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Biotic modifiers, environmental modulation and species distribution models

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ABSTRACT

The ability of species to modulate environmental conditions and resources has long been of interest. In the past three decades the impacts of these biotic modifiers have been investigated as ‘ecosystem engineers’, ‘niche constructors’, ‘facilitators’ and ‘keystone species’. This environmental modulation can vary spatially from extremely local to global, temporally from days to geological time, and taxonomically from a few to a very large number of species. Modulation impacts are pervasive and affect, *inter alia*, the climate, structural environments, disturbance rates, soils and the atmospheric chemical composition. Biotic modifiers may profoundly transform the projected environmental conditions, and consequently have a significant impact on the predicted occurrence of the focal species in species distribution models (SDMs). This applies especially when these models are projected into different geographical regions or into the future or the past, where these biotic modifiers may be absent, or other biotic modifiers may be present. We show that environmental modulation can be represented in SDMs as additional variables. In some instances it is possible to use the species (e.g. biotic modifiers) in order to reflect the modulation. This would apply particularly to cases where the effect is the result of a single or a small number of species (e.g. elephants transforming woodland to grassland). Where numerous species generate an effect (such as tree species making a forest, or grasses facilitating fire) that modulates the abiotic environment, the effect itself might be a better descriptor for the aggregated action of the numerous species. We refer to this ‘effect’ as the modulator. Much of the information required to incorporate environmental modulation effects in SDMs is already available from remote-sensing data and vegetation models.

Keywords

Ecosystem engineers, facilitation, global change, keystone species, models, niche, niche construction, species distribution models.

INTRODUCTION

It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organised creatures.

(Darwin, 1881, writing about earthworms)

Most species distribution models (SDMs) link the spatial distributions of species to spatial variation in environmental parameters via a statistical function. These models are mostly based on correlations (varying in their degree of sophistication) between the occurrences of species and selected envi-

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ronmental variables. Species distributions are then predicted, on the basis of SDM outputs, according to projected environmental (often climatic) suitability. Such predictions are used to fill in gaps in the currently known ranges, predict potential distribution ranges on other continents, or project ranges under future or past climates. Practically, this has been shown to work well for filling in the gaps in observed species occurrences. Prediction of the ranges of anthropogenically translocated species are also largely successful (Wiens *et al.*, 2010), although there are some spectacular mispredictions (Broennimann *et al.*, 2007; Medley, 2010). SDMs are based on the theory that each species has particular environmental requirements, that these requirements evolve rather slowly (are conserved), and that consequently knowledge of these requirements, and knowledge where spatially these requirements can be satisfied, allows the prediction of the spatial range (Wiens *et al.*, 2010). However, the spatial range of a species may be a poor reflection of its ecological requirements (Schurr *et al.*, 2012).

Grinnell (1917) called these requirements the species ‘niche’. The Grinnellian niche of an organism includes climatic parameters (e.g. rainfall, temperature, air humidity), habitat parameters (e.g. edaphic and light parameters), biotic interactions (e.g. predators, pollinators, dispersers) and biotic modifiers (e.g. bioturbation of soil, facilitators, biotic habitats, and other individuals of the species itself) (Chase & Leibold, 2003). Historically, most SDMs used only the climatic parameters, although some also used soil data and/or information on land cover or habitats (e.g. Pompe *et al.*, 2008, 2010). Vegetation simulation models are also primarily based on the assumption that plant distribution and abundance is regulated by climate and soil, but in addition they often consider competition between plant species in the case of forest gap models (see Hartig *et al.*, 2012). Recently, the effects of fire have also been incorporated (Bond *et al.*, 2005; Scheiter & Higgins, 2009). Like other disturbances, fires structure ecosystems, selecting for specific plant traits. But, in contrast to external factors (such as climate), fires depend on the combination of a suitable climate, ignition and adequate fuel, the latter generated by some groups of plants, such as grasses or finely branched shrubs. These plants modify habitat conditions by affecting fire regimes, and so can be regarded as biotic modifiers of the environmental niche parameters.

Biotic modifiers (species which substantially modify the environment) have been discussed under many labels, including ecosystem engineers, niche constructors, keystone species, facilitators, and foundation species. The arrival of a new biotic modifier can transform the environment, creating new opportunities, or destroying the habitats of already present species (Wardle *et al.*, 2011). This implies a reciprocal relationship between the organism and its environment, which leads to an extension of the Hutchinsonian niche concept (an n -dimensional hyperspace of all the environmental factors acting on the organism) by the additional concept that ‘the niche [is] a property not only on which the organism is dependent, but also to which the organism contributes’

(Krakauer *et al.*, 2009). Biotic modifiers change the environmental variables, thus the components of the Grinnellian niche. This obviously also affects the requirements of a species to maintain a positive growth rate (Schurr *et al.*, 2012), and so influenced realized niches *sensu* Chase & Leibold (2003). Biotic modifiers that modify the structures available may also impact species ranges. For example, bird distributions are strongly affected by vegetation structure, and changing the vegetation results in major changes in the avian diversity (Kissling *et al.*, 2010). Processes that alter these variables should be taken into account in SDMs.

Here we explore the impact of biotic modifiers on the environment, and therefore on the variables used to predict the ranges of selected (focal) species. Figure 1 shows that in species distribution models such modulation of the environment by biotic modifiers can be accounted for through modulation of specific environmental variables (e.g. temperature, T) by the modulator (e.g. forest, M), or by the presence of the biotic modifier (or engineering species, e.g. tree species). We include under this concept all interactions that modify the abiotic environment, and thereby impact on the occurrence of other species using these resources and conditions. This is consistent with the definitions of ecosystem engineers and niche constructors (Jones *et al.*, 1994; Odling-Smee *et al.*, 2003), according to which species that modify the biotic environment directly are excluded. Examples of excluded species are species that provide resources (e.g. food plants), services (e.g. pollination or dispersal), or are part of the trophic system (e.g. predators, herbivores, decomposers) of the focal species for which the SDMs are being developed. Species that are directly involved in biotic interactions are just as important in SDMs (Jones *et al.*, 1994), but different modeling techniques are

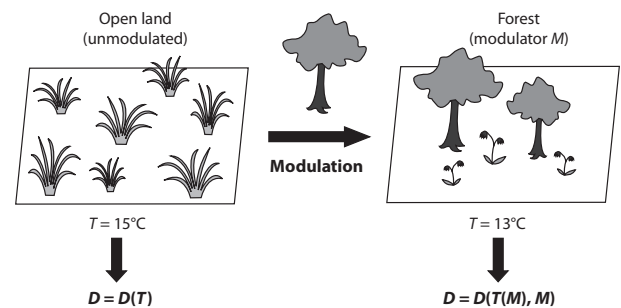


Figure 1 Schematic representation showing how modulation of the temperature (T) by a forest affects conditions of focal species and as a consequence their geographical distributions (D). For modelling, it is useful to distinguish between modulating effects that affect species conditions implicitly from those that are explicitly modelled. In the example, biotically modifying tree species modulate the environment by building a forest (modulator M), which stops grass species from growing but creates suitable conditions for understorey herbs. The structural engineering modifies the focal species’ conditions (e.g. shading, changes in water availability and soil structure), but in the model these effects are summarized in one (categorical) variable, M . However, the impact on temperature T is explicitly considered.

1 required for their inclusion (Kissling *et al.*, 2011) from the
 2 techniques we describe for biotic modifiers, as we discuss only
 3 those biotic modifiers that change the environment, whereas
 4 Kissling *et al.* (2011) deal with direct species-to-species
 5 interactions. Consequently, the probability of occurrence or
 6 abundance of the affected (focal) species is significantly
 7 different in locations where the biotic modifier is or was
 8 present from locations where it has never been active.

9 This paper focuses on explaining why ignoring modulation
 10 could result in a poorly performing SDM, and suggests ways to
 11 use the concept of environmental modulation to improve
 12 species distribution modelling. We explore the possible use of
 13 the modulation effect on statistical distribution modelling of a
 14 species (the focal species), which lives in an environment that
 15 is strongly affected by biotic modification. For the purpose of
 16 clarity, we initially briefly review the literature on ecosystem
 17 engineering and related concepts, in order to define the terms
 18 and emphasize those conceptual characteristics that are
 19 relevant to SDM.

20 WHAT ARE BIOTIC MODIFIERS?

21 A definition and classification of biotic modifiers and 22 environmental modulators

23 All species modify the environment, but we are interested in
 24 those species (here called biotic modifiers) that have a
 25 sufficiently large impact on the environment to influence the
 26 local persistence of other species. Describing or quantifying the
 27 impact of each biotic modifier is daunting, as the number of
 28 biotic modifiers in a system is potentially very large. Often,
 29 many species have qualitatively the same modulating role and
 30 their effect is a function of the sum of their biomasses. We
 31 attempt to simplify the situation by grouping biotic modifiers
 32 on the basis of the structure or factor that actually modulates
 33 the environment. We call this structure the 'modulator'. For
 34 example, fire could be the modulator, and it is facilitated by
 35 one, several or many flammable species, each of which is a
 36 biotic modifier (and could be regarded as an ecological
 37 engineer, niche constructor, facilitator, or keystone species,
 38 depending on the question addressed). In another example, a
 39 forest could be the modulator, and the biotic modifiers are in
 40 this case one or several tree species. Thus being a biotic
 41 modifier is a species-attribute, while modulators are more
 42 inclusive groupings, generally including many species (Fig. 2).
 43 In instances where the modulation effect is uniquely caused by
 44 one or two species (such as the impact of elephants in the
 45 African savanna) the biotic modifier and the modulator
 46 concepts or terms are effectively exchangeable.

47 A synonymy of biotic modifiers

48 Biotic modifiers have been described under a large number of
 49 different names or concepts, depending on the research
 50 question raised (Table 1). Perhaps the most widely used
 51 concept is that of ecosystem engineers, which was coined by

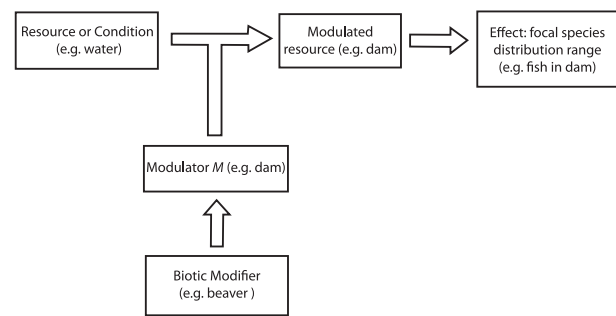


Figure 2 Simplified diagram of ecosystem engineering, showing the relative roles of the biotic modifiers, the modulators (M), the resources/conditions (e.g. water) that are modulated, and the outcome for a focal species.

Jones *et al.* (1994), and which has inspired a large number of further studies: at the time of submission of this article, Jones *et al.* (1994) had been cited 1416 times. A useful overview of the development of ecosystem engineers is given in Wright & Jones (2006). Ecosystem engineers are species that modulate the environment of other species, in ways other than by using or providing resources or biotic services themselves. The classical examples of ecosystem engineers are beavers, which change the flow of a river, thus modulating the physical environment, or earthworms, which modify the condition of the soil, modulating the soil's physical and chemical properties. Trees, by providing shade and light patches, are ecosystem engineers, because they modulate the quality of the light or temperature. Contemporary concerns over global climate change are based on the ecosystem engineering effects of the species *Homo sapiens*. Indeed, the impacts of this species are so widespread and profound that it has been argued that the Earth has entered a new geological age, the Anthropocene (Crutzen, 2002). Because every species is to some extent an ecosystem engineer, the concept is sometimes considered to be controversial and even 'useless' (Wilson, 2007). However, Wilby (2002) argues that precisely because it is ubiquitous it is particularly important, and that we need to understand the processes by which species modulate the availability of resources to other species.

Niche construction was first described by Odling-Smee *et al.* (1996), and then popularized by their book *Niche construction: the neglected process in evolution* (Odling-Smee *et al.*, 2003). They understood niche construction to occur when a species modifies its own niche. Because this also results in a modification of the biotic and abiotic environment, there is an overlap with ecosystem engineering, and consequently the distinction between niche construction and ecosystem engineering has been much discussed (e.g. Erwin, 2008; Kylafis & Loreau, 2008). We take niche construction to be concerned primarily with the evolutionary interaction between the niche constructor and the constructed niche, and the primary push for this concept came in terms of the extension of the theory of natural selection (Day *et al.*, 2003). It refers to the self-created selective regime, and the feedback system that maintains the

Table 1 Comparison of the attributes of biotic modifiers (the more inclusive concept), and the more specific concepts of ecosystem engineers, niche constructors, keystone species and facilitators. Attributes critical for the definitions of the concepts are in bold and underlined.

	Biotic modifiers	Ecosystem engineer	Niche constructor	Keystone species	Facilitator
Example	Tree species	Beaver, trees	Humans	Starfish, wolves in Yellowstone	Spiny shrub, e.g. <i>Prunus spinosa</i>
Has an impact over whole geographical range of the species	Yes	Yes	Yes	No	No
Loss always causes loss of other species	No	No	No	Yes	No
Modifies the physico-chemical (abiotic) environment	Yes	Yes	Yes	Not necessarily	Yes
Impacts other species by modulating access to resources	Yes	Yes	Not necessarily	No	No
Refers to selective regime of constructor	No	No	Yes	No	No
Always at local or community level	No	No	No	No	Yes
Trophic	No	No	No	Often	No
Allows establishment/survival/reproduction of other species under specific, otherwise unsuitable conditions	Sometimes	Often	Sometimes	Sometimes	Yes
Can have persistent effect on other species past its own presence at a site	Yes	Yes	Sometimes	No	No

process (Erwin, 2008). This can be seen as a form of self-organization (McDonald-Gibson *et al.*, 2008). An excellent example of a niche constructor is *Homo sapiens* (Kendal *et al.*, 2011), where the niche construction influences the environment, and thus also has ecosystem engineering impacts.

Keystone species were originally defined by Paine (1969), who argued that the removal of some species in a marine system led to a cascade of changes and extinctions, and contrasted this to the assumption that complexity provided stability. Keystone species might not be numerous or important in energy flow, but are critical for the survival of many species. Sole & Montoya (2001) showed that keystone species are highly connected in foodwebs, and that they usually act through trophic control. Keystone species may be ecosystem engineers [i.e. they alter the environment in such a way as to facilitate the continued existence of a high diversity of species (McMillan *et al.*, 2011) or a significant reduction in species richness (Cully *et al.*, 2010)], or they may operate as mutualists (i.e. they do not significantly alter the environment, but they themselves offer a service, e.g. pollinators) or predators (Bond, 1993). For example, removal of the wolves in the Yellowstone National Park led to an increase in the elk population, which in turn led to increased grazing and substantial vegetation changes. Reintroduction of wolves led to a trophic cascade, resulting in (at least ephemeral) vegetation changes (White & Garrott, 2005).

The concept of local facilitation (Kefi *et al.*, 2008) tends to be used where the effect is restricted to the space directly around the plants or animals. Local facilitation is a special case of ecosystem engineering, where the plant or animal essentially affects its shadow-area (broadly defined in terms of local influence) (Cushman *et al.*, 2011). Local facilitation is related to the concept of a foundation species that facilitates the establishment or survival of other species in the community,

and thus acts as the foundation of the community. Often such facilitation is ephemeral, resulting in the establishment of a new community, which, when established, can persist independently of the facilitators (Smit & Ruifrok, 2011). At least some succession models, such as the relay floristics model, rely on such ephemeral facilitation in succession, where early succession species modify the environment, making it possible for later succession species to survive (Connell & Slatyer, 1977).

Some authors regard these concepts as interchangeable, and there are indeed situations to which several concepts apply. Although all contribute to environmental modulation, there are profound differences among them (Table 1), and most biotic modifiers would probably be classified as ecosystem engineers, for three reasons. First, the ecosystem engineering concept does not include an evolutionary feedback to the ecosystem engineer (in contrast to the concept of niche construction). Such a feedback is also not part of our biotic modifier concept. Second, the modulating effect of engineering species can be expressed beyond the immediate environment of the engineering species (in contrast to facilitation). Biotic modifiers generally do not show such a spatial restriction. Third, ecosystem engineering refers solely to the modulation of environmental conditions, rather than its direct impact on other species (in contrast to keystone species). Keystone species and direct biotic interaction fit better into trophic models, as discussed in more detail by Kissling *et al.* (2011).

IMPACTS OF BIOTIC MODIFIERS

A modulator could impact the abiotic environment in one of several ways (Table 2), which suggests a functional classification of biotic modifiers and modulators. Berke (2010) proposed four functional types of ecosystem engineers: struc-

Table 2 A short selection of environmental modulators, and a summary of their characteristics and potential impacts. The biotic modifiers are the species that cause or facilitate the modulation. The resources and conditions column lists the environmental variables that are modulated. Resources (R) are depletable, conditions (C) are not depletable; this distinction is elaborated in the text. The functional type of the modulation follows the classification of Berke (2010), with two additional functional types. The spatial and temporal scale classification follows that proposed in the text.

Modulators	Biotic modifiers	Resources and conditions	Functional type	Spatial scale	Temp-oral scale	Examples
Fire	Species with flammable biomass (e.g. <i>Imperata cylindrica</i>)	Light (C), nutrients (R), biofabric (R)	Disturbance	Habitat/Biome	Decadal	Leach & Givnish, 1996; Groeneveld <i>et al.</i> , 2002; Schwilk, 2003; Bond & Keeley, 2005; Esther <i>et al.</i> , 2008
Coral reefs	Species that build corals e.g. stony corals like <i>Scleractinia</i>	Light (C), nutrients (R), biofabric (R)	Structural/ Disturbance	Habitat	Decadal, century	Kon <i>et al.</i> , 2010; Wild <i>et al.</i> , 2011
Forest	Tree species, e.g. <i>Podocarpus falcatus</i>	Light (R), Temperature (C), water (R or C), nutrients (R), biofabrics (R)	Structural/ Light/Climate	Habitat	Decadal, Century	Didham & Lawton, 1999; Micheels <i>et al.</i> , 2009; Vanwallegem & Meentemeyer, 2009; Baraloto & Coueron, 2010; Costa & Pires, 2010; Sporn <i>et al.</i> , 2010
Peatbog	<i>Sphagnum</i> spp.	Water (C), nutrients (R)	Chemical	Habitat	Century	Vanbremen, 1995
Soil biota	Earthworms (e.g. <i>Lumbricus terrestris</i>), moles (e.g. <i>Parascaptor leucura</i>), roots, fungi, ants, termites	Biofabrics (R), Chemical (R)	Bioturbation	Microhabitat	Decades	Wilkinson <i>et al.</i> , 2009; Sanders & van Veen, 2011
N-fixers	Fabaceae, <i>Azolla</i> , Cyanobacteria	Soil Nutrients (R)	Chemical	Microhabitat	Years	Bonanomi <i>et al.</i> , 2008
Mega-herbivory	Elephant, mammoths	Biofabric, light (C), soil nutrients (R), water availability (C), fire (C)	Disturbance	Biome	Decades	Jones <i>et al.</i> , 1997; Zimov, 2005; Zimov <i>et al.</i> , 2006; Johnson, 2009

tural engineers, bioturbators, chemical engineers and light engineers. Structural engineers add to the structural complexity of a region, for example: termite nests in an African savanna; bioturbators perturb the soil, adding structure, resulting in changed aeration and nutrient status; chemical engineers modify the chemical composition of the environment, such as the gas composition of the atmosphere; and light engineers modify the amount and quality of light reaching a set of organisms, such as forests or planktonic clouds. To this list we add disturbance engineers (e.g. fire, elephants) and climate engineers (e.g. plants) as additional categories. These latter two groups have major impacts on SDMs but cannot readily be assigned to any of the other categories. For example, elevated carbon dioxide can result in reduced stomatal conductance ('physiological forcing') in plants, leading to lower transpiration rates which may result in changed soil water content (Rickebusch *et al.*, 2008; Hickler *et al.*, 2009), increased river

runoff (Betts *et al.*, 2007), and decreased evaporative cooling (Cao *et al.*, 2010).

Modulating impacts can be grouped by three characteristics: whether they impact many species or a few, whether they are spatially extensive or local, and whether they persist over longer or shorter time periods. The number of species impacted by a particular environmental modulator is determined by whether the modulated resource is consumed (i.e. a real resource, a depletable pool of compounds or structures), or not (in which case the 'resource' is best referred to as a 'condition', e.g. Begon *et al.*, 2005). A typical example of a resource is nitrogen. Nitrogen-fixing bacteria in the soil can only fix a finite amount of nitrogen, while the activity of nitrogen-consuming organisms determines how much of the fixed nitrogen is available to other species. This has a complicating effect on the prediction for the occurrence of species – not only is it important to know whether the

environmental modulator is active in the area, but also whether competitor species for these resources are present. A ‘condition’ is one where it does not matter if another species is utilizing that ‘resource’. Typically, the cooler temperatures below a forest canopy can be regarded as a condition; it is not consumed, so it does not matter how many species benefit from it. Although this concept is seductively simple, many environmental factors can sometimes act like resources which are consumed (e.g. water in a savanna system), but in another context are more like a condition (e.g. water in a peatbog). In some instances the resource/condition distinction only makes sense relative to the particular species that we are attempting to model distributions for.

The spatial extent of the modulating effect ranges from highly local (i.e. a facilitation effect of one species on another) to regional/continental (i.e. climate) and global (i.e. changes in atmospheric chemistry). A local facilitation, if repeated by very many individuals, can have a cumulative global effect. These can be simplified into five categories, where the scales should be interpreted as the smallest scale at which it can operate.

1. Microhabitat effect (i.e. the effect of one species on another, for example with facilitation). An extreme case is the creation of anoxic environments in legume root nodules. This results in localized modifications.

2. Habitat effect (i.e. the effect of fast growing corals on the coral reef community composition, or forest trees which reduce the amount of light reaching the ground). This results in the modification of communities.

3. Ecosystem effect (i.e. microbial metabolic activity and changes in the water chemistry). This scale is rather variable, and this category does not fit comfortably into the spatial sequence suggested here, as it depends on the size of the ecosystem (e.g. tidal pool versus rain forest).

4. Biome effect (i.e. effect of fire on the transformation of forest into savanna). Biomes differ from the habitat and microhabitat effects in that they are usually spatially continuous.

5. Global effect (cyanobacteria and current atmosphere). This impacts virtually all ecosystems and biomes on Earth.

The duration, or time-scale, of the modulation ranges from highly ephemeral, measured in days (e.g. *Saccharomyces cerevisiae* fermentation changing the environment in ripe fruit: Goddard, 2008), to highly persistent (climate changes or atmospheric chemistry), measured in 10 million years (Fig. 3). The temporal scale measures the duration of the effect of the modulation.

IMPLICATIONS FOR SPECIES DISTRIBUTION MODELLING

Identifying biotic modifiers and environmental modulators

It may be difficult to identify all relevant biotic modifiers in order to include them in SDMs. Arguably the simplest, and most tractable, are alien plant species (neophytes). Most

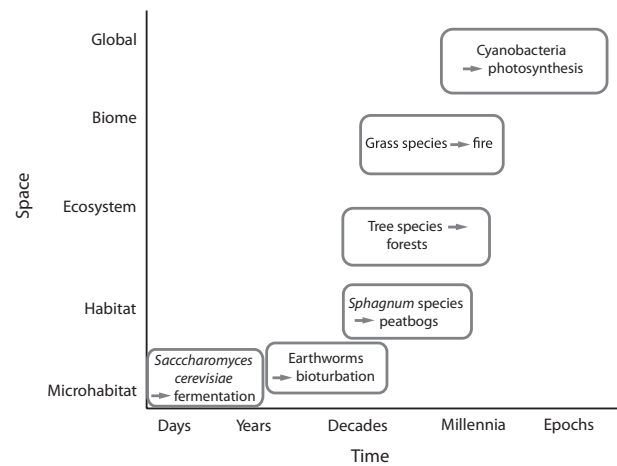


Figure 3 Diagram showing the different biotic modifiers and the modulators they affect, plus the spatial and temporal persistence of the modulators and their effects. On both the spatial and the temporal scale this is the scale at which these processes most commonly are found, but there are always exceptions.

neophytes are apparently innocuous little plants that do not significantly affect the environment. Some neophytes are strong competitors and, without significantly changing abiotic elements, replace the indigenous species. Other neophytes are biotic modifiers. For example, the increasing density of the invasive cheatgrass (*Bromus tectorum* L.) in the arid north-west of North America leads to a substantial increase in fire frequency, which results in a change in the ecosystem (D’Antonio & Vitousek, 1992; Epanchin-Niell *et al.*, 2009). Similarly, the North American black locust (*Robinia pseudo-acacia* L.) alters soil properties by invading nutrient-poor grasslands in Europe and causing nitrogen enrichment by their N-fixing symbionts (e.g. Castro-Díez *et al.*, 2009). In these cases mapping the invasive species documents its impacts as a biotic modifier.

However, in many ecosystems, a particular environmental modulating effect is the result of a large suite of species. This is exemplified by savannas which are maintained by modulators such as fire, which results from more biotic modifiers than can be listed (Beerling & Osborne, 2006). Most ‘natural’ systems may be similarly complex, with many biotic modifiers contributing to a particular environmental modulation. Mapping all these species will not be analytically or computationally tractable, and consequently other approaches may be needed. This problem is solved by replacing the individual species (biotic modifiers) by modulators, which encompass the collective modulation M (Figs 1 & 2).

Identifying the important species that predict (or cause) the modifying effect is not easy, and should ideally be based on experimental data, especially if we wish to predict these effects in different geographical areas or into future climates. Simplistically, there may be three ways of inferring environmental modulators: by first principles and observation, by experimentation and quantification, and by modelling.

1. First principle approaches are most likely to locate good starting hypotheses, such as the chemical composition of the atmosphere, and its early modulation by the biotic modifier cyanobacteria (Nisbet & Sleep, 2001).

2. Natural experimentation is used quite frequently. A typical example is the determination of the modulating effect of forest, by comparing temperature and relative humidity under forest canopy to that outside the forest (Pinto *et al.*, 2010). The search for key species often follows an experimental route, this is similar to the challenges in conservation biology, where the search is for 'keystone engineers' or 'key (ecosystem) engineers' (reviewed by Boogert *et al.*, 2006).

3. Currently a frequently used method is modelling, when the consequences of the removal of a modulator can be modelled. Such research is expected to lead to more reliable projections of future vegetation changes and will make it easier to attribute modulating effects to certain plant functional types or even species. Modelling the consequences of removing fire from ecosystems using a dynamic global vegetation model (DGVM, e.g. Bond *et al.*, 2005) is an example of this sort of test, as it evaluates the ecosystem modulating effect of fire. Modelling has also shown the importance of angiosperms in modulating tropical climates. With their higher leaf venation density and xylem structure, they have higher transpiration rates than other land plants, and consequently contribute substantially to local air humidity and rainfall (Boyce *et al.*, 2010). It might be possible to locate the key species involved in the environmental modulation, which can be regarded as biotic modifiers.

Including modulating effects in SDMs

We outline a correlative approach to modelling the spatial distribution of a species (in the following called 'focal species') that is affected by biotic modification. We assume that the modelled focal species is not a biotic modifier itself (in the sense that it does not alter modulators that co-determine its distribution), which enables us to apply the previously developed concept of modulators. If the focal species does modulate its environment, then a more complicated model, which can accommodate this interaction through feedback processes, will be required; this will not be discussed in this paper. The advantages of using the modulator concept in a SDM are: (1) Modulators directly modify resource availability, which suggests enhancing SDMs with a phenomenological description of resource modification. (2) If modulator effects are unidirectional (that is, the reciprocal impact of the modulation on the modulators can be ignored), then we can omit the response of modulators to environmental factors in SDMs. (3) The spatial distribution of modulators is often easier to determine than the distribution of the individual modifying species, as modulators such as forests or fire can be mapped from satellite images, whereas our knowledge of detailed species distribution is still incomplete. Modulators might aggregate the effect of several modifying species. (4)

Modulators can continue to exist even after the local extinction of some or even all of the individual biotic modifier species.

In the following, we show in more detail how modulators can be implemented in SDMs. Correlative SDMs infer niche conditions for particular species from observed spatial distributions of environmental factors and the focal species. In an unmodulated environment, the spatial distribution (i.e. the probability of occurrence) of the focal species is typically modelled via some transformation of a weighted linear combination D of environmental factors $P \in \{T, \dots\}$:

$$D = a_0 + \sum_{P \in \{T, \dots\}} a_P P \quad (1)$$

Note that the summation over P is over the set $\{T, \dots\}$ of all environmental factors considered. Here the effect of environmental factor P (e.g. temperature T – see Fig. 1) is described by the coefficient a_P , which, along with the intercept term a_0 , is usually inferred from data describing the observed distributions of the focal species and the environmental variable P (Guisan & Zimmermann, 2000).

In the presence of biotic modification this approach is insufficient, because modulation changes local environmental conditions for the focal species (see Fig. 1) and thereby its distribution. For example, Pinto *et al.* (2010) measured within-rain forest air temperature to be on average 10% lower and relative humidity on average 10% higher than that of the surrounding open landscape. We show how this modulation effect of forest can be incorporated in the model. Because a single modulator may impact several environmental factors we write that environmental factor P in the presence of modulator M becomes:

$$P(M) = P + \Delta_P(P, M) \quad (2)$$

where $\Delta_P(P, M)$ describes the degree of modulation as being a function of both the un-modulated environmental factor P (from the example above, the air temperature) and the modulator M (the forest). Depending on the type of impact of the modulator on its environment, the presence/absence or abundance of the modulator (both denoted by M) have to be considered. We can gain insights by approximating the modulated environmental condition as linear in M and in the interaction term $P \times M$:

$$P(M) = P + \beta_P M + \gamma_P P \times M \quad (3)$$

with parameters β_P for the direct modulator impact on the environmental factor P and γ_P for the interaction term which accounts for variation of the modulating impact dependent on the environmental condition. If the modulator impact is only weakly nonlinear, the approximation is reasonable (and in particular covers the special case of presence/absence data for the modulator – presence represented by $M = 1$ and absence by $M = 0$). In some cases, however, it may be necessary to include higher-order terms to represent nonlinearities.

We derive the full model for the distribution of the focal species by inserting equation 3 into equation 1:

$$D = \left(a_0 + \sum_{P \in \{T, \dots\}} a_P P \right) + bM + \sum_{P \in \{T, \dots\}} [c_P P \times M] \quad (4)$$

The first two terms (in brackets) are just the same as equation 1, but now modulating effects are quantified by the parameters $b = \sum_{P \in \{T, \dots\}} a_P \beta_P$ and $c_P = a_P \gamma_P$. This formulation accounts for the indirect effects of the modulator via the resource which it modifies (parameter c_P) and the direct effect on the distribution of the focal species (term bM). Such direct effects have been estimated for the effects of dominant tree species on the distribution of Iberian birds (Triviño *et al.*, 2012) and European bison (Kümmerle *et al.*, 2012). In these cases, the prevalence of the modulator was simulated with a dynamic vegetation model (using the leaf area per m² of each species as a proxy of relative cover), but one could also use forest inventory data (Brus *et al.*, 2012).

The interaction terms in equation 4, $c_P P \times M$, represent the component of the modulating effect on environmental factor P that depends on the level of P . Thus for the focal species, equation 4 accounts for the effect of the environmental factor $a_P P$, direct effects of the presence of the modulator bM , and the interaction between the modulator and each modelled environmental factor $c_P P \times M$. For factors that are not modulated, we can specify $c_P = 0$. An important caveat is that when fitting such models to data it will not be possible to distinguish biotic modulation effects from unidirectional biotic interactions, i.e. where the modulator might provide resources, prey on, or compete with the focal species (e.g. the ants studied by Sanders & van Veen, 2011). However, this is likely to be less important when the modulator results from many biotic modifiers.

SDMs: parameterization and projection

Using the approach described above, one can account for ecosystem-level modulation effects that are the result of modulation by several unspecified species. Valuable information concerning the prevalence of modulators has recently become available through advances in remote sensing. Satellite sensors are used to estimate vegetation structural characteristics, such as vegetation greenness [e.g. normalized difference vegetation index (NDVI), which also can be used as a proxy of productivity (Myneni *et al.*, 1997)], tree biomass (Saatchi *et al.*, 2011), tree cover (Hansen *et al.*, 2003) and tree height (Lefsky, 2010). Also estimates of important processes that are at least partly the result of modulation are now available from satellite sensors, such as the fire activity products (Giglio *et al.*, 2011).

In addition, dynamic vegetation or ecosystem models can be used to estimate modulator effects. Hickler *et al.* (2009), for example, estimated the effect of dynamic changes in vegetation on soil water, and Rickebusch *et al.* (2008) used the simulated soil water as a proxy for water availability in species distribution models. Most regional or global vegetation models simulate light penetration through the canopy and could easily be applied to estimate the modulating of light levels by canopy species, which has an effect on most forest plant species. An

increasing number of models also include a nitrogen cycle (e.g. Thornton *et al.*, 2007) and simulate the occurrence and effects of fire (Venevsky *et al.*, 2002; Scheiter & Higgins, 2009; Thonicke *et al.*, 2010). Hartig *et al.* (2012) discuss how DGVMs (Prentice *et al.*, 2007) can take advantage of the wealth of data being produced about ecosystems via inverse modelling techniques.

Once fitted to present-day data the models described above could be used to project future distributions of the focal species under scenarios of environmental change, if possible future distributions of both the environmental factors and the modulator are available for future times (see below). Consequently an obvious advantage of using DGVMs to produce environmental factors (e.g. fire severity or biome type) is that we can use these models to generate what these factors might be in the future, something we cannot do with remotely sensed estimates of these environmental factors. Some of the most severe environmental changes can be linked to biome shifts. Several authors have used DGVMs to project future biome shifts (Malcolm *et al.*, 2006; Scholze *et al.*, 2006; Thomas *et al.*, 2008), which would severely affect large numbers of species. Within the above framework it may be possible to utilize such information, for example current and projected fractional coverage by different biomes or plant functional traits per grid cell as a measure of modulation (Kümmerle *et al.*, 2012). However there are two key problems. The first is that the projections of the modulator distribution should account for transient effects as the modulator itself responds to changes in the environment. If the modulator is a forest, dynamic vegetation or forest models could be used to estimate transient responses (Hickler *et al.*, 2012; Triviño *et al.*, 2012), and although most of these models account for successional lags, they do not include dispersal limitations. The second problem is that static species distribution models such as those described above assume that the focal species is in equilibrium with its environment which is clearly problematic under climate change. Cabral & Kreft (submitted), Marion *et al.* (submitted) and Schurr *et al.* (2012) discuss the development of dynamic species distribution models which aim to address such issues.

Given the wealth of information on ecosystem characteristics that are relevant for describing modulation effects, the implementation of the proposed framework offers the realistic prospect of improving SDM projections. In some cases, a hierarchical approach can be used, such that, for example, the vegetation is modelled first, and then the species that depend on that particular realized vegetation structure are modelled in a second step. However, it should be noted that DGVM projections come along with their own set of uncertainties and biases (see also Dormann *et al.*, 2012), which need to be taken into account when coupling them with SDMs.

A PROPOSED RESEARCH AGENDA AND CONCLUSIONS

In order to incorporate modulating effects into our description of the environments available to focal species, and to predict

1 future changes in the environments and consequently the
 2 available space for these species, we need to incorporate three
 3 aspects.

4 First, we need to know which environmental modulators
 5 significantly change the probability of the occurrence of a
 6 species of interest at a particular location. This could be
 7 developed as a set of parameters that should be included when
 8 developing a SDM.

9 Second, we need to quantify the effect of the modulators.
 10 This should be in the form of functions that quantify the
 11 modification of the existing abiotic variables.

12 Third, we need to know the spatial distribution of the
 13 modulators, as this informs us whether they overlap with the
 14 ranges of the focal species. In the case of predictions, the spatial
 15 distributions of the modulators in the past and future should
 16 also be included.

17 Modulators affect the way the physical and consequently the
 18 biotic environment changes during global change. Earth
 19 system science suggests that both regulation of the environ-
 20 ment but also the possibility that relatively rapid biologically
 21 enhanced changes, i.e. tipping points, are possible (Lenton
 22 *et al.*, 2008; deYoung *et al.*, 2008). Forecasts of species range
 23 changes, extinction rates and ecosystem shifts without taking
 24 into account the complex impacts of modulators could result
 25 in large prediction errors. Consequently the consideration of
 26 modulation effects in SDMs is crucial.

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BIOSKETCH

Peter Linder works on the genesis and maintenance of plant diversity, with a particular focus on the Cape flora, the Restionaceae and the grass subfamily Danthonioideae.

Author contributions: All authors contributed to the development of the ideas and to the writing. H.P.L. led the writing.

Editor: Steven Higgins

The papers in this Special Issue arose from two workshops entitled 'The ecological niche as a window to biodiversity' held on 26–30 July 2010 and 24–27 January 2011 in Arnoldshain near Frankfurt, Germany. The workshops combined recent advances in our empirical and theoretical understanding of the niche with advances in statistical modelling, with the aim of developing a more mechanistic theory of the niche. Funding for the workshops was provided by the Biodiversity and Climate Research Centre (BiK-F), which is part of the LOEWE programme 'Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz' of Hesse's Ministry of Higher Education, Research and the Arts.

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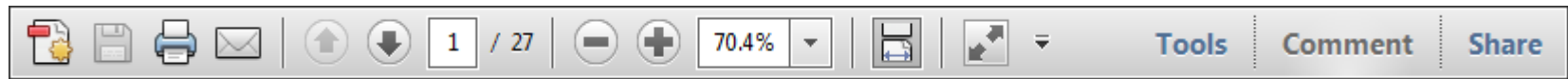
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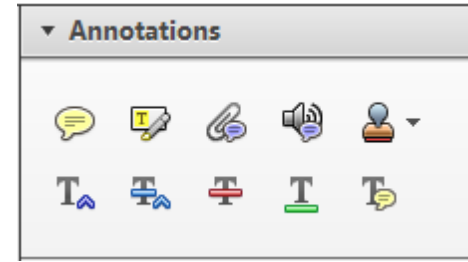
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This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the [Annotations](#) section, pictured opposite. We've picked out some of these tools below:



1. Replace (Ins) Tool – for replacing text.

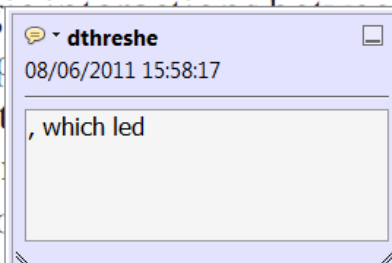


Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the [Replace \(Ins\)](#) icon in the Annotations section.
- Type the replacement text into the blue box that appears.

standard framework for the analysis of microeconomics. Nevertheless, it also led to the emergence of a new paradigm of strategic behavior. The number of competitors in the industry is that the structure of the industry is a key component of the main components of the industry. At the level, are expected to be important works on the industry by Shiraz (M henceforth) we open the 'black b



2. Strikethrough (Del) Tool – for deleting text.



Strikes a red line through text that is to be deleted.

How to use it

- Highlight a word or sentence.
- Click on the [Strikethrough \(Del\)](#) icon in the Annotations section.

there is no room for extra profits and the number of competitors are zero and the number of competitors (net) values are not determined by the number of competitors. Blanchard and ~~Kiyotaki~~ (1987), perfect competition in general equilibrium. The effects of aggregate demand and supply in the classical framework assuming monopoly power are an exogenous number of firms

3. Add note to text Tool – for highlighting a section to be changed to bold or italic.



Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the [Add note to text](#) icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

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4. Add sticky note Tool – for making notes at specific points in the text.

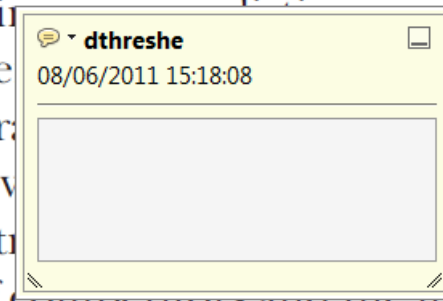


Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the [Add sticky note](#) icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.

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USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

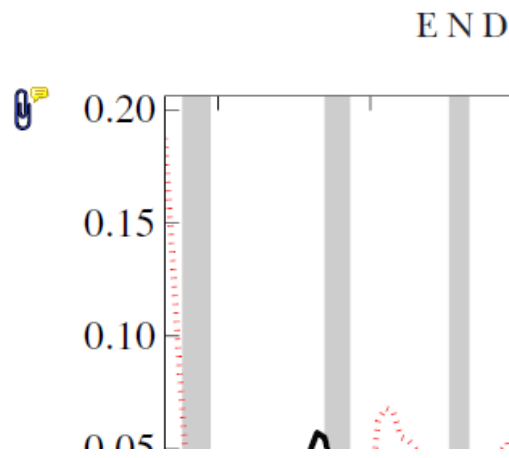
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Inserts an icon linking to the attached file in the appropriate place in the text.

How to use it

- Click on the [Attach File](#) icon in the Annotations section.
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- Select the file to be attached from your computer or network.
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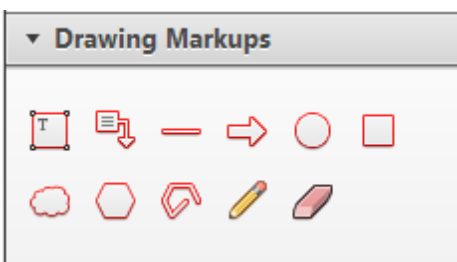
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How to use it

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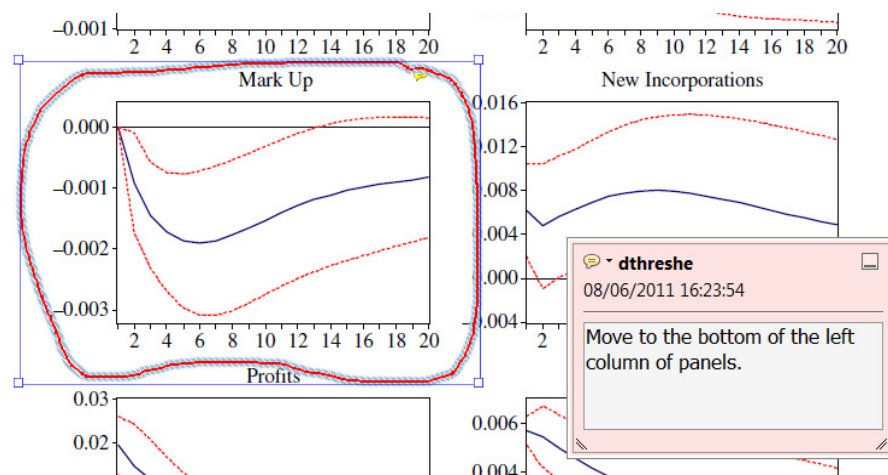


7. Drawing Markups Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks.

Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks..

How to use it

- Click on one of the shapes in the [Drawing Markups](#) section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



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