



When and how should biotic interactions be considered in models of species niches and distributions?

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ABSTRACT

Biotic interactions can influence the ranges and abundances of species, but no clear guidelines exist for integrating them into correlative models of niches and distributions. Niche/distributional models characterize environmental/habitat suitability or species presence using predictor variables unaffected by (= unlinked to) the population of the focal species. Such variables (termed ‘scenopotic’) typically have been considered to include only abiotic factors. In contrast, population–demographic approaches model the abundance of the focal species by including linked predictor variables, which frequently are biotic interactors. Nevertheless, a focal species might hold no, or negligible, population-level effects on its biotic interactors. Hence, contrary to current theory, such interactors would represent unlinked variables valid and potentially very useful for niche/distributional models. Consideration of population-level effects indicates that facilitators and affecting amensals (species that negatively affect another species but are not affected by it) constitute unlinked variables, but commensals and affected amensals do not. For competitors, mutualists, predators/prey, consumers/resources, and parasites/hosts, additional information is necessary. Specifically, available ecological/natural history information for the particular species involved (e.g. regarding specificity) and theory regarding ecological networks can allow identification of interactors that are likely to be unlinked or nearly so. Including an unlinked biotic interactor as a predictor variable in a niche/distributional model should improve predictions when the effects of the biotic interactor vary across the study region, or in another place or time period. Other relevant interactors must be taken into account by post-processing a niche/distributional model, or via population–demographic models that require abundance data over time. This framework should improve current correlative models and highlights areas requiring progress.

Keywords

abundance, biotic interactor, distribution, model, network, niche, presence, suitability

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[†]I dedicate this contribution to the late Adriana Ruiz-Espinosa, whose research addressed mutualistic nectar-feeding bats and columnar cacti across the complicated topography of north-western South America.

INTRODUCTION

Biotic interactions lie at the heart of ecology, and great interest exists in studying their effects on species distributions and communities (Ferrier *et al.*, 2007; Baselga & Araújo, 2009; Gilman *et al.*, 2010; Meier *et al.*, 2010; Guisan & Rahbek, 2011; Urban *et al.*, 2012; Blois *et al.*, 2013; D’Amen *et al.*, 2015). Nevertheless, the role of biotic interactions in influencing species distributions, and the spatial scales at which they are relevant, remain controversial (Peterson & Soberón, 2005; Soberón, 2007, 2010; Boulangeat *et al.*, 2012).

By definition, biotic interactions occur between individuals. Accordingly, much theory has considered that biotic interactions are only relevant locally and merely add random effects at coarser grains and larger geographical extents (the Eltonian Noise Hypothesis of Soberón & Nakamura, 2009; see also Pearson & Dawson, 2003; Peterson *et al.*, 2011; and Root, 1988 for summary of earlier literature). However, empirical evidence indicates that key biotic interactions often have important effects on species distributions at broad geographical extents (Gaston, 2003; Louthan *et al.*, 2006; Gotelli *et al.*, 2010; Lomolino *et al.*, 2010: 104–110, Wisz *et al.*,

2013). For example, many species only survive in the presence of—or at least strongly benefit from—a necessary or highly important pollinator, food resource or host; similarly, major competitors, predators, consumers and parasites exert strong negative influences (Ruiz *et al.*, 1997; Linder *et al.*, 2012).

In addition, it remains unclear how the effects of key biotic interactors should be modelled. Various correlative approaches for modelling the distributions of (or suitability for) individual species have seen widespread application, typically only using abiotic predictors (generally termed ecological niche modelling or species distribution modelling; Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Peterson *et al.*, 2011; Anderson, 2012). Recently, many studies have integrated biotic interactors into mechanistic niche models (Kearney & Porter, 2009) as well as correlative ones (Meier *et al.*, 2010; Godsoe & Harmon, 2012; Jaeschke *et al.*, 2012; Linder *et al.*, 2012; Blois *et al.*, 2013; Giannini *et al.*, 2013; González-Salazar *et al.*, 2013; Pellissier *et al.*, 2013; Pérez-Rodríguez *et al.*, 2013). Various other approaches consider multiple species simultaneously (Richmond *et al.*, 2010; Kissling *et al.*, 2012; Clark *et al.*, 2014; Pollock *et al.*, 2014).

Despite these advances, consideration of biotic interactions constitutes an outstanding problem even for single-species correlative models (Araújo & Guisan, 2006; Araújo & Luoto, 2007; Holt, 2009; Hellmann *et al.*, 2012; Anderson, 2013; Araújo & Rozenfeld, 2014). No guidelines exist regarding whether to consider an important biotic interactor by: (1) including it as an additional predictor variable in a niche/distributional model of the focal species, (2) integrating it later in post-processing of the prediction of a niche/distributional model of the focal species or (3) using it only in a population–demographic model of the two interacting species. Note that the latter models of linked population abundances should not be confused with ‘linked’ or ‘hybrid’ modelling approaches that build a dispersal/demographic model on top of the output from a niche/distributional model (Keith *et al.*, 2008; Engler *et al.*, 2012). Here, I consider important theoretical and mathematical issues in an attempt to provide guidelines regarding which of these three options is appropriate, and when. Other possibilities exist, such as modelling the effects of biotic interactions jointly in either a static or dynamic model (Richmond *et al.*, 2010; Pollock *et al.*, 2014). However, here I focus on the three somewhat simpler options listed above, hoping that this will shed light on key issues.

Niche perspectives and predictor variables

Two subfields of ecological modelling assess species–environment relationships in distinct ways, corresponding to differences in the kinds of processes involved and the variables employed (see also conditions versus resources, Linder *et al.*, 2012; and consumed versus non-consumed variables, Austin, 2002). First, algorithms for niche/distributional modelling have mathematical formulations that assume that the

predictor variables are density-independent factors not affected by (i.e. unlinked to) the response variable (Fig. 1; Table 1). The response variable is usually either the suitability for or presence of the focal species. Unlinked predictor variables can affect the focal species, by influencing its intrinsic population growth rate (i.e. potential for source populations and by extension carrying capacity; VanDerWal *et al.*, 2009). Hutchinson (1978: 172) termed such variables *scenopoetic*: those that ‘set the stage’ (apparently from the Greek *skene*—root of the Latin *scena*—and the Greek *poieo* or *poiesis*; Soberón, 2007, 2010; Anderson, 2015). Accordingly, predictor variables used in niche/distributional models typically consist of aspects of climate, soil or vegetation/land cover. These models reflect a niche perspective that has been termed ‘Grinnellian’ (Soberón, 2007, 2010; Peterson *et al.*, 2011). Because the predictor variables are not affected by the focal species, the suitability for (or presence of) the focal species can be estimated by niche/distributional models that use occurrence data regarding its presence (and often absence). Such models employ a variety of mathematical formulations that identify subsets of multivariate environmental space (e.g. modelling ‘response curves’; Austin & Meyers, 1996; Elith *et al.*, 2006; Elith & Graham, 2009).

Second, models of population demography also include, and indeed emphasize, the roles of predictor variables that are density dependent. The values of these variables are affected by (i.e. linked to) the population level of the focal species, and they also can affect the instantaneous population growth rate and population level of the focal species (Fig. 1; Table 1; Chase & Leibold, 2003). Hutchinson (1978) termed such variables *bionomic* because the variables classically considered were biotic interactors (especially competitors and predators/prey). These models correspond to a niche perspective that has been called ‘Eltonian’ (Soberón, 2007, 2010; Peterson *et al.*, 2011; see the latter for comparison with fundamental and realized niches). Because feedback between such variables exists, estimating the abundance of the species over time using population–demographic models requires time-series data of population abundances. Rather than identifying subsets of multivariate space (see previous paragraph), such dynamic models employ more complex mathematical formulations, including the solving of differential equations (e.g. resource–consumer models, zero-growth isoclines, impact vectors and supply points; Chase & Leibold, 2003; Soberón, 2007).

Current theory (Soberón, 2007, 2010; Peterson *et al.*, 2011) considers that the unlinked variables needed for niche/distributional models are abiotic (or reflective of habitat/vegetation structure), but this exclusion of biotic interactors may not be justified (Anderson, 2013; Lira-Noriega *et al.*, 2013). Seemingly, the only restriction prohibiting the use of a biotic interactor as a variable in building a niche/distribution model would be if its values are affected by (linked to) the population level of the focal species (Fig. 1; Table 1; Anderson, 2013). If possible, including a biotic interactor as an unlinked predictor variable would involve: (1) obtaining a representation of the range of the interactor and then (2) including that

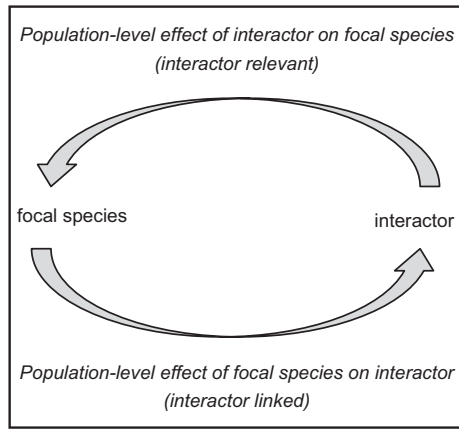


Figure 1 Illustration of the population-level effects of a focal species and its direct biotic interactor. If the population level of the interactor is affected by (linked to) that of the focal species (lower arrow), then the interactor is not valid for use as a predictor variable in a niche/distributional model of suitability or presence of the focal species. Instead, its effects must be considered in other ways (e.g. post-processing of the output of the niche/distributional model of the focal species; or in a local model of population demography of the two species; Fig. 2).

representation as a predictor along with abiotic factors to make a model for the focal species. These depictions of the range of the interactor likely would be maps of binary presence/absence or continuous representations of suitability (or probability of presence) within the areas occupied. Indeed, many recent studies have used biotic interactors as predictors (Meier *et al.*, 2010; Jaeschke *et al.*, 2012; Giannini *et al.*, 2013), although seldom considering whether or not they constitute unlinked variables (Lira-Noriega *et al.*, 2013).

Advantages and challenges of observational data

The effects of biotic interactions are inherent in observations of species occurrences, representing both an advantage and a

disadvantage for correlative niche/distributional models. Clearly, no species exists in nature impervious to the exceedingly complex biotic milieu around it. Because of this, the effects of biotic interactions pervade observational occurrence data. To a large degree, the fact that the effects of biotic interactions are built into observational data of the occurrence of a focal species represents an advantage of correlative niche/distributional models. In contrast, translating laboratory-based mechanistic niche models to the highly complex realities of field conditions, with a wide variety of known and unknown biotic interactors, presents serious challenges (Kearney & Porter, 2009).

Nevertheless, correlative niche/distributional models require two important assumptions regarding biotic interactions. First, they assume that the effects of biotic interactions on the focal species are consistent across the study region used for modelling. Second, they require that the research question can be addressed by a model characterizing the response of the species to abiotic predictor variables, given the biotic context experienced by the species. Such models also can be applied to other places and times, but only when it is reasonable to assume that the biotic context (or at least its effects) are the same as in the region/time in which the model was made. However, if the effects of biotic interactions vary across the study region (violating the first assumption), observational data for the occurrence of the focal species will be biased, at least across geography. When that is the case, observational data also may be environmentally biased (Anderson, 2013), leading to inaccurate models of the response to abiotic predictor variables. In addition, a model made in one biotic context might not be realistic when applied to a region or time period that holds a different biotic context (Blois *et al.*, 2013; Guisan *et al.*, 2014).

Hence, when the presence or average abundance of a key unlinked biotic interactor varies across the study region, including it as a predictor in a niche/distributional model could prove beneficial in two ways (Anderson, 2013; Wisz

Table 1 Summary of division of niche concepts into complementary perspectives (termed Grinnellian and Eltonian) based largely on the nature of predictor variables that define them (Soberón, 2007, 2010; Peterson *et al.*, 2011).

Niche perspective	What they characterize	Predictor variables	Generalities regarding scale	Nature of driving factors	Relationship to population growth rate	Modelling approaches
Grinnellian niche	Suitability or presence	Variables not affected by the focal species (unlinked; = scenopoetic)	Coarser grains; geographical extents	Density independent	Related to intrinsic population growth rate	Static sets of numbers (e.g. subsets of multivariate space; response curves and surfaces)
Eltonian niche	Population abundance	Emphasis on variables affected by the focal species (linked; = non-scenopoetic)*	Finer grains; local extents	Emphasis on density dependent*	Emphasis on relationship to instantaneous population growth rate*	Dynamic models (e.g. resource–consumer models; impact vectors)

*Note that although Eltonian models of population demography emphasize linked variables (affected by the focal species; = non-scenopoetic variables), such models also can include ‘abiotic stressors’ (i.e. unlinked variables that reflect density-independent factors affecting the intrinsic population growth rate).

et al., 2013). First, an unlinked biotic interactor might affect suitability for the focal species in an additive manner along with abiotic predictor variables (i.e. independent of the values of other predictor variables). Such additive effects can be modelled by many existing techniques (e.g. via a Maxent model without product features; Phillips & Dudík, 2008). Alternatively, the effects of an unlinked biotic interactor could be non-additive (\sim non-independent). For example, for the focal species, the response curve to an abiotic variable might depend on the value of the biotic interactor variable. Modelling such statistical interactions between the biotic interactor and abiotic variables could allow for better estimates of the response of the focal species to abiotic factors (Anderson, 2013). In such cases, rather than a traditional response curve, a response *surface* is needed (the response of the focal species, y ; to an abiotic variable, x ; across values of the biotic variable, z). Promising techniques for characterizing multidimensional response surfaces include boosted regression trees (Elith *et al.*, 2008; Elith & Graham, 2009) as well as hierarchical Bayesian models (Latimer *et al.*, 2006, 2009; Chakraborty *et al.*, 2010), specifically where one level considers the values of the biotic interactor, which influences the coefficients of the abiotic predictors. Therefore, determining which classes of biotic interactions could represent unlinked variables valid as predictors in single-species niche/distributional models should provide useful guidance for researchers. Complementarily, identification of linked biotic interactors should help researchers as well, leading towards relevant analytical approaches for such cases (Park, 1954; Gutiérrez *et al.*, 2014; see below).

IDENTIFYING AND INTEGRATING UNLINKED BIOTIC INTERACTORS

Typically, biotic interactions are classified by their effects on individuals, but the issues at hand require consideration of the effects of populations of each species on the other (Fig. 1). As a hypothetical example, although a lethal parasite clearly negatively affects the individual that it attacks, it might not influence the population level of the host species (or at least not substantially) beyond the stronger effects exerted by other factors (e.g. the availability of necessary resources). For terminology, I use a common classification of biotic interactions by cost/benefit to individuals of each species ($-/-$ competition; $+/+$ mutualism; $+/-$ predator/prey, consumer/resource, parasite/host; $+/0$ commensal/host; $-/0$ amensals; Begon *et al.*, 1996; Araújo & Rozenfeld, 2014). Note that in contrast to some literature where the term facilitation includes both mutualism and commensalism (Bruno *et al.*, 2003), under the classification used here individuals of a commensal benefit from association with their facilitator, whereas those of the facilitator are not affected (Begon *et al.*, 1996; Araújo & Rozenfeld, 2014).

Determination of population-level effects is straightforward only for facilitators/commensals and amensals because in those cases one species has neutral individual-level effects

on the other that can be assumed to apply at the population level as well. Specifically, the population of a facilitator by definition never is affected by the presence of the focal species (a commensal). The same is true for the population of a species that negatively affects individuals of another in an amensalism. Hence, these interactors constitute unlinked (= scenopoetic) variables valid as predictors in niche/distributional models. Conversely, populations of commensals could be affected by the presence of the focal species (a facilitator), and hence would not represent an unlinked variable. However, they are irrelevant for the focal species and need not be considered. The same applies to species negatively affected in an amensalism.

All remaining classes of interactions (competition, mutualism and predation/consumption/parasitism) require additional information to decide whether or not a particular interactor is unlinked to the focal species. In some cases, existing ecological/natural history data regarding the population-level effects of the two species involved might allow such determinations. More importantly, again taking advantage of some ecological/natural history information for the particular species involved, theory regarding ecological networks (Bascompte & Jordano, 2007; Pellissier *et al.*, 2013) should allow identification of at least some interactors that are likely to be unlinked or nearly so. Here, data regarding the specificity of the interaction for each species are paramount. For instance, despite well-known exceptions (Pellmyr & Huth, 1994; Rønsted *et al.*, 2005), studies of mutualistic networks indicate that populations of generalist species typically are only affected weakly by each of their many interactors (species that tend to be specialists); in contrast, populations of such specialist species frequently are strongly affected by their interactors (Bascompte & Jordano, 2007). In such mutualisms, the generalist species is likely to constitute an unlinked (or nearly so) interactor valid for modelling the niche/distribution of any one of the specialist species. Similarly, some research on food webs documents many weak links and few strong ones, although for such antagonistic relationships less consensus exists in the literature regarding relative effects (Berlow *et al.*, 2004; Montoya *et al.*, 2006). For these classes (competition, mutualism and predation/consumption/parasitism), unlinked interactors are valid and likely useful as predictors in niche/distributional models of the focal species. In contrast, affected yet relevant interactors must be considered in other ways (see below).

Intuitive hypothetical examples illustrate how inclusion of an unlinked biotic interactor as a predictor variable in a niche/distributional model could prove both reasonable and useful (Fig. 2). At the heart of the matter, some interactions may be important for populations of one species but only trivially affect those of the other. As mentioned above, in mutualism, predation, consumption and parasitism (with $+/+$ or $+/-$ individual-level effects), such asymmetrical population-level effects likely correspond to large differences in the specificity of the interaction. For example, a plant may depend highly on one necessary, or nearly necessary

pollinating animal (e.g. a bee, hummingbird or bat), but the animal can extract required resources from many different species of flowering plants. Here, including the range of the pollinating animal as a predictor variable would greatly improve the niche/distributional model for the plant. Similarly, a parasite may have a tight dependency on a particular host species—yet the presence of the parasite does not strongly affect the population of the host (e.g. if infection rates are consistently low). Using the range of the host as a predictor variable should prove highly beneficial in modelling the niche/distribution of the parasite. In contrast, for competition (with $-/-$ individual effects), any asymmetry of the population-level effects does not depend on uneven specificity.

Notably, slight relaxations of the definition of unlinked (scenopoetic) may prove reasonable and useful. As suggested above, if the population of the interactor is affected by the focal species—but only slightly—such a negligible effect likely could be ignored. In addition, it may prove reasonable and advantageous to take into account a set of interactors that could be considered unlinked to the population of the focal species when treated as a single predictor. For instance, an insect may need the presence of a necessary host plant (e.g. any member of a given genus or small clade) for successful development of its larvae, but the particular species of plant does not matter (Pelini *et al.*, 2010). More generally, the presence of a certain vegetation type (comprised of many species of plants) could represent a useful and valid predictor for an animal that needs but does not affect such vegetation (i.e. when the vegetation acts like a facilitator; Kissling *et al.*, 2012; Pérez-Rodríguez *et al.*, 2013). Such composite biotic predictors characterizing vegetational composition differ only slightly from those reflective of habitat/vegetation *structure* proposed recently as unlinked biotic predictors (Peterson *et al.*, 2011).

CONSIDERING LINKED BIOTIC INTERACTORS

Relevant interactors whose populations are affected by the focal species (i.e. are linked to it) must be taken into account in other ways, rather than being used as predictor variables in a niche/distributional model of suitability or presence (Grinnellian niches of Soberón, 2007, 2010; Fig. 2). First, in some cases, the focal species can be modelled using abiotic predictors separately in two biogeographical regions: one where the interactor exists and another where it does not. For example, when an important negative interactor is known or suspected to affect the focal species strongly, a niche/distributional model for the focal species could be made in a biogeographical region where the negative interactor does not occur (e.g. due to barriers to dispersal). Although this tactic would not model the effects of the interactor, it could avoid biases caused by its heterogeneity across space (Schweiger *et al.*, 2012; see Biotic Noise Assumption of Anderson, 2013). In addition, comparison of that model with one made in a biogeographical region where the negative

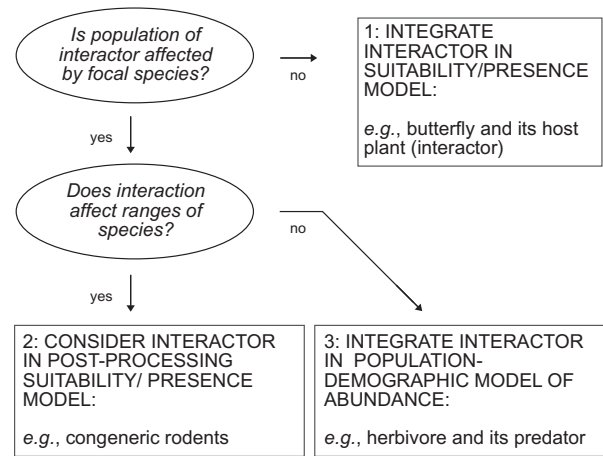


Figure 2 Decision tree illustrating the logic of how to consider a direct biotic interactor in correlative models of species niches and distributions. Ovals hold pertinent questions, and rectangles contain recommended actions. 1: Integrate interactor as an additional predictor variable along with abiotic variables in a niche/distributional model of suitability or presence of the focal species. Possible examples include a butterfly (focal species) whose larvae depend on a particular host plant (the interactor, whose population is not affected by the butterfly). 2: Consider interactor in post-processing of the niche/distributional model of suitability or presence of the focal species (after modelling each species separately based on abiotic variables). Possible examples include congeneric species of rodents of similar body sizes and diets that show parapatric ranges (contiguous but non-overlapping). 3: Integrate interactor in a local population–demographic model of the two species, using time-series data regarding abundance. Possible examples include a mammalian herbivore and its predator.

interactor is present could yield an indirect assessment of the effect of the interactor. Similarly, separate models could be made for a focal species in biogeographical regions where a key positive interactor does versus does not exist.

Second, some biotic interactors that are linked to the population of the focal species can be used in processing the output of a niche/distribution model of the focal species made using only abiotic predictors (Fig. 2; Anderson *et al.*, 2002). In general, this seems appropriate when the interaction affects the ranges of the two species in ways that depend on the values of the abiotic predictors. This approach has been developed for competition, specifically for two suspected competitors with ranges that come into contact but do not overlap (parapatric ranges). In such systems, the geographical predictions of the respective models of the two species (made using abiotic variables) can be superimposed to determine which receives the highest modelled suitability in each pixel (Anderson & Martínez-Meyer, 2004; Cornuault *et al.*, 2013). For areas suitable for both species along contact zones, occurrence records can be inspected to determine whether the particular species present in a given pixel corresponds to the one with the highest suitability. Such a pattern supports clipping the prediction of each species (removing

pixels that are more suitable for the other species), to gain a better representation of their ranges (Gutiérrez *et al.*, 2014). Notably, for such competitors, ideally each of the interacting species would be modelled in a biogeographical region where the other does not exist, with the two models then projected to a larger geographical extent that includes areas of geographical overlap (with caution regarding extrapolation in environmental space; Williams & Jackson, 2007; Fitzpatrick & Hargrove, 2009; see conflicts between Noise Assumptions and Niche Space Assumption of Anderson, 2013). Advances along similar lines should be pursued for mutualists and the various pairs of positive/negative interactions.

Third, some interactors that are linked to the population of the focal species simply are germane only in models of population demography (Eltonian niches of Soberón, 2007, 2010), requiring time-series data regarding population abundance for studying the interaction (Fig. 2). This is true when the effect of the interaction depends on the population levels of the two species, typically when they vary within small distances and over short time frames. In such cases, the interaction presumably does not affect the ranges of the species, but rather only their local abundances. Nevertheless, even in such situations it likely will prove useful to use the outputs of niche/distributional models (e.g. the suitability values for individual pixels) as additional inputs into local models of population demography, just like individual 'abiotic stressor' variables already included in such models (Chase & Leibold, 2003).

CAVEATS AND FUTURE DIRECTIONS

The assumptions of this idealized framework point to several key issues and areas requiring progress. First, some caveats concern the representation of the biotic interactor to be used as a predictor variable in the niche/distributional model. Importantly, the input data characterizing the interactor should reflect its range—i.e. the areas that it occupies, rather than all of those suitable for it. Furthermore, ideally the information regarding the interactor would indicate or at least be proportional to its average abundance in given regions (VanDerWal *et al.*, 2009; Tellería *et al.*, 2012). In reality, a continuous scaling of relative suitability (within the areas occupied), or binary estimate of the range of the interactor usually will prove easier to obtain. In addition, it is healthy to recognize that the representation of the biotic interactor carries inherent—but typically uncharacterized—uncertainty (Araújo *et al.*, 2005; Pearson *et al.*, 2006; Zurell *et al.*, 2012).

Second, strict use of niche models assumes that they were made over the full range of the response of the species to each predictor variable (both abiotic and biotic) and to combinations of them. Application to non-analogue biotic contexts—such as even higher suitability for an interactor than in any part of the study region used for model building—requires extrapolation, just as for conditions beyond the abiotic limits of the dataset used in model building (Williams *et al.*, 2007). Such extrapolation is risky and likely

will prove especially challenging for novel combinations of biotic and abiotic variables (Dormann *et al.*, 2007). Reducing model complexity whenever possible should lessen the need for unnecessary extrapolation (Guisan & Thuiller, 2005; Warren & Seifert, 2011; Radosavljevic & Anderson, 2014).

Third, niche/distributional models assume stationarity of the effect of the interaction across space and time, which may be violated in many systems (Osborne *et al.*, 2007; Finley, 2011; Wisz *et al.*, 2013). For instance, the effects of competition and predation may differ among regions, and abiotic conditions (MacLean & Holt, 1979; Harley, 2011; Cornuault *et al.*, 2013; Chamberlain *et al.*, 2014; Gutiérrez *et al.*, 2014). As mentioned above, modelling non-additive statistical interactions between biotic and abiotic predictor variables (e.g. via boosted regression trees or hierarchical Bayesian models; Latimer *et al.*, 2006; Elith *et al.*, 2008) may address such issues. Similarly, however, the outcome of the interaction between two species may itself depend on the density of a third biotic factor (Wisz *et al.*, 2013); for example, low ectoparasite densities can change a mutualism into a parasitism (Cheney & Côté, 2005), again calling for modelling such non-additive effects.

Finally, in reality, biotic interactions are web like in nature, with indirect and even cascading effects (Olesen *et al.*, 2007; Pellissier *et al.*, 2013). Hence, the intertwined nature of ecology calls for increasingly complicated models that consider multiple interacting species across large geographical extents. Such models have been proposed, both for static presence/absence occurrence data and for dynamic time-series data (e.g. regarding population abundance) at multiple sites; the latter extend local multispecies population-dynamic models to analyses across the ranges of the species (Kissling *et al.*, 2012). Nevertheless, considering even bidirectional population-level effects of two biotic interactors across space remains highly challenging. I hope that the ideas outlined here can facilitate progress towards synthesis between single-species and community-level models. In the meantime, for simplified systems containing one or more key unlinked biotic interactors, this framework should allow more realistic models of suitability or presence. Importantly, these advances should improve the application of spatially explicit estimations of dispersal, demography and range shifts under changing environmental conditions (e.g. anthropogenic climate change), which depend on the outputs of niche/distributional models (Keith *et al.*, 2008; Fordham *et al.*, 2012; Urban *et al.*, 2013).

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