

# Toward a paradigm shift in comparative phylogeography driven by trait-based hypotheses

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For three decades, comparative phylogeography has conceptually and methodologically relied on the concordance criterion for providing insights into the historical/biogeographic processes driving population genetic structure and divergence. Here we discuss how this emphasis, and the corresponding lack of methods for extracting information about biotic/intrinsic contributions to patterns of genetic variation, may bias our general understanding of the factors driving genetic structure. Specifically, this emphasis has promoted a tendency to attribute discordant phylogeographic patterns to the idiosyncrasies of history, as well as an adherence to generic null expectations of concordance with reduced predictive power. We advocate that it is time for a paradigm shift in comparative phylogeography, especially given the limited utility of the concordance criterion as genomic data provide ever-increasing levels of resolution. Instead of adhering to the concordance-discordance dichotomy, comparative phylogeography needs to emphasize the contribution of taxon-specific traits that will determine whether concordance is a meaningful criterion for evaluating hypotheses or may predict discordant phylogeographic structure. Through reference to some case studies we illustrate how refined hypotheses based on taxon-specific traits can provide improved predictive frameworks to forecast species responses to climatic change or biogeographic barriers while gaining unique insights about the taxa themselves and their interactions with their environment. We outline a potential avenue toward a synthetic comparative phylogeographic paradigm that includes addressing some important conceptual and methodological challenges related to study design and application of model-based approaches for evaluating support of trait-based hypotheses under the proposed paradigm.

biogeography | ecological traits | coalescent modeling | Pleistocene | statistical phylogeography

Paralleling its critical role in identifying biogeographic phenomena by common structuring of genetic variation across taxa, comparative phylogeography has the potential to offer unprecedented insights about the taxa themselves. We here make an argument that such a paradigm shift, in which the contribution of biotic attributes are a focal point, as opposed to an emphasis on abiotic factors, is not only a valuable endeavor in itself, but it is also critical to (*i*) understanding the relative contributions of abiotic/extrinsic (e.g., geography, geological, or climatic history) vs. biotic/intrinsic (e.g., ecological or life history traits; hereafter referred to as biotic) factors in structuring genetic variation and divergence across taxa, as well as (*ii*) determining the relative prevalence of deterministic processes versus stochasticity in the evolutionary history of taxa, and we argue that (*iii*) the key to meaningful insights is not just a function of the statistical support we might have for a model, but it also depends on the creativity of biologists to identify hypotheses that are relevant to the structuring of genetic variation. That is, the development of biologically informed model-based approaches and the application of refined hypotheses based on taxon-specific traits provides a needed balance in comparative phylogeography for addressing fundamental questions in ecology and evolution given that the field has traditionally focused (both conceptually and methodologically) on the concordance criterion as a means for identifying biogeographic

phenomena. We illustrate the unique insights that a comparative phylogeographic framework can offer about the taxa themselves through reference to some case studies in which the study design provides a predictive framework for interpreting phylogeographic concordance. We present a variety of examples to highlight some of the interesting ecological and evolutionary questions that can be addressed using refined hypotheses based on species-specific traits, but also to emphasize the broader significance of this proposed paradigm shift to ecology and evolution.

## Historical Emphasis on Concordance

Comparative phylogeography emerged three decades ago as an integrative approach to historical biogeography (1, 2), and has since offered invaluable insights into the factors that shape spatial and temporal patterns of genetic variation. An inherent emphasis on concordance in patterns of genetic variation as a criterion for evaluating hypotheses has accompanied the development of the field since its infancy. Specifically, phylogeographic congruence among several codistributed taxa has provided key evidence of the impact of biogeographic barriers, geological events, or past environmental change on today's distribution of genetic variation (3, 4). Such contributions are exemplified in classical comparative phylogeographic work, such as the study of coastal taxa from the southeast of the United States, where genetic surveys revealed concordant phylogeographic discontinuities between Gulf of Mexico and Atlantic populations in 12 of 19 species (including terrestrial, freshwater, and marine taxa), consistent with the vicariant separation of populations by Pleistocene sea level change (5). Such highly influential studies clearly demonstrated the strength of the concordance criterion, and their legacy is evident in that tests of concordance became the central paradigm in comparative phylogeographic analyses.

With concordance as a metric for testing expectations for patterns of genetic variation, comparative phylogeographic analyses have been used to address a broad array of ecological and evolutionary questions, from inferring Quaternary refugia and assigning conservation priorities (6, 7) to evaluating the stability of ecological associations between interacting organisms (8, 9). Commonly applied tests include the evaluation of spatially concordant phylogeographic breaks (10, 11), temporally synchronous population divergence (12, 13), or concerted demographic expansion/contraction (14, 15) among members of an ecological community. Methodological advances of the last decade, especially coalescent-based tools for hypothesis testing and parameter estimation (16, 17) that include statistical assessment of concordance across taxa, such as the widely used hierarchical approximate Bayesian computation (hABC)

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(18, 19), also promoted the utility of the concordance criterion. At the same time, such statistical frameworks have been critical for overcoming past perceptions of phylogeography as primarily a descriptive field that lacked rigor (20).

### Limitations of Strict Adherence to Concordance Criteria

Although the phylogeographic concordance criterion, enhanced by methodological advances that provide statistical rigor to inferences, has undoubtedly made an enormous contribution to our understanding of the historical/extrinsic factors structuring genetic variation, it has also had several consequences that have arguably limited the potential insights from comparative phylogeographic analyses. For example it has promoted a tendency to disregard discordance as uninteresting and attribute lineage-specific patterns to stochastic effects. Likewise, with the concordance criterion as a key basis for inferences, a focus on abiotic factors, and consequently on the spatial and temporal scales where the geologic/historical events are likely to have impacted codistributed taxa similarly, came to predominate the field (21). Such an emphasis has contributed to an imbalance in the perceived relative importance of extrinsic factors in structuring genetic variation (as opposed to the influence of intrinsic factors) (22). Moreover, the adherence to the concordance criterion results in tests that are often too generic and thus have reduced predictive power (23), where the rejection of concordance is often met with ad hoc explanations for the observed discordance. Last, without a correspondingly well-developed statistical framework for making predictions about discordance (24), extracting information about biotic contributions to patterns of genetic variation among codistributed species also becomes challenging. This limitation is especially critical given that if species-specific traits actually have a significant impact, then by definition, discordance will characterize genetic variation among codistributed species. Below we expand the evidence about the limitations of a strict adherence to a concordance criterion in comparative phylogeography, especially in respect to its broader impact on ecological and evolutionary thought.

**Interpreting Discordance.** As a consequence of the tendency to attribute discordance and lineage-specific patterns to stochastic effects (6, 9, 25), deterministic processes that cause discordant patterns among codistributed taxa (26) may be disregarded. Invoking the idiosyncratic nature of history makes discordant phylogeographic structure uninteresting in a comparative framework (i.e., it implies there are no conclusions to be drawn about deterministic processes from discordant patterns of genetic variation), limiting the generalizations comparative phylogeography might provide about the influence of biotic factors on genetic structure. Likewise, although the “concerted vs. individualistic responses” dichotomy can offer important insights (e.g., about the stability of ecological communities through time) (27), by considering trait-mediated responses as “individualistic,” we might miss an opportunity for drawing lessons from comparative phylogeographic study about fundamental ecological and evolutionary principles. For example, when evaluating the effect of Pleistocene glaciations on the evolutionary history of codistributed montane plant taxa, spatially discordant phylogeographic patterns are often deemed inconclusive (25), whereas they could provide insights into the interaction between species’ ecology and climatic change (26). However, the potential insights into trait-mediated effects of climate change go unrealized without a conceptual (and methodological) framework for discordant genetic structure, which is significantly underdeveloped compared with that for phylogeographic concordance.

**Imbalance in the Relative Contribution of Abiotic vs. Biotic Factors.** The inherent emphasis on phylogeographic concordance that has dominated the field since its infancy has additionally created an unbalanced focus on the spatial and temporal scales where the impact of geologic/historical events is likely to predominate. It

has been demonstrated in a range of different systems that contrasting conclusions might be drawn about the prevalence of concordant or discordant patterns depending on the spatial and temporal scale in which taxa are studied. For example, comparative phylogeography of two alpine butterfly species in the Rocky Mountains (28) or two saproxylic springtail species in southeastern Australia (29) revealed shared responses to Pleistocene climatic change across broad spatial scales, but species-specific patterns at finer spatial, and recent temporal, scales. Similarly, comparisons among three symbiotic fungal species associated with the mountain pine beetle in western Canada (30) identified congruent phylogeographic patterns at a broad geographical scale vs. incongruent structuring at a finer scale, which was linked to species-specific traits such as transmission mode or environmental tolerance. By emphasizing concordance, most phylogeographic studies tend to adhere to broader temporal and spatial scales where concordant patterns are more prevalent, whereas contemporary effects across local scales are treated separately within a landscape genetics framework (31). Although we might expect that processes at fine scales should predict patterns at broader scales, the links between mechanism (e.g., traits that limit or promote movement) and pattern (phylogeographic signal) may not be evident when relying on distinct analytical frameworks. Without a shared framework, the relative influence of extrinsic vs. intrinsic factors in structuring genetic variation, as well as the influence of contemporary vs. past processes, remain unknown, and difficult to separate from the scale of a study (32).

### Reduced Predictive Power of Generic Expectations of Concordance.

Null expectations of concordance among taxa with disparate traits are prevalent in the comparative phylogeographic literature (9, 10, 33–35), even though it is well documented that certain ecological or life history traits can influence greatly genetic structure (36, 37), especially with respect to species’ responses to biogeographic barriers and climatic change (27, 38). A main concern with such generic hypotheses of global phylogeographic concordance is their reduced predictive power (39), i.e., rejection of concordance leads to rather inconclusive statements that do not offer particularly meaningful insights (23). Refinement of the expectation for concordance is needed if concordance itself is to be a meaningful metric for making inferences about the processes structuring genetic variation (Box 1). In other words, support (or the lack thereof) for a process may simply be a function of how the concordance criterion is applied (i.e., if it is used as a generic expectation without regard to species-specific traits), as opposed to whether or not a process may drive divergence (Box 1).

### Methodological Developments Reinforce the Knowledge Gap Created by Adherence to Concordance.

Given that interpreting discordance has never been a focus in the field, currently available and newly developed comparative phylogeographic methods (18, 40, 41) are designed to quantify congruence, rather than to gain insights from discordant patterns. As a consequence, the standard comparative phylogeographic toolbox indirectly encourages users to emphasize congruence and disregard discordance as uninteresting. For example, when applying coalescent-based hypothesis testing using hABC to assess simultaneous population divergence across a set of disparate codistributed taxa (18, 42), the rejection of a global model of temporal congruence will unavoidably emphasize idiosyncratic aspects of history, if the test is not pursued under an appropriate study design allowing for an improved predictive framework based on taxon attributes (23). Similarly, some common practices in hABC implementations adopt computational shortcuts that also limit the interpretation of discordance. For example, the default option of resorting the summary statistics vector (e.g., in msBayes) (18, 42) reduces the number of simulations required for hABC analyses but comes at the expense of losing information critical to interpretation (23, 40). This lack of methodological

attention for testing predictions of discordance therefore reinforces the current knowledge gap about biotic contributions to patterns of genetic variation.

### Insights Gained from Discordance Highlight the Promise of a Paradigm Shift

Although there is a historically pervasive trend to attribute phylogeographic discordance to stochastic effects, a number of empirical studies have attempted to provide deterministic explanations based on taxon-specific traits. Morphological or life-history traits directly related to dispersal potential, such as body size, wing development, reproductive mode, or larval type (13, 38, 39, 43), have been commonly used to interpret contrasting responses to biogeographic barriers. In some cases, habitat (or microhabitat) preference has also been associated with differences in spatial genetic structure, especially when (micro)habitats differ in their long-term stability (23, 38, 44) or their responses to environmental change (26, 45). Alternatively, discordance in spatial genetic structure may be linked to the degree of ecological specialization (e.g., in habitat, diet, or host) (43, 46, 47) and differential responses to climate change among taxa may reflect differences in thermal traits (48, 49).

The range of empirical systems and suite of traits that predict species-specific patterns of genetic variation highlight the potential insights phylogeographic discordance could provide about biotic/intrinsic factors structuring genetic variation. However, this aspect still remains marginalized in comparative phylogeographic research. Specifically, species-specific or trait-based explanations are typically applied in an ad hoc manner (that is, after discordance is observed), in contrast to the more synthetic perspective applied to inferences about historical abiotic factors in which predictions are made a priori and tested within a well-developed statistical framework. Instead, the primary context for statistical tests of trait-based hypotheses has been in comparative phylogenetics, where certain clade-specific ecological traits have been linked with increased diversification rates (50, 51). The success of such inferences in macroevolutionary treatments highlights how important the biotic influence in species divergence may be. However, these tests do not provide explicit links with the underlying microevolutionary divergence processes themselves. Comparative phylogeography has the potential to bridge this gap, providing insights about the role of ecological and life history traits in driving divergence at the microevolutionary level. However, this will require a shift from the primarily historical focus and strict adherence to concordance.

### Toward a Trait-Based Comparative Phylogeography

As highlighted above, case studies provide useful insights for focal taxa and demonstrate the effect of species-specific traits on patterns of genetic variation. We are not discounting the important contributions of such work (22), which actually motivates the paradigm shift proposed here. Likewise, our attention to the limitations of the concordance criterion should not be viewed as a general call for abandoning the approach. To the contrary, our intention is to call for a conceptual and methodological shift, in which the broader significance of biological traits in shaping patterns of genetic variation can be revealed from comparative phylogeography, paralleling the field's contribution to understanding the role of historical abiotic factors (21). As phylogeography is being transformed by the unprecedented resolution of genome-wide data for demographic inference and fine-scale population structure (41, 52, 53), thus removing previous data-related constraints (54), there is an opportunity for the field to offer unprecedented insights into the interactions of taxa with their environment and to make equally important contributions to the field of ecology as it has traditionally made to historical biogeography. Specifically, the multitaxon comparative framework and the historical perspective offered by comparative phylogeography, when combined with a thorough consideration of ecological

and life-history traits, provides the potential to disentangle the relative contributions of historical vs. contemporary and abiotic vs. biotic factors to the structuring of genetic variation. However, there are both conceptual and methodological challenges to this endeavor. Here we focus on how (i) the study design is critical to providing insights about the biotic factors that might structure genetic variation and (ii) performing analyses in a model-based framework is essential for evaluating the fit of data to species-specific predictions under biologically informed hypotheses. Below we describe a synthetic model-based comparative phylogeographic paradigm that considers both biotic and abiotic factors structuring genetic variation. We fully acknowledge that this is not the only approach that might be applied. In fact, the full potential of this paradigm shift will not be realized without additional conceptual and methodological development from a diversity of researchers, in much the same way that comparative phylogeography evolved gradually to provide a robust framework for understanding the role of abiotic factors in structuring genetic variation.

**The Importance of the Study Design.** The insights provided by testing the role of biotic factors in structuring genetic variation are a direct function of a researcher's thorough knowledge of a study system, including both the thoughtful selection of hypotheses and an appropriate experimental design that can actually capture the processes of biological interest. Different approaches might be used to design comparative phylogeographic studies for testing biologically informed hypotheses. If the goal is to address questions about the possible role of a specific ecological trait in structuring genetic variation, it might be useful to focus on taxa that differ only in the targeted ecological trait (23, 24). With such a study design, refined hypotheses of concordance based on taxon-specific traits can be used, thereby providing a better predictive framework for comparative phylogeographic tests (Box 1). This approach can be applied to any set of carefully selected taxa, although for more distantly related taxa, differences in addition to the targeted ecological traits could complicate interpretations. Alternatively, study designs for testing the role of biotic factors in structuring genetic variation might be based upon predictions of phylogeographic discordance. For example, species-specific predictions for patterns of genetic variation (55) might be used to evaluate how the response to climate change may differ in a deterministic manner depending upon key ecological traits (Box 2), rather than interpreting the lack of concordance among taxa as a rejection of shared glacial refugia (53). Of course when designing a study, especially for model-based tests (16), it is imperative that the biological processes of interest are represented by the suite of hypotheses tested, as there is no way to rule out additional hypotheses that have not been evaluated. Phylogeographic analyses do not identify "the evolutionary history" of taxa per se (56), instead the insights of model-based approaches rest with demonstrating the relative support of one hypothesis relative to others where each of the different hypotheses relevant to evaluating a question are represented in the study (24).

### A Model-Based Framework for Generating Species-Specific Predictions.

The proposed paradigm shift in comparative phylogeography will require an appropriate statistical framework to accommodate and interpret phylogeographic discordance. Here we focus exclusively on model-based inference, following in the tradition of statistical phylogeography (16), given our objective is to make inferences about causation. The utility of correlative approaches for generating hypotheses should not be overlooked, but neither should their limitations for inferring processes from patterns of genetic variation. For example, general linear models (GLMs) may be used to assess the relative

importance of individual variables as predictors of spatial genetic variation (39). However, correlative approaches may misidentify the impact of candidate factors, especially when multiple processes can produce similar patterns (e.g., when multiple predictor variables are correlated), or when certain assumptions about the association between genetic variation and a predictor variable are violated. Therefore, tests of the contribution of taxon-specific traits to the structuring of genetic variation should be based on model-based approaches that provide explicit links between processes and patterns of genetic variation (57). In particular, testing hypotheses about the intrinsic factors that might structure genetic variation, requires generating species-specific predictions (Box 2). Recently developed methodologies integrating distributional, demographic and coalescent modeling (iDDC) (57) with ABC (58) provide a framework for evaluating the relative probability of alternative hypotheses based on species-specific expectations under a diverse array of models that can accommodate differences in population dynamics over space (e.g., habitat heterogeneity) or time (e.g., shifting climatic conditions), but also differences in taxon-specific

demographic processes because of disparate natural histories or ecologies (Box 2). With the analytical tools to test more complex models (59), and the power to distinguish among alternative models with genomic data, biologically informed hypotheses are poised to provide insights into questions that could not be addressed before.

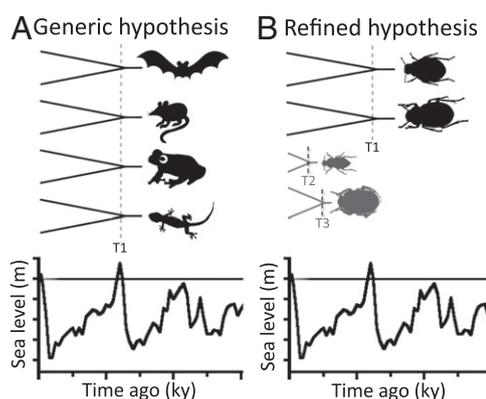
#### Methodological Challenges for Trait-Based Comparative Phylogeography.

As with any model-based approach for phylogeographic inference, there are important methodological and conceptual challenges with such tests of taxon-specific traits. For example, it is not trivial to identify from an essentially infinite set of hypotheses, those that will be the focus of statistical evaluation (16). Even though it might be possible to compare large sets of hypotheses without using any a priori biological knowledge of the study system (60, 61), that might not be particularly meaningful. The insights provided by selecting one model over another will be limited if the models only vary in nonkey parameters that do not make any important difference for their biological interpretation (24). In other words, without knowing

#### Box 1: Refined vs. Generic Hypotheses in hABC to Evaluate Climate-Driven Diversification

hABC analyses are widely used in comparative phylogeography to evaluate scenarios of climate-driven diversification by testing for simultaneous divergence among population pairs of codistributed taxa (12, 66, 67). Here we highlight two case studies that applied hABC to island taxa to assess the hypothesized “species-pump” action of rising and falling sea levels under the Pleistocene Aggregate Island Complex (PAIC) (68) model of diversification, which is expected to produce a pattern of temporally clustered divergence times coinciding with high sea level periods (35) (Fig. 1A). Consider the case in which initial hABC analyses of 22 taxon pairs spanning five orders of terrestrial vertebrates sampled from six island pairs across the Philippine archipelago fit a model of simultaneous divergence, seemingly providing support for the “species-pump” diversification hypothesis (35). However, when the authors performed a suite of simulation-based power analyses and discovered inherent bias in inferences because of improper priors on demographic and divergence-time parameters in the msBayes program (69, 70), reanalysis showed divergence times were not clustered. The merit of identifying methodological biases not withstanding, equivalent scrutiny should be given to the metric used to evaluate support for the species-pump diversification hypothesis, that is, the concordance criterion. Failure to identify clustered divergences across taxa with highly disparate dispersal capabilities and ecological traits that were sampled from different islands is not surprising and is arguably too generic of an expectation for drawing meaningful conclusions about the role of island connectivity cycles in driving diversification.

Instead of applying a generic expectation of concordance, refined hypotheses based on species-specific traits might be considered. For example, Papadopoulou and Knowles (23) generated refined expectations of concordance (Fig. 1B) to test the species-pump diversification hypothesis. Specifically, hypotheses of concordance were restricted to closely related darkling beetles species based on (i) bathymetric data that identified islands where sea-level shifts would have produced similar degrees of connectivity and (ii) ecological traits that would have mediated the effects of sea-level shifts (namely, preferences for either sand or soil; two habitats that differ in their stability over time). When hABC was applied on the full set of 13 taxa, there was moderate support for a model with two divergence events, but with considerable uncertainty and variation in divergence time estimates, as expected due to habitat-mediated differences in local extinction rate and dispersal propensity. However, when the expectations of concordance in the hABC analyses were refined based on habitat association, a model with a single divergence event was supported across all six stable-habitat specialists, demonstrating that the support for sea-level shifts as drivers of divergence is a function of the null model used in the hABC analyses. This example illustrates the reduced predictive power of generic hypotheses of concordance in hABC analyses in comparison with a refined hypothesis based on taxon-specific traits. Moreover, together the examples highlight how a bias in our understanding of the factors driving divergence may not be limited to algorithmic issues associated with comparative phylogeographic analyses, but may also be introduced by how we apply the concordance criterion to make inferences about the factors driving divergence.



**Fig. 1.** Generic vs. refined hypotheses to test the role of sea-level changes in driving diversification of island taxa. (A) A generic hypothesis assumes simultaneous divergence across taxa with disparate ecological traits and dispersal abilities. (B) A refined hypothesis limits the expectations of concordance to taxa subject to similar levels of population connectivity and persistence based on their habitat preference (top beetles in black) and excludes closely related taxa subject to high local extinction rates that would supersede divergence driven by past sea-level change (lower beetles in gray). Temporal concordance in population divergence among ecologically similar taxa provides support for the role of island connectivity cycles in driving diversification. At the same time, discordance between sets of similar taxa with different habitat preferences identifies habitat stability as a key factor structuring genetic variation in this island system (23).

what the question is, it is not clear what insights can be provided by biologically “naïve” hypotheses (i.e., models chosen without a biologically motivated hypothesis). There are of course situations where distinguishing among alternative hypotheses via some model selection procedure (62) is not the primary goal, but the aim is instead to estimate a demographic parameter, such as divergence time, taking into account the uncertainty about the actual demographic history (63). In such cases, the model itself is actually a nuisance parameter, and therefore, considering an array of models with the inclusion/exclusion of other demographic factors might be desirable so that the robustness to a variety of potential histories is accounted for.

Decisions about what biologically informed hypotheses to test need to be coupled with appropriate methods for assessing the fit of the data to the models; that is, even if one model is more probable than another, they might both fit the data poorly (64). Practical challenges with such model-based tests may include computational limitations for complex models (e.g., using parameters from spatially explicit demographic models to inform the coalescent process for thousands of independent loci unavoidably requires substantial amounts of computational resources) or methodological constraints related with the use of ABC (e.g., model posterior probabilities poorly evaluated by ABC techniques) (62). Likewise, potential

problems might be introduced when translating biological hypotheses into models for statistical tests. Specifically, the support (or lack thereof) for alternative hypotheses might reflect differences in the extent to which taxa conform to assumptions used to generate species-specific predictions, rather than key differences in the models themselves (24).

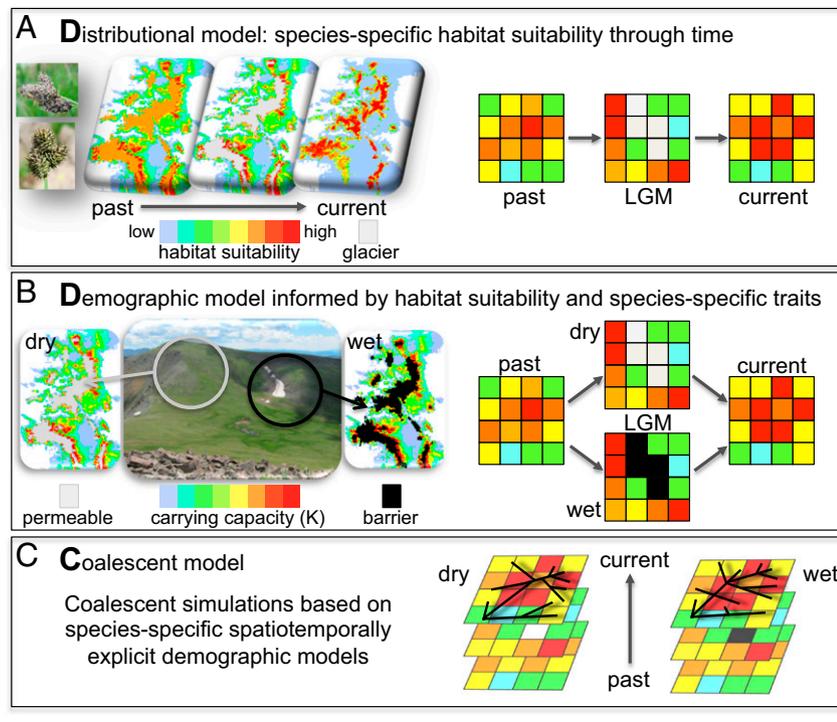
## Conclusions

After three decades of comparative phylogeography providing invaluable insights into the biogeographic factors structuring genetic variation, now is the time for the field to consider a shift that has the potential to offer equivalent insights about the biotic component: the taxa themselves and the lessons they can provide on ecological and evolutionary thought. Advances in genomic datasets will no doubt push comparative phylogeography away from the concordance-discordance dichotomy, as with increasing amounts of data, what appeared as congruent patterns of divergence or phylogeographic structure may reflect the lack of resolution or power to detect discordance (16, 65). As such, a shift toward a trait-based paradigm in comparative phylogeography may become more broadly relevant, even if the focus stays on inferences about historical/abiotic factors. That is, with the increased resolution of genomic data for resolving incongruent aspects of genetic structure that were not detectable in

### Box 2: iDDC as a Framework for Generating Species-Specific Predictions Under Biologically Informed Hypotheses

The iDDC modeling approach (57) generates species-specific expectations for patterns of genetic variation under a broad range of biologically informed hypotheses, which can then be tested against the empirical genetic data using ABC (58). In particular, it can be used to evaluate questions that focus on spatial or temporal changes in habitat suitability or to accommodate habitat heterogeneity and generate more realistic patterns of genetic variation than a simple diffusion process (e.g., when evaluating models about population expansion or colonization dynamics; Fig. 2).

A range of taxon-specific attributes can be translated into a suite of alternative models for model selection (e.g., isolation-by-distance, isolation by environment, or heterogeneity in the stability of habitats over time) (57). Alternatively, within a comparative phylogeographic framework, this approach can be used to generate contrasting expectations for patterns of genetic variation among species that differ in species-specific ecological traits (e.g., models in which a geographic region remains habitable or acts as a barrier) (24). In this context (Fig. 2), the iDDC approach can be used to make predictions about discordance (i.e., to evaluate whether trait-mediated deterministic processes contribute to observed discordance in patterns of genetic variation), making it an especially useful tool in comparative phylogeography.



**Fig. 2.** The iDDC procedure generates species-specific predictions for patterns of genetic variation, which when coupled with approximate Bayesian computation (ABC), can be used to test biologically informed hypotheses about the effect of taxon-specific traits on phylogeographic structure. For example, it has been used to address questions on how the effects of climate change differ between wet- vs. dry-adapted montane sedges from the Rocky Mountains (24). The two closely related and codistributed *Carex* species have very similar distributional models (A), based on environmental niche modeling (26). However, when considering microhabitat affinity, different carrying capacities are predicted across the glaciated area at LGM (B), and coalescent simulations produce distinct expectations for patterns of genetic variation across the spatiotemporally dynamic landscape (C). Model comparisons using ABC supported a barrier model (i.e., zero carrying capacity in the glaciated region at LGM) for the wet-adapted species, which was presumably displaced during glacial periods due to accumulation of snow in wet microhabitats (e.g., drainages). On the contrary, a permeable model (i.e., allowing for nonzero carrying capacity in the glaciated region) is supported for the dry-adapted species, which could have persisted in situ within the glaciated areas, as drier microhabitats (e.g., ridges) remained relative free of persistent snow (24). Photos reproduced from ref. 26 with permission of the publisher.

the past, a model-based framework for extracting the signature of shared responses to a barrier, as opposed to the taxon-specific contributions, may become critical. We outlined a proposal of refined hypotheses based on species-specific traits to improve the predictive power of comparative phylogeography, as well as aspects in need of methodological development for this paradigm shift to realize its full potential. Building on the foundations of phylogeography that underlies the field's prominence in ecology and evolution, its integrative approach of drawing on input from

multiple disciplines, the biologically informed hypotheses that are central to trait-based comparative phylogeography will continue to be an integral part of the field's continued success in the future.

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