Review

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Phylogeography and niche modelling: reciprocal enlightenment

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Abstract: Phylogeography examines the spatial genetic structure of species. Environmental niche modelling (or ecological niche modelling; ENM) examines the environmental limits of a species' ecological niche. These two fields have great potential to be used together. ENM can shed light on how phylogeographical patterns develop and help identify possible drivers of spatial structure that need to be further investigated. Specifically, ENM can be used to test for niche differentiation among clades, identify factors limiting individual clades and identify barriers and contact zones. It can also be used to test hypotheses regarding the effects of historical and future climate change on spatial genetic patterns by projecting niches using palaeoclimate or future climate data. Conversely, phylogeographical information can populate ENM with within-species genetic diversity. Where adaptive variation exists among clades within a species, modelling their niches separately can improve predictions of historical distribution patterns and future responses to climate change. Awareness of patterns of genetic diversity in niche modelling can also alert conservationists to the potential loss of genetically diverse areas in a species' range. Here, we provide a simplistic overview of both fields, and focus on their potential for integration, encouraging researchers on both sides to take advantage of the opportunities available.

Introduction

Traditionally, scientific disciplines are practised within rigid borders. More recently, these boundaries have become more fluid, leading to an increase in inter-disciplinary work (Van Noorden 2015). This progression, where different research fields are combined in scientific studies, is of great importance to modern scientific innovation and knowledge creation (Yegros-Yegros et al. 2015). This is especially true in ecology and conservation, where real-world environmental problems increasingly require input from multiple fields, resulting in a recent push to improve inter-disciplinary integration and co-operation (Pennington 2008, Roy et al. 2013, Goring et al. 2014, Bergstrom et al. 2015, Dick et al. 2016).

One area of increasing integration is the concomitant use of phylogeography (the field concerned with documenting the spatial distribution of genetic lineages) and environmental (or ecological) niche modelling (ENM; the field concerned with constructing the niches of species in environmental space and projecting them onto geographical space; also known as species distribution models or SDMs) (see e.g. Scoble and Lowe 2010, Chan et al. 2011). On the one hand, phylogeography can reveal a hidden complexity beneath the level of a species that appears to ubiquitously occupy a geographical range, often uncovering multiple geographically distinct lineages (Avice et al. 1987). It is, however, often very difficult to untangle the mechanisms and drivers underlying existing genetic structure without assistance from additional lines of evidence (Peterson 2009). ENM, on the other hand, can identify the environmental parameters limiting a species' distribution and project its niche onto new environmental surfaces to examine the effect of past or future environmental change (Araújo and Peterson 2012, Ashrafzadeh et al. 2018, Calixto-Pérez et al. 2018, Fuchs et al. 2018), but is limited by the assumption of a species as a homogeneous entity (Hampe 2004). Incorporating the two fields

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(e.g. by modelling the niches of geographically distinct clades) results in mutual benefit. Phylogeography benefits from an opportunity to examine the effects of historical conditions on the persistence and connectivity of geographical space beyond obvious landscape barriers (Alvarado-Serrano and Knowles 2013) while ENM benefits from a sensitivity to the variation in environmental requirements among different phylogeographical clades (D'Amen et al. 2013). Due to this opportunity for reciprocal enlightenment, there is a push from both sides to integrate the two fields (Scoble and Lowe 2010, Alvarado-Serrano and Knowles 2013), but unfortunately there has been a slow uptake with relatively few studies to date including both methods.

In this review, we provide some background to the fields of phylogeography and ENM, and end by discussing how these two fields can be used together and the benefit this provides for knowledge advancement and conservation efforts. We make use of examples to illustrate the points made here.

Phylogeography (and related fields)

Markers

The field of phylogeography was first introduced by Avise et al. (1987). In short, mitochondrial DNA (mtDNA) was suggested as the marker of choice to examine the spatial distribution of genetic lineages within and between closely related species (i.e. to combine phylogenetics with geography). MtDNA was, at the time, seen as an ideal molecular marker due to its high mutation rate and maternal, non-recombining mode of inheritance (see e.g. Brown et al. 1979, Avise et al. 1987). Typically, the mitochondrial molecule was digested with various restriction enzymes to create fragment patterns (known as restriction fragment length polymorphisms, or RFLPs), or fragments of the mitochondrial molecule were sequenced for a larger number of individuals taken from across the range of the species (cytochrome *b* was a popular choice for mammals; see Kocher et al. 1989, Johns and Avise 1998). Since then, the field has taken mammoth strides forward with various marker and methodological developments allowing for more substantive datasets to address questions more holistically (both spatially and temporally).

For example, the addition of Y chromosome markers, even if relatively conserved, provided patrilineal histories (see e.g. Sundqvist et al. 2001, Brändli et al. 2005, Cruciani et al. 2007). Nuclear markers were added in the form of

intron sequences (exons were often too conserved within species to yield a meaningful resolution) (Smit et al. 2008, Maswanganye et al. 2017) in an attempt to understand migration or address the gene tree vs species tree problem. The inclusion of highly variable microsatellite markers (short tandem repeats of between 1 and 6 base pairs scattered throughout the genome; Sunnucks 2000, Selkoe and Toonen 2006) allowed for the assessment of gene flow and connectivity between populations and lineages, as well as summary statistics describing diversity and change within populations (such as observed and expected heterozygosity, population demography and bottlenecks, and, more recently in landscape genetics, how individuals move within their respective habitat matrices) (Karsten et al. 2011, Born et al. 2012, Tensen et al. 2016, 2018, van Wyk et al. 2017). The inclusion of nuclear DNA was problematic initially in that unlinked DNA segments are constantly rearranged by meiosis and syngamy, which can result in non-homologous data, especially for divergent populations. These problems were overcome by, for example, comparing the proportion of alleles in different populations, or by isolating single locus sequences that are not rearranged (Avise 2009). Characterisation of adaptive variation (by focussing on specific adaptive markers) allowed us to address questions of local adaptations and their role in driving diversification amongst lineages or populations (Marsden et al. 2012, Mikhayev et al. 2013). The field has also made full use of next-generation technologies (Mardis 2017), notably the analyses of large numbers of single nucleotide polymorphisms (SNPs) scattered across the genomes (Vignal et al. 2002). Even if, individually, SNPs contain less information than most other marker types (Kumar et al. 2012), this is compensated for by their high frequency throughout the genome and the large number of SNPs typically included in any specific study (Brookes 1999, Portik et al. 2017). Although more limited in its application with respect to phylogeography, full or partial genomes can provide great insights into genome evolution, which may differ between distinct lineages as evidenced by vastly different chromosome numbers in distinct lineages within species (see e.g. Britton-Davidian et al. 2007).

Because different genetic markers can provide different types of information at different scales of resolution (spatial and temporal), there is a growing tendency to use different types of molecular markers together (Beheregaray 2008). This practise can greatly improve the reliability of results. Comparing mtDNA and nuclear DNA can be particularly useful as they provide glimpses of different aspects of the evolutionary history of species. Not surprisingly, many studies have found discordant patterns between the two markers (see e.g. Toews and Brelsford

2012, Teske et al. 2018). For example, Leavitt et al. (2017) found that mtDNA and nuclear DNA produced very different phylogenies in alligator lizards (*Elgaria*). This has similarly been documented for the bat genus *Myotis* where mitochondrial markers were typically used to document this extensive radiation and to understand relationships within the genus. More recently, however, phylogenetic relationships based on a large suite of nuclear markers were significantly different to those based on full mitogenome sequences (Platt et al. 2018). These authors argue that incongruences can be driven by incomplete lineage sorting, introgressive hybridisation or even phylogenetic error. As such, there is value in examining multiple nuclear loci. While all mtDNA loci have the same genealogical history due to its non-recombinant nature (but keep in mind that mtDNA fragments may experience different selection pressures), non-linked nuclear loci may have taken different genealogical pathways (Wakeley 2003). Analysing multiple nuclear loci can therefore improve estimates of the time since two clades diverged (Edwards and Beerli 2000). Thanks to next-generation sequencing (NGS) techniques, it is becoming increasingly feasible and affordable to increase both the number of loci and the number of individuals sampled (Carstens et al. 2012).

Analyses

In terms of analyses, the initial approach was to simply overlay phylogenetic trees or networks onto a map of the sampling region and attempt to identify obvious barriers or reasons for genetic discontinuities. Mathematical models were developed to more objectively identify barriers (such as Monmonier's algorithm to detect boundaries by finding the largest distances between vertices or neighbours; see Monmonier 1973, Manni et al. 2004) or test alternative hypotheses using approximate Bayesian computations to simulate alternative scenarios (ABC and DIYABC; Toni et al. 2009, Cornuet et al. 2010, see also Portik et al. 2017). Although not without its detractors, the coalescent theory was arguably one of the major steps forward in phylogeographical analyses. In essence, it is a statistical framework that allows for the estimation of past demographic changes in a population based on the genealogies of currently existing alleles (Kingman 1982, Wakeley 2003). This is possible because the processes that affect the gene tree for a selectively neutral gene (mutation and extinction of alleles) are stochastic, obeying statistical laws which allow the traces of historical demographic events to be deciphered to reveal

population histories (Hudson 1990). Using the coalescent theory, it is possible to estimate the time since two lineages diverged (Avice 2009). Other analytic developments include detecting and dating historical population growths and declines (Wakeley 2003) and to estimate the amount and direction of migration between populations (Hudson 1990, Leblois et al. 2014).

Such analyses, however, are not always clear-cut as different factors can have confusingly similar effects on genetic patterns. A lack of reciprocal monophyly between populations can indicate continuing gene flow (Knowles and Maddison 2002), but it can also be the result of polymorphisms retained from before the populations diverged (Smit et al. 2007, Smith et al. 2016), or changes in the ancestral population size (Edwards and Beerli 2000). Various (ongoing) processes can affect the estimates of divergence time and produce similar patterns to population growth (Tellier and Lemaire 2014). Natural selection can also produce patterns that mimic various demographic scenarios (Li et al. 2012). For example, balancing selection can maintain different alleles in a population for extended periods, leaving a signature that looks a lot like that left by immigration from outside a population (Hudson 1990). Selective sweeps, on the other hand, speed up the coalescent process, resulting in a pattern similar to population growth (Hudson 1990). These problems can make it difficult to establish reliable phylogenies, determine the time since populations/taxa diverged or even distinguish reproductively isolated populations from those still connected by migration.

Patterns

Various spatial and genetic patterns may emerge. First, genetically distinct, geographically separated clades suggest the presence of some biogeographical barrier preventing gene flow between populations, with higher genetic distances between groups suggesting longer periods of isolation. Secondly, genetically distinct yet geographically co-occurring clades suggest either the recent admixture of previously isolated populations, or intrinsic genetic isolation (i.e. sympatric speciation). As a third possibility, a gradual genetic change across a species' range with no sharp genetic transitions suggests a limited capacity for dispersal (low vagility) in the absence of biogeographical barriers (so-called isolation by distance). Lastly, a lack of genetic partitioning across a wide-ranging species (panmixia) suggests a high capacity for dispersal in the absence of biogeographical barriers (Avice et al. 1987).

Comparative phylogeography

Comparative phylogeography is the comparative study of the phylogeographical patterns of co-distributed taxa (Arbogast and Kenagy 2001). Species with similar ecologies and ranges often have similar phylogeographical structures (Avice 2009). This approach provides a way to discover broad patterns in the manner in which historical environmental changes have influenced the distribution and diversification of organisms (Arbogast and Kenagy 2001). This is not only valuable for understanding historical processes but can also help us to predict how communities are likely to respond to future climate change (Hickerson et al. 2010).

To date, the northern latitudes have been studied relatively extensively (Beheregaray 2008). The resulting picture is one of repeated ice-ages driving temperate species towards southern refugia, followed by northwards expansion during warmer interglacials (Hewitt 2000, 2004). Cold-adapted species show the opposite pattern, retreating to polar or high-altitude refugia during interglacials (Stewart et al. 2010). The tropical latitudes, on the other hand, are relatively understudied, despite containing the majority of our planet's diversity (Beheregaray 2008). Existing evidence, however, suggests that glacial cycles have had an important effect on aridity in the tropics and hence, forest fragmentations (Webb and Bartlein 1992). Forest lineages have experienced expansions during warm, wet interglacial periods and contractions during cool, dry glacial periods, with lineages associated with more open biomes such as savanna showing the opposite pattern (Lorenzen et al. 2012, Turchetto-Zolet et al. 2013). There are also older lineages, particularly in South America, that appear to have been shaped by orogenic events (e.g. volcanism, uplift, etc.) during the Pliocene and Miocene (Turchetto-Zolet et al. 2013).

While comparative phylogeography is typically used to look for commonalities among the organisms of a specific area (Hickerson et al. 2010), it can also be used to examine the differences between organisms with different life histories such as planktonic and restricted dispersers (Pelc et al. 2009), invasive and native species (Bossdorf et al. 2005), hosts and parasites (du Toit et al. 2013), and rupicolous (rock dwelling) and non-rupicolous species (Smit et al. 2010). Comparative phylogeography has also been used to identify areas of high genetic diversity, which can complement measures of species diversity for conservation planning (Moritz and Faith 1998). Although this approach is exceptionally good at uncovering shared patterns, the drivers of these patterns may remain obscure.

Environmental niche modelling

Terminology

ENM is known by a range of names including bioclimatic envelope modelling (Pearson and Dawson 2003), climatic envelope modelling (Kadmon et al. 2003), predictive habitat distribution modelling (Guisan and Zimmermann 2000) and species distribution modelling (Fløjgaard et al. 2009). Although the terminology within the field is far from standardised (Sillero 2011), a distinction is often made between a species' fundamental niche (the range of abiotic environmental conditions under which birth rates would exceed death rates; Hutchinson 1959), its realised niche (the subset of those conditions that can actually be occupied, limited by species interactions such as predation and competition; Hutchinson 1959) and its potential niche (the subset of the fundamental niche that is actually present in the environment; Jackson and Overpeck 2000). While the realised niche is generally a subset of the fundamental niche, it can be larger due to sink populations (Stacey and Taper 1992).

ENMs can be mechanistic or correlative. Mechanistic models create a model of a species' niche based on modelled (Dudley et al. 2016) or observed (Monahan 2009) physiological limits. These models construct the fundamental niche of a species and can project its potential niche onto a landscape (Pearson and Dawson 2003, Sillero 2011). Correlative models, on the other hand, construct models of species' niches based on the conditions at locations where the species is known to occur (i.e. presence data) (Peterson 2001). While it was originally suggested that these models can generate a species' fundamental niche (Peterson 2001), it is now more often assumed that, being based on the realised niche of a species, such models would construct the realised niche based on existing species interactions (Pearson and Dawson 2003, Sillero 2011). Due to their simplicity and ease of use, correlative models are far more common than mechanistic models (Morin and Thuiller 2009), and many studies use general terms such as ENM when actually discussing correlative models (Sillero 2011).

We will use the terms realised niche, fundamental niche and potential niche as defined earlier. Our focus here is on correlative niche models as these are more suited to use with spatial genetic data, or phylogeographical patterns. We will therefore use the term ENM to mean correlative ENM, except where specified otherwise.

Environmental niche models

ENMs use artificial intelligence algorithms to construct conceptual models of species' ecological niches (in terms of environmental parameters) which can then be projected onto geography to predict species' distributions (Peterson 2001). The models are validated by comparing the projected niches to the species' actual distributions (Peterson 2001). The statistic typically used for this is area under the receiver operating characteristic (ROC) curve (AUC) (Jiménez-Valverde 2012). AUC values are effectively the probability that a randomly selected presence site will be rated as having a higher suitability than a randomly selected absence site (Elith et al. 2006). Although the AUC is widely used, it is worth noting that there is considerable debate about its suitability as a metric of model performance (Lobo et al. 2008, Peterson et al. 2008, Jiménez-Valverde 2012, Escobar et al. 2018).

Predicting the past, present and future

The validation of a model against existing distribution patterns is often the first step in projecting models across time or space (Akhter et al. 2017). However, it is also useful in its own right. Jack-knifing of environmental variables (leaving out each variable in turn to see how the model performance is affected) can be used to determine which variables are most important in determining a species' distribution, and response curves can be generated to show how each variable affects the probability of the species' presence (Swenson 2006, Costa et al. 2008). While this is typically done across the full range of a species (Swenson 2006, Costa et al. 2008), the same technique can be used to examine how local factors such as land cover, land use and distance to roads influence a species' fine scale distribution (Sattler et al. 2007, Conde et al. 2010, Barnaud et al. 2013a,b).

In cases where the full natural range of a species is unknown, or where the range of a species is severely reduced because of anthropogenic impacts, niche modelling can be used to attempt to generate a more complete realised niche. This can be used to identify suitable reintroduction sites or areas to be surveyed for new populations (Hipólito et al. 2015, Ferrer-Sánchez and Rodríguez-Estrella 2016). The niche of an invasive species can also be projected onto areas far beyond its native range, even globally, to identify areas most at risk of invasion (Nyáiri et al. 2006). The results of such studies should, however, be interpreted with caution as invasive species often seem to occupy different ecological niches

in their invasive and native ranges (Gallagher et al. 2010) perhaps due to the absence of natural enemies in invaded areas (Keane and Crawley 2002).

Once validated against present distributions, niche models can be projected using historical climate data allowing researchers to model the geographical ranges of species under historical climatic conditions (Waltari and Guralnick 2009, Levinsky et al. 2013). This allows researchers to detect historical range shifts, expansions, contractions and changes in connectivity due to past climatic changes (Waltari and Guralnick 2009). This can help to identify likely colonisation routes to present distributions (Waltari and Guralnick 2009, Karsten et al. 2015), identify areas of long-term species persistence for conservation purposes (Rodríguez-Sánchez et al. 2010), identify likely ice-age refugia (Hewitt 2000, Rodríguez-Sánchez et al. 2010, Barlow et al. 2013), test for the historical isolation of lineages (Tolley et al. 2010, Barlow et al. 2013), reconstruct palaeobiological communities (Svenning et al. 2011) and assess climate change as a likely contributor to past extinction events (Martínez-Meyer et al. 2004). These predictions can sometimes be corroborated with other lines of evidence such as palaeoecological records (Nogués-Bravo 2009) or genetically inferred patterns (Scoble and Lowe 2010), and the comparison of historical ranges from niche modelling with those based on the fossil record has allowed researchers to test for niche conservatism, i.e. as to how long it takes for the environmental niche of a species to change due to evolution (Martínez-Meyer et al. 2004, Martínez-Meyer and Peterson 2006). Such information is, however, often unavailable, and many studies must rely on ENM alone to predict historical distribution patterns (Svenning et al. 2011).

Niche models can also be projected using future climate data to predict the effect of future climate change on the geographical ranges of species (Huntley et al. 2006, Meynard et al. 2017, Ramírez-Preciado et al. 2019) or even biomes (Eeley et al. 1999). This can be used to assess the future effectiveness of existing protected areas (Coetzee et al. 2009), identify areas of future conservation priority (Ochoa-Ochoa et al. 2012) and predict extinction risks due to climate change (Hughes et al. 2004). It has also been used to take climate change into account when identifying suitable areas for the reintroduction of endangered species (Martínez-Meyer et al. 2006) and in ecological restoration (Gelviz-Gelvez et al. 2015). Given that climate change is occurring at more alarming rates than previously expected (see e.g. Resplandy et al. 2018), climate variability is already causing changes in species' ranges (Parmesan and Yohe 2003, Chen et al. 2011) and is expected to have dramatic consequences for natural ecosystems over

the next century (see Millennium Ecosystem Assessment 2005). To this end, studies such as these will be incredibly valuable in allowing climate change to be taken into account for conservation planning.

Though typically used to model the niches of species, ENM can potentially be used to model the niche of any phenomena that is spatially distributed according to environmental variables. For example, it can be used to model the distributions of genetic clades within species (du Toit et al. 2012) or whole biomes (Eeley et al. 1999). It can be used to examine specific habitat requirements of males and females (Conde et al. 2010) or of different behaviours such as resting, hunting and denning (Vanbianchi et al. 2017). It can be used to map the risk of diseases (Du et al. 2014, Pigott et al. 2014, Sindato et al. 2016). It has also been used to model the phenological niche of large fires (De Angelis et al. 2012), model the ecological niche of land abandonment (Bajocco et al. 2016) and to identify likely adaptive alleles by comparing allele frequency to position along environmental gradients (Rolland et al. 2015).

Environmental variables and species presence data

There is little consensus on how to select environmental variables for ENM. Various stepwise selection processes have been suggested, such as starting with a large set of climatic variables and progressively removing the least contributing factor on successive model runs (Yiwen et al. 2016). Others, however, suggest choosing variables based on knowledge of the species concerned (Meynard and Quinn 2007). It is also often recommended that highly correlated variables be avoided (Merow et al. 2013), although there is some debate about this for machine learning methods such as MaxEnt which automatically determine which variables were most important in model building (Drake et al. 2006, Elith et al. 2011, Merow et al. 2013). Certainly, modellers should take care to include any variables known to be important to the study species, as accuracy will be lost if species have habitat requirements that are not fully included (Kadmon et al. 2003, Barry and Elith 2006). Although ENM typically focuses on climatic variables (Huntley et al. 2004), any environmental variable for which data are available can be used, including vegetation (Pigott et al. 2014), distance from roads (Conde et al. 2010), soil quality (Bajocco et al. 2016) and the presence of suitable prey (Rodríguez-Soto et al. 2011).

Ideally, species location data should be the result of systematic sampling across the range of the species so that differences in the density of location points reflect

differences in population density and not differences in sampling effort (Kramer-Schadt et al. 2013). In cases where species location data suffer from sampling bias, it is recommended that modellers spatially filter the number of data points in oversampled areas (Boria et al. 2014). As for the number of locations that should be included, one study concluded that 50–75 locations were required for maximum accuracy (Kadmon et al. 2003), while another found that 10 samples resulted in 90% accuracy, and 50 locations resulted in near-maximum accuracy (Stockwell and Peterson 2002). In addition, the ideal sample size is strongly dependent on the biology and distribution of the species under study (see e.g. Boria and Blois 2018 and references therein).

Criticisms of correlative ENM

Correlative niche modelling has been criticised on several points (see Table 1). It is important to understand these limitations to avoid inaccurate or misinterpreted results.

Integrating phylogeography and niche modelling

Benefits to phylogeography

A large number of taxa display some form of spatial genetic structure across their range. However, a phylogeographical structure often results in more questions than answers. Does genetic variation in space represent adaptation to different environments, or is it purely the result of stochastic processes and vicariance? Are genetic similarities across the range the result of recent connectivity or ancestral polymorphism? How is the genetic structure maintained over time? What historical factors contributed to its creation and how is it likely to change in the future? The incorporation of ENM can help to answer these questions.

Modelling existing niches (predicting the present) can be used to examine (some of) the factors currently maintaining genetic structure. Phylogeographical studies often find a rough correlation with, or between, the geographical borders of genetic clades and potential barriers or bioclimatic transitions (see e.g. Smit et al. 2007, Edwards et al. 2011, Willows-Munro and Matthee 2011, Bittencourt-Silva et al. 2017, Lavin et al. 2018, Lv et al. 2018), but proving causation is difficult. Phylogeographers must therefore

Table 1: Problems associated with ENM, and recommendations to minimise their impacts.

Problem	Explanation	Recommendation
Species interactions	Species interactions can affect the realised (potential) niche of a species (1), which can be a source of bias when niches are projected onto new landscapes with new species assemblages (2)	Niches projected onto landscapes with different species assemblages should be interpreted with caution (3) The presence or absence of important biota can be included as an environmental variable (4)
Dispersal limitations	Predicted range shifts often do not take dispersal limitations into account (5)	Researchers can compare future ranges assuming extensive and no dispersal (6) or, when possible, include species-specific dispersal rates (7)
Species out of equilibrium with their environment and unreliable presence data	Failure to accurately capture the environmental range of a species' niche can bias results. This can be due to a species not occupying its full potential niche (8) or due to incomplete (9) or inaccurate (10) species presence data; the latter two can present major challenges to the models	When species location data do not cover the full range of environmental conditions suitable for a species, reducing the complexity of models can improve the accuracy of results (11). Phylogeographical studies can provide ideal species presence data as genetic analysis prevents species misidentifications (12)
Environmental conditions with no analogue in the training data	Model projections become less reliable when projected onto environmental surfaces that are very different from those used for model training (13)	The range of environmental conditions in projection areas can be compared to those in areas used for model training, and predictions in areas beyond the range of conditions present in the data used to train the models should not be viewed as reliable (14)
Overfitting	Overfitting is when ENM programs make niches “fit” the species presence data by creating overly complex models that do not accurately reflect the actual environmental tolerances of the species (15). Such models will appear accurate but will not transfer accurately to new environments (15). However, if the ecology of the species is poorly known, one cannot avoid complex modelling. In these instances, the hypotheses raised by the models should be verified in the field	Reducing the complexity of models can prevent overfitting and improve the accuracy of niche projections onto new environments (16)
Validation problems	Validation of models typically relies on cross-validation techniques which can inflate measures of model performance due to the spatial autocorrelation of species location points (17)	Where independent data sources (such as location data from the fossil record) are unavailable, repeated cross-validation is recommended. Here, the data are divided into a number of subsets and the model is run for each subset as a test case, while another subset serves as a training data (18)

1 – Araújo and Luoto 2007; 2 – Keane and Crawley 2002, Wisz et al. 2013; 3 – Duque-Lazo et al. 2016; 4 – Rodríguez-Soto et al. 2011; 5 – Martínez-Meyer 2005; 6 – Coetzee et al. 2009; 7 – Hellmann et al. 2016; 8 – Jones 2012; 9 – Thuiller et al. 2004; 10 – Anderson 2012; 11 – Anderson and Gonzalez Jr. 2011; 12 – Avendaño et al. 2017; 13 – Robert and Hamann 2012; 14 – Elith et al. 2010; 15 – Bell and Schlaepfer 2016; 16 – Radosavljevic and Anderson 2014; 17 – Robert and Hamann 2012; 18 – Nogués-Bravo 2009.
ENM, environmental niche modelling.

often either stop at describing existing phylogeographical patterns or speculate as to their creation based on very little information (Peterson 2009). ENM can be used to correlate genetic divergence with niche divergence, suggesting environmental adaptation among lineages (Engelbrecht et al. 2011, du Toit et al. 2012, Ganem et al.

2012), and the environmental limits on each clade can be examined separately (Engelbrecht et al. 2011, du Toit et al. 2012). ENM can also be used to identify potential bioclimatic and physical barriers to gene flow (Tolley et al. 2010) and to find contact zones between lineages (Ganem et al. 2012, Meynard et al. 2012).

Modelling the ranges of genetic clades under historical climatic conditions makes it possible to test theories regarding historical distributions (Tolley et al. 2010, Barlow et al. 2013) and to generate new phylogeographical hypotheses (Carstens and Richards 2007). When phylogeographical studies find a rough correlation between the timing of divergence events and climatic changes, historical conditions are often proposed as drivers of genetic diversification (Tolley et al. 2006, Mortimer and Jansen van Vuuren 2007, Mortimer et al. 2012). In such cases, ENM provides an additional line of evidence to test for historical isolation, identify historical barriers to gene flow and identify historical refuges (Tolley et al. 2010, Barlow et al. 2013). In addition, ENM can be used to predict future distributions of genetic clades (D'Amen et al. 2013).

Benefits to niche modelling

Conversely, phylogeography opens up niche modelling to genetic diversity below the species level, allowing the different environmental tolerances of different genetic clades to be taken into account. This is important in cases where there may be adaptive variation present across a species' range, with different genetic clades adapted to different biomes or climatic conditions (du Toit et al. 2012). Modelling the ecological niches of genetic clades can highlight the different environmental requirements of these clades (du Toit et al. 2012, Neal et al. 2018), and improve the realism of projections of the niche into the past (du Toit et al. 2012) and the future (D'Amen et al. 2013). This is particularly important for predicting the effects of climate change, as ignoring genetic variation across a species' range can underestimate the physical distance genetic clades will need to alter their ranges to track suitable climates (Hampe 2004, D'Amen et al. 2013). Combining phylogeography with niche modelling can also alert conservationists to the potential loss of genetically diverse areas of a species' range (Beatty and Provan 2011).

Coalescent inferences from phylogeographical studies provide an additional line of evidence to support palaeo-distribution hypotheses generated by niche modelling. For example, periods of range reduction should coincide with reductions in population size (Fordham et al. 2014), and periods of habitat fragmentation and refugial retreat should leave traces in a species' genetic record (Scoble and Lowe 2010).

Due to this mutual benefit, there is a pull from both sides to further integrate the fields (Scoble and Lowe 2010, Alvarado-Serrano and Knowles 2013). Despite an initially slow uptake (Scoble and Lowe 2010), studies

combining phylogeography and niche modelling are becoming slightly more common (see Sánchez-Fernández et al. 2016); however, the uptake remains slow. A Scopus search using the keywords “phylogeography” and “ENM” retrieved only 10 papers for 2018, and 11 papers for 2017; although we acknowledge that our search is by no means exhaustive, and that one could broaden keywords used in the search, the point remains that relatively few studies incorporate both the approaches. Also, many of these studies still include methodological flaws (see Sánchez-Fernández et al. 2016 for a review) and have tended to focus on northern temperate regions (Alvarado-Serrano and Knowles 2013).

Examples

Studies that combine phylogeography and niche modelling commonly model the niches of phylogeographical clades to see if they occupy distinct niches and to identify the environmental factors limiting them. In South Africa, for example, it has been found that seemingly generalist species such as *Rhabdomys pumilio* (Sparrman, 1784), the four-striped mouse (du Toit et al. 2012) and *Otomys irroratus* (Brants, 1827), the Southern African vlei rat (Engelbrecht et al. 2011) are composed of two or more clades that occupy distinct climatic niches. This is often related to the seasonality of rainfall, with the winter-rainfall south-western areas of the country and the remaining summer-rainfall areas containing different genetic lineages (Engelbrecht et al. 2011, du Toit et al. 2012); these can be confirmed with additional lines of evidence such as breeding studies, etc. This method has also been used to test competing hypotheses of niche divergence and niche conservatism. In *Peromyscus maniculatus* (Wagner, 1845), the North American deer-mouse, it was found that most lineages occupied distinct niches, suggesting that niche diversification was the dominant pattern in the radiation of this species (Kalkvik et al. 2012).

Another common practice is to model the niche of a species as a whole to assess connectivity and identify barriers to gene flow. This was done with the grey long-eared bat, *Plecotus austriacus* (Fischer, 1829), in Europe (Razgour et al. 2014). It was found that climate and topography may explain the genetic connectivity across the bat's range at a large scale, while at a small spatial scale, the land cover was an important factor.

Studies have also used niche modelling to identify areas of likely co-occurrence between clades. Three clades within *Rhabdomys* (now considered species) were found to co-occur in several locations in South Africa but were

separated by microhabitat choice (Ganem et al. 2012). It was suggested that niche differentiation allowed them to coexist in areas of heterogeneous habitat, later confirmed by Dufour et al. (2015).

Studies also use palaeoclimate modelling to assess the historical persistence and connectivity of species' ranges to better understand existing phylogeographical structures or to support predictions based on current genetic patterns. To compare the effects of historical climate fluctuations on three species of Australian rainforest skinks (*Saproscincus* spp.), niches were projected using climate data from two periods during the Holocene as well as the last glacial maximum (Moussalli et al. 2009). Isolated areas of long-term persistence were identified, which, together with phylogeographical patterns, supported the idea of vicariance-driven diversification. Another study used niche modelling to independently identify the locations of the last glacial maximum refugia for 20 North American terrestrial vertebrates for which refugia had already been identified using phylogeographical methods (Waltari et al. 2007). The phylogeographical and niche modelling predictions were significantly correlated for 14 of the 20 species.

Some studies, notably on plants (see e.g. Wróblewska and Mirski 2018) and lizards (see following text), have also used future climate predictions together with phylogeographical analysis to predict the effect of climate change on species' genetic diversity (see also Pauls et al. 2013). For example, dwarf chameleons (*Bradypodion* spp.) and Burchell's sand lizard (*Pedioplanis burchelli* (Duméril and Bibron, 1839)) in the Cape Floristic Region of South Africa are expected to experience fragmentation and contraction of suitable habitat (Tolley et al. 2009). This is likely to result in a considerable loss of genetic diversity, particularly in the Western Cape Floristic Region, where the majority of phylogeographical clades can be found (Tolley et al. 2009). It would be important to expand this approach to a variety of mammalian species.

Additional areas of value

Speciation

The integration of phylogeography and niche modelling may help to shed light on the process of speciation. Ecological speciation is speciation resulting from divergent natural selection (Schluter 2001, see Rundle and Nosil 2005 for a review). Ecological explanations of speciation have been out of favour for much of the late 20th century, largely due to a lack of evidence (Morell 1999), with the

accepted wisdom being that speciation happens primarily due to allopatry (Peterson et al. 1999). More recently, however, this paradigm has been challenged by growing evidence for ecological speciation, both in sympatry and parapatry, across a range of habitat types (see e.g. Smith et al. 1997, Lu and Bernatchez 1999, Thorpe and Richard 2001, Ogden and Thorpe 2002, Barluenga et al. 2006). In a review of 40 years of laboratory experiments on speciation, Rice and Hostert (1993) concluded that “the role of geographical separation in generating allopatry (i.e. zero gene flow induced by spatial isolation) has been over-emphasised in the past, whereas its role in *diminished* gene flow in combination with strong, discontinuous and multifarious divergent selection, has been largely unappreciated”. A new view of speciation is therefore forming in which both distance and selection pressure can contribute to speciation in varying amounts (Morell 1999). Also, with the advent of new DNA technologies, notably NGS, it has become possible to examine genomic differences between isolated clades or populations across neutral and adaptive genes (see Nosil 2012). Part of the reason for the under-emphasis on natural selection in speciation has been the success of phylogenetic approaches in examining evolutionary relationships (Morell 1999). Phylogenetic studies make use of genetic information (Avise 2009) rather than phenotypic differences. The differences found between clades therefore do not necessarily relate to phenotypic differences and so researchers are understandably reluctant to ascribe genetic divergence to ecological speciation processes. By making it possible to examine the extent to which different clades occupy distinct environmental niches, the combination of niche modelling and phylogeography can argue for (du Toit et al. 2012, Kalkvik et al. 2012), or against (Peterson et al. 1999), ecological speciation.

Species concepts and evolutionarily significant units

Conservation efforts tend to focus on the preservation of species. For example, the effectiveness of conservation areas such as the global network of protected areas or the important bird areas network is often considered in terms of their ability to protect diversity at the species level (Rodrigues et al. 2004, Coetzee et al. 2009) and the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2017) identifies species in need of protection. The species concept used therefore has an important impact on conservation and biodiversity studies. For example, the phylogenetic species concept

often results in a greater number of species, each with smaller ranges and population sizes, resulting in a larger number of endangered species (Agapow et al. 2004). Through the identification of phylogenetic species, based on phylogenetic concepts such as monophyly (De Queiroz 2007), and ecological species, based on the occupation of distinctive niches (De Queiroz 2007), phylogeography and niche modelling have the potential to encourage conservation efforts in groups not covered by the biological species concept.

Conservation units such as evolutionarily significant units (ESUs) (see Moritz 1994) or distinct population segments (May et al. 2011) have a similar value. They identify taxonomic groups of conservation value below the species level and have the advantage of side-stepping extensive arguments regarding what constitutes a species. ESUs should ideally be based on ecological and genetic data (Crandal et al. 2000). However, the availability of genetic data for many species or groups in recent times has resulted in a reliance on genetic data alone. ENM, in conjunction with phylogeography, can be used to identify the niche differentiation among genetic lineages, providing an additional, ecologically relevant line of evidence for the identification of ESUs (Martínez-Gordillo et al. 2010, May et al. 2011).

Conclusion

Phylogeography and ENM work well together. Both can provide a great deal of information on the evolution and ecology of species, and both have potential sources of error that make corroborative evidence valuable. Phylogeographical studies (*sensu lato*) can provide information on the timing of divergence events (Avice 2009), historical changes in population size (Wakeley 2003) and migration rates (Hudson 1990) and ensures greater accuracy in the identification of species as true biological entities although the effects of different factors on genetic patterns can be hard to disentangle (Tellier and Lemaire 2014). ENM can describe the ecological niches of species or clades, and project them across time and/or space (Moussalli et al. 2009), but models are difficult to validate and sensitive to limitations of presence data (Anderson 2012) and environmental data (Barry and Elith 2006). In combination, these two lines of evidence can support each other and provide reciprocal enlightenment. Furthermore, where phylogeography provides information on the existence and demographic histories of genetic clades, niche modelling can be used to investigate potential present and historical drivers of spatial structure and develop hypotheses relating to the

effects of future environmental changes. We suggest that the main limitations going forward are likely to be the availability of reliable, unbiased, georeferenced genetic data from natural populations and ecologically appropriate environmental data sets. Increased collection and sharing of such data would be of great assistance to studies combining phylogeography and ENM, and thereby to ecological research and conservation in general. Comprehensive data (ecological, distribution and genetic) exist for several well-studied mammalian species, and these present ideal models to further test predictions and develop methodologies and understanding of biological responses to changes in local environments.

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