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A framework for using niche models to estimate impacts of climate change on species distributions

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Predicting species geographic distributions in the future is an important yet exceptionally challenging endeavor. Overall, it requires a two-step process: (1) a niche model characterizing suitability, applied to projections of future conditions and linked to (2) a dispersal/demographic simulation estimating the species' future occupied distribution. Despite limitations, for the vast majority of species, correlative approaches are the most feasible avenue for building niche models. In addition to myriad technical issues regarding model building, researchers should follow critical principles for selecting predictor variables and occurrence data, demonstrating effective performance in prediction across space, and extrapolating into nonanalog conditions. Many of these principles relate directly to the niche space, dispersal/demographic noise, biotic noise, and human noise assumptions defined here. Issues requiring progress include modeling interactions between abiotic variables, integrating biotic variables, considering genetic heterogeneity, and quantifying uncertainty. Once built, the niche model identifying currently suitable conditions must be processed to approximate the areas that the species occupies. That estimate serves as a seed for the simulation of persistence, dispersal, and establishment in future suitable areas. The dispersal/demographic simulation also requires data regarding the species' dispersal ability and demography, scenarios for future land use, and the capability of considering multiple interacting species simultaneously.

Keywords: biotic interactions; climate change; dispersal; ecological niche model; land use; species distribution

Introduction

Predicting changes in species geographic distributions into the future is an important yet exceptionally challenging endeavor. Here, biology and the spatial and computational sciences have the opportunity to provide society with information critical for a variety of pressing environmental issues, including applications to agriculture, public health, and conservation biology.[1–4] Two fundamental items must be predicted. First, we aim to estimate changes in which particular areas will hold suitable abiotic conditions for the species (sometimes also taking into account key biotic interactions). Second, we then need to forecast changes in the species' distribution in response to those environmental changes. Some modeling strategies aim to predict changes in species distributions by combining factors related to niches and suitable environmental conditions with those related to occurrence, dispersal, and establishment into a single modeling framework.[5–8] In contrast to that paradigm, a purely niche-based model first estimates suitability on the basis of present environmental data. That niche model is then applied to future conditions to estimate the areas that will be suitable, a critical input for a spatially explicit dispersal/demographic simulation that then considers factors affecting the species' occurrence, dispersal, and establishment. Following a copious literature,[9] I provide an overview of the latter, niche-modeling paradigm, emphasizing key principles, necessary assumptions, and relevant procedural designs.

Species niches can be estimated via either mechanistic or correlative models, with some recent efforts to integrate them.[10–13] Mechanistic models based

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Table 1. **Summary of division of niche concepts into complementary Grinnellian and Eltonian perspectives**

Niche perspective	Relevant environmental variables	Generalities regarding scale	Nature of driving factors	Relationship to population growth rate	Relevant modeling approach
Grinnellian niche	Variables not affected by the presence of the focal species (scenopoetic variables)	Coarser grains; geographic extents	Density-independent	Related to intrinsic population growth rate	Static sets of numbers (e.g., subsets of multivariate space)
Eltonian niche	Variables affected by the presence of the focal species (nonscenopoetic variables)	Finer grains; local extents	Density-dependent	Related to instantaneous population growth rate	Dynamic models (e.g., resource–consumer models)

NOTE. Although full understanding of species geographic distributions requires consideration of Eltonian processes as well, I focus here on models of Grinnellian niches.

directly on physiological tolerances (and sometimes behavior) hold certain advantages and will prove useful in some systems.[14,15] However, such models require laborious and often costly experiments. Hence, for the vast majority of species, correlative approaches—which leverage vast digital data sources regarding species occurrences and environmental conditions across the globe—represent a more feasible avenue.[16–18] Whichever means is used to characterize the species' niche and hence estimate future changes in the areas suitable for it, the overall problem of estimating a species' future distribution remains tremendously complex—because it will depend on multiple classes of driving factors, each of which likely will change. These factors include the areas holding suitable abiotic conditions; the distributions of species that interact with the focal species and influence its distribution (biotic interactors); human modifications of the environment; and the areas that are accessible to the focal species via dispersal, within which it may be able to establish and maintain populations. Although the particular challenges in building a niche model differ substantially between mechanistic and correlative approaches, many relevant principles hold true for either.

Here, I aim to sketch a conceptual overview of what must be done and where the challenges lie. To do so, I cover several areas: (1) the theoretical paradigm of niche models, linked to spatially explicit dispersal/demographic simulations; (2) principles for building niche models and transferring them to other places and time periods (selecting environmental and occurrence data, evaluating performance on spatially independent data, and considering nonanalog conditions); (3) issues requiring progress in niche modeling (regarding abiotic and biotic variables, genetic heterogeneity, and uncertainty); and (4) an overall framework for predicting species future distributions by linking niche models to dispersal/demographic simulations (including inputs and outputs of various classes of data). I focus on correlative approaches, specifically those modeling what have been termed *Grinnellian niches* (Table 1), but attempt to provide an overview relevant for mechanistic models as well. In addition to these conceptual principles, many critical methodological issues affect the output of correlative niche models. These include topics related to errors and biases in occurrence and environmental data, grain of analysis, algorithm selection, model complexity (controlling overfitting to noise and bias), and details of model evaluation. However, treatments of those issues appear elsewhere,[9,17,19–21] and I refrain from further discussion of them here. Notably, most of the issues affecting transfer of niche models across space (e.g., for invasive species) match those for transferring them across time. Therefore, I maintain dual mention of the two transfers throughout for clarity and completeness. Finally, I place emphasis on transfers to future conditions but note that issues discussed here are also germane for application to past conditions.

Theoretical paradigm: niche models, linked to dispersal/demographic simulations

Theory regarding niches and distributions

In studying niches and distributions, we must continually make the distinction between environmental space and geographic space, yet maintain conceptual and practical links between them. In environmental space, the aim of niche modeling is to characterize the conditions suitable for the species (for the dimensions of its niche examined in a given analysis). Projecting such a model onto geography then identifies the areas that fulfill those conditions. Purely niche-based models hold predictive power across space or time because they estimate the *conditions* suitable for the species in environmental space—and by extension, can identify where suitable conditions exist in geographic space. In contrast, models of the particular *areas* that the species truly occupies include (directly or indirectly) the influence of other factors that do not transfer across space or time.[17]

This discrepancy exists because—owing to limitations related to dispersal and demography or to biotic interactions—most species do not occupy all of the areas that are abiotically suitable for them (Fig. 1). Situations where species occupied distributions are smaller than the areas abiotically suitable for them have been termed *nonequilibrium distributions*, because those other classes of factors prevent the species' distribution from being in equilibrium with abiotic variables.[9] Such reductions derive from the geographic realities imposed by the spatial configuration of the study region (e.g., the size and arrangement of areas holding suitable conditions), as well as by the contingent effects of Earth history (e.g., continental drift, orogeny, formation of lacustrine and riverine systems, development of prevailing weather patterns) and biotic history (e.g., where various taxa originated, the areas to which they have dispersed, and where they have persisted). Hence, in projections between environmental and geographic spaces, a key distinction exists between estimates of abiotically suitable conditions, versus characterizations of what areas and conditions the species truly occupies.

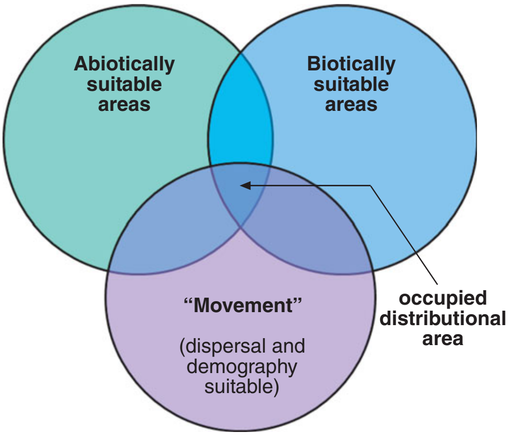

Figure 1. Diagram illustrating the three classes of factors affecting species distributions: abiotic variables, biotic interactions, and contingent factors related to "movement" (dispersal and demography).[9] This diagram can be thought of as geographic space, rearranged to group together those pixels that have the same characteristics for each of the three classes. Each circle contains the pixels suitable for that respective class, and the species only occurs where all three are favorable. Note that as used here, the "movement" class includes contingent factors associated with both dispersal and demography (e.g., minimum patch size necessary to maintain populations).

Transfers between environmental and geographic spaces are only bidirectional when considering the conditions and areas suitable for the species (Table 2). The abiotic conditions suitable for a species in environmental space (if known) can be applied to geographic space to identify those areas matching its requirements for the examined environmental variables. Conversely, environmental information from areas matching a species' abiotic requirements (if known) can be extracted from geographic space and then projected to environmental space. That subset of environmental space represents, with regard to the variables considered, the abiotically suitable conditions that exist in the study region in question. It has been termed the *existing fundamental niche*:[9] that portion of the fundamental niche that exists in the study region and time period of analysis (sometimes termed the *potential niche*).[22]

Inversely, however, transfers between environmental and geographic spaces are not bidirectional when considering the conditions and areas that the species truly occupies (i.e., the contingent realities of nonequilibrium distributions; Table 2). For example, environmental information from areas that a species occupies can be extracted from geographic space and then projected to environmental space—representing the abiotic conditions that the species occupies in the study region in question. Nonetheless, and of paramount importance, a characterization in environmental space of the abiotic conditions occupied in the study region cannot be projected back onto geography for the purpose

Table 2. Summary of transfers between environmental and geographic spaces

Geographic space	Directionality of transfer	Environmental (niche) space
Abiotically suitable area	⟷	Existing fundamental niche
Abiotically and biotically suitable distributional area	⟶	Biotically reduced niche space
Occupied distributional area	⟶	Occupied niche space

NOTE. Bidirectional transfers between geographic space and environmental space only are possible for regions in which the species is at equilibrium with abiotic variables (top row). In contrast, for study regions where biotic interactions and/or factors related to dispersal/demography cause nonequilibrium distributions, transfers only can occur from geographic to environmental space (second and third rows; see Fig. 1).

of identifying the areas actually occupied by the species. For instance, abiotic conditions occupied by the species in one area may exist in another part of the study region, but the species does not occur in the second area because it never dispersed there or went locally extinct (e.g., an isolated mountain range for a montane species, or a small patch of suitable conditions where the species cannot maintain populations), or the biotic context is not favorable (e.g., a superior competitor exists there, or a necessary mutualist is absent).[a]

Practical ramifications

The unidirectional nature of projections from geographic to environmental space when including the realities of nonequilibrium distributions forms a central tenet to understanding, building, evaluating, and applying niche models.[9] It also leads to principles for selecting predictor variables and occurrence data for niche models of suitability (outlined in section "Selecting data and transferring niche models"). These principles, subject to clearly defined assumptions, aim to minimize the effects of latent correlations of species occurrences with dispersal/demographic limitations and the distributions of biotic interactors. Such associations can lead to biases that restrict and distort estimates of the abiotically suitable conditions for a species.[28–32] Correlative models that follow these principles yield estimates of the conditions (and, by extension, areas) suitable for the species (Fig. 2). Such models differ from correlative models that intend instead to estimate the areas (and conditions) occupied by the species.[b] The latter models include the effects of dispersal/demographic limitations and biotic

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[a] For example, in northwestern South America, the spiny pocket mice *Heteromys australis* and *Heteromys anomalus* exhibit distributions that illustrate patterns consistent with both dispersal-related and biotic limitations. The species inhabit overlapping abiotic conditions (in environmental space) but show spatially complementary (parapatric) distributions in geographic space.[23–25] For each species, correlative niche models projected onto geographic space indicate disjunct areas of abiotically suitable conditions that the species does not inhabit, apparently because of barriers to dispersal in this topographically complex system.[26] Furthermore, in regions where the two species' distributions come into contact, *H. australis* consistently inhabits the areas that the models indicate as holding suitable abiotic conditions for either species (consistent with competitive exclusion of *H. anomalus*).[27]

[b] Because models estimating suitable conditions and areas differ in aim, assumptions, and required data from those that estimate occupied areas and conditions, the use of different terms would provide clarity of meaning.[17] Nevertheless, the field has yet to reach consistently used terminology to refer to the theory and methodologies employed in producing models for the two respective objectives. For example, varied meanings—implicitly or explicitly—have been given to the words bioclimatic envelope modeling, ecological niche modeling, habitat suitability modeling, species distribution modeling, and other related terms. Various methods and algorithms can be applied to fulfill one or both the two aims. Furthermore, even given data appropriate for the aim of a given study (see section "Selecting data and transferring niche models"), the particular method, algorithm, and settings (especially those regarding model complexity) employed can cause failure to achieve the stated goal, leading to models that predict an entity in between the conditions/areas suitable and the areas/conditions occupied.[33]

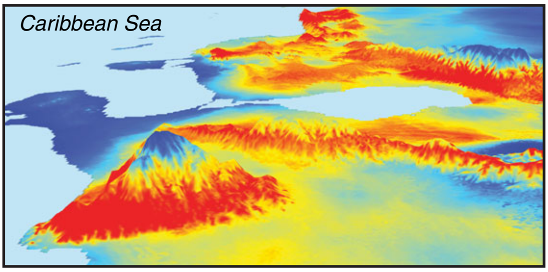

Figure 2. Example of a correlative niche model applied to geographic space to estimate the abiotically suitable area for the focal species (Table 2). Here, the modeled suitability gradient for the Caribbean spiny pocket mouse (*Heteromys anomalus*) is shown draped over a three-dimensional representation of elevation (note, scale for elevation does not match that for horizontal distances).[34] The color ramp illustrates the gradient of suitability from low (blue) to high (red). This species inhabits mesic forests at low and intermediate elevations but cannot survive in arid conditions (such as along the Caribbean coast) or cold environments (above ca. 1600 m).[24,35]

interactions upon species distributions, via their correlations with occurrence data and predictor variables. Only niche models of suitability are expected to hold predictive ability across space and time, subject to important additional assumptions detailed below (see section "Transfer across space or time").

Hence, this theoretical structure calls for joining two distinct analyses in order to predict species future distributions (but see a differing perspective).[5–8] Although predictions of future distributions need niche-based estimates of suitability (to allow transfer across time), they also require spatially explicit post-processing to reflect the reality that species do not disperse to or establish and maintain populations in all areas that are abiotically suitable for them.[36] Therefore, rather than a single step of modeling, these conflicting needs lead to two steps: (1) a niche model (characterizing suitability as a function of environmental variables), which can be transferred across time to predict future suitable areas for the species; and (2) a dispersal/demographic simulation that estimates the species' future occupied distribution, by considering the areas suitable for it then as well as spatially explicit realities regarding its occurrence, dispersal, and establishment. When used in tandem, niche models and dispersal/demographic simulations have been termed *coupled models*, *linked models*, or *hybrid models.*[12,37–40]

Selecting data and transferring niche models

Selecting predictor variables: three parallel classifications

To make fully niche-based models, researchers must follow important principles regarding the selection of predictor variables and occurrence data. Three parallel classification schemes provide helpful guidance when selecting variables and considering their utility under spatial or temporal transfer (Table 3). On the basis of the physiological effects for a given species, the first classification assigns variables as indirect, direct, or resource.[28] Indirect variables hold no physiological effect on organisms of the focal species but are correlated with the species' distribution because of correlations with other factors. Direct variables affect organisms of the focal species physiologically but are not consumed by them. Resource variables affect organisms of the focal species physiologically and *are* consumed by them. The second classification reflects the relative degree of causality of the focal species' response, with variables being either proximal or progressively more distal in causation (i.e., not in space). "Proximal and distal refer to the position of the predictor in the chain of processes that link the predictor to its impact" on the organism of the focal species (p. 105).[28] A proximal variable determines the organism's response. In contrast, a distal variable is only linked to the proximal variable (either causally or even more distally via noncausal correlation). Finally, variables may be classified by the effect that the focal species has on the variable itself. Scenopoetic variables are not affected by the presence of organisms of the focal species (scenopoetic derives from Greek roots for "setting the stage.").[9,41] On the other hand, nonscenopoetic variables *are* affected by the presence of organisms of the focal species. Because a variable's categorization under each of the three schemes relates to its relationship with the focal species, it can vary according to the particular species being studied. Furthermore, a given variable can be categorized into each of the three schemes, although not always independently. For example, indirect variables never can be proximal. Note that although direct variables often constitute abiotic scenopoetic variables, and resource variables frequently represent nonscenopoetic biotic factors, classification of biotic interactions into these three schemes requires

Table 3. **Three parallel classifications of environmental variables, with recommendations for correlative models of Grinnellian niches (Table 1)**

Basis of classification	Category	Definition	Abiotic examples	Recommendations
Physiological effect on focal species	Indirect variable	Does not affect organisms of the focal species physiologically but can be correlated with the species' distribution because of correlations with other factors	Elevation; latitude or longitude	Avoid if correlated with the focal species' distribution because of associations with factors related to dispersal/demography or with the distributions of important biotic interactors; use if correlated with the focal species' distribution because of correlations with driving abiotic variables; furthermore, use in models designed for spatial or temporal transfer only if the correlation with the driving variable is likely to hold across space/time
	Direct variable	Affects organisms of the focal species physiologically but is not consumed by them	Aspects of temperature; pH	Use whenever available
	Resource variable	Affects organisms of the focal species physiologically and is consumed by them	Water or nutrients in the soil	Use if scenopoetic
Relative degree of causality of focal species' response	Proximal variable	Determines the organism's response	(1) Available soluble soil phosphate concentration at root hair; (2) freeze durations that affect survival of cacti along poleward range margin	Use whenever available
	Distal variable	Linked to the proximal variable that determines the organism's response	(1) Total soil phosphate; (2) mean temperature of coldest month, or annual mean temperature (relatively more distal than the former)	Use if distal and direct; if distal and indirect, see "indirect variables" above; in either case, use in models designed for spatial or temporal transfer only if the correlation with the driving variable is likely to hold across space/time
Effect of focal species on predictor variable	Scenopoetic variable	Not affected by the presence of the focal species	Aspects of temperature or precipitation	Use
	Nonscenopoetic variable	Affected by the presence of the focal species	Water or nutrients consumed by a plant	Avoid

further development (see section "Issues requiring progress").

These classifications aid in selecting valid and useful predictor variables, especially for models that will be transferred across space or time. Researchers should consider a variable's classification into each of the three schemes to decide whether to use it in a niche model (Table 3). Direct and proximal variables should be used whenever possible.[28] Indirect and distal variables can be employed and may provide useful information due to their correlation with important direct and proximal variables (which commonly are either unknown or unobtainable). However, models based on indirect and distal variables will only retain their predictive ability in other places and times if the correlation with the underlying driving variable remains intact. Hence, when considering variables known or suspected to be indirect or distal, researchers should avoid using those likely to have inconsistent correlations with the driver across space and time. For example, as an indirect variable, elevation may provide a good proxy of temperature (a driving direct variable) within a given latitudinal band of a local-to-regional area. However, that association will differ at other latitudes and likely in areas with different prevailing winds or rainfall patterns. Similarly, models utilizing proximal variables more likely to affect survival or phenology of the organism (e.g., freeze durations affecting survival) likely will transfer better than those based on commonly used distal variables that summarize climate via annual or quarterly means.[42,43] In contrast to these circumstances where indirect and distal variables can prove useful for modeling suitability—and sometimes for spatial or temporal transfer—researchers should avoid using indirect and distal variables that are correlated with the species' distribution not because of correlations with driving abiotic variables, but rather because of associations with factors related to dispersal/demography or with the distributions of important biotic interactors. Indirect and distal variables of this variety (e.g., spatial, nonenvironmental variables like latitude and longitude), likely would aid in estimating the species' occupied distribution but restrict the prediction to less than all of the abiotically suitable areas (see discussion on the noise assumptions below), both in the present and under spatial or temporal transfer.

Finally, correlative models of Grinnellian niches assume that predictor variables are scenopoetic (not affected by the presence of the focal species; Tables 1 and 3). Scenopoetic variables represent density-independent factors that characterize the conditions permitting positive intrinsic population growth rates for the focal species.[41] Such factors can be modeled using static sets of numbers, via many existing correlative methods (that identify subsets of multivariate space).[9,44] In contrast, nonscenopoetic variables constitute density-dependent factors whose values are dynamically linked to the population level of the focal species (affected by, and in turn affecting the instantaneous population growth rate of the focal species). Because of that dynamic feedback, including consideration of their influence on species distributions requires more complex (e.g., resource–consumer) models of the Eltonian niche.[45] Frequently, biotic interactors represent nonscenopoetic variables, leading to many of the challenges of integrating biotic interactions into niche models, especially for transfer across space or time (see section "Issues requiring progress").

Selecting occurrence data: environmental domain, bias, and noise

The assumptions. Similarly, the theoretical framework provided above guides the selection of occurrence data for correlative niche modeling, both regarding records of the species' presence, and for sites that provide absence, absence-like, or background information with which to compare (hereafter referred to as comparison data). Most correlative niche modeling techniques contrast the environmental information found at presence records to that in a comparison data set.[44] Such data sets typically consist of either sites where biological sampling has not detected the species, or a sample of sites designed to provide a characterization of the environments available to the species (whether or not it occupies those sites).[c] Comparison of the two data sets (presence records versus comparison sites) allows for the production of models that characterize the signal of the species' niche: its response to the examined abiotic variables.

Interpreting the output of correlative niche models as an estimate of abiotic suitability requires several assumptions, which apply to all types of comparison data. By definition, presence records come from the species' occupied distribution, which is influenced by several classes of factors. The abiotic conditions found in those occupied areas correspond to the species' occupied niche space (often termed the *realized niche*) in the study region of analysis. Even assuming that all occurrences represent demographic sources and that biological sampling was unbiased, presence records may provide incomplete and/or distorted characterizations of the species' fundamental niche for the examined abiotic variables. Two issues contribute to this problem: (1) a limited range of environmental conditions in the study region; and (2) nonequilibrium distributions.

First, estimation of the fundamental niche requires what I term the *niche space assumption*: that the study region (for correlative niche modeling) or experiments (for mechanistic niche modeling) contain the full range of abiotic conditions that the species can inhabit, for the examined abiotic variables (Table 4). When the study covers a smaller environmental domain, this assumption is not met. In such cases, niche modeling can, at best, estimate the subset of the fundamental niche that exists in the study region (for correlative niche modeling) or in the experimental conditions (for mechanistic niche modeling)—that is, the existing fundamental niche[9] (= potential niche of some authors).[22] Clearly, we

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[c] Varied usage of terms regarding comparison data exists in the literature, but I follow the following definitions:[9] (1) assumed absences (sites where biological sampling occurred but the species was not observed, ideally via repeated sampling);[46] (2) pseudo-absences (sites where the species was not observed, whether or not biological sampling occurred there); or (3) background information (sites used to characterize the conditions available for the species, generally via random samples from the study region). In practice, pseudo-absence and background samples will prove very similar when biological sampling has been sparse across the study region, but they can differ substantially in situations where a sizeable proportion of the pixels in a study region have been sampled.

Table 4. Four assumptions associated with data used in niche models estimating abiotic suitability for a species, with recommendations for correlative models of Grinnellian niches

Name of assumption	Assumption	Consequences of violation	Recommendations
Niche space assumption	The study contains the full range of conditions that the species can inhabit (for the examined abiotic variables)	The existing fundamental niche is smaller than the fundamental niche; the species' response is truncated for one or more abiotic variables	Use presence records from many portions of the species' range and over multiple time periods; examine response curves and detect truncations in calibration region
Dispersal/ demographic noise assumption	Factors related to dispersal, establishment, and persistence do not cause the species to occupy an environmentally biased subset of the abiotically suitable areas	The occupied niche space is smaller than the existing fundamental niche; the species' response is truncated and/or distorted for one or more abiotic variables	Use occurrence data (presence records and comparison data) only from regions where the species is at equilibrium with abiotic variables or where limitations caused by dispersal/demography, biotic interactions, or human modifications do not cause the species to occupy an environmentally biased subset of the abiotically suitable areas
Biotic noise assumption	Biotic interactions do not cause the species to occupy an environmentally biased subset of the abiotically suitable areas	Same as above	
Human noise assumption	Human modifications of the environment do not cause the species to occupy an environmentally biased subset of the abiotically suitable areas	Same as above	

Note. The niche space assumption applies to both mechanistic and correlative niche models (Fig. 3). Similarly, the noise assumptions apply to both but in practice hold most relevance for correlative models. For correlative models, the study region for selecting occurrence data (both positive records and comparison data) is key for considering the three noise assumptions (Fig. 1). In contrast, for mechanistic models, those assumptions apply with regard to the environmental conditions of the experiments.

would like to know how closely the existing fundamental niche of a given study approximates the full fundamental niche.

Researchers can assess some aspects of the niche space assumption using response curves generated from either correlative or mechanistic niche models. Such curves correspond to a graph of the species' response (some measure of suitability) on the y-axis, versus the variable itself on the x-axis.[47,48] The relevant issue is whether the environmental domain of the study truncates the species' response curve to a given abiotic variable at a suitability value sufficiently high to support the presence of the species (Fig. 3).[22] Such a truncation indicates a violation of the niche space assumption. However, if a violation is detected, mere examination of response curves cannot determine the extent of the violation, which would require further correlative modeling or mechanistic experiments in the environmental domain beyond the conditions of the initial study. Furthermore, such inspections may fail to detect some truncations. Unfortunately, low estimated suitability values could be caused not by the abiotic variable itself but rather by an unfavorable biotic context associated with those values of it (see discussion on the biotic noise assumption, and section "Issues requiring progress"). The same confounding situation could derive from human modifications of the environment (see discussion on the human noise assumption). In any case, when a truncation is detected, researchers must take special care when transferring the model to a second region or time period. Complications for transfer exist if the new region or time period holds conditions more extreme (for one or more abiotic variables, or for combinations of variables) than those available in model calibration. Such situations are termed *nonanalog conditions*, which limit the confidence that can be drawn from predictions into such regions (see section "Transfer across space or time").[49–51]

Second, dispersal/demographic limitations, biotic interactions, and human modifications of the environment can cause presence records to represent a reduced and/or distorted estimate of the species' existing fundamental niche. Correlative niche models assume that presence records constitute unbiased samples reflecting the species' niche signal (its response to the abiotic predictor variables). In an idealized study region where the species is in equilibrium with abiotic variables, by definition these factors do not cause a violation of this assumption. Because of this, recent literature has considered equilibrial distributions necessary to fulfill the assumptions required for model

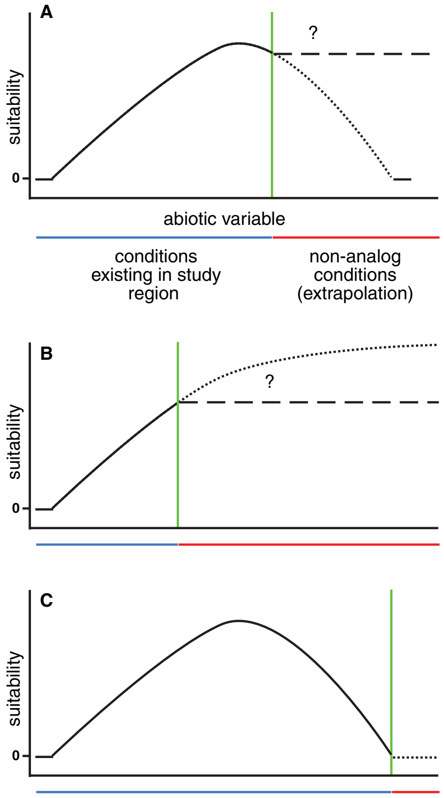

Figure 3. Hypothetical univariate response curves illustrating environmental truncations in the study region (for correlative niche modeling) or experimental conditions (for mechanistic niche modeling), highlighting issues related to environmental extrapolation into nonanalog conditions. Each panel illustrates a species' modeled response curve for a given abiotic variable (x-axis), plotted against suitability (y-axis). Conditions within the environmental domain of the study region or experimental conditions are indicated in blue, and red denotes those beyond that domain (nonanalog conditions). Application of a niche model to regions or time periods (or experimental conditions) holding nonanalog conditions (beyond the vertical green bar) requires extrapolation in environmental space. The panels show various possible scenarios: (A) a response curve truncated at a high but decreasing suitability value; (B) a response curve truncated at a high and increasing suitability value; and (C) a response curve where the environmental domain of the study encompasses the species' full response to the abiotic variable. Extrapolations in environmental space constitute risky endeavors when the species' response is truncated (A and B). Two possibilities are shown: allowing the model to estimate the response without any constraint (dotted line) versus "clamped" to the modeled suitability value at the point of truncation (dashed line).

calibration.[8,9,29,30] However, in nonequilibrium situations, the effects of these nonabiotic factors do not necessarily lead to *biases* in the information provided regarding the species' niche signal. Rather, out of all of the abiotically suitable areas, the particular ones occupied versus not occupied might merely add noise to the data set, without distorting the species' niche signal. Furthermore, it is possible that variation in the species' abundance due to these nonabiotic factors would only generate noise, rather than bias. Therefore, rather than strict equilibrial conditions, correlative modeling of the existing fundamental niche requires assumptions regarding bias versus noise in the sample of occurrence data.

I formalize these assumptions regarding occurrence data as the dispersal/demograpic noise assumption, the biotic noise assumption, and the human noise assumption (Table 4). Each relates to the situation for a particular species in a given study region. They acknowledge the pervasiveness of nonequilibrium distributions, where a species occupies a subset of the *geographic* areas that are abiotically suitable for it, and instead focus on the relevant issue of the corresponding *environmental* information. First, in the *dispersal/demographic noise assumption*, factors related to dispersal, establishment, and persistence do not cause the species to occupy an environmentally biased subset of the areas abiotically suitable for it. Similarly, in the *biotic noise assumption*, biotic interactions do not cause the species to occupy an environmentally biased subset of the areas abiotically suitable for it.[d] As

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[d] A recent theoretical treatment of niches and distributions proposed a concept closely related to, but not exactly equivalent to, the biotic noise assumption defined here. Biotic interactions often influence the dynamics of Eltonian niches, which can determine the particular species present in a local community, as well as their abundances (Table 1). These processes typically occur at grain sizes smaller than those relevant for the scenopoetic variables used in correlative niche models of Grinnellian niches.[53] Owing to this difference in scale, biotic interactions might not have any manifestations, or at least not consistent ones, when local small-grain pixels are aggregated to the coarser grain of (typically abiotic) scenopoetic variables. Rather, local differences in the outcomes of Eltonian processes might only lend noise to the coarser-grain information relevant for Grinnellian niches. The idea leads to the conjecture that at the grain of the Grinnellian niche, the areas abiotically suitable for a species generally will be biotically suitable as well, termed the *Eltonian noise hypothesis*.[9] This general hypothesis requires empirical testing for specific systems, and many counter examples exist where biotic interactions do influence species distributions at broad geographic extents.[54,55]

a predictor variable, humans, of course, technically represent a biotic interactor. However, our actions lead to strong and pervasive effects upon local environments, those effects can vary over relatively short time frames, and many variables exist that characterize the results of human modifications of the environment (especially remotely sensed variables associated with vegetation/land cover; see section "Issues requiring progress"). Therefore, it is useful to ponder human-caused biases separate from those of other species. This leads to the *human noise assumption*: that human modifications of the environment do not cause the species to occupy an environmentally biased subset of the areas abiotically suitable for it.[e]

If any of these assumptions are not met in a given study (or, more likely, to the degree to which they are violated), the niche model will constitute an incomplete and/or distorted estimate of the species' existing fundamental niche. This theoretical structure leads to principles for selecting occurrence data, specifically regarding the characteristics of study regions more likely to match these assumptions and allow for niche models that provide more realistic forecasts when transferred across space or time. Situations that add only noise (not environmental bias) are probably more common at local-to-regional scales and over shorter time spans, for example via metapopulation dynamics.[52] Nevertheless, the topic of nonequilibrium distributions and violation of these assumptions remains an empirical question for research.

The principles. These assumptions lead to principles for selecting presence records and comparison data, although conflict may sometimes exist between the niche space assumption and the three noise assumptions. Overall, presence records should derive from many portions of the species' range and, ideally, from various time periods.[31,32,36] However, presence records must be matched to environmental data from the same time period as when they themselves were collected. Owing to heterogeneities in the abiotic conditions available, broad spatial and temporal sampling increases the likelihood that the data encompass the full environmental domain of the species' tolerances, and hence fulfill the niche space assumption (Table 4). Following this principle is relevant whether or not the application at hand requires transfer. However, combining data collected in different regions and time periods assumes no genetic differences across space or time (for traits related to the species' response to the examined abiotic variables), or heterogeneity in the nature of relevant biotic interactions (see section "Transfer across space or time").

While broad spatial and temporal sampling should tend to help match the niche space assumption, it can either increase or decrease the likelihood of fulfilling the noise assumptions. For example, broad spatial and temporal sampling can either dilute or reinforce any environmental biases caused by dispersal-related or demographic factors (violation of the dispersal/demographic noise assumption), depending on whether individual regions or time periods suffer similar or different biases. The same applies to the biotic noise assumption and human noise assumption. However, it seems likely that combining data from a variety of biotic contexts present across space and time would tend to yield less biased information regarding the species' response to the abiotic predictor variables, at least regarding the extreme values of its tolerances.

Additionally, the three noise assumptions lead to principles for selecting occurrence data for use in niche models (Table 4). These principles apply simultaneously to both presence records and comparison data, although emphasis usually lies on the latter. In selecting a study region for modeling, a researcher aims to avoid regions where nonequilibrium distributions reduce or distort the species' response to abiotic variables. For example, if the focal species is absent from a region of abiotically suitable conditions because it never dispersed there (or went extinct), using comparison data from that region can send a false negative signal (if the dispersal/demographic noise assumption is violated).[29,30] Similarly, if the biotic context does

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[e] The human noise assumption is especially important in regions of high human modification of the environment. In such situations, older records (e.g., from natural history museums and herbaria) can provide documentation of abiotically suitable areas where the species no longer occurs (e.g., due to habitat modification by humans). If those areas hold abiotic conditions different from the places with abiotically suitable conditions that still hold appropriate habitat for the species, the older records prove critical for estimating the species' response to the abiotic variables.

not allow a species' persistence in an area that is abiotically suitable, violation of the biotic noise assumption or human noise assumption would do the same. Furthermore, even if biotic interactions or human modifications do not prohibit the species' presence in an abiotically suitable area, they still can violate the corresponding noise assumptions by reducing its abundance and, hence, distorting its response curves to abiotic variables. Technically, the same is true for dispersal/demographic limitations as well, if small patches of suitable habitat receive dispersing individuals but are not large enough in area to maintain a population at the carrying capacity that would be commensurate with the abiotic conditions. However, that issue seems less likely to affect occurrence data profoundly.

Hence, occurrence data should derive from a study region where the species is in equilibrium with abiotic conditions, or where any reductions caused by dispersal/demography, biotic interactions, or human modifications only add noise (i.e., not bias) to the data.[f] Clearly, full information regarding these factors never will be available. However, these assumptions can be tested, for example via comparison of the results of mechanistic and correlative models. Furthermore, researchers can and should take advantage of relevant available information regarding the species and study region, such as the position of obvious or likely geographic barriers to dispersal. Furthermore, the distributions of important known or suspected interacting species, such as congeneric species with parapatric distributions, represent prime candidates for consideration.[54] To whatever degree the study region employed more closely approximates these assumptions, the resulting niche model should be correspondingly more realistic. The effects of study region selection on niche estimates—and corresponding predictions of abiotically suitable areas in geography—apply whether or not the model is transferred across space or time.

Unfortunately, fulfilling or at least more closely approximating the noise assumptions may necessitate the use of a smaller study region that corresponds to a smaller subset of the species' fundamental niche (i.e., a greater violation of the niche space assumption). Frequently, barriers to dispersal can cause this situation. For example, a region on the other side of a dispersal barrier might contain areas holding suitable conditions that are more extreme for one or more abiotic variables than are any suitable areas that exist in the region where the species actually occurs. For biotic interactions and human modifications of the environment, environmental biases may occur even if those factors do not prohibit the occurrence of the focal species, but rather merely reduce its abundance. As a hypothetical example, a species might co-occur with an important competitor through half of its range, where the competitor reduces the focal species' abundance but does not prohibit its occurrence. If the two parts of the range differ in abiotic conditions, the effect of the competitor would distort the focal species' response curves for those abiotic variables. In such situations, making models with data from only the portion of the focal species' range where the competitor is absent should lead to more realistic estimates of the species' response curves. Similar examples, at least in theory and likely also in practice, exist for other classes of biotic interactors. The possibility of such biases may be quite important with regard to the human noise assumption.

In all of these situations, use of a smaller study region (to accommodate the noise assumptions) could lead to a reduction in the existing fundamental niche modeled, requiring extrapolation in environmental space if the model is transferred to nonanalog situations. Nevertheless, it is better to gain an unbiased estimate in a smaller subset of environmental space, rather than a biased estimate in a larger subset of environmental space. The former situation

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[f] The principles for study region selection outlined here differ somewhat from those in some of the recent literature, which considered that niche models should be both calibrated and evaluated in regions where the distribution of the focal species is in equilibrium with abiotic conditions.[9,29,30] Here, the three noise assumptions instead clarify that the relevant issue is whether the areas occupied in the study region represent an environmentally biased subset of the areas abiotically suitable for the species. Equilibrial distributions are sufficient but not necessary conditions for fulfilling those assumptions. It is important to note, however, that *assessing* a niche model of suitability (rather than a model of the species' occupied distribution) does require equilibrial conditions for the study region used for evaluation.[9] To the degree that this assumption is violated (with a study region holding unoccupied areas of abiotically suitable conditions), the evaluation will tend to underestimate the performance of a correct model of suitability.

corresponds to a niche model that encompasses a smaller existing fundamental niche (fulfilling the relevant noise assumption but more strongly violating the niche space assumption). In contrast, the latter estimates a larger existing fundamental niche (better matching the niche space assumption, at the expense of violations of the noise assumption). As a possible resolution to some of these unsatisfying tradeoffs, the possibility of integrating biotic interactors as predictor variables may alleviate such dilemmas (see section "Issues requiring progress").

Transfer across space or time

Two conceptual issues come to the forefront when transferring correlative niche models across space or time: strategies for evaluation, and extrapolation in environmental space. Normally, models are evaluated in the same study region as they were made. However, models can perform well under those conditions yet fail in others. Therefore, in order to afford confidence for transfers across space or time, some demonstration of effective transfer should be provided. Except for relatively rare situations when data for past time periods are available,[32] evaluations of predictive ability must be undertaken across space as an, albeit imperfect, substitute for time.[56] Sometimes, "natural experiments" provide meaningful distinct geographic regions for such evaluations, for example nonnative (especially invasive) species or others found in multiple biogeographic regions.[57,58] In other cases, researchers can divide occurrence data spatially for model building and model evaluation;[59,60] such strategies require assumptions that match or mirror those necessary for transfer across time.

Key in any transfer is the general assumption of stationarity: that the species' response to predictor variables does not vary across space or time.[61] Specifically, no genetic differences (e.g., local adaptation across space, niche evolution over time) should exist across space or time for traits associated with abiotic suitability. Similarly, neither the nature of important biotic interactions nor the presence of key interactors should differ between the calibration and projection regions or time periods (but see section "Advancements regarding biotic variables"). Furthermore, if the second region or time period contains nonanalog conditions, the required extrapolation in environmental space rests on further assumptions detailed below.[62–64]

Transferring niche models (either correlative or mechanistic) into nonanalog environmental conditions constitutes a risky endeavor. Although details of the shape of the species' response can vary tremendously, abiotic variables that are continuous in nature typically elicit curves with two tails: low suitability at low values for the variable, increasing to high suitability at intermediate values, and then decreasing to low suitability at high values (Fig. 3). Response curves truncated at a high suitability value raise a cautionary flag for transfer. The situation is especially hazardous when the response curve is increasing at the point of truncation.[17] In contrast (and assuming unimodal responses), response curves presenting low suitability at the extreme of the examined environmental domain pose relatively little danger when transferred to another place or time. In addition to conditions more extreme for single predictor variables, researchers also should take into account combinations of conditions that do not exist in the calibration region. For that purpose, Multivariate Environmental Similarity Surfaces (MESS) analysis allow a researcher to identify regions holding nonanalog conditions and characterize the degree of extrapolation necessary.[65,66]

If a species' response is truncated and the second region or time period includes environmental conditions that are more extreme, some assumption must be made in order to make a prediction.[29,51,67] Various approaches exist for making predictions into nonanalog conditions. Two tactics spanning the spectrum of possibilities are (1) setting the prediction to zero outside the range of conditions used to build the model; and (2) allowing the models to estimate the response without any constraint (e.g., in some implementations of generalized additive models; GAMs).[60,67,68] An intermediate option is "clamping" the species' response at the suitability level of the truncation point (e.g., in Maxent).[69] For generalized linear models (GLM) and GAMs, particular kinds of splines that are either constant or linear beyond the range of the calibration data can be used (a constant response is equivalent to clamping in Maxent).[66] Notably, although intermediate methodologically, clamping does not necessarily constitute a more reasonable tactic than allowing extrapolation without constraint, for example when a response curve is decreasing when truncated (Fig. 3A). When projection into

Table 5. **Summary of research agenda for correlative niche models of Grinnellian niches (aimed at estimating suitability), including applications requiring transfer across space or time**

Category	Issue requiring progress
Abiotic variables	Model interactions between pairs of abiotic variables (including nonclimatic ones) Integrate rapidly changing abiotic variables as predictors, ensuring temporal correspondence with occurrence data (e.g., for remotely sensed variables)
Biotic variables	Determine whether biotic variables are scenopoetic or not; integrate scenopoetic biotic variables as predictors, and model their interactions with abiotic variables Determine how to take into account biotic variables that are nonscenopoetic and therefore cannot be used as predictor variables in Grinnellian niche models (i.e., instead, use them in post-processing or in Eltonian niche models) Use probability of occurrence or abundance of the interacting species
Genetic heterogenetity	Integrate genetic heterogeneity into calibration of niche models and into dispersal/demographic simulations
Uncertainty	Quantify uncertainty for each constituent factor/step Calculate uncertainty with full error propagation Display uncertainty spatially

nonanalog conditions is necessary, researchers should document the method of extrapolation and illustrate the extrapolated portion of the response curve. Furthermore, in geographic space, researchers should provide maps identifying the geographic areas involved and quantifying the degree of environmental extrapolation.

Issues requiring progress

Advancements regarding abiotic variables

I highlight two underappreciated issues regarding abiotic variables: (1) interactions among variables; and (2) and complications regarding variables whose values change rapidly over time. Ideally, researchers would include consideration of the effects of interactions among abiotic variables (Table 5). For example, a species may be able to inhabit fairly broad ranges of both temperature and precipitation, leading to seemingly simple characterizations of their response curves to each respective variable. In reality, however, only some values of one of those variables may be suitable for the species, depending on the value experienced for the other. For example, in northwestern South America the spiny pocket mouse *Heteromys australis* can inhabit areas with lower precipitation if at high elevations; these altitudes experience much lower evapotranspiration (primarily because of cooler temperatures), leading to a functionally more mesic environment than lowland areas with the same precipitation.[27] Although considerations of such relationships are not commonplace in current studies, they likely will prove important for all uses of niche models, including those requiring transfer. One avenue for doing so is via modeling interactions between pairs of variables (e.g., via use of product features in Maxent).[70] Another is to include variables that themselves represent derived combinations of variables.[71]

Furthermore, nonclimatic abiotic variables may interact with climatic ones. Such interactions include what have been termed *associations* with edaphic, atmospheric, or hydric factors.[72] For instance, the existence of a given soil type may prevent the presence of a tree species (or entire forest ecosystem) that would normally be supported in a given climate. Similarly, local atmospheric conditions—such as windy ridges or fog-enveloped mountain peaks—alter the environment beyond that expected by macroclimatic variables.[73,74] Finally, surface water (e.g., streams and lakes) clearly supersedes macroclimate to alter the suitability at a site, either increasing or decreasing the suitability for a species. The effects of any of these classes of associations may bias the species' relationship with other variables, affecting the modeled response curve. Effective consideration of such issues in correlative models requires substantial development, even without transfer across space or time. Whereas edaphic features likely will remain fairly constant in the near future, modeling future atmospheric and hydric associations presents serious methodological challenges.

Additionally, special issues exist when researchers use variables whose values change rapidly over time (Table 5). Temporal correspondence between occurrence data and environmental data constitutes a key principle for any correlative niche model. If such correspondence does not exist, the researcher must assume no change in the environmental variable between the time that the data regarding it were collected and the period corresponding to the occurrence records. For example, it may be reasonable to associate occurrences from various decades of the early and middle 20th century with climatic averages for the 1950s. In contrast, such associations may prove highly problematic for some variables whose values have changed rapidly. For example, remotely sensed data can hold important benefits for niche modeling, especially when human modifications of the environment have been substantial.[g, 75–78] Similarly, some studies aim to assess distributional shifts and their possible relationship to relatively rapid climatic changes over recent decades.[46] In either case, the use of rapidly changing variables requires recent occurrence data. Additionally, temporal transfer of models that include remotely sensed variables requires projections of the same variables into the future. Although true measurements obviously will not exist, simulations of land use change do, albeit with their own uncertainty.[79]

Advancements regarding biotic variables

Consideration of biotic variables in correlative niche models remains one of the areas most in need of theoretical and methodological advances. The intertwined nature of ecology makes it impossible to collect observational records of any species divorced from the effects of species interactions. Nevertheless, correlative models based solely on abiotic variables have proven informative and useful for myriad species. Indeed, much literature considers that biotic interactions hold effects only at local scales (Eltonian noise hypothesis, see footnote *d*).[9] However, many studies have demonstrated that biotic interactions can and often do impose strong effects on species distributions at large geographic extents.[54,55,80,81] This issue profoundly affects choices regarding the study regions from which to select occurrence data for modeling (see section "Selecting occurrence data: environmental domain, bias, and noise"). Furthermore, in recent years, many researchers have explored ways to improve niche models by including consideration of biotic interactions in model calibration or in post-processing.[27,82–86]

No consensus yet exists regarding whether a known or suspected biotic interactor should be included as a predictor variable, or considered later in interpretation and post-processing of the prediction for the species (made using only abiotic variables; Table 5). Clearly, many biotic variables represent resources, which intuitively seem appropriate as predictor variables; however, including such variables violates principles of modeling Grinnellian niches if they are substantially affected by the focal species.[28] One path towards progress would be to assign classes of interactors as either variables unaffected by the presence and abundance of the focal species (scenopoetic variables), versus those that are affected by it. By extension of existing theory, scenopoetic variables—even if biotic in nature—could then be included as predictors in models of Grinnellian niches (Table 1).[9]

Such advances could make niche models much more realistic, but various associated topics require development. Progress is needed regarding detection of truncations in a species' response to an abiotic variable, caused by biotic interactions rather than by the lack of available conditions in the study region (see discussion on the niche space assumption).[86] More generally, the presence or absence of an interacting species (and its abundance) indeed could affect the focal species in either a positive *or* negative manner, as well as distort its response curve substantially without producing a full truncation.[87] In either case, when not considered explicitly in model calibration, the (latent) effects of a biotic interaction upon the focal species' response to abiotic variables are in effect built into the model. Furthermore, transferring such a model across space or time requires assuming that both the nature of the biotic interaction and the presence of

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[g] Note that many remotely sensed variables reflect aspects of vegetation/land cover. Although not constituting abiotic variables in the strict sense, such vegetation-related variables correlate with physical aspects of the environment and behave more like abiotic factors than like biotic variables characterizing species interactions.

the interactor do not differ in the new region or time period.[88,89]

Therefore, including the distribution of an interacting species as a predictor variable (ideally its abundance) should allow for better estimation of the focal species' response curves for abiotic variables. Two possible tactics to disentangle the effects of the two classes of factors could be via modeling of interactions between abiotic and biotic variables; or perhaps via hierarchical modeling.[8,90] Notably, inclusion of biotic interactors as predictor variables offers a solution to the dilemma mentioned above regarding conflicts between the niche space assumption on one hand and the biotic noise assumption and human noise assumption on the other, potentially allowing unbiased characterization of the species' niche over a broader environmental domain. Furthermore, inclusion of the biotic interactor as a predictor variable should allow for transfer to places or time periods where the presence or abundance of the interactor differs from the calibration region and time. In contrast, however, both model calibration and transfer assume that the *nature* of the biotic interaction (the effect of the interactor on the focal species) does not vary. This assumption sometimes is not reasonable, for example in mutualisms that switch to predator–prey relationships in parts of the ranges of the co-occurring species.[91]

Other challenges exist for incorporating the effects of biotic interactions. Foremost, progress is needed in determining how to consider the effects of biotic interactors that cannot be used as predictors (i.e., that do not constitute scenopoetic variables; Table 5). In some cases, using them only in post-processing may be reasonable.[27] In contrast, other biotic interactions may prove feasible and appropriate for inclusion only in models of Eltonian niches relevant at local scales. Additionally, whether used as a predictor or in post-processing, the distributions of interacting species often are represented merely as binary maps. Continuous (ideally probabilistic) representations of biotic interactors represent a substantial step forward but should be at least proportional to probabilities of *occurrence* (or, ideally, abundance estimates),[92,93] rather than merely to probabilities of *suitability*—since the species must truly be present in order to interact with the focal species. Finally, similar to the situation with remotely sensed variables mentioned above, the use of biotic interactors as predictors will require projections of the distributions of those species in the future (notably, of their occupied future distributions, not merely the areas suitable for them in the future). These complications illustrate the serious complexity of integrating information from various classes of driving factors to make realistic predictions of species distributions in the future.

Genetic adaptation across space and time

Overwhelmingly, recent studies transferring niche models assume that no niche differentiation exists across the species' range, or over time. For some species, the causal factors limiting the distribution have been shown to differ across range margins (e.g., poleward versus equatorial; or upper versus lower elevational limits).[43,94] More importantly, in some documented cases, genetic variation among populations corresponds to traits that directly affect range boundaries or that influence their response to climatic change.[95,96] Complementarily, the burgeoning literature assessing niche evolution versus conservatism highlights the fact that, at least over longer time spans, species niches indeed evolve.[97] Key outstanding questions include how often, how substantially, how quickly, under what conditions, and how predictably niches evolve.[98–102] Studies of the distributions and evolution of non-native species provide an important knowledge base for future research regarding these issues.[58,103] Of promise, dispersal/demographic simulations can consider the effects of local adaptation (or non-adaptive genetic differences) related to the species' response to abiotic variables, when such data are available.[102,104,105] Ultimately, information regarding genetic heterogeneity should be integrated into the calibration of the correlative models,[99] for example by explicit consideration of genetically differentiated entities within currently recognized species (Table 5). Overall, however, the repercussions of geographic and temporal genetic heterogeneity in predictions of future species distributions remain even less understood than consideration of the effects of biotic interactions.

Quantifying uncertainty

Very few studies quantify uncertainty in predictions of species niches and associated suitable areas, but emerging methodologies allow for this necessary, cross-cutting issue (Table 5). Uncertainty enters into the modeling endeavor at every step, for example, due to error, bias, or incompleteness

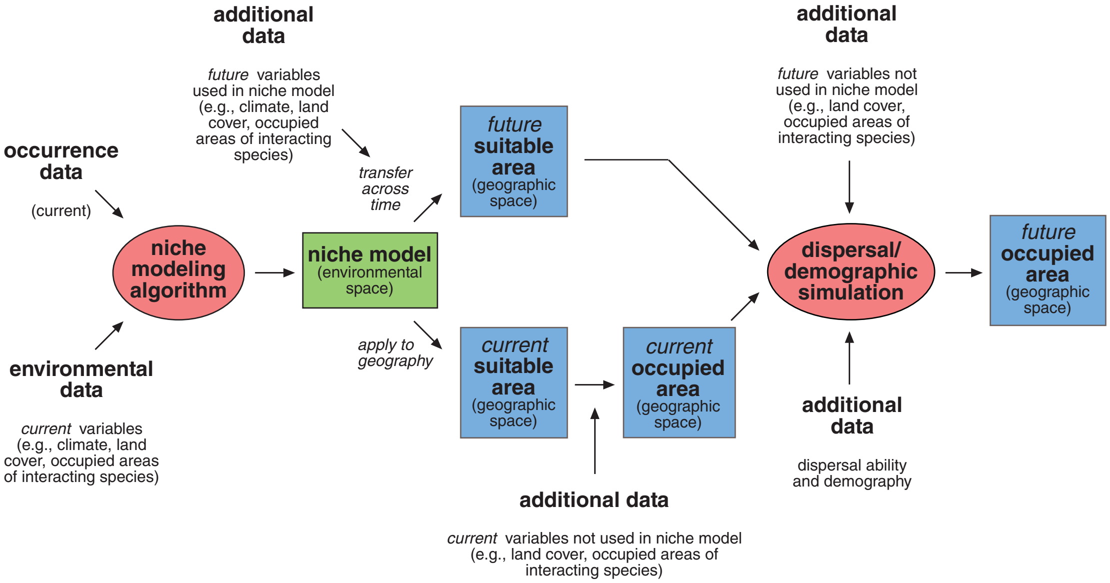

Figure 4. Flowchart illustrating the use of correlative niche models linked to dispersal/demographic simulations to approximate a species' future occupied distribution. Ovals represent algorithms (red), and rectangles denote the entities being estimated (green indicates environmental space; blue signifies geographic space). Note that the needs of the dispersal/demographic simulation depend on which classes of variables were used as predictors in the niche model. Specifically, future land cover (or vegetation) and the future occupied areas of interacting species enter into consideration in transferring the niche model across time if they were used as predictor variables in the niche model; otherwise, they constitute inputs into the dispersal/demographic simulation.

of occurrence data or environmental data; grain of analysis; study region; modeling technique and settings; assumptions regarding truncated response curves and extrapolation in environmental space; and issues regarding data for and implementation of dispersal/demographic simulations. Recent work provides frameworks for quantifying uncertainty at multiple steps, including propagation of error through each stage of modeling.[38,106–108] Ideally, quantifications of uncertainty should be spatially explicit, providing a map of uncertainty along with the value of predicted suitability itself. Maturation and widespread use of these approaches will provide users the relevant quantitative context in which model predictions should be interpreted. Furthermore, it could guide both research and data-collection efforts aimed at reducing uncertainty at the steps identified as most needing improvement.

Linking niche models to dispersal/demographic simulations

Once built following the principles outlined above, a niche model can be linked to a dispersal/demographic simulation to estimate the areas that the species will occupy in the future. Such simulations require substantial data inputs, many of which depend on the nature of the variables included (or not) as predictors in the niche model (Fig. 4). Hence, although the two modeling steps remain distinct coupled or linked procedures (but see a differing viewpoint),[5–8] they must be undertaken with a single coherent vision. As mentioned before, the dispersal/demographic simulation requires a seed: an estimate of the species' current occupied distribution. Fortunately, selection of a study region approximating the noise assumptions leads to an estimate of the abiotically suitable distribution that typically should be very similar to the occupied distribution (at least if the niche model is projected to the same study region as was used for calibration). Nevertheless, researchers still need to take into account issues of sampling adequacy, local dispersal, and demographic limitations (e.g., small patches of suitable conditions), and any remaining known biotic interactions that limit the species' distribution.[27,109] Furthermore, unless variables reflecting current vegetation/land cover were included as predictors, models should be processed to remove areas where the current land cover does not permit the species' presence.[110] Such processing requires natural history data (e.g., the general habitat/vegetation/land cover requirements of the species) and/or analyses comparing such variables with current records of the species.

The dispersal/demographic simulation then models—in a spatially explicit fashion—dispersal to and establishment in areas identified as suitable by applying the niche model to projections of future environmental conditions.[36–38,111–114] In addition, the simulations model the persistence of populations in areas no longer suitable according to the niche model. These analyses require either data or assumptions regarding the species' dispersal ability and demography (e.g., shape of the dispersal kernel, intrinsic population growth rates, and minimum areas necessary to maintain a population). Some advanced techniques conduct a population viability analysis (PVA) in explicit geographic space for each time period, linking succeeding time slices with the results of the PVA from the previous iteration.[40] The simulations should integrate information regarding the distributions and abundances of key biotic interactors not included as predictors in the niche model itself.[115] This requires knowledge not only of the current occupied distribution and future suitable distribution of the interacting species, but also its own future dispersal/demographic simulation. Ideally, dispersal/demographic simulations also would take into account data regarding genetic heterogeneity among populations regarding factors relevant for survival, dispersal, and establishment.[104] Finally, most species will be faced with dispersal through a nonpristine matrix of seminatural, agricultural, and urban areas. If land use or other variables reflecting human modifications of the environment were not used as predictors in the niche model, then relevant binary masks or probabilistic overlays representing estimates of future conditions after human modification should be employed in the dispersal/demographic simulation, on the basis of either data or assumptions regarding the species' use of such areas.[114]

Finally, interesting and likely important differences may exist between leading and trailing edges of shifting distributions. As mentioned above, in addition to dispersal to and establishment in newly suitable areas, species may persist for some time in areas no longer suitable for long-term positive population growth (i.e., demographic sinks). Such "extinction lags" or "extinction debts" will lead to occupied distributions that include sites outside the future suitable distributional areas.[116] As such, this phenomenon could act as a buffer to extinction of the focal species both directly (by maintaining additional populations for some time) and indirectly, by fostering dispersal via increased metapopulation connectivity. Notably, however, populations at the trailing edge of a species' distribution may affect the dispersal and demography of populations of an interacting species on the leading edge of its own shifting distribution (e.g., reducing the expansion of a competitor).[85,94] For these reasons, increasingly realistic simulations will consider multiple interacting species simultaneously, in dynamic future landscapes.

Conclusions

The overall framework now exists for building correlative niche models and using them to predict species distributions in the future, but full implementation remains difficult, especially when including consideration of biotic interactions, land-use change, and genetic heterogeneities. Many of the same principles and difficulties apply to mechanistic niche models as well. To a great extent, the fundamental theory and methodologies are available for building correlative models of Grinnellian niches on the basis of present-day abiotic variables. However, the critical details of making and evaluating high-quality models remain time consuming and have been inconsistently undertaken in the literature. This calls for automation that facilitates implementation of best practices while still requiring the user to make necessary biological decisions, especially regarding data that fulfill or reasonably approximate modeling assumptions.[9,17] In addition, substantial opportunity for progress remains for considering interactions among abiotic variables. Regarding biotic interactions, even in static models of current distributions, taking interactors into account requires further theoretical development and knowledge of the interactions themselves—but paths for progress have been identified. In contrast, including land use in current predictions appears to constitute a simpler endeavor, at least when recent occurrence records for the species exist.

However, integration of biotic interactions and land use into estimates of *future* species distributions remains highly challenging. In large part, the difficulty derives from the reality that, in addition to changes in climate, these two other driving factors themselves likely will change. Furthermore, dispersal/demographic simulations require detailed species-specific information (e.g., regarding dispersal ability, population growth rates, biotic interactions, genetic differences, and tolerance to human environmental modifications). The ramifications of genetic adaptations, across both space and time, represent an area seldom considered by current studies, yet one likely to prove of considerable importance for many species. In addition to increased collection of relevant ecological and genetic information, the situation calls for research into scenarios for future land use and the development of algorithms capable of simulating the dispersal and demography of multiple interacting species simultaneously. More generally, a synthesis is needed between research that builds upon single-species models to integrate biotic interactions (as here), and that focusing on community-level processes.[4,117,118] Together, these challenges pose exciting opportunities for theoretical and computational advancements. In tackling them, researchers may find inspiration and motivation by recalling the high societal need for forecasts of future species distributions, which likely will prove feasible on a large scale only via correlative niche models harnessing occurrence data from natural history museums, herbaria, and other reservoirs of primary biodiversity information.[16–18,119]

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Conflicts of interest

The author declares no conflicts of interest.

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