Nei (1987)
	segregating sites (S)	Number of polymorphic sites among aligned haplotypes, excluding insertion-deletion mutations	Watterson (1975)
	phylogenetic diversity	Sum of branch lengths on a phylogeny that unites haplotypes from a given group (or location)	Faith (1992)
Connectivity among populations	F_{st}	Partitioning of genetic variance among groups; ranges from 0 (panmixia) to 1 (fixed differences)	Weir and Cockerham (1984)
	isolation-by-distance	Correlation between pairwise genetic distances (e.g., F_{st}) vs. corresponding geographic distances	Wright (1943)
	population graphs	Genetic co-variance among populations represented by a graph's minimum edge set	Dyer and Nason (2004)
	MIGRATE	Bi-directional (i.e., potentially asymmetrical) coalescent estimates of long-term migration rates	Beerli and Felsenstein (2001)
Population divergence	IMa2	Distinguishes incomplete lineage sorting from post-divergence gene flow, estimates splitting time	Hey (2010)
Effective population size (*Ne*)	LDNE	LD-based estimate of contemporary *Ne* from a single temporal sample using multilocus data	Waples and Do (2008)
	Watterson's theta	Mutation-scaled *Ne* (the observed S in sample size *n*, divided by the expected S given a neutral model)	Watterson (1975)
Changes in *Ne* over time	Tajima's *D*	Neutrality test that compares the mean number of pairwise nucleotide differences against S	Tajima (1989)
	Extended Bayesian skyline plot	Coalescent estimator of the directionality, magnitude, and timing of past changes in Ne	Heled and Drummond (2008)
Multispecies comparative analyses	population graphs	Assessment of shared edges between two (or more) co-distributed species' minimum pop graph topologies	Dyer (2015)
	MTML-msBayes/ hABC	Test for simultaneous divergence among corresponding pairs of populations from co-distributed species, using hABC	Huang et al. (2011)
	aSFS/hABC	Test for simultaneous growth among corresponding populations from co-distributed species, using aSFS and hABC	Xue and Hickerson (2015)
	PARAFIT	Test for global cophylogenetic structure between a pair of co-distributed species (e.g., host vs. parasite/pollinator)	Legendre et al. (2002)
	JANE	Event-based tree reconciliation between a pair of co-distributed species (e.g., host vs. parasite/pollinator)	Conow et al. (2010)
	Phylogeographic Concordance Factors	Quantify phylogeographic congruence among population trees of co-distributed species	Satler and Carstens (2016)
	Community Trees	Identify species that fit a community tree model, and those species that are a poor fit to the model	Carstens et al. (2016)

Abbreviations are as follows: aSFS, aggregate Site Frequency Spectrum; DA, Discriminant Analysis; hABC, hierarchical ABC; HWE, Hardy–Weinberg Equilibrium; LD, Linkage Disequilibrium; LE, Linkage Equilibrium; MCMC, Markov chain Monte Carlo; PC, Principal Component

to be calculated. Superficially, this may appear to be a reasonable response to the criticism that model choice experiments may mislead researchers because the "true" model is probably not included in the model set under comparison. In practice, however, as the number of models increases, the models generally become more similar and thus the parameter space among the models decreases, which causes the posterior probability to be divided amongst several similar models. This makes differentiating among many models a difficult challenge due to the use of thresholds in ABC (i.e., the retention of datasets that are arbitrarily close to the empirical data in Euclidean space) to calculate the relative posterior probability. Both empirical (Fagundes et al. 2007) and simulation-based theoretical studies (Pelletier and Carstens 2014) suggest that model choice with ABC is best conducted with two to four models. However, these same studies indicate that the use of hierarchical model sets, where models are grouped by similarity and then the best models from each group are selected for comparison in a second round of model evaluation, may be a useful strategy for expanding the size of the model set under consideration.

To circumvent the limitations inherent to the use of ABC in model selection, other researchers utilize information theory to calculate the model probabilities of multiple models (see Anderson 2008 for a justification of this approach in the historical sciences). Superficially, this approach is similar to ABC in the sense that multiple models can be compared in a statistical framework. Researchers who use information theory, however, are typically able to differentiate among a greater number of models because this approach relies on direct (or indirect, see Jackson et al. 2017) calculations of the likelihood of the model given the data. For example, consider Hotaling et al. (2018), who used this approach to investigate the demographic history of the stonefly *Lednia tumana*. Hotaling et al. (2018) inferred population genetic structure and then assigned samples to three genetic populations. These populations served as the basis for a complex set of 20 models that represented different historical scenarios and included different degrees of population divergence, gene flow, and admixture. After calculating the maximum likelihood score of each model, the Akaike (1974) Information Criterion (AIC) and model probabilities (Burnham and Anderson 2002) were used to identify one of these models as the most probable with a probability of 0.96 indicting strong superiority to all other models included in the set. This model was then used as the basis for parameter estimation and inferences regarding the empirical system. Given the similarities between this and other models in the set, it is unlikely ABC would have enabled the same discriminatory power.

The Many Aspects of Insect Phylogeography

Understanding Evolution in Space

After several decades of phylogeographic studies on insects, it may now seem obvious that the demographic history, spatial genetic structure, and the timing of divergence of intraspecific genetic groups can be at least partly explained by past environmental changes and by spatial and topographic features within a species' range. It is important to realize that the strong development of phylogeography as a field led to the formal investigation and integration of evolutionary and spatial scales into species evolution. Further, this contribution set the foundation for understanding the history of ecosystems, and general species responses to environmental change. Evaluating this has provided key information on how past climatic and topographic changes affected the histories and genetic compositions of species (Hewitt 1996, Roderick

1996, Hewitt 1999). Indeed, several of the first phylogeographic studies were based on insect species (e.g., grasshoppers, beetles, moths). It is possible that the usual short life cycles and ability of these species to maintain viable populations within relatively small habitat patches, along with sometimes limited dispersal (e.g., low flight ability) and/or habitat specialization leading to patchy distributions, may have helped make insects useful study systems for understanding how landscape and environmental processes structure genetic variation within a species (e.g., Roderick 1996). Finally, insects are the most widespread and speciose group of animals, enabling them to be used as models for understanding landscape evolution across the world.

The study of insects was at the foundation of Palearctic and Nearctic phylogeography (Hewitt 1996, Taberlet et al. 1998, Hewitt 1999, Shafer et al. 2010, Riddle 2016), allowing researchers to start to understand how temperate species retracted into refugia during glacial periods, and expanded their ranges in response to subsequent warming (but see Knowles 2000, and DeChaine and Martin 2006, for counter-examples from alpine-adapted insects). Although the northern hemisphere has received the bulk of research attention (Riddle 2016; Fig. 2), insect phylogeography has been central to clarifying the responses of species to environmental change in other regions of the world. For instance, we now understand the main phylogeographic patterns of insects in South Africa (de Jager and Ellis 2017, Matenaar et al. 2018), a region in which plant species have historically been the main focus of research due to exceptional diversity and endemism in the Cape Floristic Region. The study of hexapod phylogeography also provided insights into their response to climatic changes in Antarctica (Stevens et al. 2006, McGaughran et al. 2011, Collins et al. 2019, McGaughran et al. 2019, Collins et al. 2020), clarified the spatial response of species in the Tropics (Solomon et al. 2008, Leite and Rogers 2013, Su et al. 2014), and shed light into species' histories in southern temperate regions (Chinn and Gemmell 2004, McCulloch et al. 2010, Sosa-Pivatto et al. 2020). Besides the importance of these studies for conservation and taxonomic purposes, these studies demonstrated that patterns in the Tropics or southern temperate regions do not match those in the northern hemisphere.

Phylogeography and Species Conservation

Through the combined understanding of the spatial distribution of genotypes and their associated response to past environmental changes, one has the power to make predictions about likely responses to future environmental changes. From this perspective, the integrated toolbox of phylogeographic analysis methods (Table 1) can inform conservation decision-making (Box 2). For instance, detailed information about the number and geographic distribution of divergent intraspecific lineages across a species' range can facilitate the maintenance of genetic diversity (e.g., Collins et al. 2020). Likewise, estimates of the timing, nature, and magnitude of past demographic changes allow the likely drivers of those changes to be identified, as well as a prediction about such changes in the future. Along with the combination of phylogenetic and purely spatial methods (e.g., species distribution modeling and other geospatial analyses), phylogeography allows combining range and genetic predictions, which can be used to inform decisions (Espíndola et al. 2012), including the establishment of habitat corridors that facilitate the persistence of unique genetic lineages (Robillard et al. 2015).

In the context of major changes in climatic and land use conditions, the contributions of phylogeography are impressive (Schierenbeck 2017). Such studies have informed researchers about the conservation
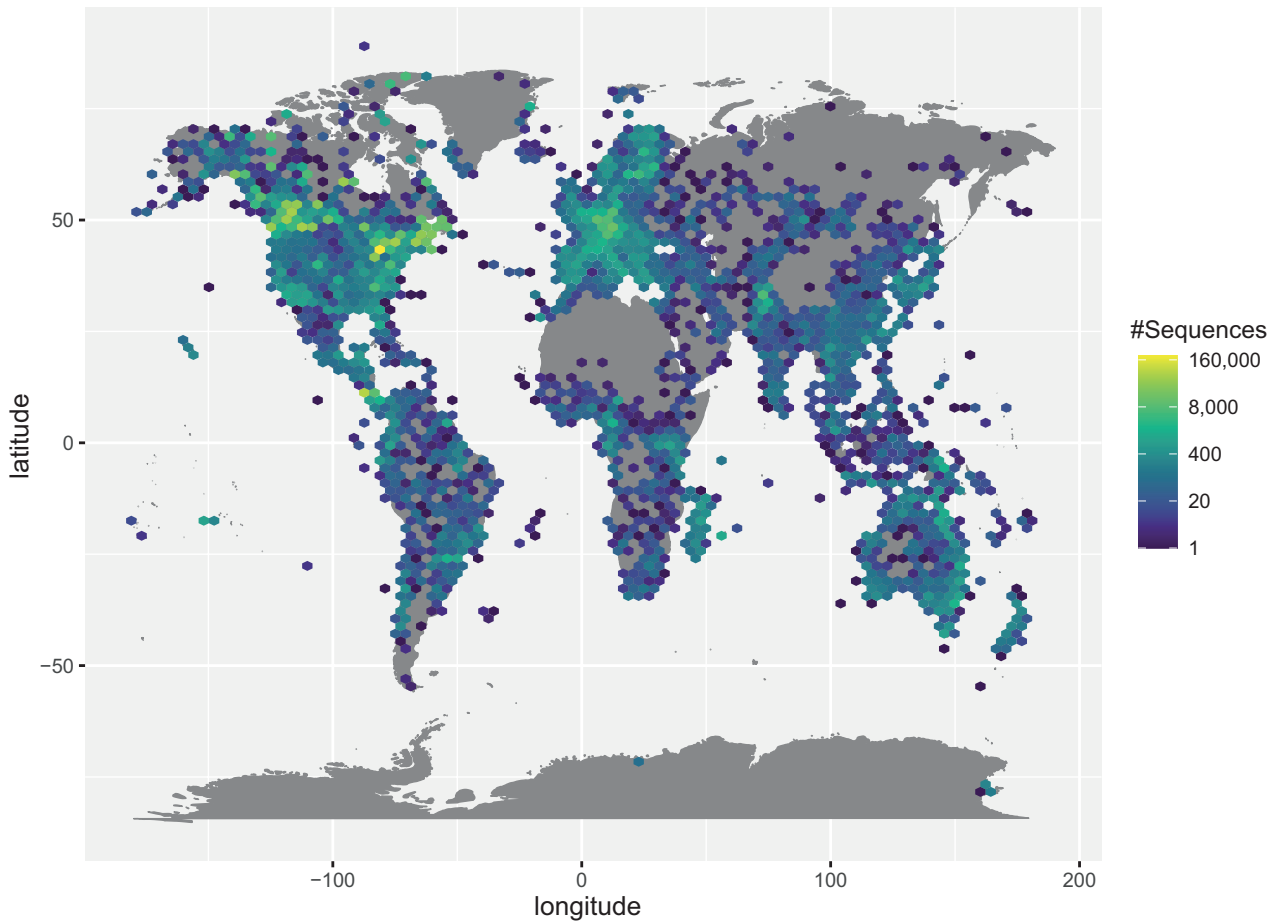
Fig. 2. Distribution and number of sequences available on GenBank for insect species, as obtained from the PhylogatR database (www.phylogatR.org). Cell colors represent the number of unique sequences at localities falling within that cell (see figure scale).

needs of butterflies in response to climate change (Zakharov and Hellmann 2008, Wells et al. 2015, Brunetti et al. 2019) and investigated the effect of landscape changes in bees (Dellicour et al. 2015a, b). Further, studies on Trichoptera (Múrria et al. 2020) provided specific recommendations on how to best protect species with extremely restricted ranges. As a result of this and other work, phylogeographic studies are now recommended for improving conservation decision-making (Andrew et al. 2013, Ghisbain et al. 2020).

The example of the study of Antarctic arthropods (most of them Hexapoda) represents a clear illustration of how the investigation of arthropod phylogeography can lead to understanding the spatial and biological history of understudied regions while informing conservation (e.g., Stevens et al. 2006, McGaughran et al. 2019, Collins et al. 2020). Even though Antarctica is one of the few regions of the world that remains almost completely isolated from human activity, climate change has allowed humans to reach previously inaccessible regions of the continent. Phylogeography is contributing to a developing understanding of how best to protect endemic Antarctic species. In the past million years, Antarctica experienced both expansion and contractions of ice sheets, with associated changes in land exposure and likely effects on species range changes. Studying the demographic and spatial history of Antarctic organisms enables conservation actions to target the preservation of unique genetic types and to predict connections between regions that may appear under higher temperatures. In present-day ice-free regions of Antarctica

small invertebrates such as Diptera, Collembola, and Acari dominate the fauna. To understand the effect of past environmental changes on the distribution of species and their genetic clusters (see Box 3 for a discussion of phylogeography and landscape genetics), studies have investigated the phylogeographic history of a number of Antarctic Collembola (Stevens et al. 2006, McGaughran et al. 2011, Collins et al. 2019, McGaughran et al. 2019, Collins et al. 2020). Jointly, these works demonstrate that these groups harbor high intraspecific diversity, with most genetic clusters restricted to small refugial areas. Importantly, these studies demonstrate that Antarctic springtails likely harbor substantial cryptic diversity. While a common finding is that present-day populations are isolated from each other, past patterns of long-distance dispersal have also been identified, especially in coastal species (Rogers 2007, McGaughran et al. 2019). This suggests that Antarctica's land fauna has been mostly evolving in nunatucks, and that conservation actions will be needed to conserve the often highly endemic lineages from being lost with the reestablishment of connections among currently isolated populations.

Phylogeography and Insect Taxonomy

Phylogeographic investigations can make important contributions to species delimitation (e.g., Sites and Marshall 2004) and integrative taxonomy (e.g., Dayrat 2005), particularly in groups such as insects where the Linnean shortfall—the large discrepancy between

Box 2

The study of representative species for conservation: There are many single-species phylogeographic studies that have conservation implications for the focal taxon. However, given limited resources, taxonomically far-reaching conservation benefits are critical. Thus, it may be efficient to target "umbrella species"; keystone species (i.e., functionally important ecosystem engineers; Paine 1969) or flagships (i.e., charismatic icons for the plight of threatened taxa such as butterflies; New 1997) that may be used as proxies for decision-making at the level of the ecosystem. This is based on the premise that species-specific conservation interventions such as enhancing quality, quantity, and continuity of essential habitat, or mitigating other threats (e.g., undirected use of insecticides) can indirectly benefit other community members. For the umbrella species itself, phylogeographic analyses can help set conservation priorities by determining whether isolated populations warrant treatment as evolutionarily significant units vs. management units (Moritz 1994). In turn, this can inform the planning of captive breeding or assisted translocation / genetic rescue programs through a better appreciation of the risks of outbreeding depression. Also, an understanding of what types of landscape features have historically represented barriers vs. conduits for dispersal and gene flow can aid in the identification of habitat linkages that are likely to be critical in the present day, and future.

Two European beetles illustrate the potential value of understanding the demographic histories of umbrella species for advancing the conservation of whole communities. The Alpine longhorn (*Rosalia alpina*) and stag beetle (*Lucanus cervus*) are icons for biodiversity associated with veteran trees and dead wood. Both are widely considered threatened by habitat fragmentation and loss, as well as by forest sanitation practices (e.g., removal of fallen logs or firewood collection), and in the case of *L. cervus*, also by the illegal pet trade. The former is IUCN Red-listed as Vulnerable (IUCN 2020), whereas the latter is currently on the Red List of the European saproxylic beetles as Near Threatened (Nieto & Alexander 2010) and is the subject of an intensive monitoring program conducted by citizen scientists. Drag et al. (2018) conducted a phylogeographic investigation of *R. alpina* and compared patterns of spatial-genetic structure with the distribution of the species' primary host tree (European beech, *Fagus* spp.), as well as host trees classified as either "marginal" or "occasional" habitat host trees. The authors discovered several divergent lineages, one of which was considered suggested to represent a new subspecies. Other notable inferences were that *R. alpina* had closely tracked its primary main host only but not others, it seemed unable to persist in small isolated refugia, and that most genetic diversity is concentrated at the extreme southern range margin of *Fagus* spp., where these forests are vulnerable to climate change. Thus, a high priority conservation intervention for *R. alpina* is the protection of beech forests in montane regions of Greece, Italy, and Turkey (Drag et al. 2018). Interestingly, conclusions from a study of *L. cervus* had several similarities, despite oaks (*Quercus* spp.) being this beetle's main host tree (Cox et al. 2019). These similarities included the detection of deeply divergent lineages (albeit fewer that *R. alpina*), and the identification of montane

regions in Greece and Italy as centers of phylogeographic endemism. Again, this information indicates that conservation efforts should be focused on protecting key oak habitats in the southern portion of the species range, including modification of intensive forestry practices so that mean tree age does not continue to decline (e.g., via longer rotation times; Nieto & Alexander 2010). Such changes would clearly also benefit a suite of dead-wood-associated fauna in the region.

the number of described species versus the number of actual species (Lomolino 2004)—is substantial. Both single locus (e.g., Pons et al. 2006, Vondráček et al. 2017) and multilocus (e.g., Montagna et al. 2017, Liu et al. 2019) datasets have been used to delimit insect species. In particular, phylogeographic investigations often discover cryptic species, where populations phenotypically indistinguishable, are genetically distinct (Bickford et al. 2007). While some investigations have found that mitochondrial DNA sequence data are not consistent with the morphological characters used to differentiate species (e.g., Vondráček et al. 2017), other investigations have demonstrated that putatively cryptic species discovered by phylogeographic investigations using mitochondrial data are not supported with nuclear genomic data (e.g., Huang et al. 2020). For this reason, and because any single marker might not reflect population history due to biological processes (deep coalescence, introgression) or non-biological (gene tree estimation error) factors, it is clear that single-locus data should not form the basis for the description of new species and are best applied in the discovery phase of species delimitation (Carstens et al. 2013). Taken together, these analyses indicate that performing studies at the phylogeographic level can assist in the identification of independently evolving lineages, which can be used to describe much of the still-undescribed insect diversity (Stork 2018).

Phylogeography for Pest Management and Biocontrol Agents

Reconstructions of colonization history provide important context for understanding the range expansion of pest species. For instance, phylogeographic analyses can identify the geographic origin(s) and the number of independent introductions into newly-invaded areas. Such inferences have management-relevant implications. In the case of multiple independent introductions, several gene pools may converge and recombine at the wave front, producing an invasive population with elevated genetic variation and adaptive potential (e.g., Kolbe et al. 2004, Kébé et al. 2017). Alternatively, if there is a single primary source of spread following initial arrival, targeted control of this bridgehead population should be possible (e.g., Grapputo et al. 2005, Du et al. 2020). Furthermore, insights into the relative importance of natural vs. human-mediated long-distance dispersal can help set priorities for enhanced surveillance of stowaways, with an informed focus on road, rail, or shipping transportation networks, depending on which one is implicated in accelerating spread.

Owing to contributions from phylogeography, historical events leading to the colonization of North America by several exotic insects that have become major pests are now well understood. The red imported fire ant (*Solenopsis invicta*) provides a good example. These ants are native to central south America and were accidentally introduced by humans via shipping cargo to the southern USA in the 1930s. Since then, the species rapidly expanded into other regions in the USA (Ahrens et al. 2005) and has now also invaded

Box 3. The integration of phylogeography with landscape genetics/population genomics

Phylogeography (Avise et al. 1987) and population genetics—particularly spatially explicit approaches such as those implemented in landscape genetics (Manel et al. 2003)—lie along a continuum, and with the advent of next-generation sequencing datasets, there is increasing overlap among them (Rissler 2016). Perhaps the most widely acknowledged distinction relates to the timescale under consideration, whereby phylogeography typically addresses questions that focus on long-term Pleistocene-aged (or earlier) events and processes, whereas landscape genetics studies are often most concerned with recent drivers of spatial-genetic structure (e.g., landscape-level changes that occurred over tens to just a few hundred generations, depending on the species). A secondary distinction might include the proportion of a species' known geographic range that is sampled, where phylogeographic studies usually attempt complete coverage, whereas landscape genetics studies may deliberately focus on subsets to allow for meta-replication (e.g., Short Bull et al. 2011; Burgess & Garrick 2020). Nonetheless, analytical tools developed for population and landscape genetics have considerable cross-discipline utility. Accordingly, we briefly summarize some examples.

Spatially explicit simulation tools that model genetic divergence through time while considering environmental heterogeneity, habitat carrying capacity, and genetic connectivity in the presence of a "hostile" matrix have been used extensively in landscape genetics. For example, SPLATCHE (Currat et al. 2004) integrates with SIMCOAL (Excoffier et al. 2000) to simulate molecular data for discrete local populations via neutral coalescence, whereas CDPOP (Landguth & Cushman 2010) takes an individual-based forward-in-time approach. While these have been useful for identifying which characteristics of intervening areas between sampled locations affect dispersal and gene flow (and for understanding trade-offs between number of loci and number of alleles per locus, or number of locations and number of individuals per location), they do not explicitly leverage the power of genomic datasets. Recent developments that redress this gap include msprime (Kelleher et al. 2016) and SLiM (Haller et al. 2019). For example, SLiM, which uses individual-based forward-in-time simulations to model evolution of whole chromosomes within multiple user-defined population gene pools that can have complex demographic histories including variable gene flow dynamics and fluctuating effective sizes. ConStruct (Bradburd et al. 2018) is another useful tool population genomics analysis tool that, although tailored toward the short timescales most relevant to landscape genetics, has the potential to serve as an important precursor to deeper timescale phylogeographic analyses of genomic data. This is because conStruct is directly informative about the nature of present-day population structure (i.e., distinguishing between clusters vs. clines, given the geographic sampling at hand), which is critical to the biological interpretation of downstream analyses that are conditioned on initial decisions about the basic units of analysis.

other continents, including parts of Asia and Australia. Ascunce et al. (2011) reconstructed the global invasion history of *S. invicta* to inform mitigation efforts through identifying source populations and transportation routes. The authors found that northeastern Argentina was the likely origin of invasion into the southern USA; phylogeographic analysis of *S. invicta* in the native range (Ahrens et al. 2005) identified this region as containing one of two major lineages. The southern USA was the primary source of almost all subsequent global spread (i.e., eight of nine independent introductions), with one exception involving secondary long-distance colonization of California as the precursor to the invasion of Taiwan. Ultimately, the global invasion history of the fire ant can be largely attributed to one critical bridgehead population in the southern USA, plus one serial introduction (Ascunce et al. 2011). If this type of information had been available during the initial spread of *S. invicta*, intensive control efforts could have been targeted at locations of high cargo movement out of the southern USA. Today, this knowledge has practical applications via informing monitoring and quarantine programs in *S. invicta* and other invasive pests.

Not all invasive species are exotic, and native species that colonize and rapidly spread throughout previously unoccupied neighboring regions can cause negative economic and ecological impacts. They also present a conundrum regarding classification of pest status and prediction of future impacts (Havill et al. 2019, and references therein). An illustration of the insights that come from investigating the demographic history of native invasives comes from research on the mountain pine beetle (*Dendroctonus ponderosae*). Briefly, this species recently expanded its range from western North America into new parts of the midwestern USA and Canada, increased its host breadth to include jack pine, and extended the duration of outbreaks (Cullingham et al. 2019). To reconstruct historical dispersal dynamics, Janes et al. (2018) coupled broad sampling across the native and invaded ranges with model-based phylogeographic analyses of alternative colonization scenarios. The authors found that *D. ponderosae* was already present in Canada, albeit at very low levels, long before the species was thought to have arrived there. Thus, it appears that small and isolated founding populations can potentially persist for extended periods, despite low effective population sizes and associated negative consequences of drift and inbreeding (Janes et al. 2018). Accordingly, current management practices for irruptive pests that focus on the removal of infested trees in emerging outbreak areas may be ineffective in preventing future outbreaks.

In addition to understanding colonization history and the context for the ongoing spread of invasive insects, phylogeography can contribute to evaluating the potential of natural enemies to act as high-fidelity biocontrol agents. Faithful host-tracking by parasitoids or prey-tracking by highly specialized predators is expected to generate signatures of strong congruence (e.g., codivergence of lineages, synchronous range expansions or contractions, closely matching gene flow dynamics), whereas host-switching is not (Page and Charleston 1998, Espíndola and Alvarez 2011). Comparative phylogeographic analysis of an insect pest and its candidate biocontrol agent can reveal the strength and antiquity of their trophic interaction. Furthermore, this information can guide choice of the source population(s) for progenitors used in mass rearing of the natural enemy prior to release (e.g., Kruitwagen et al. 2018).

Auger-Rozenberg et al. (2015) assessed long-term host specialization of two wasps that parasitize eggs of the pine processionary moth (*Thaumetopoea pityocampa-wilkinsoni* species complex), a major pest of conifers in the Mediterranean that is rapidly

expanding poleward owing to climate change. The authors used phylogeographic approaches to show that current differences in the degree of host specificity of the natural enemies, *Baryscapus servadeii* (only known to parasitize *T. pityocampa-wilkinsoni*) and *Ooencyrtus pityocampae* (which also parasitizes other Lepidoptera and Hemiptera) are long-standing. Whereas 40% of the variance in spatial-genetic structure of *B. servadeii* was explained by that of the host, for *O. pityocampaei,* only 15% was (Auger-Rozenberg et al. 2015). Furthermore, *B. servadeii* and *T. pityocampa-wilkinsoni* were inferred to have shared common habitat refuges during glacial cycles, yet *O. pityocampaei* only recently recolonized areas where the pine processionary moth is found today. From the perspective of Integrated Pest Management professionals, this research is confirmatory with respect to the existing life history information for these parasitoids. Nonetheless, it should provide added confidence when evaluating the risks (e.g., host-switching or host generalization upon introduction into novel communities) of biocontrol agent candidates.

Phylogeography as a Tool for Insect Domestication and Breeding

Few insects have been domesticated via a deliberate selective breeding of wild species ("directed domestication"; Lecocq 2018; e.g., honey bees, *Bombyx mori* silkworms). However, some species are considered semi-domesticated. Nonetheless, in all cases, the initial basic requirements are a pool of standing genetic variation with an associated phenotypic variation that can be recombined so that artificial selection can be imposed. Characterizing the evolutionary history of wild populations of a species with an economically valuable trait can facilitate directed domestication in several ways. For example, the identification of distinct lineages could guide the design of artificial breeding experiments that optimize the potential for generating novel phenotypes. Also, given that depth of phylogeographic structure is positively correlated with reproductive isolation (Singhal and Moritz 2013), this information would represent a useful framework for interpreting the success or failure of different controlled crosses.

Phylogeographic studies of semi-domesticated silkmoths from India have provided baseline information about the nature of standing genetic variation, and by extension, the capacity to enhance quantity, quality or variety of silk through selective breeding. For example, the muga silkmoth (*Antheraea assama*) is endemic to a narrow region of northeast India where it produces luminous golden silk that has been used to make garments for over 2,300 yr. The reputation and authenticity of the species' silk have been protected by Geographical Indications status, and there is interest in the potential to harness new genetic resources. Arunkumar et al. (2012) reevaluated the assumption that intraspecific genetic variation was low by performing spatially explicit analyses of population genetic data. They uncovered a divergent localized gene pool in close proximity to (and potentially spatially nested within) a more broadly distributed unstructured genetic cluster, well within the expected flight range of individuals. Similarly, Chakraborty et al. (2015) identified marked spatial-genetic structure in the economically important tasar silkmoth (*A. mylitta*), again with two major groups. In this latter case, however, variation was previously expected to be much higher owing to the existence of numerous well-defined ecotypes each with different host-plant specificities, and which do not appear to freely interbreed in nature. Collectively, this research showed that an as-yet untapped potential source of novel phenotypic variation may exist for *A. assama*, whereas the considerable phenotypic variation observed in *A. mylitta* is attributable to contemporary genotype ×

environment interactions, rather than long-standing differences in evolutionary trajectories.

A second example comes from bees. Attempts to enhance pollination services of bumble bees, particularly for greenhouse crops through directed domestication (i.e., "bombiculture"), began in the early 20th century, progressed through several steps of the process, but were then temporarily abandoned because of difficulties with rearing them in captivity (Lecocq 2018). However, with the advent of a suite of molecular resources for bumble bees (Woodard et al. 2015), phylogeographic methods can now be used to assess evidence for cryptic diversity within currently-recognized bumble bee species that still remain as candidates for domestication. Indeed, species with broad geographic ranges can include reproductively isolated lineages (e.g., Lozier et al. 2016), and those that span steep environmental gradients may include high elevation populations with unique local gene pools (e.g., Lozier et al. 2011). This information could inform the design of controlled crosses, and perhaps also pinpoint unique reservoirs of adaptive variation that could be leveraged during the domestication process. Additional applications of phylogeography for guiding bumble bee domestication include understanding the potential for hybridization with native *Bombus* species (Woodard et al. 2015).

Phylogeography of Vectors of Disease

Vector-borne diseases kill over 700,00 people per year, with tropical and subtropical regions most impacted. Among insect vectors of disease, female mosquitos, particularly *Aedes*, *Anopheles*, and *Culex* spp., transmit a suite of viruses and parasites that infect humans. Other blood-feeding dipterans such as tsetse flies, blackflies, and sandflies also have enormous human health consequences in the world's poorest countries (WHO 2020). Responses to outbreaks, and prevention of disease, often focus on vector control. In this context, the identification of isolated populations provides opportunities for local eradication, whereas an understanding of mechanisms of long-distance dispersal can inform strategies to prevent further spread.

The dengue and yellow fever mosquito (*Ae. aegypti*) exemplifies the role phylogeography can play in understanding the past and on-going spread of an insect whose evolution has been intricately connected to humans, and for which improved strategies for control are needed. Brown et al. (2014) reconstructed an "out-of-Africa" expansion of *A. aegypti* in considerable detail. The authors showed that there are two distinct lineages, one strictly African, which includes both forest-dwelling zoophilic as well as anthropophilic populations, and the other globally widespread (i.e., in the tropics and subtropics) and strictly human-associated. Brown et al.'s (2014) data were consistent with at least one dispersal event associated with human-trade routes (i.e., to the New World via slave trade, and subsequent serial invasion from the New World to Asia and Oceania), which caused genetic bottlenecks associated with founder effects. This study, along with follow-up work with expanded molecular sampling for this species (e.g., Gloria-Soria et al. 2016), provides an important reference database of global genetic diversity for determining the geographic origins of new introductions and their associated traits.

The tsetse fly (*Glossina fuscipes*), which transmits a parasitic trypanosome that causes sleeping sickness leading to thousands of deaths per year in sub-Saharan Africa, provides an illustration of how phylogeography can inform vector control. To be effective, such interventions depend on an understanding of the spatial scale over which vector populations are connected by dispersal

and gene flow, in the present and the past. To address this, Beadell et al. (2010) examined spatial-genetic patterns of diversity across Uganda, and parts of Kenya, Sudan and the Democratic Republic of the Congo. Molecular data identified two deeply divergent lineages, attributable to ancient north-south vicariance. This division includes a narrow contact zone across central Uganda, where gene flow is currently occurring. Subsequent work has identified additional admixture zones, likely resulting from the historical reorganization of river networks during the formation of the West African Rift system (Saarman et al. 2019). Within the two major phylogeographic regions, Beadell et al. (2010) found that gene flow is generally high and that contrary to expectations, island populations within Lake Victoria are not genetically isolated from the mainland. Importantly, populations at the species' southeastern range margin are largely genetically isolated. This region could therefore be prioritized as a target for intensive trapping and insecticide treatment, as well as other complementary eradication strategies (e.g., sterile insect technique, or symbiont-induced cytoplasmic incompatibility; see Alam et al. 2011), with the goal of achieving complete local eradication.

Phylogeography in a Comparative Framework

Phylogeography reaches its full potential in a comparative framework. Although single-species studies make valuable contributions to understanding the abiotic and biotic factors that structure genetic diversity within a species, studies of codistributed species can reveal how historical events have shaped biodiversity and community structure across entire landscape systems (Moritz et al. 1998, Avise 2000, Riddle et al. 2000). In particular, a comparative framework provides replication for testing how landscape and environmental processes (e.g., Pleistocene glacial cycles, mountain orogeny, river formation) have shaped taxonomic and genetic diversity among codistributed species (Arbogast and Kenagy 2001, Carstens et al. 2005). In this context, congruent phylogeographic patterns suggest a shared response to historical events.

Since the earliest days of the discipline, comparative phylogeographic studies have revealed that biogeographic barriers, glacial refugia, and other landscape and environmental processes influence the genetic diversity of codistributed species. In one influential project, Riddle et al. (2000) used genetic data from 12 species to test hypotheses about the role vicariance played in structuring genetic diversity in Baja California, Mexico, and found shared phylogeographic patterns among several taxa supporting multiple vicariance events. Comparative studies, however, have also commonly revealed discordant phylogeographic patterns, suggesting that species responded idiosyncratically to landscape-level environmental processes. For example, Marske et al. (2012) identified shared glacial refugia for three of four codistributed beetle species across New Zealand's South Island, but variation in temporal patterns suggested different responses by the species to environmental changes best explained current distributions. Although congruent phylogeographic patterns reveal broader processes influencing genetic structure in a region, incongruent patterns are useful for understanding how differences in life-history traits, behavior, and ecology may allow species to vary in their responses to a changing environment (Papadopoulou and Knowles 2016, Zamudio et al. 2016). When testing the species-pump hypothesis for 13 species of beetles from the Aegean archipelago, Papadopoulou and Knowles (2015) found evidence for multiple divergence episodes but considerable uncertainty among demographic models. When the authors refined their

hypothesis to include six beetle species that share similar habitat preferences, a single divergence episode was the best-supported model. Thus, a comparative framework is important for testing and refining hypotheses, including how intrinsic life-history traits (and extrinsic biotic interactions) can generate congruent or incongruent phylogeographic patterns.

Darwin's (1859) tangled bank envisioned species spanning the tree of life, living in an ecological entanglement because they are interdependent in some manner. These biotic interactions may be loose and fleeting in time or may result in species evolving dependence on each other for survival and reproduction. For example, in pollination mutualisms such as those exhibited by figs and wasps, each member is dependent on the other for reproduction; figs require fig wasps for pollination services, and fig wasps require figs as a nursery for egg-laying and larval development (Herre et al. 2008). Given a continuum of ecological associations among interacting species of a community—ranging from nonexistent to facultative to obligate—a comparative framework can be used to test hypotheses about the evolution of species interactions, how species interactions contribute to shaping phylogeographic patterns, and how these interactions shape community structure in space and time. This is the focus of community phylogeography (Satler and Carstens 2016).

Community phylogeography considers several topics, such as understanding the correlation between the degree of ecological association and shared evolutionary history, the potential (in)congruence in dispersal and gene flow among interacting species, or quantifying the (dis)similarity in diversification patterns within and/or across trophic levels. In addition to revealing the abiotic factors structuring genetic diversity within a region, studying species from the same ecological community enables testing hypotheses on the nature of species interactions, their importance in shaping spatial and temporal community structure, and in identifying evolutionary communities: ecological communities maintained over evolutionary time.

Numerous examples of community phylogeography have revealed the processes structuring ecologically interacting species. Below, we first discuss several exemplar studies of plant-insect associations and then highlight how community approaches can help define and establish conservation decisions.

Mutualistic Interactions

Insect pollinators range in their level of association with many (generalists) or few (specialists) host plant species. At one end of the continuum are specialists involved in obligate pollination mutualisms, which provide exemplar systems for studying the history of ecological interactions and their importance in shaping evolutionary history. In these systems (e.g., yuccas and moths, figs and wasps), each lineage is solely dependent on the other for survival and reproduction. Thus, we might predict a shared response to landscape and environmental changes. For example, Smith et al. (2011) tested if Joshua Trees (*Yucca brevifolia*) and their four associated prodoxid pollinators responded in a similar manner to climatic changes of the Pleistocene glacial cycles. The authors provided evidence for concerted demographic changes between host plant and pollinator, suggesting these lineages responded similarly to the changing environment. This suggests the ecologically dependent plant-pollinator association has persisted through evolutionary time, with this community responding to abiotic processes as a unit. Phylogeography can also inform researchers about the community structure of the system (e.g., Satler et al. 2020), providing an important connection between ecological and evolutionary processes.

Although we might predict obligate mutualisms to show similar phylogeographic patterns, differences in life history traits may contribute to discordant patterns. Espíndola et al. (2014) investigated the phylogeographic history of the European globeflower (*Trollius europaeus*) and three of their obligate *Chiastocheta* fly pollinator species. In contrast to the Smith et al. (2011) findings, Espíndola et al. (2014) recovered discordant phylogeographic histories among the pollinators and host plant. The authors suggested this discordance was due to independent responses to historical events shaped by differences in dispersal ability.

Antagonistic Interactions

Given the interactions between hosts and antagonists (e.g., parasites, herbivores), we might predict lower levels of phylogeographic congruence (Espíndola and Alvarez 2011). As only one lineage is dependent on the other—and even then, antagonists can vary between generalists and specialists—a community phylogeographic framework can reveal processes shaping the evolution of these interactions. For example, Bunnefeld et al. (2018) investigated the evolutionary history of a community of oak gall wasps (four species) and their parasitoids (nine species). They did not find evidence of codivergence, codispersal, or a history of host tracking within the community, but rather, recovered idiosyncratic population histories. As some shared patterns were observed, Bunnefeld et al. (2018) suggested that a more diffuse pattern of coevolution—restricted in geographic scale—characterized this community.

Another example of the comparative study of antagonistic interactions is of *Araptus attenuatus*, a bark beetle found in Baja California and mainland Mexico. Placed in the context of previous research done on the beetle's only known host plant, *Euphorbia lomelii* (Garrick et al. 2009), Garrick et al. (2013) tested hypotheses on the abiotic and biotic processes shaping phylogeographic patterns in the beetle. The authors recovered similarities in phylogeographic histories between the two species, suggesting the bark beetle has tracked its host's distribution, while also recovering phylogeographic patterns specific to the beetle. Their results suggest ecological interaction—and constraints imposed by the host-specific relationship—can contribute to generating shared phylogeographic patterns, while also allowing for species-specific responses to past climatic and other landscape-level changes.

Ecological Communities

Investigations that focus on members of ecological communities spanning different trophic levels can provide opportunities for testing hypotheses on how ecological association correlates with evolutionary history and how sets of taxa sharing life-history traits may partition their response to abiotic and biotic factors. Carnivorous pitcher plants provide excellent model systems for community phylogeographic research. In addition to their prey items, pitcher plants are often host to a diverse set of inquilines (i.e., non-prey species) that span the tree of life, from bacteria to fungi to protists to arthropods (Adlassnig et al. 2011). These communities encompass a broad suite of ecological interactions, where some species are found in the habitat, but weakly associated with the host plant, while others are dependent on the plant for most or all of their life cycle. Thus, these self-contained and clearly-delimited systems are excellent for testing hypotheses about how ecological interactions contribute to shaping phylogeographic patterns among community members.

The *Sarracenia alata* pitcher plant system has been the subject of considerable phylogeographic research. The host plant is structured along the landscape with the deepest break at the Mississippi River (Koopman and Carstens 2010, Zellmer et al. 2012), with evidence suggesting the presence of two cryptic species (Carstens and Satler 2013). Species that interact ecologically with the plant share similar population genetic structure, from bacteria (Koopman et al. 2010, 2011) to several different groups of eukaryotes (Satler et al. 2016). In particular, a mite (*Macroseius biscutatus*), a moth (*Exyra semicrocea*), and multiple flesh flies (*Fletcherymia celarata*, *Sarcophaga sarraceniae*) are dependent on the host plant for their entire life cycles, and are only ever found in these unique habitats. As predicted based on life history traits, these species share phylogeographic patterns with the host pitcher plant, suggesting that degree of ecological association is positively correlated with evolutionary history (Satler and Carstens 2016, 2017, 2019). In contrast, two spider species (*Misumenoides formosipes*, *Peucetia viridans*) found in but not restricted to this habitat show discordant phylogeographic patterns as compared with the host plant. These studies suggest landscape processes structuring genetic diversity in the host plant have similarly-structured genetic diversity in several associated species, with degree of ecological association being positively associated with a shared evolutionary history.

Conservation

The identification of multi-species centers of endemism can assist managers in prioritization of geographic areas for conservation. Comparative phylogeographic studies are particularly informative for community-focused conservation when they include a broad suite of distantly-related species, although it is not uncommon for such studies to focus on a particular ecological guild or microhabitat type. Assessments of the extent to which multiple members of the same community respond to past environmental change can be based on the level of similarity in their spatial patterns of intraspecific diversity, such as the number and geographic distributions of distinct lineages (e.g., Rissler and Smith 2010). Congruence can also be assessed based on inferred underlying processes, including shared vs. different historical refuge areas into which populations contracted, persisted, and subsequently expanded from, as well as the estimated temporal synchrony with which such events occurred (e.g., Huang et al. 2011, Xue and Hickerson 2015). Geographic areas that contain distinct lineages of multiple species (i.e., high phylogeographic endemism) can be directly targeted for protection. Indeed, conservation prioritization of areas that harbor deeply divergent intraspecific lineages will not only protect irreplaceable diversity but also promotes the maintenance of the underlying processes that generated it (Moritz 2002).

Several examples from eastern Australia illustrate how comparative phylogeographic studies provide actionable information, and more granularity than the "single large or several small" debate over conservation reserve design (see Fahrig 2020). In the northeast Wet Tropics rainforests, a marked phylogeographic break across the Black Mountain Corridor (BMC) has been documented in multiple vertebrate taxa (Schneider et al. 1998). More recently, Bell et al. (2007) extended this assessment to dung beetles, including a pair of tropical rainforest specialist sister species (*Temnoplectron aeneopiceum* and *T. subvolitans*). They each exhibited strong intraspecific spatial-genetic structure, as well as deep species-level divergence across the BMC (i.e., each species was restricted to a different side of the barrier). This suggested that ecologically-specialized invertebrates may show finer-scale

phylogeographic structure than more mobile vertebrates, and they may also speciate more readily. Indeed, Schiffer et al. (2004) identified a cryptic species of *Drosophila serrata* for which the southern range limit coincides with the BMC. In the same landscape setting, Hugall et al. (2002) showed that phylogeographic patterns in an ecologically-specialized low-mobility land snail (*Gnarosophia bellendenkerensis*) represented a composite of those seen in lizards and frogs. Those authors also highlighted the potential importance of microrefugia—blocks of montane rainforest habitat too small to support populations of vertebrates, but suitable for invertebrates—during Pleistocene glacial cycles. These findings also extend to temperate forests in southeastern Australia. In Tallaganda National Forest on the Great Dividing Range, a suite of dead-wood-dependent invertebrates, including springtails, terrestrial flatworms, spiders, and velvet worms typically exhibit strong phylogeographic structure over relatively short distances (i.e., ~100 km; Beavis et al. 2011, Garrick et al. 2012 and references therein, Bull et al. 2013). Notwithstanding some species-specific idiosyncrasies, marked spatial clustering of deep breaks are evident, and as a group, the invertebrates fully capture patterns of intraspecific diversity seen in a co-distributed lizard. Ultimately, the superimposition of multi-species phylogeographic lineage boundaries can be used to propose conservation of specific areas of endemism (Garrick et al. 2012) that are appropriate for different taxonomic groups.

Future Prospects and Opportunities

Insect phylogeography continues to evolve and provide new insights into the history of species, their interacting partners, and ecosystems. There are, however, several areas where opportunities are underutilized, and knowledge gaps remain.

Soil-Dwelling and Subterranean Hexapod Species

Even though we have increased our understanding of how surface-dwelling terrestrial species respond to environmental change, little is known of those that live underground. For example, soil communities have been called the "poor man's tropical rainforest" (Giller 1996), reflecting their high levels of biodiversity. Considering that much of this biodiversity is represented by arthropods, there is a large knowledge gap in that area. The few studies that have investigated this usually have found considerable cryptic diversity, and made insightful discoveries about how species living in the soil or cave habitats responded to environmental change (e.g., Juan and Emerson 2010, Guzik et al. 2011, Faille et al. 2015, Katz et al. 2018, Langille et al. 2020) or how these habitats served as important refugia that enabled in situ persistence in glaciated areas (Faria et al. 2019).

Increasing the Geographic and Taxonomic Coverage

Phylogeographic studies are being conducted in many parts of the world, but they remain concentrated in the northern hemisphere (Riddle 2016; Fig. 2). More work is needed globally, particularly in the tropics, where most insect diversity is found yet likely undescribed and where it is urgent to understand how habitat loss and climate change may impact species survival and the retention of genetic diversity. We found an alarming "phylogeographic shortfall" in entomological phylogeography. Indeed, there is not always a direct relationship between the proportions of phylogeographic studies and of taxa present in different orders. Further, it also seems that the research focus is phylogenetically clustered (Fig. 3). These observations are worrisome because they suggest that some groups are grossly

understudied and that most phylogeographic insights come from a small and potentially unrepresentative subset of Hexapoda clades. Future work should focus on redressing this taxonomic unevenness.

Integration of Methodological and Other Non-Genetic Data

More work can also be done to improve the integration of ecological spatial methods with the estimation of genetic diversity and demographic history. For example, sample occurrence data can be used to estimate a statistical model of the climatic niche of a given species, which can then be projected onto climatic models at different time points (see Alvarado-Serrano and Knowles 2014). These models of how a species' range may have changed over time can form the basis for hypothesis tests in phylogeography (e.g., Richards et al. 2007) and are particularly useful in comparative studies (e.g., Espíndola et al. 2014) or for species of conservation concern (e.g., Brunetti et al. 2019, Françoso et al. 2019). Researchers have also combined phylogeographic investigations with acoustic data (e.g., Mahamoud-Issa et al. 2017, Liu et al. 2019), morphological data (e.g., Vondráček et al. 2017, Henriques et al. 2020) or both (e.g., Liu et al. 2018). In combination, these data allow researchers to address questions of importance related to species boundaries, and thus appropriate for species delimitation and taxonomy (e.g., Wade et al. 2015).

Repurposing Georeferenced Genetic Data

The availability of millions of georeferenced DNA sequences present new opportunities for analysis and synthesis. Gratton et al. (2017) suggested that these data can be accessed and analyzed automatically via the construction of custom pipelines using *R* and *Python*. For example, Pelletier and Carstens (2018) automated analysis of data from >10,000 species, including thousands of hexapod species, to investigate the factors that lead to genetic isolation by distance, and then used machine learning to identify variables that predicted the presence of isolation by geographic or environmental distance. Investigations that apply data repurposing, where existing data are reanalyzed using a common analytical framework (Sidlauskas et al. 2010) are particularly relevant in a field such as phylogeography where methods for data analysis are continually improving.

The Emergence of Community Phylogeography

As a relatively new subfield of research, community phylogeography harbors a lot of potential and is currently underutilized. Comparative studies often focus on codistributed species within a similar taxonomic group (e.g., reptiles, mammals), whereas relatively few studies focus on ecologically-interacting taxa sampled from across the tree of life. We recommend more studies concentrate on sampling species from ecological communities. In addition to questions of community response to historical events, these studies can address fundamental questions and hypotheses on the evolution of species interactions, how species interactions contribute to shaping codiversification patterns, and how ecological communities evolve.

Integrated Analysis of Codistributed Species

Methods development will help improve our ability to test hypotheses and make inferences about the evolution of codistributed species. A popular approach in comparative phylogeography is to generate parameter estimates on a species-by-species basis, and then compare estimates across species. For example, methods based on the site frequency spectrum (e.g., fastsimcoal2; see Table 1) can be used to estimate demographic models and generate parameter estimates with
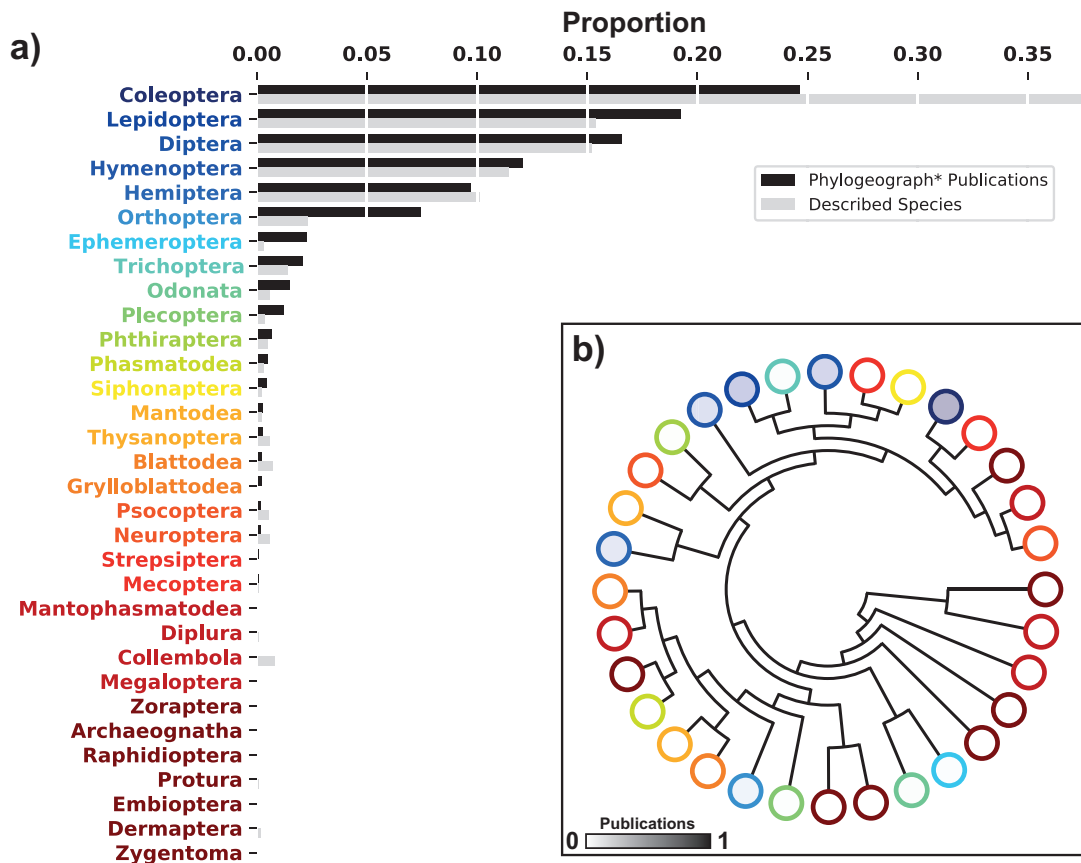
Fig. 3. Distribution of phylogeography studies by major insect group. We conducted a literature search in Web of Science for publication titles including the term "Phylogeograph*" and insect order (the rank of class was used for Protura, Collembola, and Diplura). The search returned 1,955 total hits. (a) The proportion of phylogeography studies (black) and the proportion of described species (gray) for each group. Species numbers are from Stork (2018). (b) A phylogeny of Hexapoda (with relationships as estimated from Misof et al. 2014) matching our major insect groups, with colors matching those in panel a. Transparency in circles reflects the proportion of phylogeography publications for that group. Circles with bluer shades indicate groups with the bulk of insect phylogeography publications; circles with redder shades show insect groups receiving little or no phylogeographic attention.

genome-wide SNP data sets. While useful, posthoc comparisons of parameter estimates across species are often challenging to interpret. For example, how many years difference is acceptable for a population splitting event or speciation to be considered "simultaneous" among multiple species? And if parameter estimates require a mutation rate and generation length (as generally needed with coalescent-based approaches) to be converted to real units (e.g., years), how do we account for differences in mutation rate and generation length among species, and especially uncertainty in those values, when our assumptions of either can drastically alter interpretation? To respond to this need, we suggest a focus on developing methods that use community data simultaneously for testing hypotheses on the evolution of codistributed species. For example, methods using ABC have been used to test for simultaneous divergence (e.g., MTML-msBayes) or concerted demographic changes (e.g., aSFS) among a community of species (see Table 1 for details). Further, Oaks (2019) improved upon the msBayes approach by developing a full-likelihood method—capable of handling genomic data—to test for simultaneous divergence. Additional methods for handling community data would improve our ability for testing hypotheses about the evolution of ecological communities. In particular, process-based methods that can model the interaction of species and how these interactions can generate phylogeographic patterns will be critical for addressing hypotheses in this field. Given that generating comparative genomic data sets

is becoming easier, a focus on method development will be necessary to address outstanding questions in the evolution of ecological communities.

Acknowledgments

References Cited

Adlassnig, W., M. Peroutka, and T. Lendl. 2011. Traps of carnivorous pitcher plants as a habitat: composition of the fluid, biodiversity and mutualistic activities. Ann. Bot. 107: 181–194.

Ahrens, M. E., K. G. Ross, and D. D. Shoemaker. 2005. Phylogeographic structure of the fire ant *Solenopsis invicta* in its native South American range: roles of natural barriers and habitat connectivity. Evolution 59: 1733–1743.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. on Autom. Control 19: 716–723.

Alam, U., J. Medlock, C. Brelsfoard, R. Pais, C. Lohs, S. Balmand, J. Carnogursky, A. Heddi, P. Takac, A. Galvani, et al. 2011. Wolbachia symbiont infections induce strong cytoplasmic incompatibility in the Tsetse fly *Glossina morsitans*. PLoS Pathogens 7: e1002415.

Alvarado-Serrano, D. F., and L. L. Knowles. 2014. Ecological niche models in phylogeographic studies: applications, advances, and precautions. Mol. Ecol. Res. 14: 233–248.

Anderson, D. R. 2008. Model-based inference in the Life Sciences: a primer on evidence. Springer Science, New York, NY.

Andrew, N. R., S. J. Hill, M. Binns, M. H. Bahar, E. V. Ridley, M.-P. Jung, C. Fyfe, M. Yates, and M. Khusro. 2013. Assessing insect responses to climate change: what are we testing for? Where should we be heading? PeerJ 1: e11.

Arbogast, B. S., and G. J. Kenagy. 2001. Comparative phylogeography as an integrative approach to historical biogeography. J. Biogeogr. 28: 819–825.

Arunkumar, K. P., A. K. Sahu, A. R. Mohanty, A. K. Awasthi, A. R. Pradeep, S. R. Urs, and J. Nagaraju. 2012. Genetic diversity and population structure of Indian golden silkmoth (*Antheraea assama*). PLoS ONE 7: e43716.

Ascunce, M. S., C.-C. Yang, J. Oakey, L. Calcaterra, W.-J. Wu, C.-J. Shih, J. Goudet, K. G. Ross, and D. Shoemaker. 2011. Global invasion history of the fire ant *Solenopsis invicta*. Science 331: 1066–1068.

Auger-Rozenberg, M.-A., M. Torres-Leguizamón, C. Courtin, J.-P. Rossi, and C. Kerdelhué. 2015. Incongruent evolutionary histories of two parasitoids in the Mediterranean Basin: influence of host specialization and ecological characteristics. J. Biogeogr. 42: 1040–1051.

Avise, J. C. 2000. Phylogeography: the history and formation of species. Harvard University Press, Cambridge, MA.

Avise, J. C., J. Arnold, R. M. Ball, E. Bermingham, T. Lamb, J. E. Neigel, C. A. Reeb, and N. C. Saunders. 1987. Intraspecific phylogeography: the mitochondrial bridge between population genetics and systematics. Annu. Rev. Ecol. Evol. Syst. 18: 489–522.

Bain, A., R. M. Borges, M. H. Chevallier, H. Vignes, N. Kobmoo, Y. Q. Peng, A. Cruaud, J. Y. Rasplus, F. Kjellberg, and M. Hossaert-Mckey. 2016. Geographic structuring into vicariant species-pairs in a wide-ranging, high-dispersal plant-insect mutualism: the case of *Ficus racemosa* and its pollinating wasps. Evol. Ecol. 30: 663–684.

Baird, N. A., P. D. Etter, T. S. Atwood, M. C. Currey, A. L. Shiver, Z. A. Lewis, E. U. Selker, W. A. Cresko, and E. A. Johnson. 2008. Rapid SNP discovery and genetic mapping using sequenced RAD markers. PLoS ONE 3: e3376.

Barrios-Leal, D. Y., J. Neves-da-Rocha, and M. H. Manfrin. 2019. Genetics and distribution modeling: the demographic history of the cactophilic *Drosophila buzzatii* species cluster in open areas of South America. J. Hered. 110: 22–33.

Beadell, J. S., C. Hyseni, P. P. Abila, R. Azabo, J. C. K. Enyaru, J. O. Ouma, Y. O. Mohammed, L. M. Okedi, S. Aksoy, and A. Caccone. 2010. Phylogeography and population structure of *Glossina fuscipes fuscipes* in Uganda: Implications for control of tsetse. PLoS Negl. Trop. Dis. 4: e636.

Beaumont, M. A., W. Zhang, and D. J. Balding. 2002. Approximate Bayesian computation in population genetics. Genetics 162: 2025–2035.

Beavis, A. S., P. Sunnucks, and D. M. Rowell. 2011. Microhabitat preferences drive phylogeographic disparities in two Australian funnel web spiders. Biol. J. Linn. Soc. 104: 805–819.

Beerli, P., and J. Felsenstein. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. Proc. Nat. Acad. Sci. U.S.A. 98: 4563–4568.

Bell, K. L., C. Moritz, A. Moussalli, and D. K. Yeates. 2007. Comparative phylogeography and speciation of dung beetles from the Australian Wet Tropics rainforest. Mol. Ecol. 16: 4984–4998.

Bickford, D., D. J. Lohman, N. S. Sodhi, P. K. L. Ng, R. Meier, K. Winker, K. K. Ingram, and I. Das. 2007. Cryptic species as a window on diversity and conservation. Trend. Ecol. Evol. 22: 148–155.

Bradburd, G. S., G. M. Coop, and P. L. Ralph. 2018. Inferring continuous and discrete population genetic structure across space. Genetics. 210: 33–52.

Bransetter, M. G., and J. T. Longino. 2020. Ultra-conserved element phylogenomics of New World *Ponera* (Hymenoptera: Formicidae) illuminates the origin and phylogeographic history of the endemic exotic ant *Ponera exotica*. Ins. Syst. Div. 3: 1.

Branstetter, M. G., B. N. Danforth, J. P. Pitts, B. C. Faircloth, P. S. Ward, M. L. Buffington, M. W. Gates, R. R. Kula, and S. G. Brady. 2017. Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. Curr. Biol. 27: 1019–1025.

Brito, P. H., and S. V. Edwards. 2009. Multilocus phylogeography and phylogenetics using sequence-based markers. Genetica 135: 439–455.

Brown, J. E., B. R. Evans, W. Zheng, V. Obas, L. Barrera-Martinez, A. Egizi, H. Zhao, A. Caccone, and J. R. Powell. 2014. Human impacts have shaped historical and recent evolution in *Aedes aegypti*, the dengue and yellow fever mosquito. Evolution. 68: 514–525.

Brunetti, M., G. Magoga, M. Iannella, M. Biondi, and M. Montagna. 2019. Phylogeography and species distribution modelling of *Cryptocephalus barii* (Coleoptera: Chrysomelidae): Is this alpine endemic species close to extinction? ZooKeys 856: 3–25.

Buckley, T. R., K. Marske, and D. Attanayake. 2010. Phylogeography and ecological niche modelling of New Zealand stick insect *Clitarchus hookeri* (White) support survival in multiple coastal refugia. J. Biogeogr. 37: 682–695.

Bull, J. K., J. Sands, R. C. Garrick, M. G. Gardner, N. N. Tait, D. A. Briscoe, D. M. Rowell, and P. Sunnucks. 2013. Environmental complexity and biodiversity: the multi-layered evolutionary history of a log-dwelling velvet worm in Montane Temperate Australia. PLoS ONE 8: e84559.

Bunnefeld, L., J. Hearn, G. N. Stone, and K. Lohse. 2018. Whole-genome data reveal the complex history of a diverse ecological community. Proc. Nat. Acad. Sci. U.S.A. 115: E6507–E6515.

Burgess, S. M., and Garrick, R. C. 2020. Regional replication of landscape genetics analyses of the Mississippi slimy salamander, *Plethodon mississippi*. Landscape Ecology. 35: 337–351.

Burham, K. P., and D. R. Anderson. 2002. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research 28: 111–119.

Carling, M. D., and R. T. Brumfield. 2007. Gene sampling strategies for multilocus population estimates of genetic diversity (θ). PLoS ONE 1: e160.

Carstens, B. C., and J. D. Satler. 2013. The carnivorous plant described as *Sarracenia alata* contains two cryptic species. Biol. J. Linn. Soc. 109: 737–746.

Carstens, B. C., S. J. Brunsfeld, J. R. Demboski, J. M. Good, and J. Sullivan. 2005. Investigating the evolutionary history of the Pacific Northwest mesic forest ecosystem: hypothesis testing within a comparative phylogeographic framework. Evolution 59: 1639–1652.

Carstens, B. C., H. N. Stoute, and N. M. Reid. 2009. An information theoretical approach to phylogeography. Mol. Ecol. 18: 4270–4282.

Carstens, B. C., T. A. Pelletier, N. M. Reid, and J. D. Satler. 2013. How to fail at species delimitation. Mol. Ecol. 22: 4369–4383.

Carstens, B. C., M. Gruenstaeudl, and N. M. Reid. 2016. Community trees: identifying codiversification in the Páramo dipteran community. Evolution 70: 1080–1093.

Chakraborty, S., M. Muthulakshmi, D. Vardhini, P. Jayaprakash, J. Nagaraju, and K. P. Arunkumar. 2015. Genetic analysis of Indian tasar silkmoth (*Antheraea mylitta*) populations. Scientific Reports 5: 15728.

Chinn, W. G., and N. J. Gemmell. 2004. Adaptive radiation within New Zealand endemic species of the cockroach genus *Celatoblatta* Johns (Blattidae): a response to Plio-Pleistocene mountain building and climate change. Mol. Ecol. 13: 1507–1518.

Collins, G. E., I. D. Hogg, P. Convey, A. D. Barnes, and I. R. McDonald. 2019. Spatial and temporal scales matter when assessing the species and genetic diversity of springtails (Collembola) in Antarctica. Front. Ecol. Evol. 7: 18.

Collins, G. E., I. D. Hogg, P. Convey, L. G. Sancho, D. A. Cowan, W. B. Lyons, B. J. Adams, D. H. Wall, and T. G. A. Green. 2020. Genetic diversity of soil invertebrates corroborates timing estimates for past collapses of the West Antarctic Ice Sheet. Proc. Natl. Acad. Sci. U.S.A. 117: 22293–22302.

Conow, C., D. Fielder, Y. Ovadia, and R. Libeskind-Hadas. 2010. Jane: a new tool for the cophylogeny reconstruction problem. Algorithms Mol. Biol. 5: 16.

Corander, J., P. Waldmann, and M. J. Sillanpää. 2003. Bayesian analysis of genetic differentiation between populations. Genetics 163: 367–374.

Cox, K., N. McKeown, G. Antonini, D. Harvey, E. Solano, A. Van Breusegem, and A. Thomaes. 2019. Phylogeographic structure and ecological niche modelling reveal signals of isolation and postglacial colonisation in the European stag beetle. PLoS ONE 14 (4): e0215860.

Csilléry, K., M. G. B. Blum, O. E. Gaggiotti, and O. François. 2010. Approximate Bayesian Computation (ABC) in practice. Trends Ecol. Evol. 25: 410–418.

Cullingham, C. I., J. K. Janes, R. C. Hamelin, P. M. A. James, B. W. Murray, and F. A. H. Sperling. 2019. The contribution of genetics and genomics to understanding the ecology of the mountain pine beetle system. Can. J. For. Res. 49: 721–730.

Currat, M., N. Ray, and L. Excoffier. 2004. SPLATCHE: a program to simulate genetic diversity taking into account environmental heterogeneity. Molecular Ecology Notes. 4: 139–142

Darwin, C. 1859. The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, UK.

Dayrat, B. 2005. Towards integrative taxonomy. Biol. J. Linn. Soc. 85: 407–415.

DeChaine, E. G., and A. P. Martin. 2006. Using coalescent simulations to test the impact of quaternary climate cycles on divergence in an alpine plant-insect association. Evolution 60: 1004–1013.

Dellicour, S., D. Michez, and P. Mardulyn. 2015a. Comparative phylogeography of five bumblebees: impact of range fragmentation, range size and diet specialization. Biol. J. Linn. Soc. 116: 926–939.

Dellicour, S., D. Michez, J. Y. Rasplus, and P. Mardulyn. 2015b. Impact of past climatic changes and resource availability on the population demography of three food-specialist bees. Mol. Ecol. 24: 1074–1090.

Derkarabetian, S., S. Castillo, P. K. Koo, S. Ovchinnikov, and M. Hedin. 2019. A demonstration of unsupervised machine learning in species delimitation. Mol. Phylogenet. Evol. 139: 106562.

Drag, L., D. Hauck, O. Rican, T. Schmitt, D. F. Shovkoon, R. J. Godunko, G. Curletti, and L. Cizek. 2018. Phylogeography of the endangered saproxylic beetle Rosalia longicorn, *Rosalia alpina* (Coleoptera, Cerambycidae), corresponds with its main host, the European beech (*Fagus sylvatica*, Fagaceae). J. Biogeogr. 45: 2631–2644.

Du, Z., Y. Wu, Z. Chen, L. Cao, T. Ishikawa, S. Kamitani, T. Sota, F. Song, L. Tian, W. Cai, and H. Li. 2020. Global phylogeography and invasion history of the spotted lanternfly revealed by mitochondrial phylogenomics. Evol Appl. 14: 915–930.

Dupanloup, I., S. Schneider, and L. Excoffier. 2002. A simulated annealing approach to define the genetic structure of populations. Mol. Ecol. 11: 2571–2581.

Dyer, R. J. 2015. Population graphs and landscape genetics. Annu. Rev. Ecol. Evol. Syst. 46: 327–342.

Dyer, R. J., and J. D. Nason. 2004. Population Graphs: the graph theoretic shape of genetic structure. Mol. Ecol. 13: 1713–1727.

Edwards, S. V., and P. Beerli. 2000. Perspective: gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. Evolution 54: 1839–1854.

Espíndola, A. and N. Alvarez. 2011. Comparative phylogeography in a specific and obligate pollination antagonism. PLoS ONE 6: e28662.

Espíndola, A., L. Pellissier, L. Maiorano, W. Hordijk, A. Guisan, and N. Alvarez. 2012. Predicting present and future intra-specific genetic structure through niche hindcasting across 24 millennia. Ecol. Lett. 15: 649–657.

Espíndola, A., B. C. Carstens, and N. Alvarez. 2014. Comparative phylogeography of mutualists and the effect of the host on the genetic structure of its partners. Biol. J. Linn. Soc. 113: 1021–1035.

Excoffier, L., J. Novembre, and S. Schneider. 2000. SIMCOAL: A general coalescent program for the simulation of molecular data in interconnected populations with arbitrary demography. J Hered. 91: 506–509.

Excoffier, L., I. Dupanloup, E. Huera-Sánchez, V. C. Sousa, and M. Foll. 2013. Robust demographic inference from genomics and SNP data. PLoS Genetics. 9 (10): e1003905.

Fagundes, N. J. R., N. Ray, M. Beaumont, S. Neuenschwander, F. M. Salzano, S. L. Bonatto, and L. Excoffier. 2007. Statistical evaluations of alternative models of human evolution. Proc. Nat. Acad. Sci. U.S.A. 104 (45): 17614–17619.

Fahrig, L. 2020. Why do several small patches hold more species than few large patches? Glob. Ecol. Biogeogr. 29 (4): 615–628.

Faille, A., R. Tanzler, and E. F. Toussaint. 2015. On the way to speciation: shedding light on the karstic phylogeography of the microendemic cave beetle *Aphaenops cerberus* in the Pyrenees. J. Hered. 106: 692–699.

Faircloth, B. C. 2017. Identifying conserved genomic elements and designing universal bait sets to enrich them. Methods Ecol. Evol. 8: 1103–1112.

Faircloth, B. C., J. E. McCormack, N. G. Crawford, M. G. Harvey, R. T. Brumfield, and T. C. Glenn. 2012. Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. Syst. Biol. 61: 717–726.

Faircloth, B. C., M. G. Branstetter, N. D. White, and S. G. Brady. 2015. Target enrichment of ultraconserved elements from arthropods provides a genomic perspective on relationships among Hymenoptera. Mol. Ecol. Resources 15: 489–501.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61: 1–10.

Faria, C. M. A., P. Shaw, and B. C. Emerson. 2019. Evidence for the Pleistocene persistence of Collembola in Great Britain. J. Biogeogr. 46: 1479–1493.

Finn, D. S., D. M. Theobald, W. C. IV Black, and N. L. Poff. 2006. Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. Mol. Ecol. 15: 3553–3566.

Françoso, E., A. R. Zuntini, and M. C. Arias. 2019. Combining phylogeography and future climate change for conservation of *Bombus morio* and *B. pauloensis* (Hymenoptera: Apidae). J. Ins. Conserv. 23: 63–73.

Garrick, R. C., J. D. Nason, C. A. Meadows, and R. J. Dyer. 2009. Not just vicariance: phylogeography of a Sonoran Desert euphorb indicates a major role of range expansion along the Baja peninsula. Mol. Ecol. 18: 1916–1931.

Garrick, R. C., D. M. Rowell, and P. Sunnucks. 2012. Phylogeography of saproxylic and forest floor invertebrates from Tallaganda, South-Eastern Australia. Insects 3: 270–294.

Garrick, R. C., J. D. Nason, J. F. Fernández-Manjarrés, and R. J. Dyer. 2013. Ecological coassociations influence species' responses to past climatic change: an example from a Sonoran Desert bark beetle. Mol. Ecol. 22: 3345–3361.

Garrick, R. C., I. A. S. Bonatelli, A. E. Morales, T. A. Pelletier, M. F. Perez, E. Rice, J. D. Satler, R. E. Symula, M. T. C. Thomé, and B. C. Carstens. 2015. The evolution of phylogeographic datasets. Mol. Ecol. 24: 1164–1171.

Ghisbain, G., D. Michez, L. Marshall, P. Rasmont, and S. Dellicour. 2020. Wildlife conservation strategies should incorporate both taxon identity and geographical context—further evidence with bumblebees. Divers. Distrib. 26: 1741–1751.

Giller, P. S. 1996. The diversity of soil communities, the 'poor man's tropical rainforest'. Biodiv Conserv. 5: 135–168.

Gloria-Soria, A., D. Ayala, A. Bheecarry, O. Calderon-Arguedas, D. D. Chadee, M. Chiappero, M. Coetzee, K. B. Elahee, I. Fernandez-Salas, H. A. Kamal, et al. 2016. Global genetic diversity of Aedes aegypti. Mol. Ecol. 25: 5377–5395.

Gratton, P., S. Marta, G. Bocksberger, M. Winter, E. Trucchi, and H. Kuhl. 2017. A world of sequences: can we use georeferenced nucleotide databases for a robust automated phylogeography? J. Biogeogr. 44: 47–486.

Grapputo, A., S. Boman, L. Lindstrom, A. Lyytinen, and J. Mappes. 2005. The voyage of an invasive species across continents: genetic diversity of North American and European Colorado potato beetle populations. Mol. Ecol. 14: 4207–4219.

Grummer, J. A., R. W. Bryson, and T. W. Reeder. 2014. Species delimitation using bayes factors: simulations and application to the *Sceloporus scalaris* species group (Squamata: Phrynosomatidae). Syst. Biol. 63: 119–133.

Gueuning, M., J. E. Frey, and C. Praz. 2020. Ultraconserved yet informative for species delimitation: ultraconserved elements resolve long-standing systematic enigma in Central European bees. Mol. Ecol. 29: 4203–4220.

Guzik, M. T., S. J. B. Cooper, W. F. Humphreys, S. Ong, T. Kawakami, and A. D. Austin. 2011. Evidence for population fragmentation within a subterranean aquatic habitat in the Western Australian desert. Heredity. 107: 215–230.

Haller, B. C., J. Galloway, J. Kelleher, P. W. Messer, and P. L. Ralph. 2019. Tree-sequence recording in SLiM opens new horizons for forward-time simulation of whole genomes. Mol. Ecol. Resour. 19: 552–566.

Hamilton, C. A., A. R. Lemmon, E. Moriarty-Lemmon, and J. E. Bond. 2016. Expanding anchored hybrid enrichment to resolve both deep and shallow relationships within the spider tree of life. BMC Evol. Biol. 16: 212.

Havill, N. P., A. I. Cognato, E. del-Val, R. J. Rabaglia, and R. C. Garrick. 2019. New Molecular tools for *Dendroctonus frontalis* (Coleoptera: Curculionidae: Scolytinae) reveal an East–West genetic subdivision of early Pleistocene origin. Insect Syst. Divers 3: 2.

Heled, J., and A. J. Drummond. 2008. Bayesian inference of population size history from multiple loci. BMC Evol. Biol. 8: 289.

Henriques, D., J. Chávez-Galarza, J. S. G. Teieira, H. Ferreira, C. J. Neves, T. M. Francoy, and M. A. Pinto. 2020. Wing geometric morphometrics of workers and drones and single nucleotide polymorphisms provide similar genetic structure in the Iberian Honey Bee (*Apis mellifera iberiensis*). Insects 11: 89.

Herre, E. A., K. C. Jandér, and C. A. Machado. 2008. Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. Ann. Rev. Ecol. Evol. Syst. 39: 439–458.

Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biol. J. Linn. Soc. 58: 247–276.

Hewitt, G. M. 1999. Post-glacial re-colonization of European biota. Biol. J. Linn. Soc. 68: 87–112.

Hey, J. 2010. Isolation with migration models for more than two populations. Mol. Biol. Evol. 27: 905–920.

Hotaling, S., C. C. Muhfield, J. J. Giersch, O. A. Ali, S. Jordan, M. R. Miller, G. Luikart, and D. W. Weisrock. 2018. Demographic modelling reveals a history of divergence with gene flow for a glacially tied stonefly in a changing post Pleistocene landscape. J. Biogeogr. 45: 304–317.

Huang, W., N. Takebayashi, Y. Qi, and M. J. Hickerson. 2011. MTMLmsBayes: approximate Bayesian comparative phylogeographic inference from multiple taxa and multiple loci with rate heterogeneity. BMC Bioinform. 12: 81.

Huang, J.-P., J. G. Hill, J. Ortego, and L. L. Knowles. 2020. Paraphyletic species no more—genomic data resolve a Pleistocene radiation and validate morphological species of the *Melanoplus scudderi* complex (Insecta: Orthoptera). Syst. Entomol. 45: 594–605.

Hubby, J. L., and R. C. Lewontin. 1966. A molecular approach to the study of genic heterozygosity in natural populations I: The number of alleles at different loci in *Drosophila pseudoobscura*. Genetics 54: 577–594.

Hugall, A., C. Moritz, A. Moussalli, and J. Stanisic. 2002. Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). Proc. Nat. Acad. Sci. U.S.A. 99: 6112–6117.

International Union for Conservation of Nature. 2020. The IUCN Red List of Threatened Species. Version 2020–3. Available from https://www.iucnredlist.org. Accessed on 31 December 2020.

Jackson, N. D., A. E. Morales, B. C. Carstens, and B. C. O'Meara. 2017. PHRAPL: phylogeographic inference using approximate likelihoods. Syst. Biol. 66: 1045–1053.

de Jager, M. L., and A. G. Ellis. 2017. Evolutionary history of a keystone pollinator parallels the biome occupancy of angiosperms in the Greater Cape Floristic Region. Mol. Phylogenet. Evol. 107: 530–537.

Janes, J. K., J. R. P. Worth, P. D. Batistia, and F. A. H. Sperling. 2018. Inferring ancestry and divergence events in a forest pest using low-density single nucleotide polymorphisms. Insect System Divers 2: 3.

Jombart, T., S. Devillard, and F. Balloux. 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genet. 11: 94.

Juan, C., and B. C. Emerson. 2010. Evolution underground: shedding light on the diversification of subterranean insects. J. Biol. 9: 17.

Kapun, M., M. G. Barrón, F. Staubach, D. J. Obbard, R. A. W. Wiber, J. Vieira, C. Goubert, O. Rota-Stabelli, M. Kankare, M. Bogaerts-Márquez, et al. 2020. Genomic analysis of European Drosophila melanogaster populations reveals longitudinal structure, Continent-wide selection, and previously unknown DNA viruses. Mol. Biol. Evol. 37: 2661–2678.

Katz, A. D., S. J. Taylor, and M. A. Davis. 2018. At the confluence of vicariance and dispersal: phylogeography of cavernicolous springtails (Collembola: Arrhopalitidae, Tomoceridae) codistributed across a geologically complex karst landscape in Illinois and Missouri. Ecol. Evol. 8: 10306–10325.

Kébé, K., N. Alvarez, M. Tuda, G. Arnqvist, C. W. Fox, M. Sembène, and A. Espíndola. 2017. Global phylogeography of the insect pest *Callosobruchus maculatus* L. (Coleoptera: Bruchinae) relates to the history of its main host, *Vigna unguiculata* L. J. Biogeogr. 44: 2515–2526.

Kelleher, J., A. M. Etheridge, and G. McVean. 2016. Efficient coalescent simulation and genealogical analysis for large sample sizes. PLoS Computat Biol. 12: e1004842.

Knowles, L. L. 2000. Tests of Pleistocene speciation in montane grasshoppers (genus *Melanoplus*) from the sky islands of western North America. Evolution 54: 1337–1348.

Knowles, L. L., and W. P. Maddison. 2002. Statistical phylogeography. Mol. Ecol. 11: 2623–2635.

Koopman, M. M., and B. C. Carstens. 2011. The microbial phylogeography of the carnivorous plant *Sarracenia alata*. Microbial Ecol. 61: 750–758.

Koopman, M. M., and B. C. Carstens. 2010. Conservation genetic inferences in the carnivorous plant *Sarracenia alata* (Sarraceniaceae). Conserv. Genet. 11: 2027–2038.

Koopman, M. M., D. M. Fuselier, S. Hird, and B. C. Carstens. 2010. The carnivorous pale pitcher plant harbors diverse, distinct, and time-dependent bacterial communities. Appl. Environ. Microbiol. 76: 1851–1860.

Kolbe, J. J., R. E. Glor, L. R. Schettino, A. C. Lara, A. Larson, and J. B. Losos. 2004. Genetic variation increases during biological invasion by a Cuban lizard. Nature 431: 177–181.

Kruitwagen, A., L. W. Beukeboom, and B. Wertheim. 2018. Optimization of native biocontrol agents, with parasitoids of the invasive pest *Drosophila suzukii* as an example. Evol. Appl. 11: 1473–1497.

Landguth, E. L., and S. A. Cushman. 2010. cdpop: A spatially explicit cost distance population genetics program. Molecular Ecology Resources. 10: 156–161.

Langille, B. L., J. Hyde, K. M. Saint, T. M. Bradford, D. N. Stringer, S. M. Tierney, W. F. Humphreys, A. D. Austin, and S. J. B. Cooper. 2020. Evidence for speciation underground in diving beetles (Dytiscidae) from a subterranean archipelago. Evolution 75: 166–175.

Leaché, A. D., M. K. Fujita, V. N. Minin, and R. R. Bouckaert. 2014. Species delimitation using genome-wide SNP data. Syst. Biol. 63: 534–542.

Lecocq, T. 2018. Insects: the disregarded domestication histories, pp. 35–68. In: F. Teletchea, (ed.), Animal domestication. IntechOpen, Rejika, Croatia.

Legendre, P., Y. Desdevises, and E. Bazin. 2002. A statistical test for host-parasite coevolution. Syst. Biol. 51: 217–234.

Leite, R. N., and D. S. Rogers. 2013. Revisiting Amazonian phylogeography: insights into diversification hypotheses and novel perspectives. Org. Divers. Evol. 13: 639–664.

Lemmon, A. R., S. A. Emme, and E. M. Lemmon. 2012. Anchored hybrid enrichment for massively high-throughput phylogenomics. Syst. Biol. 61: 727–744.

Lindtke, D., K. Lucek, V. Soria-Carrasco, R. Villoutreix, T. E. Farkas, R. Riesch, S. R. Dennis, Z. Gompert, and P. Nosil. 2017. Long-term balancing selection on chromosomal variants associated with crypsis in a stick insect. Mol. Ecol. 26: 6189–6205.

Liu, Y., Y. Qiu, X. Wang, Y. Huan, M. Hayashi, and C. Wei. 2018. Morphological variation, genetic differentiation and phylogeography of the East Asia cicada *Hyalessa maculticollis* (Hemiptera: Cicadidae). Syst. Entomol. 43: 308–329.

Liu, Y., C. H. Dietrich, and C. Wei. 2019. Genetic divergence, population differentiation and phylogeography of the cicada *Subpsaltria yangi* based on molecular and acoustic data: an example of the early stage of speciation? BMC Evol. Biol. 19: 1–17.

Lomolino, M. V. 2004. Conservation biogeography, in frontiers of biogeography: new directions in the geography of nature. Sinauer Assoc., Sunderland, MA. pp. 293–296.

Lozier, J. D., J. P. Strange, I. J. Stewart, and S. A. Cameron. 2011. Patterns of range-wide genetic variation in six North American bumble bee (Apidae: *Bombus*) species. Mol. Ecol. 20: 4870–4888.

Lozier, J. D., J. M. Jackson, M. E. Dillon, and J. P. Strange. 2016. Population genomics of divergence among extreme and intermediate color forms in a polymorphic insect. Ecol. Evol. 6: 1075–1091.

Mahamoud-Issa, M., T. Marin-Cudraz, V. Party, and M. D. Greenfield. 2017. Phylogeographic structure without premating barriers: do habitat fragmentation and low mobility preserve song and chorus diversity in the European bushcricket? Evol. Ecol. 31: 865–884.

Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol. 18: 189–197.

Manni, F., E. Guérard, and E. Heyer. 2004. Geographic patterns of (genetic, morphologic, linguistic) variation: how barriers can be detected by using Monmonier's algorithm. Hum. Biol. 76: 173–190.

Marske, K. A., R. A. Leschen, and T. R. Buckley. 2012. Concerted versus independent evolution and the search for multiple refugia: comparative phylogeography of four forest beetles. Evolution 66: 1862–1877.

Martin, S. H., K. K. Dasmahapatra, N. J. Nadeau, C. Salazar, J. R. Walters, F. Simpson, M. Blaxter, A. Manica, J. Mallet, and C. D. Jiggins. 2013. Genome-wide evidence for speciation with gene flow in *Heliconius* butterflies. Genome Res. 23: 1817–1828.

Matenaar, D., M. Fingerle, E. Heym, S. Wirtz, and A. Hochkirch. 2018. Phylogeography of the endemic grasshopper genus *Betiscoides* (Lentulidae) in the South African Cape Floristic Region. Mol. Phylogenet. Evol. 118: 318–329.

McCulloch, G. A., G. P. Wallis, and J. M. Waters. 2010. Onset of glaciation drove simultaneous vicariant isolation of alpine insects in New Zealand. Evolution 64: 2033–2043.

McGaughran, A., M. I. Stevens, I. D. Hogg, and A. Carapelli. 2011. Extreme glacial legacies: a synthesis of the Antarctic springtail phylogeographic record. Insects 2: 62–82.

McGaughran, A., A. Terauds, P. Convey, and C. I. Fraser. 2019. Genome-wide SNP data reveal improved evidence for Antarctic glacial refugia and dispersal of terrestrial invertebrates. Mol. Ecol. 28: 4941–4957.

Misof, B., S. Liu, K. Meusemann, R. S. Peters, A. Donath, C. Mayer, P. B. Frandsen, J. Ware, T. Flouri, R. G. Beutel, et al. 2014. Phylogenomics resolves the timing and pattern of insect evolution. Science. 346: 763–767.

Montagna, M., D. Kubisz, M. A. Mazur, G. Magoga, R. Ścibior, and L. Kajtoch. 2017. Exploring species-level taxonomy in the *Crytocephalus flavipes* species complex (Coleoptera: Chrysomelidae). Zool. J. Linn. Soc. 179: 92–109.

Morales-Hojas, R., A. Gonzalez-Uriarte, F. A. Iraizoz, T. Jenkins, L. Alderson, T. Kruger, M. J. Hall, A. Greenslade, C. R. Shortall, and J. R. Bell. 2020. Population genetic structure and predominance of cyclical parthenogenesis in the bird cherry-oat aphic *Rhopalosiphus padi* in England. Evol. Appl. 13: 1009–1025.

Moritz, C. 1994. Defining "Evolutionarily Significant Units" for conservation. TREE 9: 373–375.

Moritz, C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. Syst. Biol. 51: 238–254.

Moritz, C., and D. P. Faith. 1998. Comparative phylogeography and the identification of genetically divergent areas for conservation. Mol. Ecol. 7: 419–429.

Múrria, C., M. Sáinz-Bariáin, A. P. Vogler, A. Viza, M. González, and C. Zamora-Muñoz. 2020. Vulnerability to climate change for two endemic high-elevation, low-dispersive *Annitella* species (Trichoptera) in Sierra Nevada, the southernmost high mountain in Europe. Insect Conserv. Divers. 13: 283–295.

Nei, M. 1987. Molecular evolutionary genetics. Columbia University Press, New York, NY, USA.

New, T. R. 1997. Are Lepidoptera an effective 'umbrella group' for biodiversity conservation? J. Ins. Conserv. 1: 5–12.

Nieto, A., and K. N. A. Alexander. 2010. European Red List of Saproxylic Beetles. Pp. 1–56. Publications Office of the European Union, Luxembourg.

Oaks, J. R. 2019. Full Bayesian comparative phylogeography from genomic data. Syst. Biol. 68: 371–395.

Olazcuaga, L., A. Loiseau, H. Parrinello, M. Paris, A. Fraimout, C. Guedot, L. M. Diepenbrock, M. Kenis, J. Zhang, X. Chen, et al. 2020. A whole-genome scan for association with invasion success in the fruit fly *Drosophila suzukii* using contrasts of allele frequencies corrected for population structure. Mol. Biol. Evol. 37: 2369–2385.

Page, R. D. M., and M. A. Charleston. 1998. Trees within trees: phylogeny and historical associations. TREE 13: 356–359.

Paine, R. T. 1969. A note on trophic complexity and community stability. Am. Nat. 103: 91–93.

Papadopoulou, A., and L. L. Knowles. 2015. Species-specific responses to island connectivity cycles: refined models for testing phylogeographic concordance across a Mediterranean Pleistocene aggregate island complex. Mol. Ecol. 24: 4252–4268.

Papadopoulou, A., and L. L. Knowles. 2016. Toward a paradigm shift in comparative phylogeography driven by trait-based hypotheses. Proc. Nat. Acad. Sci. U.S.A. 113: 8018–8024.

Pelletier, T. A., and B. C. Carstens. 2014. Model choice in phylogeography using a large set of models. Mol. Ecol. 23: 3028–3043.

Pelletier, T. A., and B. C. Carstens. 2018. Geographic range size and latitude predict population genetic structure in a global survey. Biol. Lett. 14: 20170566.

Peterson, B. K., J. N. Weber, E. H. Kay, H. S. Fisher, and H. E. Hoekstra. 2012. Double digest RADseq: an inexpensive method for de novo SNP discovery and genotyping in model and non-model species. PLoS ONE 7: e37135.

Pons, J., T. G. Barraclough, J. Gomez-Zurita, A. Cardoso, D. P. Duran, S. Hazell, S. Kamoun, W. D. Sumlin, and A. P. Vogler. 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. Syst. Biol. 55: 595–609.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155: 945–959.

Puillandre, N., A. Lambert, S. Brouillet, and G. Achaz. 2012. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Mol. Ecol. 21: 1864–1877.

Richards, C. L., B. C. Carstens, and L. L. Knowles. 2007. Distribution modeling and statistical phylogeography: an integrative framework for generating and testing alternate biogeographical hypotheses. J. Biogeogr. 34: 1833–1845.

Riddle, B. R. 2016. Comparative phylogeography clarifies the complexity and problems of continental distribution that drove A. R. Wallace to favor islands. Proc. Natl. Acad. Sci. U.S.A. 113: 7970–7977.

Riddle, B. R., D. J. Hafner, L. F. Alexander, and J. R. Jaeger. 2000. Cryptic vicariance in the historical assembly of a Baja California Peninsular Desert biota. Proc. Nat. Acad. Sci. U.S.A. 97: 14438–14443.

Rissler, L. J. 2016. Union of Phylogeography and landscape genetics. Proc. Natl. Acad. Sci. U.S.A. 113: 8079–8086.

Rissler, L. J., and W. H. Smith. 2010. Mapping amphibian contact zones and phylogeographical break hotspots across the United States. Mol. Ecol. 19: 5404–5416.

Robillard, C. M., L. E. Coristine, R. N. Soares, and J. T. Kerr. 2015. Facilitating climate-change-induced range shifts across continental land-use barriers. Conserv. Biol. 29: 1586–1595.

Roderick, G. K. 1996. Geographic structure of insect populations: Gene flow, phylogeography, and their uses. Ann. Rev. Entom. 41: 325–52.

Rogers, A. D. 2007. Evolution and biodiversity of Antarctic organisms: a molecular perspective. Philos. Trans. R. Soc. Lond. B Biol. Sci. 362: 2191–2214.

Saarman, N. P., R. Opiro, C. Hyseni, R. Echodu, E. A. Opiyo, K. Dion, T. Johnson, S. Aksoy, and A. Caccone. 2019. The population genomics of multiple tsetse fly (*Glossina fuscipes fuscipes*) admixture zones in Uganda. Mol. Ecol. 28: 66–85.

Satler, J. D., and B. C. Carstens. 2016. Phylogeographic concordance factors quantify phylogeographic congruence among co-distributed species in the *Sarracenia alata* pitcher plant system. Evolution. 70: 1105–1119.

Satler, J. D., and B. C. Carstens. 2017. Do ecological communities disperse across biogeographic barriers as a unit? Mol. Ecol. 26: 3533–3545.

Satler, J. D., and B. C. Carstens. 2019. The *Sarracenia alata* pitcher plant system and obligate arthropod inquilines should be considered an evolutionary community. J. Biogeogr. 46: 485–496.

Satler, J. D., A. J. Zellmer, and B. C. Carstens. 2016. Biogeographic barriers drive co-diversification within associated eukaryotes of the *Sarracenia alata* pitcher plant system. PeerJ 4: e1576.

Satler, J. D., E. A. Herre, K. C. Jandér, D. A. R. Eaton, C. A. Machado, T. A. Heath, and J. D. Nason. 2019. Inferring processes of coevolutionary diversification in a community of Panamanian strangler figs and associated pollinating wasps. Evolution 73: 2295–2311.

Satler, J. D., K. K. Bernhard, J. O. Stireman III, C. A. Machado, D. D. Houston, and J. D. Nason. 2020. Community structure and undescribed species diversity in non-pollinating fig wasps associated with the strangler fig *Ficus petiolaris*. Insect System. Divers. 4: 1–13.

Schierenbeck, K. A. 2017. Population-level genetic variation and climate change in a biodiversity hotspot. Ann. Bot. 119: 215–228.

Schiffer, M., M. E. Carew, and A. A. Hoffmann. 2004. Molecular, morphological and behavioural data reveal the presence of a cryptic species in the widely studied *Drosophila serrata* species complex. J. Evol. Biol. 17: 430–442.

Schneider, C. J., M. Cunningham, and C. Moritz. 1998. Comparative phylogeography and the history of endemic vertebrates in the Wet Tropics rainforests of Australia. Mol. Ecol. 7: 487–498.

Shafer, A. B., C. I. Cullingham, S. D. Cote, and D. W. Coltman. 2010. Of glaciers and refugia: a decade of study sheds new light on the phylogeography of northwestern North America. Mol. Ecol. 19: 4589–4621.

Short Bull, R. A., S. A. Cushman, R. MacE, T. Chilton, K. C. Kendall, E. L. Landguth, M. K. Schwartz, K. McKelvey, F. W. Allendorf, and G. Luikart. 2011. Why replication is important in landscape genetics: American black bear in the Rocky Mountains. Mol. Ecol. 20: 1092–1107.

Sidlauskas, B., G. Ganapathy, E. Hazkani-Covo, K. P. Jenkins, H. Lapp, L. W. McCall, S. Price, R. Scherle, P. A. Spaeth, and D. M. Kidd. 2010. Linking big: the continuing promise of evolutionary synthesis. Evolution 64: 871–880.

Singhal, S., and C. Moritz. 2013. Reproductive isolation between phylogeographic lineages scales with divergence. Proc. R. Soc. B: Biol. Sci. 280: 20132246.

Sites, J. W. Jr, and J. C. Marshall. 2004. Operational criteria for delimitating species. Annu. Rev. Ecol. Evol. Syst. 35: 199–227.

Smith, M. L., and B. C. Carstens. 2020. Process-based species delimitation leads to identification of more biologically relevant species. Evolution 74: 216–229.

Smith, C. I., D. S. Tank, W. Godsoe, J. Levenick, E. Strand, T. Esque, and O. Pellmyr. 2011. Comparative phylogeography of a coevolved community: Concerted population expansions in Joshua trees and four Yucca moths. PLoS ONE 6: e25628.

Solomon, S. E., M. Bacci, Jr, J. Martins, Jr, G. G. Vinha, and U. G. Mueller. 2008. Paleodistributions and comparative molecular phylogeography of leafcutter ants (*Atta* spp.) provide new insight into the origins of Amazonian diversity. PLoS ONE 3: e2738.

Song, W., L.-J. Cao, B.-Y. Li, Y.-J. Gong, A. A. Hoffman, and S.-J. Wei. 2018. Multiple refugia from penultimate glaciations in East Asia demonstrated by phylogeography and ecological modelling of an insect pest. BMC Evol. Biol. 18: 152.

Sosa-Pivatto, M., G. A. Camps, M. C. Baranzelli, A. Espíndola, A. N. Sersic, and A. Cosacov. 2020. Connection, isolation and reconnection: quaternary climatic oscillations and the Andes shaped the phylogeographical patterns of the Patagonian bee *Centris cineraria* (Apidae). Biol. J. Linn. Soc. 131: 396–416.

Stork, N. E. 2018. How many species of insects and other terrestrial arthropods are there on Earth?. Ann. Rev. Entom. 63: 31–45.

Stevens, M. I., P. Greenslade, I. D. Hogg, and P. J. Sunnucks. 2006. Southern Hemisphere springtails: Could any have survived glaciation of Antarctica? Mol. Biol. Evol. 23: 874–882.

Su, Y. C., J. F. Wang, R. J. T. Villanueva, O. M. Nuneza, and C. P. Lin. 2014. Hopping out of Mindanao: Miocene-Pliocene geological processes and cross-island dispersal as major drivers of diversity for Philippine treehoppers. J. Biogeogr. 41: 1277–1290.

Suchan, T., C. Pitteloud, N. S. Gerasimova, A. Kostikova, S. Schmid, N. Arrigo, M. Pajkovic, M. Ronikier, and N. Alvarez. 2016. Hybridization capture using RAD probes (hyRAD), a new tool for performing genomic analyses on collection specimens. PLoS ONE 11: e0151651.

Taberlet, P., L. Fumagalli, A. G. Wust-Saucy, and J. F. Cosson. 1998. Comparative phylogeography and postglacial colonization routes in Europe. Mol Ecol 7: 453–464.

Tajima, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123: 585–595.

Tembrock, L. R., A. E. Timm, F. A. Zink, T. M. Gilligan. 2019. Phylogeography of the recent expansion of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in South America and the Caribbean Basin. Ann. Entom. Soc. Am. 112: 388–401.

Tian, E. W., J. D. Nason, C. A. Machado, L. N. Zheng, H. Yu, and F. Kjellberg. 2015. Lack of genetic isolation by distance, similar genetic structuring but different demographic histories in a fig-pollinating wasp mutualism. Mol. Ecol. 24: 5976–5991.

Vondráček, D., A. Fuchsová, D. Ahrens, D. Král, and P. Šípek. 2017. Phylogeography and DNA-based species delimitation provide insight into the taxonomy of the polymorphic rose chafer *Protaetia* (*Potosi*) *cuprea* species complex (Coleoptera: Scarabaeidae: Cetoniinae) in the Western Palearctic. PLoS ONE 13: e0192349.

Wachi, N., K. W. Matsubayashi, and K. Maeto. 2017. Application of next-generation sequencing to the study of non-model insects. Entomol. Sc. 21: 3–11.

Wade, E. J., T. Hertach, M. Gogala, T. Trilar, and C. Simon. 2015. Molecular species delimitation methods recover most song-delimited cicada species in the European Cicadetta montana complex. J. Evol. Biol. 28: 2318–2336.

Waples, R. S., and C. Do. 2008. LDNE: a program for estimating effective population size from data on linkage disequilibrium. Mol. Ecol. Resour. 8: 753–756.

Watterson, G. A. 1975. On the number of segregating sites in genetical models without recombination. Theor. Popul. Biol. 7: 256–276.

Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38: 1358–1370.

Wells, C. N., P. B. Marko, and D. W. Tonkyn. 2015. The phylogeographic history of the threatened Diana fritillary, *Speyeria diana* (Lepidoptera: Nymphalidae): with implications for conservation. Cons. Genet. 16: 703–716.

Woodard, S. H., J. D. Lozier, D. Goulson, P. H. Williams, J. P. Strange, and S. Jha. 2015. Molecular tools and bumble bees: revealing hidden details of ecology and evolution in a model system. Mol. Ecol. 24: 2916–2936.

World Health Organization. 2020. Vector-borne diseases. Published on-line, 2 March 2020. Available at: https://www.who.int/en/news-room/fact-sheets/detail/vector-borne-diseases. Accessed on 31 December 2020.

Wright, S. 1943. Isolation by distance. Genetics 28: 114–138.

Xue, A. T., and M. J. Hickerson. 2015. The aggregate site frequency spectrum for comparative population genomic inference. Mol. Ecol. 24: 6223–6240.

Yang, Z., and B. Rannala. 2010. Bayesian species delimitation using multilocus sequence data. Proc. Nat. Acad. Sci. U.S.A. 107: 9264–9269.

Zakharov, E. V., and J. J. Hellmann. 2008. Genetic differentiation across a latitudinal gradient in two co-occurring butterfly species: revealing population differences in a context of climate change. Mol. Ecol. 17: 189–208.

Zamudio, K. R., R. C. Bell, and N. A. Mason. 2016. Phenotypes in phylogeography: species' traits, environmental variation, and vertebrate diversification. Proc. Nat. Acad. Sci. U.S.A. 113: 8041–8048.

Zellmer, A. J., M. M. Hanes, S. M. Hird, and B. C. Carstens. 2012. Deep phylogeographic structure and environmental differentiation in the carnivorous plant *Sarracenia alata*. Syst. Biol. 61: 763–777.

Zhang, Y. M., J. L. Williams, and A. Lucky. 2019. Understanding UCEs: a comprehensive primer on using ultraconserved elements for arthropod phylogenomics. Ins. Syst. Div. 3: 3.