

PRIMER

Ecological niche models in phylogeographic studies: applications, advances and precautions

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*Department of Ecology and Evolutionary Biology, Museum of Zoology, University of Michigan, Ann Arbor MI 48109-1079, USA***Abstract**

The increased availability of spatial data and methodological developments in species distribution modelling has led to concurrent advances in phylogeography, broadening the scope of questions studied, as well as providing unprecedented insights. Given the species-specific nature of the information provided by ecological niche models (ENMs), whether it is on the environmental tolerances of species or their estimated distribution, today or in the past, it is perhaps not surprising that ENMs have rapidly become a common tool in phylogeographic analysis. Such information is essential to phylogeographic tests that provide important biological insights. Here, we provide an overview of the different applications of ENMs in phylogeographic studies, detailing specific studies and highlighting general limitations and challenges with each application. Given that the full potential of integrating ENMs into phylogeographic cannot be realized unless the ENMs themselves are carefully applied, we provide a summary of best practices with using ENMs. Lastly, we describe some recent advances in how quantitative information from ENMs can be integrated into genetic analyses, illustrating their potential use (and key concerns with such implementations), as well as promising areas for future development.

Keywords: coalescent modelling, ecological niche models, phylogeography

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Background

Building upon a tradition of interdisciplinary approaches, recent integration of ecological niche models (ENMs) in phylogeographic studies is improving our understanding of the processes structuring genetic variation across landscapes (Knowles 2009; Chan *et al.* 2011). Because ENMs generate information about abiotic preferences and tolerances of species (i.e. the existing fundamental niche *sensu* Peterson *et al.* 2011), and hence, estimates of the current, past and possible future potential distribution of species, they are invaluable tools (Soble & Lowe 2010; Chan *et al.* 2011; Svenning *et al.* 2011). ENMs are an independent data source that can be used to evaluate or develop phylogeographic hypotheses about the processes generating patterns of genetic variation in disparate taxa from virtually anywhere across the globe (reviewed in Richards *et al.* 2007).

Given the broad applicability of ENMs and the increasing availability of environmental data in the form of GIS (Geographic Information Systems) layers and of species' distribution data (the main inputs for ENMs,

Box 1), it is perhaps not surprising that ENMs are becoming widely used in phylogeographic studies, although its use remains taxonomically and regionally biased (Fig. 1). Developments in the different uses of ENMs in phylogeography have also progressed quickly. This includes the use of ENMs to: identify the potential location of past populations (e.g. Swenson 2006; Knowles *et al.* 2007; Morgan *et al.* 2011), characterize species environmental preferences and tolerances (e.g. Stockman & Bond 2007; Wooten *et al.* 2010), evaluate adaptation to local environmental conditions across populations (Fournier-Level *et al.* 2011; Banta *et al.* 2012), test whether niche divergence accompanies species divergence (e.g. McCormack *et al.* 2010; Kalkvik *et al.* 2012), evaluate alternative biogeographic hypotheses about community responses to climate change (e.g. Galbreath *et al.* 2009; Edwards *et al.* 2012), and provide quantitative information for predicting how distributional shifts might leave species-specific signatures in patterns of genetic variation (e.g. Knowles & Alvarado-Serrano 2010; He *et al.* 2013).

In the following section, we review the different uses of ENMs in phylogeographic studies, highlighting the advantages and limitations of ENMs in each of these applications. In particular, we focus on the integration of

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ENMs with coalescent-based approaches, some of the potentially most insightful, but also challenging, applications of ENMs in phylogeography. We provide some guidelines for the successful implementation of ENMs, including a brief discussion of the assumptions and limitations of ENMs (Warren 2012). However, we do not

cover in detail the theory behind ENMs or specifics of individual modelling approaches, for which there is an extensive literature (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Peterson *et al.* 2007; Elith & Leathwick 2009; Franklin & Miller 2009; Elith *et al.* 2010; Pearson 2010; Sillero 2011).

Box 1 ENMs: an overview

ENMs can be divided into correlative and mechanistic approaches (Peterson *et al.* 2011; but see Sillero 2011). Mechanistic approaches use biophysical properties of organisms to directly link functional traits with environmental conditions to determine areas where species may exist (Kearney & Porter 2009; Dormann *et al.* 2012). Correlative approaches, on the other hand, focus on identifying statistical associations between the distribution of a species (or set of species) and environmental conditions without the identification of causal links. Although both mechanistic and correlative approaches can be integrated into phylogeographic studies and can be used in combination (Elith *et al.* 2010; Dormann *et al.* 2012), mechanistic approaches have had limited use because of the detailed information, beyond the sampling coordinates, they require. In this box, we focus on correlative approaches (hereafter referred to generically as ENMs), which rely on two sources of information: (i) distribution data and (ii) environmental layers. Below, we present a brief description of the steps involved in generating ENMs with some general guidelines (see also Table 2).

Distribution data

Distribution data can be compiled from primary surveys, natural history collections, published species ranges (e.g. Barnes & Wagner 2004), or public databases (e.g. NatureServe, Patterson *et al.* 2007; GBIF, Telenius 2011). Although different sources contain information relevant for ENMs, the accuracy and precision of distributional data is tightly linked to their origin and format, and hence, all distributional data should be vetted (e.g. confirm taxonomic identities and screen for possible errors in recording collection point information). Once distribution data have been compiled and vetted, all presence records (and sometimes absence records) should be mapped into a predefined map coordinate system that matches the one from the environmental data. If geographic coordinates are not available, georeferencing that ideally quantifies geographic uncertainty (e.g. Wiczorek *et al.* 2004) might be used. Tools for removing redundant data (i.e. points in the same locality or that fall within the same grid cell of environmental data), which can artificially bias ENM predictions, are available (e.g. Warren *et al.* 2010); more complex methods of filtering redundant data, such as those based on spatial variograms (Goovaerts 1998), could also be used.

Environmental data

Environmental data in the form of digital grids can be derived from field data, interpolated surfaces (e.g. climatic data from WorldClim; Hijmans *et al.* 2005), or remote sensing (e.g. landcover from MODIS, Friedl *et al.* 2002; for additional examples of available data see Richards *et al.* 2007; Pearson 2010). Once compiled, all environmental data (i.e. both data used to train the model and for projecting the distribution) need to be processed. Most commonly this involved either transforming the environmental data into raster grids with a single predefined map coordinate system with GIS software (Bolstad 2008). Techniques to deal with correlated variables, such as orthogonal transformations (e.g. principal component analysis) are available and should be considered whenever the goal of the study does not include the identification of the relative contribution of different environmental variables to the model.

Model generation and calibration

The performance of different algorithms for determining the association between species distribution and environmental variables (Table 1) may vary. Likewise, data requirements (e.g. requirement of presence/absence or presence only data or ability to deal with categorical environmental variables) and output (e.g. continuous vs. discrete prediction) differ among algorithms. Thus, algorithm selection choice depends on the characteristics of the data and goal of the study. Although no simple basis for algorithm selection exists, general guidelines for deciding which approach to use are available (reviewed in Thuiller *et al.* 2003; Elith *et al.* 2006; Peterson *et al.* 2007; Elith & Graham 2009). After deciding upon an approach or group of approaches, sensitivity analyses of parameter settings (Haegeman & Etienne 2010; Anderson & Gonzalez 2011; Royle *et al.* 2012), as well as sensitivity analyses for the inclusion/exclusion of

variables in the model (especially when the variables are highly correlated with each other, as it is commonly the case), should be conducted in conjunction with model selection procedures (e.g. Warren & Seifert 2011). Tools for identifying optimal ENM models are freely available (Warren *et al.* 2010); yet, uncertainty associated with model selection and parameterization should always be assessed.

Model validation

Assessing the accuracy of a model is essential and can be accomplished by different means (Liu *et al.* 2009; Jimenez-Valverde 2012), depending upon the model and data type used (for review of validation procedures see Pearson 2010; Peterson *et al.* 2011). Model validation should be performed using multiple alternative accuracy measurements (Hernandez *et al.* 2006; Lobo *et al.* 2008; Liu *et al.* 2009) and on independent data (e.g. occurrence data from a new survey of the species), or if sample size is limited, on pseudo-replicated partitions of the data (e.g. bootstrapping or jackknifing the data). It is important to note that model utility depends on the application intended, and hence, that the accuracy required from a model should be considered on a case-by-case basis. If generating projections of species distributions in the past or future, it may be possible to validate these projections using historical data (e.g. palynological, or fossil records) or using biophysical models as reference (e.g. Kearney *et al.* 2009), respectively.

Model projection

Once the model has been validated, it can be projected across different regions and/or for different time periods (PMIP2, Braconnot *et al.* 2007; e.g. using climatic variables estimated for the past or future; CliMond, Kriticos *et al.* 2012). However, it is always important to consider all potential errors that might impact both the accuracy of the model and the projection (see Table 2), and ideally, this uncertainty should be considered in all downstream analyses. The robustness of the projections to different climatic estimates (e.g. MIROC, CCSM3; Braconnot *et al.* 2007) and model parameterizations should also be considered.

Ecological niche models

The approaches collectively referred to as ENMs (Warren 2012) include different methods that aim to identify the environmental niche and potential distribution of species and/or communities (Ferrier & Guisan 2006; Peterson *et al.* 2011; Svenning *et al.* 2011) (Box 1). This is accomplished by statistically establishing an association between the locations where a species (or set of species) live and the environmental conditions of these locations, or, as in the case of mechanistic models, by directly calculating the physiological tolerances of a species based on biophysical principles (Kearney & Porter 2009). Although the exact procedure followed varies among methods (Table 1), all of them first establish the environmental space the species under study inhabits (hereafter referred to as suitable, as is commonplace in the literature; however, note that in this context, suitable refers only to the set of inhabited environmental conditions; see Anderson 2013). This environmental space is then projected onto a geographic space, finding the geographic areas where the suitable environment is represented (for details see Box 1). Although in principle both correlative and mechanistic ENMs can be used in phylogeographic studies, mechanistic approaches have seldom been used in phylogeography. Hence, our review is focused on correlative approaches.

Despite the insights of an integrative perspective in phylogeography (Knowles 2009) that ENMs can bring to

phylogeography, ENMs are not without their own set of challenges and potential pitfalls (Elith *et al.* 2010). The realized distribution of a species at any point in time is of course conditioned by a plethora of factors, including those that may not be accounted for in an ENM but play an important role in structuring distributions, such as biotic interactions (Davis *et al.* 1998; Meier *et al.* 2010; but see Anderson 2013). In addition, individual populations may differ in their responses to particular environmental conditions because of local adaptation (Fournier-Level *et al.* 2011). This raises the possibility of not only inaccurate inferences from ENMs based on the entire species range (see below), but also that phylogeographic analyses might be compromised (i.e. local adaptation may impact gene flow rates and evolutionary responses to climate change, but the impact of such fitness variation on population genetic structure is not directly accommodated by typical phylogeographic models). These and other caveats should be considered and best practices used to minimize errors with ENMs (see Table 2). Fortunately, there have been significant advances for the generation and refinement of ENMs (Peterson *et al.* 2011).

To guard against inaccurate inferences, it is also important to first clearly define the phylogeographic question that is being addressed with information from an ENM. Because the assumptions, performances and data requirements differ among potential methods for ENMs construction (Table 1) (Elith *et al.* 2006; Peterson *et al.* 2011), the choice of a particular modelling approach

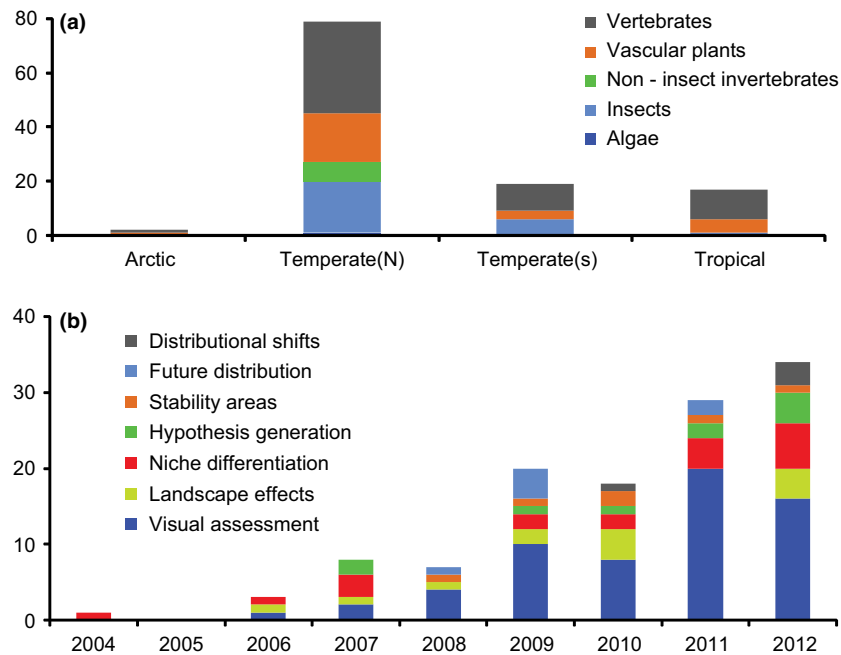


Fig. 1 Uses of ecological niche models (ENMs) in the phylogeographic literature. Number of articles recovered according to (a) the region and organism studied, and (b) how the ENM was applied given the year of publication; note that overall, 77.5% of studies to date used ENMs in a corroborative application (bottom three categories in legend), and only 22.5% of studies used ENMs to generate phylogeographic hypotheses independent of genetic data. This summary is based on a search of articles containing the topic terms 'phylogeography' and 'niche model*' or 'distribution model*' on the Web of Science (the asterisk represents a wild card used to find words with alternative endings, for example, model* = model, models, modelling). The results of this search were filtered to exclude all articles that did not include any of the following phrases in the abstract: 'niche model*', 'distribution model*', 'potential distribution*', 'ENM*', 'SDM*'. Although not exhaustive, this search procedure probably provides a fair representation of the available literature.

Table 1 Main distribution modelling methods available

Method	Procedure	Input	Reference
BIOCLIM	Environmental envelope	Presence	Busby (1991)
HABITAT	Environmental envelope	Presence	Walker & Cocks (1991)
DOMAIN	Gower distances	Presence	Carpenter <i>et al.</i> (1993)
GARP	Genetic algorithm	Presence/pseudoabsence	Stockwell & Peters (1999)
Classification and Regression Trees	Regression	Presence/absence	De'ath & Fabricius (2000)
Artificial Neural Networks (ANNs)	Machine learning	Presence/absence	Hilbert & Ostendorf (2001)
Ecological Niche Factor Analysis (ENFA)	Eigensystem computation	Presence/background	Hirzel <i>et al.</i> (2002)
Generalized Linear Models (GLMs)	Regression	Presence/absence	Lehmann <i>et al.</i> (2002)
Generalized Additive Models (GAMs)	Regression	Presence/absence	Lehmann <i>et al.</i> (2002)
Support Vector Machines (SVMs)	Environmental envelope	Presence or presence/absence	Guo <i>et al.</i> (2005)
MAXENT	Maximum entropy	Presence/background	Phillips <i>et al.</i> (2006)
Multivariate Adaptive Regression Splines (MARS)	Regression	Presence/absence	Elith & Leathwick (2007)
Boosted Regression Trees (BRTs)	Boosting	Presence/absence	Elith <i>et al.</i> (2008)
Deduced Distribution Model (DDM)	Expert knowledge	Presence/absence	Kitchener & Rees (2009)
BIOMOD	Model combination ¹	Presence/absence	Thuiller <i>et al.</i> (2009)

Depending upon the input, the specific procedures used in ecological niche models vary across methods. With presence only data, an environmental envelope approach is used in which environmental tolerances are determined from the environmental variables associated with specific occurrence records. In contrast, suitable areas are identified by contrasting the environmental conditions from known species occurrences against those (i) where the species is known to be absent (presence/absence models), (ii) is presumed to be absent (presence/pseudoabsence models), or (iii) against the environmental variation across the study region (presence/background algorithms).

¹Combining models should be carefully considered as there is a risk of obtaining positively mislead answers (analogous to problems with concatenation in phylogenetics).

Table 2 Summary of some basic considerations when generating ecological niche models (ENMs) (for a more extensive discussion and details see Barry & Elith 2006; Soberón & Nakamura 2009; Elith *et al.* 2010; Peterson *et al.* 2011)

Assumptions that may compromise ENM accuracy	Specific considerations	Relevant references
1. Data compilation		
Are species presences (and absence) records representative of the actual distribution?	<ul style="list-style-type: none"> • effects of species' natural history • geographic/environmental bias • intraspecific variability • positional uncertainty • sample size • sampling bias (e.g. towards more accessible areas) • taxonomic accuracy (e.g. subspecies or races) • temporal coverage in relation to environmental data 	Stockwell & Peterson (2002), Hernandez <i>et al.</i> (2006), Pearson <i>et al.</i> (2007), Hortal <i>et al.</i> (2008), Jackson <i>et al.</i> (2009), Lozier <i>et al.</i> (2009), Phillips <i>et al.</i> (2009), Barve <i>et al.</i> (2011) and Gonzalez <i>et al.</i> (2011)
Do environmental variables accurately capture the association between species subsistence and the environment at the relevant scale?	<ul style="list-style-type: none"> • data quality and biases • effect on species distribution (direct vs. indirect) • resolution in space and time • spatial autocorrelation • spatial extent • temporal coverage and stability • type (categorical vs. continuous) 	Van Niel <i>et al.</i> (2004), Barry & Elith (2006), Anderson & Raza (2010), Kriticos & Leriche (2010), Pearson (2010), Barve <i>et al.</i> (2011), Peterson <i>et al.</i> (2011) and Syne & Osborne (2011)
2. Model generation and calibration		
Is the modelling algorithm appropriate given the data available and research question?	<ul style="list-style-type: none"> • algorithm assumptions • algorithm performance under different scenarios • input data type (e.g. presences only vs. presence/absences) • output generated (e.g. presence/absence vs. continuous prediction) • sensitivity to model parameters 	Austin (2002), Segurado & Araujo (2004), Pearson <i>et al.</i> (2006), Guisan <i>et al.</i> (2007), Elith & Graham (2009) and Barbet-Massin <i>et al.</i> (2012)
Is the model appropriately calibrated for the data available and research question?	<ul style="list-style-type: none"> • model complexity • model selection procedure • setting of model parameters • variable selection strategy 	Maggini <i>et al.</i> (2006), Anderson & Gonzalez (2011), Austin & Van Niel (2011) and Warren & Seifert (2011)
3. Model validation		
Is validation performed on truly independent data and under appropriate settings?	<ul style="list-style-type: none"> • assumptions/limitations of accuracy measurement • importance of use of multiple metrics • sensitivity to model parameters • threshold transformation of continuous predictions 	Fielding & Bell (1997), Liu <i>et al.</i> (2005), Hirzel <i>et al.</i> (2006), Peterson <i>et al.</i> (2008) and Elith & Graham (2009)
4. Model projection		
Is the species–environment relationship likely to be maintained in space and/or time?	<ul style="list-style-type: none"> • availability of validation data in projected regions • likelihood of niche shifts • model uncertainty • model transferability • risks of interpolation and extrapolation 	Thuiller <i>et al.</i> (2004), Randin <i>et al.</i> (2006), Peterson <i>et al.</i> (2007), Elith <i>et al.</i> (2010), Peterson (2011) and Wenger & Olden (2012)

will vary depending upon the application. For example, if the goal is to estimate the similarity of niches between phylogeographic lineages, a regression-based model, which is not particularly robust to spatial autocorrelation, should be avoided (Sokal & Rohlf 1981). Likewise, if the goal is to generate projections of past distributions, ENM approaches, such as environmental envelope models, should be avoided as they are not ideal for such applications because of sensitivities with extrapolating to conditions that are beyond those used in the training set (i.e. when current environmental conditions are a small subset of those present at different time periods) (Fielding & Bell 1997; Roberts & Hamann 2012a). The spatial structure of the taxon of interest is another important consideration when selecting a modelling approach. For example, broadly distributed species are often composed of locally adapted populations with distinct environmental tolerances and potential ranges (Fournier-Level *et al.* 2011; Banta *et al.* 2012). Under this scenario, community-based approaches that allow for the modelling of each population independently may be a well-suited alternative to species-based models that assume a common response of populations across the entire species range (Crego *et al.* 2013; Gray & Hamann 2013; for a comparison of these approaches see Chapman & Purse 2011).

Applications of ENMs in phylogeographic studies

Here, we review some of the common uses of ENMs in phylogeographic studies. The application of ENMs vary, with ENMs most commonly used in a correlative (or corroborative) manner vs. as tools for generating hypotheses (or predictions) that can be tested with genetic data (Fig. 1). This reflects in part the differences in the type and availability of required data for specific applications (i.e. whether physiological data or genomic data might be needed), as well as differing levels of analytical development across applications (i.e. some new applications discussed below show promise but require further development for their full potential to be realized).

Visual assessments of concordance with genetic variation

One of the most common applications of ENMs in phylogeography (Fig. 1b) is to interpret patterns of genetic variation based on the post hoc concordance between patterns of genetic divergence and projections of the species distribution. For example, a deep phylogenetic split between geographically proximate populations may be suggestive of long-term isolation. Support for this hypothesis might be obtained by visual inspection of projections of past species distributions (i.e. from ENMs

based on paleoclimatic variables), where the distributional disjunctions correspond to the genetic differentiation observed between regions (e.g. Moussalli *et al.* 2009).

These analyses are typically qualitative, seeking corroborative evidence visually from the ENMs, and are often implemented in one of two ways. An ENM may be generated for the entire species of interest and compared visually to the pattern of genetic variation, for example, to identify plausible isolating barriers (e.g. areas of low suitability) or past distributions during glaciations that may explain observed genetic breaks (e.g. Beatty & Provan 2010; Lawson 2010). Buckley *et al.* (2009), for example, compared the spatial arrangement of genetic diversity of a New Zealand stick insect (*Argosarchus horridus*), to past distribution models created from all reliable records of the species. With geographic regions of high and low genetic diversity coinciding with suitable and unsuitable regions identified by the ENMs, respectively, these authors conclude that it is probably that differences in genetic diversity across the species range reflects differences in population persistence during glacial periods.

Alternatively, ENMs can be generated separately for each group of individuals (or populations) identified from genetic analyses and the geographic overlap of the projected distributions of the different genetic groups assessed (Jezkova *et al.* 2009; Banta *et al.* 2012; Hornsby & Matocq 2012). For example, to evaluate the role of environment differentiation in the divergence of three distinct genetic lineages of the Spanish lizard (*Psammotromus hispanicus*), Fitze *et al.* (2011) modelled the current distribution of these three distinct genetic lineages. With marginal overlap in their predicted distributions, the authors conclude that the ENMs support a hypothesized role of environmentally driven isolation as a driver of divergence in this lizard.

Because these applications are correlative, *ad hoc* interpretations might be misleading given that other processes might have generated the observed genetic patterns (Box 2; Wagner & Fortin 2013). This is especially a concern when the landscape has been dramatically altered (such that genetic variation may be associated with past, rather than current, landscape configurations; see Zellmer & Knowles 2009), the species distribution has been historically dynamic (as with climate induced distributional shifts; see Hewitt 2000; Greenstein & Pandolfi 2008), or the distribution of a species is structured by biotic interactions not captured by the ENM model (Wiszt *et al.* 2013).

Identification of landscape effects

This application is focused on correlative tests between landscape features and patterns of genetic variation and/or gene flow (inferred from genetic data). Using

habitat suitability scores from ENMs, the impact of the landscape on population connectivity can be predicted. For example, habitat suitability information can be translated into probable migration paths between populations using either least-cost path analysis or isolation by resistance calculations (McRae 2006). The resulting matrix of pairwise connectivity values among populations is then statistically compared with a corresponding matrix of pairwise genetic distances or genetic diversity using regression or ordination methods (e.g. canonical correspondence analysis; ter Braak 1986) or correlation methods (e.g. Mantel tests; Mantel 1967). For example, using a series of Mantel tests, Ortego *et al.* (2012) examined the explanatory power of current vs. the past distribution (during the last glacial maximum) from ENMs with respect to patterns of genetic relatedness of an endemic oak from southern California (*Quercus engelmannii*). Their analyses showed that both current and past distributions, in addition to elevation, were significant predictors of pairwise genetic distance, even after accounting for the geographic distance between populations, indicating the joint influence of current and historical landscape configurations on genetic structure of the species.

Alternatively, spatial association methods (e.g. boundary overlap statistics, Jacquez 1995) can be used to statistically determine whether spatial breaks in the ENM-based suitability of habitats (as identified from boundary delineation methods; Fortin *et al.* 1996) overlap with genetic boundaries (such as those estimated using Monmonier's or Womble's bilinear algorithm; Monmonier 1973; Barbujani *et al.* 1989) (reviewed in Legendre & Fortin 2010; Wagner & Fortin 2013). Such analyses, for example, were used to assess whether the dispersal of foxsnakes in Canada and northern US was limited by habitat degradation (Row *et al.* 2010). Using assignment tests that explicitly incorporate spatial information of the samples (e.g. Corander & Marttinen 2006; Chen *et al.* 2007) coupled with spatial interpolation to identify the location of genetic breaks, Row *et al.* (2010) were able to show that patterns of genetic differentiation were spatially coincident with areas of low habitat suitability, as determined by the ENMs, supporting the impact of habitat suitability on population connectivity in these snakes.

As with applications that seek concordance (discussed in the previous section), the correlation between the landscape, or habitat suitability and genetic data may not be causal. For example, genetic patterns may not be exclusively linked to the present landscape configuration, but instead reflect the past configuration of habitats or the effects of range shifts themselves (Knowles & Alvarado-Serrano 2010; He *et al.* 2013). Tests of the role of past population connectivity in shaping current patterns of genetic diversity (e.g. when past and present landscape configurations differ; Zellmer & Knowles 2009) are

also for populations in mutation–drift equilibrium (i.e. they assume that the rate of input of new mutations is equal to the rate of loss of mutations by genetic drift). Furthermore, they generally view current genetic diversity as a simple product of environmental isolation (i.e. they do not consider how species-specific characteristics that might affect local population demography would impact the relationship between genetic divergence and landscape configurations; Chan & Hadly 2011).

Niche differentiation

There are several different ways ENMs can be used to examine whether different phylogeographic lineages may have diverged in their respective niches (Peterson *et al.* 2011). Niche similarity can be assessed by evaluating whether an ENM generated for one phylogeographic lineage recovers the distribution of another (Peterson *et al.* 1999; Warren *et al.* 2008). Alternatively, the spatial or environmental overlap of ENMs generated for different phylogeographic lineages can be assessed (e.g. Warren *et al.* 2008; McCormack *et al.* 2010). For example, niche divergence across many different environmental factors might be assessed by ordination, in which the distribution of phylogeographic lineages across environmental space, or differentiation along environmental axes, is characterized (e.g. Graham *et al.* 2004). Regardless of the chosen method, a diversity of questions related to niche differentiation can be addressed with the coupling of genetic data and ENMs in this context. These include the importance of local adaptation among populations (Fournier-Level *et al.* 2011; Banta *et al.* 2012) and species diversification (e.g. Beukema *et al.* 2010; Kozak & Wiens 2010), tests of the likelihood of niche conservatism (e.g. Cordellier & Pfenninger 2008), delimitation of species (e.g. Rissler & Apodaca 2007), or even cryptic speciation (e.g. Florio *et al.* 2012).

When ENMs are applied to study niche differentiation, some interpretations need to be made cautiously. As a sole measure of niche differentiation, ENMs obviously may not capture all dimensions relevant to defining a species niche (for discussion see Guisan & Thuiller 2005; Soberón & Peterson 2005; Kearney 2006; Soberón 2007; Sillero 2011; Warren 2012). Tests of niche divergence, including those that test for divergence relative to a particular background level (e.g. McCormack *et al.* 2010; Warren *et al.* 2010) can be sensitive to the environmental variables included in the analyses (see McCormack *et al.* 2010; Rodder & Lotters 2010). Likewise, when species distributions don't overlap spatially, differences in the niches characterized from the ENMs may not have an adaptive explanation (Ree & Sanmartin 2009). It may, for example, reflect that the taxa simply occupy different geographic regions, which could reflect the mode of

speciation (e.g. isolation by a geomorphic feature that acts as a barrier to dispersal). Nevertheless, to the extent that ENMs capture relevant aspects of the niche (e.g. environmental tolerances), ENMs can provide valuable insights about niche similarity or divergence (as highlighted by the studies referenced above), not withstanding certain limitations.

Generation of hypotheses

Rather than seeking visual corroboration or correlations between information from ENMs and patterns of genetic variation, ENMs can instead be used to generate hypotheses that are subsequently tested with genetic data (Richards *et al.* 2007). This approach generally consists of using ENMs to identify population distributions for the present and/or past that can inform the choice of particular phylogeographic models to test (e.g. Lehrian *et al.* 2010; Ralston & Kirchman 2012). With the identification of discrete populations, demarcated by regions of low predicted occurrence from an ENM (and perhaps different ancestral source populations in the past), expected patterns of genetic variation can be generated for these ENM-informed scenarios using coalescent simulations (Carstens & Richards 2007). This general framework can also be used to test hypotheses (Knowles 2009). For example, genetic simulations were used to test whether contemporary populations were founded from one common glacial refugial population, as opposed to different ancestral source populations in montane grasshoppers (*Melanoplus marshalli*) from the Rocky Mountain sky islands (Knowles *et al.* 2007). The hypotheses were in this case inspired by an ENM based on paleoclimatic data that identified more than one possible refugial population. The estimated habitat suitability differed between refugial areas, which raised the question of whether the montane populations were actually colonized from only one of the two putative glacial refugia – a hypothesis that was rejected based on coalescent simulations tested under the models (Knowles *et al.* 2007).

A primary challenge with this application of ENMs revolves around the translation of information from the ENMs into models (i.e. hypotheses about the processes generating patterns of genetic variation). There may be many different configurations of possible current populations and/or routes of colonization from past populations. For example, differing habitat suitability levels may not clearly delimit geographic regions that have been more or less isolated. The models generated from the visual inspection of projected distributions from ENMs also may not capture the primary demographic events experienced by a species. Co-distributed species may not exhibit similar patterns of genetic variation for a particular landscape configuration, for example, because

of differing dispersal capabilities, ecologies and/or natural histories that leave different genetic signatures as taxa experience species-specific bottlenecks and/or rates of population expansion as they move across a landscape (Knowles & Alvarado-Serrano 2010; Marske *et al.* 2012).

Although it is important to remain cognizant of these caveats, these challenges represent a more general constraint of model-based inference in phylogeography. In fact, the independent information ENMs provide are an important source for generating hypotheses about the processes impacting patterns of genetic variation. As such they can be key in developing models that can then be tested using a variety of statistical phylogeographic approaches (reviewed in Knowles 2009; Beaumont *et al.* 2010; Hickerson *et al.* 2010).

Areas of stability

Predictions for species distributions at different time periods from ENMs can be used to identify regions of environmental stability where a species may (in principle) have persisted overtime, in contrast to unstable areas (i.e. areas where climatic changes would have made the region uninhabitable during particular periods). For example, Carnaval *et al.* (2009) assessed the geographic overlap between projected distributions of tropical forests along the Brazilian coast to identify areas of stability over the last 21 000 years (i.e. since the last glacial maximum) that might have served as refugia. Such areas represent areas of critical conservation concern given the extent of deforestation of the Brazilian coastal forest and as species survival under climate change scenarios become increasingly more pressing. By collecting genetic data on three frog species, they were able to show that, as predicted, populations from stable areas identified from the ENMs not only exhibited a genetic signature that differed from those in unstable areas, but that the genetic patterns were also consistent with long-term population persistence in all three species (based on a hierarchical approximate Bayesian computation analysis).

Of course the environmental (or climatic) stability of an area may not correspond to the ecological stability of an area. Nonanalogue communities can be common, indicating that even for co-distributed species, areas of stability may differ among taxa (Williams & Jackson 2007; Polly & Eronen 2011). There can also be potential problems with identifying areas of stability associated with the statistical procedure of projecting the ENM beyond the data used to train it (i.e. projecting the distributions for combinations of environments not present today). Different ENM algorithms deal with this problem in different ways, but the majority of methods constrain the suitability of novel environments to remain within that of the training environment (a procedure referred to as

'clampling'; Elith *et al.* 2011). To deal with this issue, for example, recent implementations of Maxent generate lower suitability scores in areas with environmental conditions not represented in the training data, effectively extending the suitability values of the maximum (or minimum) environment conditions to all environments outside the range of the data used in the training set (cf. Maxent help file; Phillips *et al.* 2006). This introduces a risk of identifying areas of stability from the models simply because of the increased uncertainty of the projected distributions across different time periods (e.g. larger areas of suitability will be represented in ENMs across time periods characterized by conditions not present in today's climate, which may fall outside the physiological tolerances of the species; Soberón & Nakamura 2009). Inflation of the geographic scope of suitable habitats that leads to the false characterization of stable areas overtime will create downstream problems when interpreting the results from phylogeographic analyses. For example, the importance of stable areas as a key determinant of population genetic structure might be rejected because of mis-specification of what were stable and unstable areas. Unfortunately, accounting for uncertainty in ENMs is area in need of further development (see discussion below), but approaches for identifying areas with non-analogue conditions (see Roberts & Hamann 2012b) could be used to guard against misleading conclusions in phylogeographic tests of the importance of climatic stability.

An additional concern with identifying regions of stability reflects the inherent limited temporal resolution of climatic data for generating ENMs. Specifically, ENMs are typically generated for fixed temporal snapshots (but see Brown & Knowles 2012), leaving open the possibility that suitable habitats (and populations) could have shifted repeatedly in a manner that was not always spatially concordant overtime, and/or with a frequency that is beyond the temporal resolution of the climatic data used for generating ENMs for different time periods (Graham *et al.* 2010). Despite these potential limitations, when coupled with tests of expected genetic signatures for areas of stability (e.g. higher genetic diversity, no evidence of bottlenecks) and/or a statistical hypothesis-testing framework (e.g. likelihood or Bayesian methods; for review see Nielsen & Beaumont 2009), using ENMs to identify areas of stability for phylogeographic studies can be particularly revealing (e.g. Werneck *et al.* 2012; Fuchs *et al.* 2013).

Future distributions

With rising concerns about the impact of current climate change on species, ENMs offer a potential tool for assessing potential future consequences. However, because of a number of challenges, such applications have been

limited (Fig. 1b). Not only could there be errors in accurately predicting the configuration of climatic variables in the future, the factors that limit species distributions today may not be the same in the future. This may be especially true if climate change produces unique combinations of environmental conditions that a taxon has not experienced in the past (Williams & Jackson 2007) or if the response of a species to climate change is compromised by mismatches between the distribution of adaptive alleles and local environmental conditions (Banta *et al.* 2012; Gray & Hamann 2013), making predictions about the genetic consequences of future climate change challenging.

Nevertheless, by creating ENMs for independent phylogeographic lineages under different climate change scenarios, a suite of possible effects on the genetic diversity of species can be considered. For example, by assessing the overlap between protected areas and future ENM-predicted distributions of distinct lineages of nine species of African large mammals, D'Amen *et al.* (2013) were able to forecast the likelihood of lineage persistence, and hence, the expected impact of global warming on genetic diversity in these mammals. Examination of the ENMs for similar distributional effects between the future and past (e.g. similar range reductions or levels of fragmentation) may also provide a window into how future climate change will impact species by drawing analogies from genetic signatures of past distributional shifts (e.g. Taubmann *et al.* 2011). Such inferences may be improved upon further by incorporating physiological data that identifies what environmental factors are key to predicting the response of species to environmental change. For example, using physiological data on larval mosquitoes (*Aedes aegypti*), Kearney *et al.* (2009) were able to not only predict, but also to show that expected distributional shifts from ENMs were realized in Australia under recent historical changes in human water-storage practices. Their results demonstrate how human practices mediate the impact of global climate change on species, assessing the expected effects of physiological evolution in these mosquitoes in response to climate change. Yet, translating the genetic consequences of expected distributional shifts can be difficult because of the varying demographic effects that can accompany these shifts (Excoffier *et al.* 2009; Arenas *et al.* 2012).

Expanding the content from ENMs used in phylogeographic studies

Although ENMs provide quantitative spatial information that is commonly used in phylogeographic studies (i.e. the suitability of an area, and hence, how the predicted occurrence of a species varies across the landscape), ENMs contain additional information, and in particular

quantitative information, that is seldom incorporated into phylogeographic studies. In this section, we overview some promising areas of development related to developing suites of phylogeographic hypotheses/models and generating species-specific genetic expectations. Like the applications discussed above, these too share some of the common challenges (see Table 2), and they are not repeated here. Moreover, such applications have not been explored thoroughly, and therefore, should be used cautiously. We include them here primarily to highlight directions for future development and to suggest new ways in which ENMs might be integrated with genetic analyses to broaden the scope of phylogeographic hypotheses that might be tested.

Accounting for uncertainty in an ENM

The process of translating information from an ENM into a hypothesis and/or model has the potential to incorporate uncertainty of the ENM into phylogeographic tests with genetic data. The goal here is to avoid treating the information contained in an ENM as fixed and without potential biases or errors. For example, a suite of different biogeographic histories might be translated from an ENM if we consider how the number and/or levels of connectivity among populations may vary depending on the threshold used to infer occurrence across the landscape, (e.g. 4 isolated populations might be apparent for habitat suitabilities above 85%, but only 2 regions with a narrow connecting corridor might be inferred for habitat suitabilities above 40%). In other words, different interpretations of the ENM can alter the spatial configuration of potential populations and consequently have important ramifications for intuiting phylogeographic hypotheses from ENMs. Likewise, uncertainty associated with the quality of the available data could be quantified (e.g. issues with irregular sampling or spatial dependency; Latimer 2007) and ideally incorporated into downstream analyses. However, this area remains undeveloped.

Incorporating information about distributional shifts

Environments are not constant and populations are not static (in location or size), as evidenced by the vast literature on climate-induced distributional shifts (e.g. Stewart 2009; Shafer *et al.* 2010; Allal *et al.* 2011). Although paleoclimatic data provide an opportunity to estimate past distributions (e.g. Knowles *et al.* 2007; Buckley *et al.* 2009; Smith *et al.* 2011; Marske *et al.* 2012) and there have been advances on studying movement patterns across spatially or temporally variable landscapes in other fields, such as conservation planning (e.g. Iverson *et al.* 2004; Lawler *et al.* 2013), little phylogeographic research has explored the issue of how to represent the movement

of species from one point to another on the landscape across different time periods (but see Graham *et al.* 2010; Brown & Knowles 2012). Theoretical work suggests disentangling the effects of spatial vs. spatio-temporal processes may be difficult (Wegmann *et al.* 2006). Considering both the spatial and spatiotemporal components of distributional shifts may nonetheless be important from a biological perspective. For example, it may be the rate of change in available habitats, not the spatial configuration itself, that is key to understanding why some species diversify during dynamic geologic periods and others do not (Knowles 2000). Nevertheless, the predominant approach of incorporating information from ENMs for different time periods focuses on the spatial component of distributional shifts, and they do not consider associated demographic changes in populations' size accompanying shifts in the distribution predicted by ENMs at different time points (Richards *et al.* 2007).

A couple of different recent approaches have taken advantage of the quantitative information contained in ENMs (i.e. differences in the habitat suitability scores across the landscape) to extract more detailed information about the spatiotemporal component of distributional shifts by coupling ENMs projected for different time periods. For example, an amalgam of the ENMs from different periods might be generated (e.g. an average habitat suitability surface; Knowles & Alvarado-Serrano 2010). Alternatively, local suitability scores might be defined by a weighted average that varies for each time period according to the amount of time that separates these periods from the projected ENMs (see Brown & Knowles 2012; He *et al.* 2013), to account for gradual shifts in habitability of geographic regions over time. When coupled with independent information about the rate of climate change, such as information from oxygen isotope ratios, different rates of climatic change, and accompanying shifts in the distributions, might also be calculated for the intervening periods for which paleoclimatic data is available (see Brown & Knowles 2012).

These promising (albeit underdeveloped) approaches all address the spatiotemporal component of distributional shifts, but do not consider how species are moving across the landscape. Such a static view of what is a complex dynamic process could potentially be misleading (Dyer *et al.* 2010; Wagner & Fortin 2013). For example, high levels of genetic differentiation among populations might reflect long-term isolation of the current populations, founding of the populations from separate refugial populations, or, as recently shown by simulations, result from the demographic process of colonizing contemporary populations from a single shared ancestral population (Knowles & Alvarado-Serrano 2010). In the following section, we highlight two approaches that utilize the quantitative information contained in ENMs to

inform the demographic component of distributional shifts, as well as other phylogeographic models more generally.

Generating species-specific predictions for patterns of genetic variation

With quantitative information on differences in habitat suitability across a landscape at different time periods, there is the potential to use this information on predicted distributions to infer how individuals have possibly dispersed (Crandall *et al.* 2012). For example, an estimate of the history of population connectivity over time might be generated using an optimization algorithm to identify a probably migration path (Graham *et al.* 2010). Specifically, with suitable areas identified at different time points from ENMs (i.e. those generated from contemporary climatic data and paleoclimatic data, respectively), the most likely spatiotemporal path can be selected using a pre-defined criterion, such as minimum cost path. As with landscape genetic approaches, there are still potential problems with selecting a single path given that multiple, complex migration paths may be involved (see McRae 2006). Yet, with such a species-specific estimated history of population connectivity over time, the resulting information can be used for testing models of isolation by distance that account for how genetic differentiation may have been impacted by population connectivity patterns that change over time.

Alternatively, expected patterns of genetic variation can be generated for a diversity of different models for testing phylogeographic hypotheses using iDDC modelling (integrative distributional, demographic and coalescent modelling; He *et al.* 2013) (see also the approaches described in Ray *et al.* 2005; Neuenschwander *et al.* 2008). Briefly, with the iDDC approach (Fig. S1) habitat suitability scores are extracted from an ENM across a landscape to inform a spatially explicit demographic model, in which population sizes and migration rates track local habitat suitabilities, and the parameters from the demographic model are used to inform a spatially explicit coalescent model. DNA sequences are simulated upon these coalescent genealogies to generate expected patterns of genetic variation across the landscape (see Knowles & Alvarado-Serrano 2010 for details). As local population sizes and migration probabilities are informed from the local habitat suitabilities estimated from the ENM, the iDDC modelling approach generates patterns of genetic variation that reflect the interaction of the biological and physical factors that determine population connectivity, not just landscape features alone. Moreover, the likelihood of different models can be assessed, along with the estimation of demographic parameters, with the iDDC approach using flexible

statistical tests, like Approximate Bayesian Computation, ABC (Beaumont 2002), which can accommodate complex, biologically informed models. For example, He *et al.* (2013) used iDDC modelling to test hypotheses about the factors structuring patterns of genetic variation in a southwestern Australian lizard, *Lerista lineopunctulata*. As a sand dune specialist, it was conceivable that population divergence could reflect the contemporary habitat configuration, which limits migration among the small geographically isolated populations (Excoffier *et al.* 2009). Alternatively, genetic variation might reflect the colonization patterns associated with historical shifts in suitable coastal sand habitats, which expanded and contracted during glacial and interglacial periods, respectively. Tests based on multilocus sequence data showed that a dynamic model that takes into account the demographic consequences of the species tracking its habitat under shifting climatic conditions was a more probable model than either a static model of isolated populations or one based on contemporary landscape features alone.

With the complex models accommodated by iDDC modelling, tests with ABC will not only require multilocus data, but also careful evaluation of the ABC tests (Bertorelle *et al.* 2010; He *et al.* 2013). This includes meaningful selection of model priors in the light of empirical data (Lombaert *et al.* 2011; Hickerson *et al.* 2013), an appropriate number of simulations run for each model being tested (Beaumont 2002; Wegmann *et al.* 2010), the selection of informative statistics to summarize genetic variation under each model and the assessment of their interaction (Wegmann & Excoffier 2010; Robert *et al.* 2011), and appropriate model selection and parameter estimation procedures (Neuenschwander *et al.* 2008; Leuenberger & Wegmann 2010; Wegmann *et al.* 2010). Such quality control measures involve the use of pseudo-observed data (pods), which are simulations generated under a known scenario or set of scenarios and compared against a fixed set of parameter values, providing an assessment of whether the data (and summary statistics used) are sufficient for accurate estimation (Neuenschwander *et al.* 2008; Estoup *et al.* 2012) (for further details on model robustness and accuracy assessment see Thornton & Andolfatto 2006; Guillemaud *et al.* 2010). If these precautions are followed, the ABC approach allows not only for the identification of the most likely scenario that may have generated observed patterns of genetic variation but also estimation of the parameters in the models (e.g. migration rates, times of divergence and population sizes).

Conclusions

The incorporation of ENMs into phylogeographic studies has made a significant contribution to the field of

phylogeography, broadening the suite of hypotheses that can be tested, as well as advancing integrative methodological approaches. These contributions, in large part, reflect the utility of species-specific information obtained from ENMs, whether ENMs are applied in a corroborative manner, as most commonly done, or a formal hypothesis testing framework (reviewed here through illustrative examples, as well as a discussion of the caveats with specific applications). As such, the use of ENMs in phylogeography is instrumental for identifying the processes structuring genetic variation and revealing previously unrecognized mechanisms shaping the evolutionary trajectories of species and populations. In this regard, ENMs have also been key to moving the field of phylogeography towards the development of biologically informed hypotheses and away from generic statistical tests that provide little biological insight. The rapid methodological advances in the construction of ENMs, together with the increasing availability of geospatial environmental and species distribution data, will no doubt expand the ways in which ENMs might be used to address phylogeographic questions, continuing the impressive trajectory of their applications in phylogeography to date. While we highlight some of these new promising developments, more research is clearly needed, especially with regards to translating not just the qualitative information, but also the quantitative information contained in ENMs, into testable phylogeographic hypotheses.

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Data Accessibility

This review is based on data already available in ISI Web of Science.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1 Schematic describing iDDC (integrative distributional, demographic, and coalescent modelling). Using information on the local habitat suitabilities derived from ENMs generated for different time points in the past (a), a time forward demographic simulation using the program SPLATCHE 2 (Ray *et al.* 2010) is conducted, where local carrying capacities and migration probabilities of individuals varies across the landscape (b). Based on this ENM-informed demographic history, coalescent simulations are used to generate patterns of genetic variation (c). By simulating over a broad range of parameter sets, as specified by priors derived from alternative models, expectations for patterns genetic data, as characterized using summary statistics (e.g. F_{ST} and Tajima's D), can be generated under an ABC approach and compared with summary statistics obtained from empirical data (d) (for details see Beaumont 2002; Csillery *et al.* 2010). Note that tools to perform these analyses have already been developed and are freely available (e.g. Ray *et al.* 2010; Wegmann *et al.* 2010).