

Stitch the niche – a practical philosophy and visual schematic for the niche concept

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ABSTRACT

By over-focusing on precise definitions, ecology has produced a confused idea of the niche concept. This, our second paper, develops a practical philosophy for the niche that approaches the concept at the correct level of abstraction. We deconstruct the niche into effect and response components and then reconstruct those parts into a general, visual schematic of the niche and ecology. Using this schematic we examine the relationship of particular niche ideas to ecology, and examine the relationship between niche and ecological sub-disciplines, particularly species distribution modelling (SDM). This general description clarifies the duality of the niche concept, as both a *facet of species* and a *facet of environments*. Unclear use of these dual concepts can confuse the scientific approach, and our ideas about uncertainty and error. By misclassifying models as concepts, ecology has confused the niche. Our practical philosophy uses the current wealth of ecological and niche ideas as a panoramic view of a general niche concept. We argue that stitching the niche produces a concept that underpins straightforward ecological thinking.

Keywords

Distribution, environment, fundamental niche, model, model selection, niche concept, policy, range, realized niche, species.

STITCH THE NICHE

The multiplicity of ‘niche’ concepts is often interpreted as problematic (McInerny & Etienne, 2012a; see also Elton, 1927) – producing a conflated terminology that uses different terms for very similar ideas, and similar terms for very different ideas. This means that the term ‘niche’ has an any-purpose meaning which does not discriminate between different concepts (McInerny & Etienne, 2012a). This criticism can encourage very precise definitions to be constructed (Peterson *et al.*, 2011). However, that can be counterproductive if generality is lost in favour of precision. Any comparison between ‘definitions’ can then become artificial because precision comes from the details of particular enquiries and different interpretations of scale. We need a general niche concept from which precise definitions originate and can be compared.

This second paper (of three) examining the utility of the niche concept (see also McInerny & Etienne, 2012a,b) searches for a general concept and is tolerant of the differences that could stand in the way of that goal. We deconstruct the different general ideas included in various niche concepts

and then *stitch the niche* to demonstrate the compatibility of these concepts as a whole and to provide a consensus definition from the literature. We do not linger on history that could distract from this task and that is well discussed elsewhere (e.g. Chase & Leibold, 2003; Schoener, 2009).

The niche components

There are two broad niche concepts, as follows.

1. The niche as a *facet of environment* – a recess, a part of environments, resources or ecological communities in which a species is found (see Grinnell, 1917; Schoener, 2009), where the environment is everything except the species. Two interpretations of the environment should be separated:

1a. The environment as a structure that itself is the niche (e.g. Ehrlich, 1989), a literal recess, constructed from abiotic or biotic factors or both. This concept permits species to occupy niches, or to leave niches empty if they become extinct, and allows other species to fill them or for niches to be destroyed.

1b. The environmental niche as a pattern delimited by a species’ distribution (Guisan & Zimmermann, 2000). In

lieu of knowing what processes determine that pattern, this niche definition may include any factor that co-varies with species' distributions. Thus, variables could be assumed to be important when they are not, because of similar patterns to a species' occupancy (e.g. Dormann, 2007).

2. The niche can be posed as a *facet of species* – i.e. adaptations or traits that determine what biotic and abiotic factors a species interacts with, and how species respond to and affect those variables/factors (Elton, 1927; Chase & Leibold, 2003). This collection of effect and response traits describes causal mechanisms underpinning species' distributions (e.g. Austin, 2002). Thus, an environmental recess or pattern could be modelled based on the facets of species, but the facets of species cannot necessarily be modelled from the recess or pattern. Below, we list these responses and effects relative to a focal species and define the environmental object as those that species respond to and have effects on. Thus, two interacting species may form each other's biotic environment, but can otherwise occupy distinct environments. The two directions of interaction (see Fig. 1) can be distinguished as:

2a. Species' responses to environmental objects – i.e. tolerances and requirements. These may be positive or negative responses, and can be divided into:

2a.i. Abiotic environmental response – the response of a species to non-living factors (Grinnell, 1917), e.g. a response to temperature or sunlight.

2a.ii. Response to biotic environment – the response of a species to living, biotic factors that also have

biological/ecological traits (Hutchinson, 1957), e.g. a competitive or facilitative response.

2b. The effects of species on environmental objects – e.g. biotic or abiotic environment, the *role* of the species (Elton, 1927).

2b.i. Environmental effects – i.e. the effect of species on the abiotic environment, physical factors that are not living (Leibold, 1995), e.g. water uptake or shading.

2b.ii. Interspecific effects – effects of species X on species Y, biotic interactions and network links (Elton, 1927; Gause, 1934), e.g. competitive or facilitative effects.

2b.iii. Intraspecific effects – effects of species X on X (Gause, 1934; Pulliam, 1988), i.e. the effect of a species on itself, frequency dependence, density dependence, dispersal and spatial processes which can alter a species' tolerance/position, or alter its role by changing how that species affects and responds to other objects.

Ecology

From this scheme of abstraction for ecological objects (Fig. 1) emerges a general and visual schematic of ecology (Fig. 2) that is using the *facet of species* concept; we shall return to *facet of environment* later. A unification of niche and ecology should not be surprising because niche concepts are so entangled with ecology (Kingsland, 2004). Ecological thinking is based on interdependence between species and their environments. From this simple conceptual lexicon, we can build causal, ecological explanations of why species occur where they do. We could call that collection of effects and responses their niche, i.e. their ecology (Elton, 1927; Chase & Leibold, 2003).

Unlike specific niche definitions, this general schematic is not dependent on particular scales (e.g. see Peterson *et al.*, 2011, p. 7). By incorporating some details into effects and responses (i.e. parameters and functional forms), and trimming certain niche components out, this scheme is relevant to all ecological studies: from individual behaviour and ecophysiology, to population dynamics and macroecology. It is unlikely that Grinnell, Elton or Hutchinson would disagree with the components of Fig. 1, or would argue with their compatibility as a description of ecology (Fig. 2). We can now see a fuller panorama of ecology than our colleagues of the early 1900s could. Focusing on any single view of this panorama moves us towards precise definitions and particular scales.

Ecosystems as combinations of niche components

Through effects and responses (Fig. 1), the niche describes relationships between species and their environments (Fig. 2). The existence of a species in an area may depend on other species and environmental objects, so depends on the species' place in an ecosystem (an ecological system) – 'The niche concept is a systems concept because it addresses how objects fit together...' (Patten & Auble, 1981, p. 893). We can build

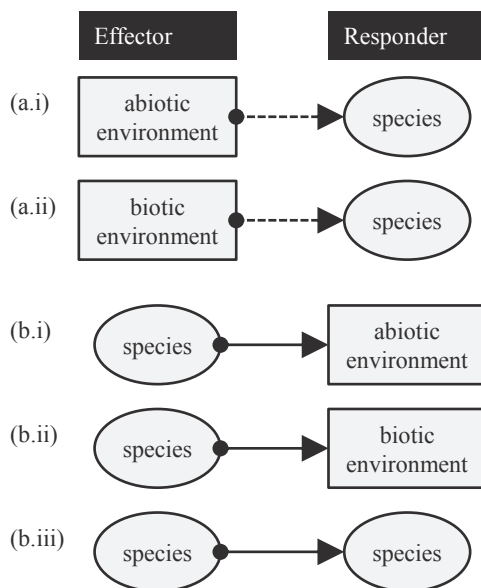


Figure 1 Five components of different niche concepts (see text) where niche is a facet of species. We can distil the components of the niche into two groups: (a) the response of species to other objects; and (b) the effect of species on those objects. The list of effects and responses follows the text in this paper.

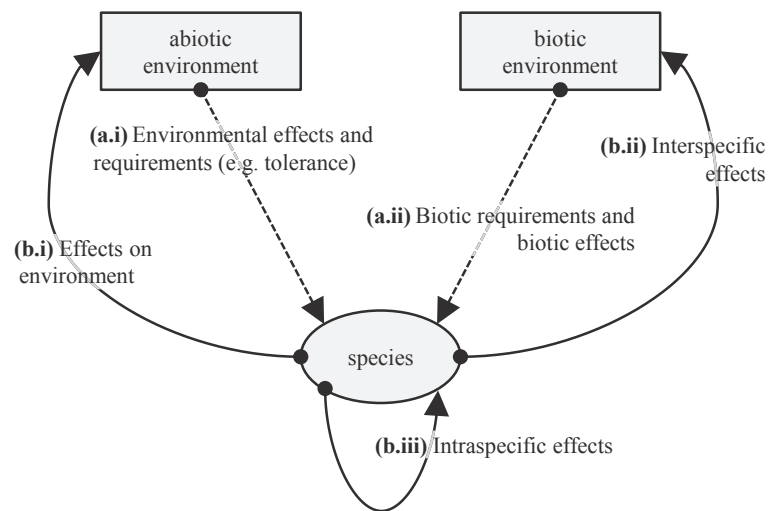


Figure 2 Linkage of the five different 'niche' concepts (see Fig. 1 and text) produces an ecosystem from the focus of one species. This is also a general representation of ecology (see also Meszéna *et al.*, 2006).

ecosystems from these components that could have more than one species of interest, more than one abiotic/biotic environmental object, and multiple links between species and between objects. These links may be unique to each object in a system or shared amongst many objects (Fig. 3). Configuring this relational structure of objects is the basis of understanding how ecosystems work (e.g. Loreau, 2010) and how species distributions are determined (e.g. Grinnell, 1917). Different subsets of components could produce ecosystems representing many different and similar views of ecology (e.g. Gause, 1934; Hutchinson, 1957; Lenton, 1998; Loreau, 2010).

Ecological terminology derives from positions of objects within ecosystems (see also Fig. 2.6 of Chase & Leibold, 2003). For instance, species respond to both conditions and resources, but only resources are affected by a species (Fig. 3a,b; see also 'bionomic' variables as resources and 'scenopoetic' variables as conditions in Peterson *et al.*, 2011). Thus, resources are characterized by feedbacks and can exhibit behaviours that conditions cannot (Fig. 3c). Similarly, the full suite of ecological interactions can be defined by different permutations of both positive and negative effects and responses between two species: e.g. two-way interactions with resources objects such as competition $-/-$, mutualism $+/+$, and predation $+/-$; and one-way interactions with conditions such as facilitation and commensalism $+/0$, and amensalism $-/0$. Likewise, species may be named by characteristics of their effects and responses such as based on what species is eaten (herbivores interact with plants, carnivores with animals), the positions species hold in that interaction (predators eat, prey are eaten); or through the magnitude of effect a species has in a ecosystem, for example ecosystem engineers (where species create new physical features; Jones *et al.*, 1994) or keystone species (where species have large impacts on ecosystems' stability; Paine, 1995). This terminology is based on what species do ecologically (Elton, 1927), i.e. what their niche is within ecosystems.

Feedbacks between objects may also occur indirectly, such as those mediated by effects on and responses to common

resources rather than direct interference (Fig. 3e). This can produce apparent effects and responses between objects, similar to the principle of apparent competition for prey objects with a common predator (Holt, 1977). Important ideas in ecology are based on some very similar systems. For instance, interactions occur through feedbacks with common resources in Gause's (1934) experiments, and in the daisy-world model (Lenton, 1998) through feedbacks with common environmental factors (Fig. 3e). Both produce qualitatively similar dynamic interactions and apparent effects between objects. Despite dramatic differences in details and scale, the similarity of these niches can produce similar general behaviours and have a similar ecology.

Ecology revisited – observation, context dependence and emergent properties

Observing the structure and dynamics of systems can be difficult. Many different types of dynamics and properties can potentially emerge from a particular structure (e.g. balance and persistence, decoupling and transience, cycling and complex dynamics). The dynamics may also be heterogeneous across ecosystems with different subsystems and objects exhibiting different behaviours. These differences may be driven by: initial conditions and time elapsed – the role of history and memory in systems' transient dynamics (Hastings & Higgins, 1994); spatial context – effects of heterogeneity and geometry on spatially restricted processes (Huffaker, 1958); available environments – the particular set of variables and patterns of variation found through time and space (Thuiller *et al.*, 2008); and perturbations – unpredictable effects of exogenous factors on system components (Lande *et al.*, 2003).

Our observations also depend on what tools we use, such as: methods of observation – sampling, measurement and modelling (Huston, 2002; McNerny & Purves, 2011); the abstractions used – how we abstract real objects in models (Hastings, 2002), e.g. selection and recording of state variables (for pattern, or objects); and how we conceptualize

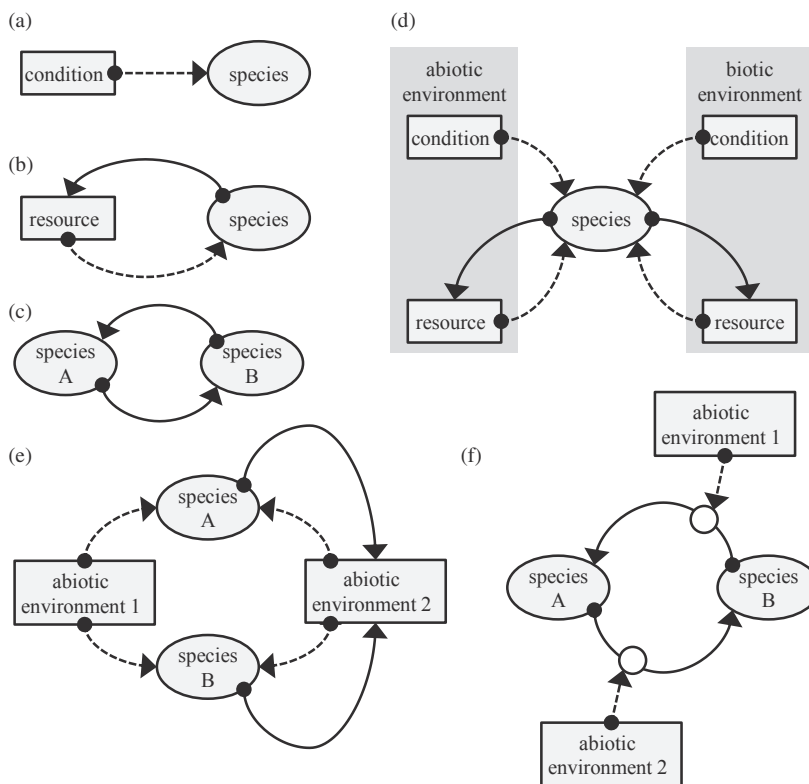


Figure 3 Different ecosystems created from different sets of niche components (see Fig. 1 and text). For instance (a) ‘conditions’ are objects that species have a response to but no effect on; (b) ‘resources’ have feedbacks with species through response and effect, and (c) where one species has an effect on another species. Different terminologies could be used for similar objects, for instance abiotic and biotic objects may act as resources or as conditions, because of the similar functional forms of these interactions (d). In (e), we show an ecosystem representing the ideas of both Gause’s fundamental work in community ecology (Gause, 1934) and the Gaia hypothesis as found in ‘daisyworld’ (Lenton, 1998). This graphical notation (f) could include indirect effects of objects on species through processes (see also Kissling *et al.*, 2012).

‘species’ within metrics such as abundance, biomass, demographic rates, occupancy, or by other traits. Observations of ecosystems, subsystems, interactions or objects can then be characterized as context-dependent realizations across potentially large numbers of ecological and observational factors (see also Hutchinson, 1957). Observations may be only one realization within a whole universe of possible states of the system (see above). Hence, observing the state of the system (all objects and their interactions) at any particular time may not lead to a full ecosystem model, and we might not be able to explain individual species’ properties (e.g. its distribution) without understanding ecosystems’ properties.

Because ecology often relies on a limited number of imperfect, or indirect observations of systems we might consider a more tractable approach. For instance, rather than studying models of systems we might study models of outcomes, i.e. investigating patterns instead of causal processes. This uses niche as *facets of environment*, frequently based on delineations of specific outcomes such as survival, existence and persistence (Hutchinson, 1957; Holt, 2009; Ricklefs, 2010).

These more easily observable outcomes of ecosystems – e.g. where species reproduce, grow or die – facilitate the building of models to explore which factors may be important without recomposing ecosystems themselves (Peterson *et al.*, 2011). This activity does not necessarily produce a model explaining why species occur where they do. Rather, it produces models of where species occur – a model of an outcome, pattern or geography – and what objects co-occur with that outcome, e.g. species distribution modelling (Guisan & Zimmermann, 2000). Depending on the niche compo-

nents assumed in a model, controlled in an experiment, or interpreted post hoc, different names have been used for different outcomes, e.g. fundamental niche for outcomes in a monoculture, and realized niche for outcomes within the community setting of a polyculture [Hutchinson, 1957; see also the ‘BAM’ (biotic, abiotic, movement) diagram of Soberón & Peterson (2005) and ZNGI (zero-net growth isocline; e.g. Chase & Leibold, 2003)].

Modelling patterns has no interest in causation by default. Instead, inductive approaches capture correlation and co-variation between factors: the indicator of scientific success being reproduction of observed patterns (niche concept 1b above). Such models should not be expected to predict outcomes beyond the conditions of observation (Thuiller, 2004). Inductive methods could use ‘ecological’ functional forms (*facet of species*) to suggest what happens beyond observed conditions (Austin, 2002) but without including any other ecological aspects to the model. Then, this extension is not necessarily complementary to what we know about the ecosystems’ underlying distributions. Mixing up concepts will produce confused inferences about patterns, cause and effect, what are species’ traits and covariates, and how we should extract knowledge from those inferences. A general niche concept can explain these different approaches to ecology and enable us to rationalize our inferences.

The scope of individual niches

Our visual scheme can also highlight similarities and differences between the thoughts of Grinnell (1917), Elton (1927)

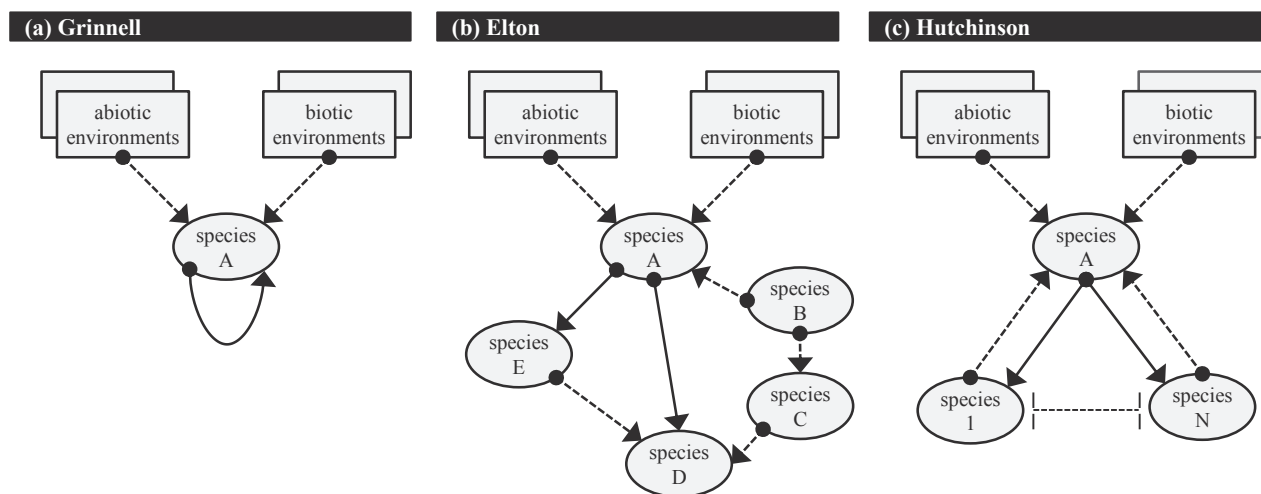


Figure 4 Graphical representations of the subsystems considered by authors in particular niche definitions for (a) Grinnell (1917), (b) Elton (1927) and (c) Hutchinson (1957). All these definitions consider different kinds of subsystems; see text for details but note that none include effects of species on environmental factors. In some cases, we have simplified the details that may have been included in the original text, e.g. compare our interpretation of Grinnell (1917) with the ‘Forrester’ diagram in Patten & Auble (1980).

and Hutchinson (1957) (Fig. 4, see also Patten & Auble, 1980). Using niche as a *facet of species* these authors constructed explanations of why species occur where they do (Fig. 4). Interestingly, they all pose abiotic variables as conditions, never as resources with feedbacks. This is a clear conceptual omission (see also Leibold, 1995; McInerney & Etienne, 2012a). Aside from these similarities each niche definition considers different but complementary aspects of ecology – Grinnell (1917), as a predecessor of contemporary neutral theory (Etienne & Alonso, 2007), considers the role of dispersal (a species property, not an interaction), Elton (1927) emphasizes interactions with ‘food & enemies’ and Hutchinson (1957) focuses on competition (though briefly considers ‘negative competition’, i.e. facilitation). Thus, each definition has unique features and is an essential contribution to a whole general concept. For this reason, our general scheme is a logical level for comparing these specific niche models/definitions (see below). An important detail of Grinnell’s (1917) and Hutchinson’s (1957) ideas is that they were explored as a *facet of species* (Fig. 4) but then turned into definitions posed as a *facet of environment* by subsequently defining an outcome based on those ecosystems (see 1b above; Hutchinson, 1957; Soberón, 2007; BAM diagram of Peterson *et al.*, 2011).

The scope of sub-disciplines

Most research focuses on interactions between pairs or small groups of objects (Fig. 3). Rarely are more complete ecosystems considered (Loreau, 2010) and few species distributions models are explained by species’ position within ecosystems (Hampe, 2004; Thuiller *et al.*, 2008). This is because ecology’s intensional aims are very complex and ecological sub-disciplines have developed around more tractable questions

(Weiner, 1995, pp. 156; the *centrifugal force* of ecological study). Thus ecology might be of limited scope because the sub-disciplines comprising ecology are of limited scope.

Sub-disciplines are not necessarily alternative views of ecology. Instead, like different individual’s definitions, smaller tractable subsystems are selected for study given the data and methods at ecologists’ disposal. Fig. 5 highlights these conceptual omissions using caricatures of ecological sub-disciplines. Redefining ecology by any of these sub-disciplines would patently produce an incomplete explanation. Hence, these terms carry prefixes (population, community, food web ecology) or a different name (neutral theory, species distribution modelling). Likewise, we should declare niche definitions that have a trimmed scope (Fig. 2 vs. Fig. 4). Different sub-disciplines may also describe effects and responses differently. For instance, food web ecology most often considers the qualitative existence of interspecific interactions (e.g. does species 1 eat species 2? – e.g. Williams & Martinez, 2000), whereas community ecology may consider quantitative measures of interaction strength (e.g. how much can species 1 affect species 2? – May & MacArthur, 1972; see also Kissling *et al.*, 2012). Further innovation in ecology will be built by expanding the scope of our sub-disciplines.

The scope of species distribution modelling (SDM)

SDM has a well recognized ecological scope (Hampe, 2004; Thuiller *et al.*, 2008), being principally focused on abiotic environmental responses (Figs 1a.i & 5e). SDM is also characterized by the data used (mostly large-scale occurrence and environmental layers), methods applied (correlative) and technology selected (software). A change in any of these characteristics can change the type of modelling and its scope.

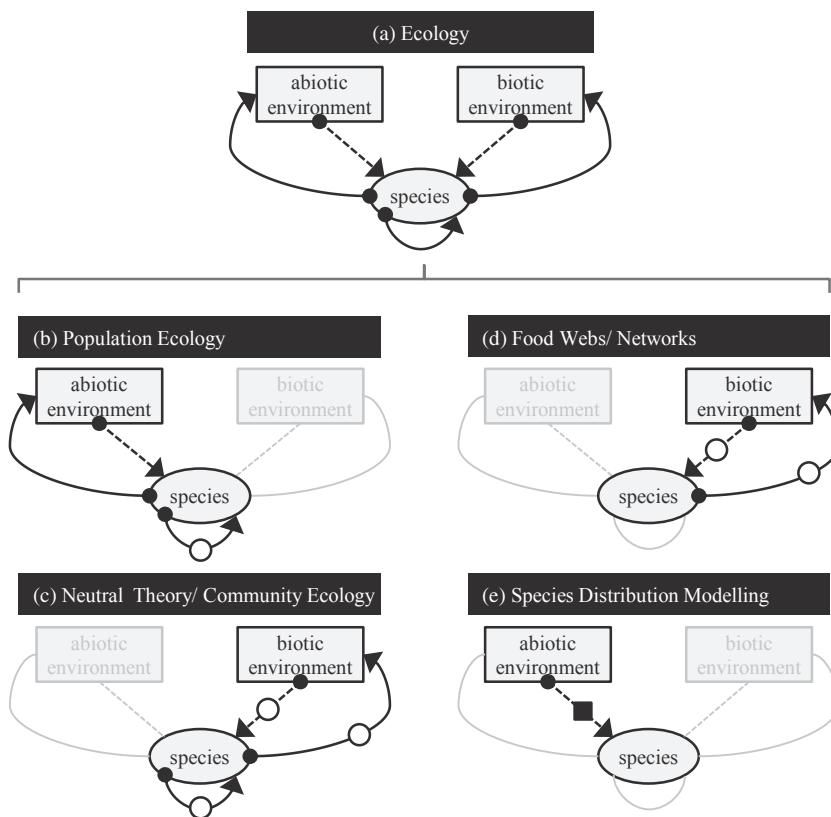


Figure 5 The scope of niche concepts in different areas of ecological study. Black boxes refer to correlative models and open circles to explicit mechanisms linking objects. See text for more information.

‘Correlative modelling’ almost exclusively considers environments as conditions using inductive SDM approaches to combine environmental and occurrence data (Fig. 6a; see also Guisan & Zimmermann, 2000), whilst ‘ecophysiological models’ (Fig. 6b) still consider environments as conditions, but models are built from experimental observations of individuals’ responses (rather than backward regressions) (e.g. Kearney & Porter, 2009; see also Dormann *et al.*, 2012). The difference in data drives a shift from inductive approaches (pattern matching, e.g. Pimm, 2008) to deductive approaches using niche as a *facet of species* (Austin, 2002). Ecophysiological models could be seen as expanding the black box explanation to a mechanistic explanation, but they do not necessarily expand the ecological scope of SDM (shown in Fig. 6a,b).

‘Dynamic range models’ (Schurr *et al.*, 2012) have an expanded scope by including otherwise unaccounted-for intraspecific interactions (Fig. 6c; e.g. Allee effects and spatial processes). This modelling is driven by more detailed abundance data. SDM has rarely modelled biotic interactions (Araújo & Luoto, 2007; Meier *et al.*, 2011; Kissling *et al.*, 2012) and these ‘correlative models with biotic interactions’ (Fig. 6d) expand the scope of SDM using slight variations in data and methodology. However, interacting species are considered as conditions (Araújo & Luoto, 2007; Meier *et al.*, 2011) and these models still focus on outcomes and modelling covariates of outcomes (see also Kissling *et al.*, 2012).

SDM uses imperfect observations from ecosystems of far greater complexity than the models can possibly consider. This disparity is understandable but these omissions of ecol-

ogy must be recognized as errors or uncertainties in models (Beale & Lennon, 2012) rather than as reasons to search for alternative interpretations that have less uncertainty and error (e.g. Franklin, 2009). Justification of models should consider what the possible sources of variation are in our data and what has been included in a model (Fig. 6a,b,d). We should be particularly cautious that the scope of interpretations and model predictions are not being stretched, for instance, if niche as *facets of species* is used for model prediction but niche as *facets of environments* was used in model construction (Hampe, 2004; Thuiller, 2004).

‘Hybrid models’ (Fig. 6e) attempt to broaden SDM’s scope by attaching spatial demographic models to traditional correlative models (e.g. Keith *et al.*, 2008). Because these models are parameterized separately, this method assumes that spatial demographic processes are unimportant in determining distributions and do not alter observed abiotic responses (Fig. 6e). In reality, the hybrid model is doubly accounting for the effect of spatial processes: once in the spatial model and once by ignoring spatial effects in the occupancy data. A co-parameterized joint model [$distribution = f(environment, space)$] and separately parameterized hybrid model [$distribution = f(environment) + f(space)$] may not retrieve equivalent functions for *environment* or *space*. Concepts behind the hybrid approach seem to be related to those of biotic and abiotic filters that can be separated and statistically modelled (see Figs 3.4 & 3.5 in Franklin, 2009; see also Guisan & Thuiller, 2005). Again, our general niche concept forces us to be clear about what different model components mean and how they relate.

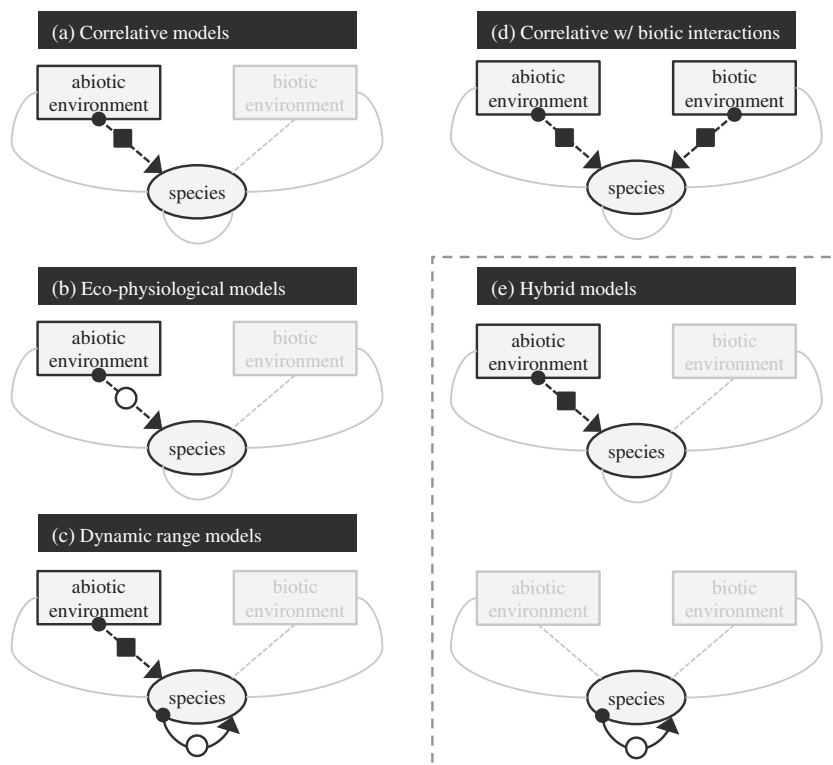


Figure 6 Different species distribution modelling approaches and their scope. Black boxes refer to correlative models and open circles to explicit mechanisms linking objects. See text for more information.

DISCUSSION

The definition of ecology is relatively stable (Haeckel, 1870 in Allee, 1949; Begon *et al.*, 1996) and is bounded by a small set of general principles (Fig. 2; see also Kingsland, 2004). It could be criticized for being imprecise as any application requires more specific assumptions and methodology, but such criticism does nothing but undermine a high-level, general abstraction on the basis of criteria suited to precise models. And so, for the niche concept, many criticisms come from staging false rivalries between very specific models rather than observing the generality.

The stitched niche concept we have presented here is unambiguously connected to ecology. It is both holistic and heuristic. In comparison, specific models and definitions are incomplete abstractions of the niche concept, because specific details are required by particular applications. Concepts quickly turn into models within specific definitions (e.g. Hutchinson, 1957; Patten & Auble, 1980), and forgetting the difference between concept and model distracts us from discussing integrative concepts that might actually stitch our science together and will cause us to falsely assign properties of models to concepts. For example, the competitive exclusion principle (Grinnell, 1917) is frequently cited as a property of the niche (Chase & Leibold, 2003), but it is a property of some only some models and not all of those models, for which competitive exclusion is a property, were derived from niche concepts. Believing that precise models represent the general concept can then be dangerous, not least because it constrains a full view of the world.

Elton (1927, pp. 63–64) describes the niche within the following text:

Animals have all manner of external factors acting upon them – chemical, physical and biotic – and the “niche” of an animal means its place in the biotic environment, its relations to food and enemies. The ecologist should cultivate the habit of looking at animals from this point of view as well as from the ordinary standpoints of appearance, names, affinities and past history. When an ecologist says “there goes a badger” he should include in his thoughts some definite idea of the animal’s places in the community to which it belongs ...

Food web research has been highly influenced by these ideas (Williams & Martinez, 2000), but mostly by focusing on species’ places in communities. This was a novel feature of Elton’s thoughts but has largely been re-interpreted as an alternative concept. Really, Elton offers an ecological grammar that separates ecology from natural history and systematics, as niche is a species’ relationship to the ecosystem (a facet of species – an ecological niche). Importantly, that ecosystem includes chemical, physical and biotic factors (Elton, 1927). This more general concept is often missed because headlines are made of the differences in concepts rather than seeing the similarities. Let us *stitch the niche* and observe the depth of ecology from this higher level concept.

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BIOSKETCHES

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