Does the Study of Facilitation Require a Reform of the Hutchinsonian Niche Concept?

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Abstract

This paper revisits the debate over whether the study of facilitation requires ecologists to revise their understanding of the relationship between the Hutchinsonian realized and fundamental niches. Following Rodriguez-Cabal et al. (2012), I argue against Bruno et al.'s (2003) claim that facilitation can make a species' realized niche larger than its fundamental niche. However, I also maintain that the abstract Hutchinsonian conceptualization of the niche makes a whole range of facilitative interactions—which I propose to call *ameliorative facilitation*—invisible to niche-based approaches to the study of ecological communities. I propose a way to incorporate ameliorative facilitation into niche-based approaches to the study of ecological communities. The proposed way involves supplementing the Hutchinsonian realized/fundamental dyad with a third concept: the *potential niche*. This concept was introduced by ecologists studying the effects of environmental changes on species distributions (Jackson and Overpeck 2000), but I show how it could also be fruitfully used in facilitation studies. I argue that this proposed solution is more appealing than Stachowicz's (2012) suggestion to apply Hutchinson's realized/fundamental contrast to a spatial-geographical, as opposed to an abstract-conceptual, notion of the niche.

Keywords: Ecological niche; facilitation; G. Evelyn Hutchinson; ecological interactions; ecological communities; competition.

1. Introduction

The ecological niche is one of the most influential and widely discussed ecological concepts. Historically, it has occupied a prominent place in ecological studies of competitive interactions among species, and in associated investigations of the factors

that enable species that use similar resources and habitats to coexist within communities (Kingsland 1985, chap. 7; Schoener 1989; Colwell 1992). This association of the niche with interspecific competition has a long history in ecology, which can be traced back to animal ecologist Joseph Grinnell (1914, 1917, 1928), the first introducer of the niche concept (Schoener 1989, pp. 80–85), and to the seminal theoretical and experimental explorations of Alfred J. Lotka (1925), Vito Volterra (1926), and Georgy F. Gause (1934) on the "competitive exclusion principle." With G. Evelyn Hutchinson's (1944, 1957, 1978, chap. 5) influential "hypervolume concept" of the niche and his contrast between a species' *fundamental* and *realized* niches, competition became nearly built in the concept—competition being seen as the main process that differentiates the respective sizes of the fundamental and realized niches.

Hutchinson (1944, 1957, 1978, chap. 5) introduced a characterization of the niche as a set of points in an abstract space representing intersections between ecological factors (e.g. sizes of food, temperature, etc.). Within such a space, he proposed, a species' *fundamental niche* can be defined as "an area … each point of which corresponds to a possible environmental state permitting the species to exist indefinitely." (Hutchinson 1957, p. 416) A species' *realized niche* can then be defined as the subset of this area representing environmental states under which the species is capable to exist in the presence of another species whose fundamental niche partly overlaps with its own (Hutchinson 1957, p. 418). This theorization emphasized the *negative* impacts that co-occurring species can have on the size of each other's niches, mainly through competition. Hutchinson's approach has then been extended to other interactions, like predation, parasitism and even mutualism (e.g. Colwell and Fuentes 1975), but the niche concept has remained predominantly tied to the study of negative interactions among species.[1]

[1] This is in part reflected by the fact that ecologists who did not use the term "niche" but discussed competition and competitive exclusion at around the same time as the above-cited authors (e.g. Tansley 1917; Salisbury 1929) are at times recognized as part of the history of the niche concept (see Jackson 1981; Chase and Leibold 2003, pp. 7–8).

Recently, however, some ecologists studying the phenomenon of *facilitation* in ecological communities have explored the possibility of applying the Hutchinsonian niche to the study of positive interactions among species (e.g. Bruno et al. 2003). *Facilitation* can be defined as an ecological interaction that is beneficial to at least one participant and detrimental to none of them (see Stachowicz 2001, p. 235; Callaway 2007, p. 2). The current interest of many ecologists in this type of interaction can be situated as part of a more general surge of interest within the field in non-competitive and non-trophic interactions among species, like *ecosystem engineering* (e.g. Jones et al. 1997; see Holt 2009, p. 3).

In an influential paper on facilitation and its purported implications for ecological theory, Bruno et al. (2003) argue that facilitation should lead ecologists to revise their understanding of the relationship between the realized and the fundamental niches. They state: "Incorporating facilitation into niche theory leads to the paradox that the spatial extent of the realized niche of a species can be larger than the spatial range predicted by the fundamental niche." (Bruno et al. 2003, p. 119) This proposal has sparked debate among ecologists interested in facilitation, some of them criticizing Bruno et al.'s proposal as conceptually confused (Rodriguez-Cabal et al. 2012).

This paper aims to revisit the debate between Bruno et al.'s (2003) and Rodriguez-Cabal et al. (2012) (see also Stachowicz 2012; Bulleri et al. 2016), and to propose a way to incorporate facilitation into niche-based approaches to the study of ecological communities that avoids some drawbacks of Bruno et al.'s proposal. I will maintain that, although Rodriguez-Cabal et al.'s (2012) criticism of Bruno et al.'s (2003) proposal is well-founded, incorporating facilitation in niche-based approaches to the study of ecological communities nevertheless requires some expansion of established conceptualizations. I will maintain that facilitation could promisingly be incorporated into niche-based approaches to the study of ecological communities through the use of Jackson and Overpeck's (2000) *potential niche* concept. Jackson and Overpeck (2000) introduce this concept for other research aims, but I will contend that it provides the expansion of niche-based approaches to the study of communities that facilitation requires.

My discussion will be organized as follows. In section 2, I will introduce Bruno et al.'s (2003) claim about facilitation and the niche, and review its reception by other ecologists and the criticism it received from Rodriguez-Cabal et al. (2012). I will support Rodriguez-Cabal et al.'s point that facilitation cannot make a species' realized niche larger than its fundamental niche. In section 3, I will review Stachowicz's (2012) response to Rodriguez-Cabal et al., and his suggestion that Hutchinson's contrast between the realized and the fundamental can as much be applied to a spatial-geographical as to an abstract-conceptual notion of the niche. I will also propose an analysis of why, and in what respects, the Hutchinsonian conceptualization of the relationship between the realized and fundamental niches hinders the development of niche-based ecological approaches that fully incorporate facilitation. In section 4, I will give reasons not to adopt Stachowicz's spatial-geographical reconceptualization of the Hutchinsonian niche, and present what I think is a more fruitful way to incorporate facilitation into a niche-based approache to the study of ecological communities.

2. Facilitation and the realized niche: an alleged paradox

As I mentioned in the introduction, ecologists' recent interest in facilitation can be seen as part of a broader surge of interest in non-competitive and non-trophic interactions in ecology. This surge of interest has led to the introduction of various new concepts for describing those interactions, concepts such as *ecosystem engineering*, *niche construction* and *facilitation*. Facilitation, as I said above, can be defined as an ecological interaction that is beneficial to at least one participant and detrimental to none of them. It has some commonalities with *ecosystem engineering* and *niche construction* (Jones et al. 1997; Odling-Smee et al. 2003). Like *ecosystem engineering*, facilitation refers to non-competitive and non-trophic interactions. Facilitation, however, is in some respects narrower and in some respects broader than ecosystem engineering. It is narrower in in that it includes, among instances of ecosystem engineering, only those that are beneficial to at least one of the species involved. It is broader in that in includes indirect effects that species have on each other via more direct effects on other species (e.g. a species that benefits another one by controlling its predators), whereas ecosystem engineering includes only indirect effects that occur via effects on abiotic factors. *Niche construction*

includes, among other things, beneficial interactions between organisms from different species, which is essentially what facilitation consists in. Niche construction, however, is in some respects broader and in some respects narrower than facilitation. It is broader in that facilitation includes only beneficial effects, whereas niche construction also includes detrimental interactions. It is narrower in that facilitation includes interactions irrespective of potential evolutionary effects, whereas niche construction is usually restricted to interactions that affect the selective pressures that organisms face.[2]

Reviews on facilitation make clear that it is an ubiquitous ecological phenomenon (e.g. Callaway 1995; Bertness and Leonard 1997; Stachowicz 2001). As Stachowics (2001, pp. 238–242) summarizes, some species facilitate others by providing them refuges from physical stresses. For instance, plants, reef-forming corals, and giant kelps facilitate many other species by reducing wind or water flow in a way that enhances the deposition and stabilization of the substrate on which they live. Some species facilitate others by providing them refuges from predation. For instance, the complex habitat structures formed by seaweeds, seagrasses, and corals provide shelters from predators to many mobile animals, and some unpalatable plants provide refugees from herbivory to the more palatable plants that grow close to them. Some species facilitate others by enhancing their nutrient acquisition. For instance, mycorrhizal fungi and symbiotic bacteria enhance many terrestrial plants' nutrient acquisition, and some marine sponges do something similar with respect to mangrove trees. And some species facilitate others by providing them refugees from competition. For instance, in some well-lit tropical habitats where corals grow slowly, herbivores that feed on seaweeds benefit corals by preventing their overgrowth by seaweeds.

Given the focus of established ecological theory on negative interactions, the apparent ubiquity of facilitation suggests the need for some revisions of approaches classically used in ecology. This perceived need provides the context for Bruno et al.'s controversial proposal:

[2] Niche construction *sensu* Odling-Smee et al. (2003) encompasses both intraspecific and interspecific interactions between organisms, and both positive and negative interactions between them.

> The niche concept implicitly assumes that neighboring species have negative impacts (or a niche-shrinking affect) on one another and is firmly bound to the notion or 'principle' of competitive exclusion (that no two species can occupy the same niche). Incorporating facilitation into niche theory leads to the paradox that the spatial extent of the realized niche of a species can be larger than the spatial range predicted by the fundamental niche. (Bruno et al. 2003, p. 119)[3]

Bruno et al. (2003) illustrate this proposal with a few examples—e.g. canopies of seaweeds in intertidal environments expand the distributional rage of many species, by reducing thermal and desiccation stresses, early successional plants and trees expand the distributional range of many species by modifying soil conditions after glacial retreat. They then contend: "In all of these cases, the niche or physical space occupied by a species in the presence of interspecific interactions is actually greater than that occupied when the species lives alone." (Bruno et al. 2003, p. 120)

Bruno et al.'s claim seems reasonable at first glance: negative interactions make a species' realized niche smaller than its fundamental niche; hence, symmetrically, positive interactions should make a species' realized niche larger that its fundamental niche. Many commentators simply take Bruno et al.'s suggestion at face-value (e.g. Callaway 2007, pp. 295–296; Holt 2009, p. 3). For Colwell and Rangel (2009), Bruno et al.'s (2003) suggestion in fact involves no paradox at all:

> The consequence, that positive species interactions (mutualism and commensalism) might imply a realized niche larger than the fundamental niche for one or both partners, has been viewed by some as a ''paradox'', but in fact is simply a logical and meaningful consequence of Hutchinson's definitions, a consequence that might very well not have troubled him at all. (Colwell and Rangel 2009, p. 19654, in footnote *)

They note that the possibility highlighted by Bruno et al. (2003) was already recognized by Gause and Witt (1935, pp. 603–604), and highlighted by Hutchinson (1957, p. 417), himself, who referred to it with the odd term "negative competition."

Bruno et al.'s (2003) claim, however, has also sparked criticism. In a commentary, Rogdriguez-Cabal et al. (2012) object that what Bruno et al.'s (2003) examples illustrate

[3] For antecedent claims similar to Bruno et al.'s, see Higashi (1993), van der Maarel et al. (1995), and Wilson et al. (1995).

is only the possibility that facilitation expands a species' *spatial range of distribution*, and that this, in itself, does not prove that the facilitated species involved have expanded their realized niche beyond their fundamental niche. They state: "whether the new range of conditions experienced by the recipient species is greater than that predicted by the fundamental niche is uncertain because, in most cases, we do not even know what is the fundamental niche." (Rodriguez-Cabal et al. 2012, p. 38) Another possible explanation of the facilitated species' expanded range of distribution is that the facilitator species creates environmental conditions that are part of the facilitated species' fundamental niche at locations where those conditions would not otherwise be present. The facilitated species expands its distributional range, but its fundamental niche hasn't changed.

I think that, in fact, the latter possibility is the only one permitted by the Hutchinsonian concept. This is because, as defined by Hutchinson (1957, 1978, chap. 5), the fundamental niche is an abstract volume that includes *all* environmental conditions that underlie a species' ability to persist at a location. Hence, *by definition*, the conditions created by a facilitator species *must* be included in the fundamental niche of the species it facilitates. What the facilitator species changes is the *instantiation* of factors that are part of the facilitated species' fundamental niche in the environment, not the fundamental niche itself. The facilitator species creates an environment that exhibits more of the features that are included in the facilitated species' fundamental niche than the environment would otherwise exhibit. Hence, I would put the point more strongly than Rodriguez-Cabal et al.: the issue is not just, as they suggest, that *we do not know* what the fundamental niche of the facilitated species is, but rather, that whatever this fundamental niche is, it must, *by definition*, include *all* facilitative environmental conditions potentially created by another species. This nevertheless only reinforces Rodriguez-Cabal et al.'s (2012, p. 39) verdict (see fig. 1): "facilitation cannot cause the expansion of the realized niche over the fundamental niche."

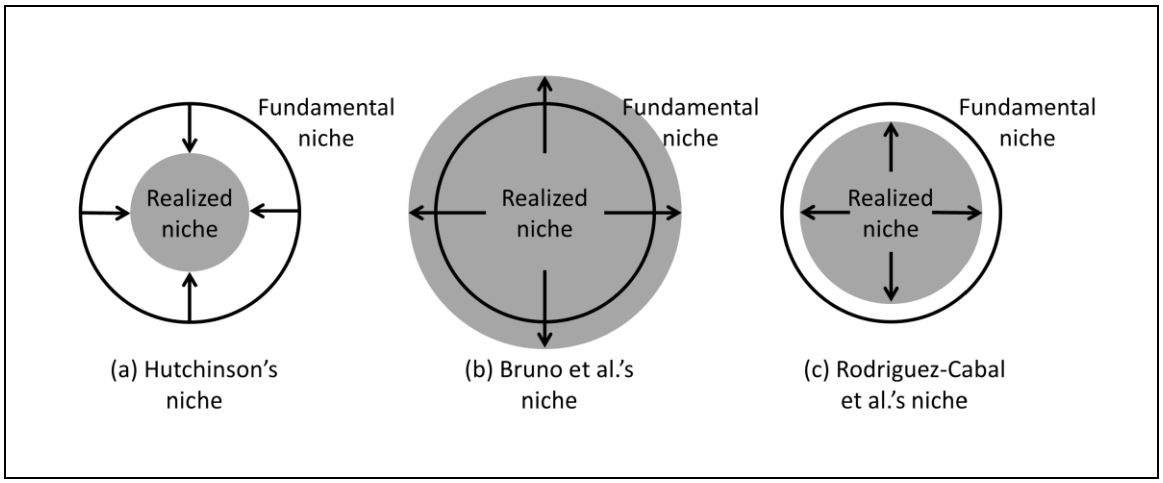

Figure 1: The relationship between the realized and fundamental niches according to (a) Hutchinson (1957), (b) Bruno et al. (2003), and (c) Rodriguez-Cabal et al. (2012). In (a), negative interactions (competition, predation parasitism) make the realized niche (grey circle) smaller than the fundamental niche (black line). In (b), facilitation makes the realized niche (grey circle) larger than the fundamental niche (black line). In (c), facilitation mitigates the effects of negative interactions and makes the realized niche (grey circle) larger than it would be without facilitation (its size in a), but does not make it larger than the fundamental niche (black line). Redrawn from Rodriguez-Cabal et al. (2012, p. 37).

By definition, Hutchinson's niche concept entails that only niche evolution can change a species' fundamental niche (Rodriguez-Cabal et al. 2012, p. 38). If a facilitative interaction triggers evolutionary change on the part of the facilitated species by opening new opportunities, then it could lead to an expansion of that species' fundamental niche (for some examples, see Rodriguez-Cabal et al. 2012, p. 38). But one should note that, in such cases, it is the species' *fundamental* niche that would become expanded, not the realized niche beyond the fundamental niche. Hence, the idea that a species' realized niche can be larger than its fundamental niche is incompatible with Hutchinson's definition of the fundamental niche.

From these considerations, Rodriguez-Cabal et al. (2012, p. 39) draw the following conclusion: "[T]he inclusion of facilitation into niche theory may be better characterized as the processes, both physical and/or biological, that can expand the n-dimensional hypervolume of the realized niche that meets the requirements of the fundamental niche, and can alleviate the effects of negative interactions and abiotic stress." In the next section, I will argue that, although Rodriguez-Cabal et al. are correct about what

Hutchinson's conceptualization of the realized and fundamental niches implies, this conceptualization has an important drawback as regards the possible incorporation of facilitation into niche-based approaches to the study ecological communities.

3. Facilitation: a Hutchinsonian dead angle?

3.1 Stachowicz's response to Rodriguez-Cabal et al.

In a short response, Stachowicz (2012)—one of Bruno et al.'s (2003) coauthors—attempts to counter Rodriguez-Cabal et al. (2012) objections. He argues that Rodriguez-Cabal et al.'s disagreement with Bruno et al. is based on a particular interpretation of Hutchinson's fundamental niche, for which there is an alternative. Rodriguez-Cabal et al. (2012) interpret the fundamental niche as an *abstract* or *conceptual* entity, whereas Bruno et al. interpret it as a *spatial* or *geographical* entity (Stachowicz 2012, pp. 42–43).

Stachowicz concedes that facilitation cannot expand a species' realized niche beyond its fundamental niche when the fundamental niche is understood as an *abstract conceptual* entity. For instance, when some plants facilitate other plant species by shading the substrate and reducing temperature or desiccation, the factors that limit the facilitated species' fundamental niche remain unchanged. Nevertheless, in such cases, Stachowicz insists, "geographically, the niche has expanded," since "the spatial extent of the fundamental niche increased under such interactions." (Stachowicz 2012, pp. 42–43) Hence, according to Stachowicz:

> Both viewpoints are correct. The fundamental niche in a conceptual sense has not changed, rather the environmental conditions in an area have shifted to fall within those specified by the fundamental niche. … [W]hether this represents an expansion of the fundamental niche or not depends on whether one conceptualizes the niche in an abstract sense, or as a physical location. (Stachowicz 2012, p. 43)

A concern with Stachowicz's response is that the fundamental niche as defined by Hutchinson is unmistakably an *abstract conceptual* entity. As seen above, the fundamental niche, for Hutchinson (1957, 1978, chap. 5), is a hypervolume representing all the environmental states that would permit a species to persist indefinitely at a location if not hindered by another species whose fundamental niche partly overlaps with its own. The fundamental niche, as classically defined by Hutchinson, is thus not a spatial

or geographical entity. In fact, a commonly-highlighted specificity of Hutchinson's niche is its being an attribute of species or population rather than an attribute of the environment (Schoener 1989, p. 90; Griesemer 1992, p. 238; Colwell 1992, p. 241). The hypervolume represents *the niche of a particular species*, not a niche that exists independently in the environment. In this respect, Hutchinson's introduction of his hypervolume concept is commonly thought to have amounted to a "radical" and even "revolutionary" shift from Grinnell's (1917) and Elton's (1927) prior understandings of the niche as an attribute of the environment (Schoener 1989, p. 90; Griesemer 1992, p. 238). To be sure, as Stachowicz's (2012, p. 43) notes (see also Bulleri et al. 2016, p. 71), the niche concept has been continuously debated since its initial introduction by Grinnell and Elton, and, clearly, some ecologists still construe the niche as an attribute of the environment. However, that the *Hutchinsonian* niche concept—the concept in relation to which the realized/fundamental niche contrast is classically defined—construes the niche as an abstract entity is not up for debate.

So, I think that the question ultimately raised by Bruno et al.'s (2003) proposal and Stachowicz's (2012) response to Rodriguez-Cabal et al. (2012) is whether we should *reform* the Hutchinsonian conceptualization of the niche. Perhaps studying facilitation requires ecologists to apply Hutchinson's contrast between the realized and the fundamental niches to a (non-Hutchinsonian) notion of the niche as a spatial-geographical entity (i.e. as an attribute of the environment) (see fig. 2). Scientific concepts are subject to being redefined according to the theoretical needs of researchers. Hence, if, as Stachowicz's (2012) response to Rodriguez-Cabal et al. (2012) suggests, the established Hutchinsonian abstract-conceptual conceptualization of the niche is unsuited to the study of facilitation, then this may call for a reform of this conceptualization. And as Stachowicz (2012, p. 43) suggests, the choice to use the abstract or the spatial construal "could be a matter of … the particular question/application under consideration."

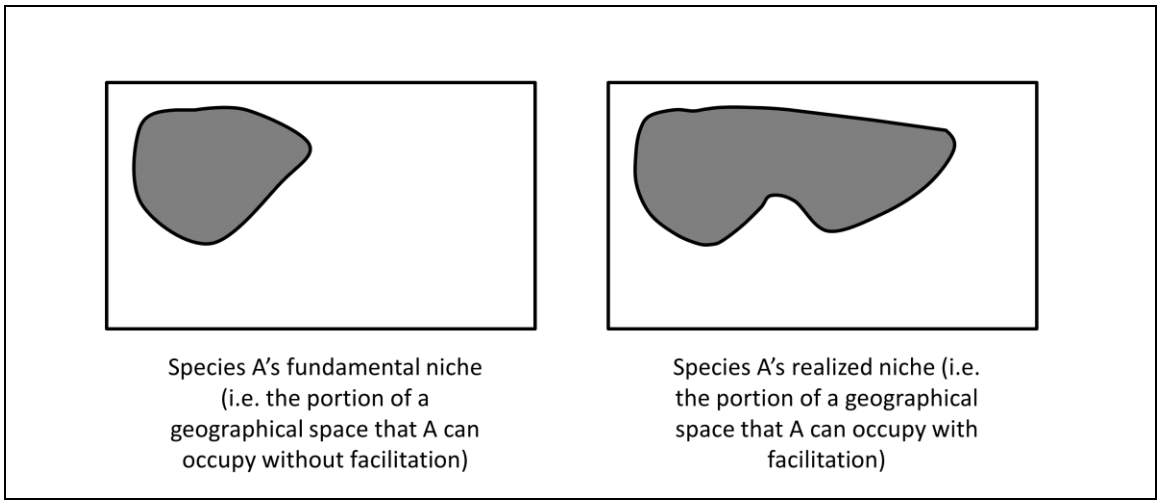

Figure 2: A geographical application of the realized/fundamental niche contrast. The species' niche without facilitation (left) covers less geographical space than its niche with facilitation (right). If the niche without facilitation (right) is assumed to represent what the species' (geographical) niche would be if no interaction with other species occurred, then this niche can be called its (geographical) fundamental niche, and its geographical niche as expanded by facilitation (right) can be called its realized (geographical) niche.

I will now highlight an important way in which the abstract Hutchinsonian conceptualization of the niche hinders the development of niche-based ecological approaches that fully incorporate facilitation. I will contend that the Hutchinsonian conceptualization makes a whole range of facilitative interactions—which I will call *ameliorative facilitation*—invisible to niche-based models of ecological communities.

3.2 Mitigating vs. ameliorative facilitation

The Hutchinsonian conceptualization of the niche implies that facilitation can be incorporated into niche-based models of ecological communities only when it *counteracts* or *mitigates* the effects of some negative interactions. I will refer to such occurrences as *mitigating facilitation*. Rodriguez-Cabal et al. at times speak as if they recognized only the possibility of mitigating facilitation (Rodriguez-Cabal et al. 2012, p. 37, figure legend, p. 39). However, as Bruno, Stachowicz and colleagues emphasize in a subsequent publication, facilitation may not only *counteract* the effects of some negative interactions (or dispersal limitation), it can also *ameliorate* some abiotic conditions that would otherwise be too stressful for a species to be able to establish itself, and, in so

doing, enable that species to persist at a location where it would otherwise not be able to persist (Bulleri et al. 2016, p. 71). This occurs, for instance, in cases where a species facilitates another one by providing it a refuge from physical stress (see examples by Stachowicz 2001 in section 2, above, and those presented by Bulleri et al. 2016, p. 71). I will refer to such occurrences as *ameliorative facilitation*.

The Hutchinsonian conceptualization of the niche makes ameliorative facilitation invisible to niche-based models of communities because of the asymmetric way in which it theorizes positive and negative ecological factors. The reasoning that underlies the relationship between the fundamental and the realized niches involves identifying two types of factors: *niche factors*—i.e., components of a species' niche (both fundamental and realized), and what I will call *interaction factors*—i.e., factors that explain the difference between a species' realized and fundamental niches. Importantly, niche factors in the Hutchinsonian conceptualization of the niche are always *positive* ones. The niche variables represented in Hutchinson's hypervolume denote *requirements* for the persistence of a species in a given environment (Chase and Leibold 2003, pp. 5–6), and, as such, they represent factors whose presence in an environment is *beneficial* to a species. Hutchinson (1978, pp. 171–173) identifies two categories of niche factors: *scenopoetic* factors, that is, physical and chemical factors that "set the stage" for the lives of organisms, i.e. that pertain to their ranges of tolerance (e.g. temperature, illumination, humidity), and *bionomic* factors, that is, factors "that are directly involved in the lives of organisms" as resources that they consume and which they may compete for when they become rare.

The Hutchinsonian concept thus acknowledges the presence of positive factors in the ecological world from the outset. However, by theorizing these factors as *niche factors* rather than *interaction factors*, the Hutchinsonian conceptualization of the niche forecloses the possibility of treating them as ones that result from the presence of other species, that is, as factors that result from ecological interactions. Whether positive factors result from interactions with other species (i.e. from ameliorative facilitation), or are present out of purely physical processes does not matter when identifying them as

niche factors (relatively to a particular species), and when determining whether they are available at a given location.

Once the (positive) niche factors pertaining to a particular species are identified and found to exist at a given location, researchers can then look at the extent to which the species has access them. That is, they can consider how *interaction factors* (i.e. interactions with other species) affect the ability of the species to access to those factors, that is, affect the difference between the species' realized and fundamental niches. The fact that niche factors are positive factors imposes that interaction factors will primarily be negative ones, that is, factors that *hinder* the species' ability to access the factors that are constitutive of its fundamental niche. Since the factors that are constitutive of its fundamental niche form the background against which the potential effects of interspecific interactions are considered, and since what is at issue is whether the species will or will not have access to those factors, then the relevant interactions, at this stage, can only be negative ones.

Only at a second time, once the negative effects of some interspecific interactions on a species' access to its niche factors available at a location have been considered, it then becomes possible to consider how some facilitative interactions—i.e. some *mitigating facilitation*—can counteract those negative effects and restore the species' access to some of the factors constitutive of its fundamental niche. Negative interactions had deprived the species access to those factors, *mitigating facilitation* partly restores this access.

Hence, by theorizing positive factors primarily as niche factors rather than interaction factors, the Hutchinsonian niche concept makes itself able to consider only *mitigating facilitation* (besides negative interactions) as able to change the size of a species' realized niche with respect to its fundamental niche. Its theorization of positive factors as niche factors makes it blind to *ameliorative facilitation.* A niche-based model of ecological communities adopting Hutchinson's conceptualization cannot distinguish the results of *ameliorative facilitation* from those of purely physical processes. Both results form the background against which the possible effects of (other) interspecific interactions on a species' realized niche can be investigated. One can of course *recognize* the occurrence of ameliorative facilitation and then use the Hutchinsonian approach to

study other types of ecological interactions, but one cannot use this approach to study ameliorative facilitation *as an ecological interaction*. Hence, although the Hutchinsonian conceptualization of the niche does not *deny* the occurrence of ameliorative facilitation, it sends its occurrence to the background, and thus makes an investigative approach based on it blind to how ameliorative facilitation may be crucial to many species' ability to persist at some locations. The Hutchinsonian conceptualization of the niche sets ameliorative facilitation in a dead angle.

3.3 Competition, facilitation, and counterfactuals

By setting ameliorative facilitation in a dead angle, the Hutchinsonian conceptualization limits the kind of questions that ecologists can formulate within a niche-based research framework. Hutchinson's contrast between the realized and the fundamental niche is a powerful tool to formulate questions about what might be called *competition-* and *predation-counterfactuals*. It provides a framework to structure research around questions of the type: "how would species A's ability to persist at a location be increased if competitor B and/or predator C were not present?"; or "how would species A's ability to persist at a location be reduced if competitor B and/or predator C were introduced?". These questions can be formulated in terms of how B and/or C affect the difference between A's realized and fundamental niches. Answering such counterfactual questions improves our understanding of how a particular community hangs together.

The Hutchinsonian conceptualization, however, does not permit the formulation of questions about what might be called *facilitation-counterfactuals*—at least ones concerned with *ameliorative facilitation*. It provides no way to structure research around questions of the type: "how would species A's ability to persist at a location be reduced if ameliorative facilitator B were not present?"; or "how would species A's ability to persist at a location be increased if ameliorative facilitator B were introduced?". Answering such counterfactual questions would also improve our understanding of how a particular community hangs together. However, given that, as seen above, ameliorative facilitation cannot affect the difference between a species' realized and fundamental niches, the Hutchinsonian conceptualization does not provide a framework within which to formulate such questions. At best, it provides a framework within which to formulate

questions about the possible effects of a *mitigating* facilitator, that is, questions of the type: "how would species A's ability to persist at a location, when competitor B and/or predator C are present, be increased if facilitator D were introduced?"; or "how would species A's ability to persist at a location, when competitor B and/or predator C are present, be reduced if facilitator D were removed?"

A common criticism of the Hutchinsonian niche concept asserts that it is biased towards negative interactions (Vázquez 2005, p. 151; Polechová and Storch 2008, p. 1090). What I explained in this section sheds some light on the subtle way in which it is. The Hutchinsonian conceptualization of the relationship between the realized and fundamental niches sends a whole range of positive ecological interactions—i.e. ameliorative facilitative ones—to the background. A framework for studying ecological communities based on it will therefore set these positive interactions in a dead angle.

4. A path to solution: the potential niche

Is it really a problem that niche-based approaches to the study of communities set ameliorative facilitation in a dead angle? One could indeed argue that it is not. Scientific models need not pretend to give a complete picture of reality, and researchers can use a model while keeping in mind that the picture of the world it conveys is partial and incomplete. Hence, the study of ameliorative facilitation may simply require a different research framework than that used to study negative interactions and mitigating facilitation.

However, even if we grant this, we must still recognize that a unifying picture of how negative interactions, mitigating facilitation, and ameliorative facilitation relate to each other in their respective ways to shape the conditions that enable a species to persist at a location would improve our understanding of communities. Such a picture could be given in either of the two following ways. One could elaborate a *non-niche-based framework* for studying ameliorative facilitation, and then explain how it complements niche-based understandings of how negative interactions and mitigating facilitation shape the conditions that enable a species to persist at a location. Or one could elaborate a *unificatory niche-based framework* that incorporates both the types of interactions that

the Hutchinsonian concept (in its classical formulation) is suited to study—i.e. negative interactions and mitigating facilitation—and those that it is unsuited to study—i.e. ameliorative facilitation. The choice between these two ways might be a matter of a researcher's taste for (or indifference towards) conceptual unification, but it might also partly depend upon how appealing a candidate unificatory framework that takes the second way might be. This, I think, motivates the exploration of how the Hutchinsonian conceptualization of the niche might be reformed, or perhaps expanded, to incorporate ameliorative facilitation.[4]

I do *not* think that a *reform* of the Hutchinsonian conceptualization of the niche along the lines proposed by Stachowicz (2012) is an appealing strategy for incorporating ameliorative facilitation into a niche-based research framework. Applying Hutchinson's contrast between the realized and the fundamental niches to a (non-Hutchinsonian) *spatial-geographical* notion of the niche, as suggested by Stachowicz (2012), would have important drawbacks. One of them is that such a reform would leave us in need for a concept that does precisely what Hutchinson's (abstractly construed) fundamental niche does. In order to be able to determine whether some factors instantiated at a location are

[4] A possible damaging effect of models that send ameliorative facilitation to the background is that they can foster a picture of ecological communities that misguidedly underappreciates the importance of species interactions within them. Ecology has a long history of controversies over whether and to what extent communities are interactive entities or mere sets of co-occurring populations (Levins and Lewontin 1980; Odenbaugh 2007). Ecologists studying facilitation insist on how the recognition of facilitation brings support to the interactive view (Callaway 1997; Lortie et al. 2004). In that it is bound to reflect only a subset of the interspecific interactions that take place within communities, a niche-based ecological model that adopts the Hutchinsonian conceptualization thus seems prone to fuel unwarranted doubts about how interactive communities really are. It can falsely make the question of whether communities are interactive entities or mere sets of co-occurring species seem to hinge on the question of how important competitive and predatory interactions are within them. Of course, in line with what I say above, ecologists could attempt to eschew this problem by keeping in mind that niche-based models reflect only an incomplete picture of ecological reality. But, arguably, this could hardly cancel entirely the risk that, as the use of a (competition- and predation-biased) niche-based model becomes entrenched, the picture of the world it conveys gets falsely taken for reality.

or are not part of a species' *spatial-geographical* fundamental niche, we would need to know whether those factors are among that species' ecological requirements. Hutchinson's abstract fundamental niche concept tells us precisely this: what combinations of environmental conditions would enable a species to persist if instantiated at a given location. A reform of the Hutchinsonian conceptualization that would apply the realized/fundamental contrast to a spatial-geographical notion of the niche would thus require ecologists to introduce a new term to refer to Hutchinson's abstract concept.

Moreover, a reason for not, as Stachowicz (2012, p. 43) proposes, letting the choice to use the abstract or the spatial construals "be a matter of … the particular question/application under consideration," is that this would promote an unsteady use of terms that would be prone to generate miscommunication and confusion among ecologists. Ecology has historically been plagued with such confusion-generating unsteady uses of terms, and the niche concept has not been spared (Real and Levin 1991, p. 180). Many ecologists consider such unsteady uses of ecological terms as hindering the progress of their science (e.g. Mills et al. 1993; Fauth et al. 1996; Stroud et al. 2015), and the possible detrimental effects of such unsteady use (with respect to "community") has even been quantified (Trombley and Cottenie 2019). Hence, what seems advisable is a better stabilization of the usage of niche-related terms, not more terminological wobble.[5]

[5] Another reason against adopting a reform like that suggested by Stachowicz is that, to obtain the result illustrated in figure 2 above, it is in fact not sufficient to apply Hutchinson's contrast between the realized and the fundamental niches to a spatial-geographical notion of the niche. We also need to stipulate that some geographically instantiated ecological conditions are part of a species' fundamental niche only if they exist strictly out of purely physical processes. Only if we make this stipulation, do we get the result that a species' geographical realized niche (its niche after interactions, including facilitative ones) can be larger than its fundamental geographical niche (its niche prior to interactions). Without this stipulation, it remains possible to consider that the fundamental niche is the (geographical) niche prior to negative interactions and the realized niche is the (geographical) niche after negative interaction. We would then get the result that facilitation may make a species' *fundamental* (geographical) niche larger than what it would otherwise be, not the result that facilitation may make a species' *realized* (geographical) niche larger than its *fundamental* (geographical) niche. The stipulation highlighted here seems unappealing in that it requires one to adopt the rather strange view that the very same ecological factor (e.g. some temperature range) is or is not part of a species' (geographical) fundamental niche, depending on whether it is produced exclusively by physical

These considerations suggest that if elaborating a *unificatory niche-based framework* that incorporates ameliorative facilitation required us to reform the Hutchinsonian concept along the lines proposed by Stachowicz (2012), then we should probably abandon the project of elaborating such a framework. We should instead take the first way delineated above, and recognize that ameliorative facilitation needs to be studied through a *non*-niche-based research framework.

However, I think that there is a more appealing alternative to Stachowicz's (2012) proposed reform, as a strategy for incorporating ameliorative facilitation in a niche-based ecological framework. What the study of facilitation calls for, I submit, is *not* a *reform* of the Hutchinsonian abstract understanding of the niche, but instead the introduction of a spatial-geographical concept that *supplements* Hutchinson's realized/fundamental dyad. I think that the *potential niche* concept introduced by Jackson and Overpeck (2000) as a tool to study the effects of environmental changes on species distributions provides the adequate supplement.

An often highlighted limitation of the Hutchinsonian niche concept is that, because of its abstract character, it represents combinations of ecological factors irrespective of whether they are actually instantiated at some existing locations (Jackson and Overpeck 2000, p. 195; Vázquez 2005, p. 150; but see nuances in Colwell and Rangel 2009). For instance, it can represent all the possible combinations of summer mean temperature and annual precipitation, including high precipitation combined with low temperature, even though, in fact, this combination is not instantiated at any existing site (because mean annual precipitation and summer mean temperature are positively correlated). In general,

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processes or whether it partly results from biotic processes. Besides being an odd way to parse ecological factors, this view would demand ecologists to determine how a given ecological factor has come to be available at a given location before being able to decide whether to count it as part of a species' fundamental niche or as part of its realized niche. Such an epistemic demand would likely hinder research on facilitation rather than facilitating it. In a more recent publication Bruno, Stachowics and colleagues (Bulleri et al. 2016, p. 71) shift to the view that what facilitation may expand is a species' *fundamental* niche, not its *realized* niche beyond the limits of its *fundamental* niche. With this shift, their view comes close to the one I will propose below, but I think that my proposal, which introduces the concept of the *potential niche* to facilitation research, offers a cleaner conceptualization.

among the possible combinations of factors under which a species could theoretically persist, only a subset is instantiated at existing locations. Moreover, this subset is prone to change over time given that environments change, and that such changes will often affect the ability of species to persist at given locations. Because it does not discriminate between instantiated and uninstantiated combinations of ecological factors, the Hutchinsonian abstract concept, however, is unable to capture the possibility that a species' ability to persist at a location changes, not because some competitors or predators have been removed or introduced (leading the species to realize a larger or smaller portion of its fundamental niche), but rather because the degree of instantiation in the environment of some factors included in its fundamental niche has changed.

Their aim to study the effects of environmental changes on species distributions thus leads Jackson and Overpeck (2000) to introduce new niche-related concepts. Jackson and Overpeck's concepts will be useful for our purposes, because the phenomenon that they aim to study is, in significant respects, similar to the one studied by ecologists working on facilitation. In both cases, what is emphasized is the possibility that a species' ability to persist at a location be affected not only by the presence or absence of competitors or predators preventing it to exploit the favorable ecological conditions available there, but also by the prior presence or absence of those favorable ecological conditions. Jackson and Overpeck focus on ecological factors produced by physical processes, whereas ecologists studying facilitation focus on factors produced by biological processes (i.e. other species), but in both cases, attention is drawn to the fact that the pre-competition or pre-predation availability of ecological conditions that are favorable to a species should not be taken for granted.[6]

Jackson and Overpeck (2000, p. 197) introduce two new concepts to study how environmental changes can affect species distributions: the *realized environmental space*,

[6] As they note, Jackson and Overpeck (1981, p. 195n1) focus on non-resource factors that belong to what Hutchinson calls *scenopoetic* niche factors (see section 2), and that are mainly produced by physical processes. Nothing, however, prevents the application of a reasoning similar to theirs to what Hutchinson calls *biogenic* factors, factors that are produced by other species inhabiting the environment, such as those that result from facilitation.

and the *potential niche.* They situate these concepts with respect to Hutchinson's realized and fundamental niches (see fig. 3). The *realized environmental space* is "the particular realization of environmental conditions that occur in nature at a particular time." With respect to two ecological conditions that vary in degrees, the realized environmental space will include all the values at which the first condition intersects with values of the other condition. The *potential niche* is "the intersection of [a species'] fundamental niche with the realized environmental space at a particular time." It thus is "a subset of the fundamental niche, comprising the portion of the fundamental niche that corresponds to realized combinations of the environmental variables at a given time." (Jackson and Overpeck 2000, p. 197) Thus, the *potential niche,* as defined by Jackson and Overpeck, includes the subset of the possible combinations of factors under which a species could theoretically persist (i.e. its fundamental niche) that are instantiated at some existing locations. As they highlight, a species' potential niche will therefore change in relation to changes in the environment: if the combinations of ecological conditions realized at a given time changes, "the potential niche will change in shape, size, and/or position in environmental space." (Jackson and Overpeck 2000, p. 197) Defined in relation to the potential niche, the *realized niche* thus "comprises a subset of the potential niche, owing to constraints imposed by biotic processes." (Jackson and Overpeck 2000, p. 197).

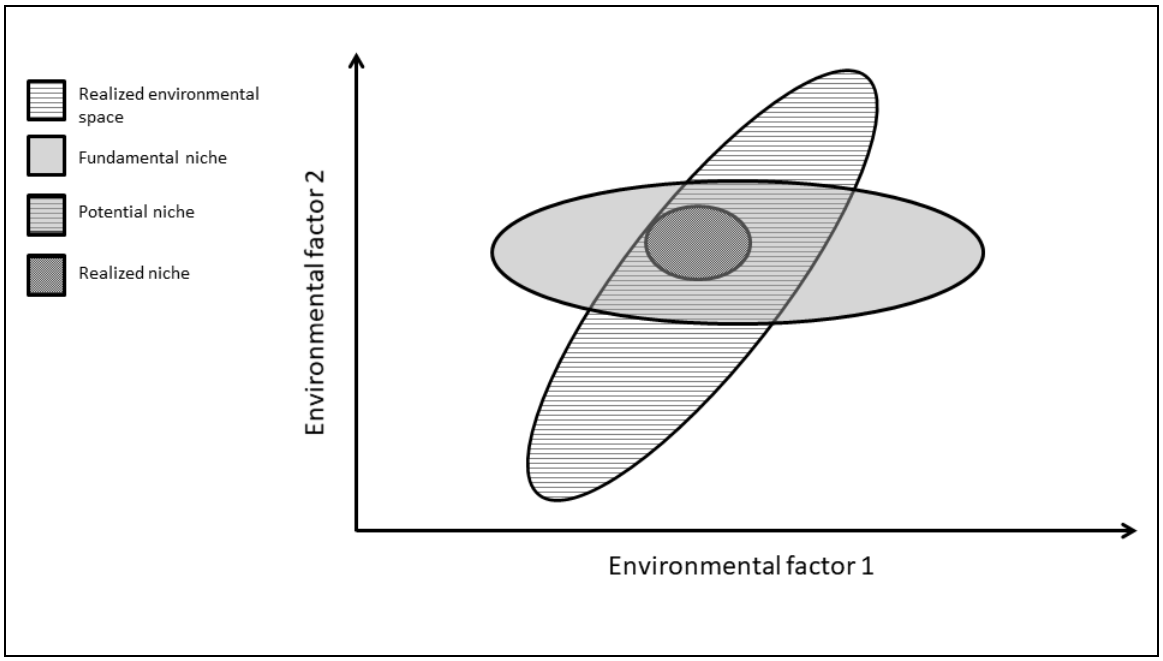

Figure 3: The realized environmental space with respect to two ecological factors, and a species' fundamental, potential, and realized niches with respect to these two factors. The *realized environmental space* comprises the combinations of values of the two factors that are instantiated at a location. The species' *fundamental niche* comprises the combinations of values of the two environmental factors that would permit the species to persist indefinitely if not hindered by another species. The *potential niche* comprises the intersection of the realized environmental space and the fundamental niche. The *realized niche* comprises the portion of the potential niche in which the specie's presence it not hindered by the presence of another species whose fundamental niche partly overlaps with its own. Redrawn from Jackson and Overpeck (2000, p. 197).

Jackson and Overpeck's (2000) conceptualization makes it possible to identify three reasons why a species may not be able to exploit all the combinations of factors that are included in its fundamental niche (see Colwell and Rangel 2009, p. 19654). First, portions of its fundamental niche may simply not be instantiated at any existing site; second, portions of its fundamental niche may be instantiated at existing sites, but the species might be unable to reach those sites because of dispersal limitations; third, portions of its fundamental niche may be instantiated at existing sites and reachable by the species, but the presence of competitors or predators at those sites may prevent the species from exploiting them. The relationship between the realized and the fundamental niches captures only the third possibility, while the first possibility is captured by the relationship between the fundamental and the potential niche.

I contend that Jackson and Overpeck's (2000) *potential niche* concept provides exactly what ecologists require in order to be able to incorporate ameliorative facilitation into a niche-based framework for studying ecological communities. As seen through the prism of Jackson and Overpeck's conceptualization, what an ameliorative facilitator does is to construct another species' *potential niche*. As we have seen in section 3, ameliorative facilitation makes available some ecological factors that are part of a species' (abstract) fundamental niche but would not otherwise be available, and this is exactly what constructing a potential niche amounts to.[7] By changing the environmental

[7] A slight shift of my proposal with respect to Jackson and Overpeck's use of the potential niche, I should note, is that they focus on the instantiation of factors included in a species' fundamental niche at *any* location on earth, whereas I focus on their instantiation at a particular location (where a facilitator species creates them). Another possible difference has to do with the choice between two distinct modeling approaches that may be applied to the study of niches: *correlative* and *mechanistic* approaches (on the

space that is realized at some location in a way that makes available some antecedently unavailable ecological condition that are part of a species' fundamental niche, an ameliorative facilitator constructs that species' potential niche. In so doing, the facilitator expands the species' potential niche in comparison to what it would otherwise be. All else equal, this expansion of the species' potential niche will expand the geographical range under which a species is able to persist, but the species' fundamental niche will remain unchanged.[8]

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contrast between these approaches, see Kearney and Porter 2009; Kearney et al. 2010). As a reviewer of this paper pointed out, Jackson and Overpeck introduce their *potential niche* concept in the context of their use of a *correlative* modeling approach to niches, whereas, given that facilitation is a causal mechanism, its study would seem to require a more *mechanistic* modeling approach. Here, I should make clear that my proposal to import Jackson and Overpeck's potential niche concept to the study of facilitation entails no claim that the occurrence of facilitative interactions between species could reliably be inferred from correlative descriptions of species distributions. A full understanding of how a facilitator species creates a potential niche for a facilitated species would, I think, require consideration of how the traits of individual organisms that form populations of these species determine their ecological requirements and their potential effects on the habitat at different stages of their life-cycle, as well as of how all these requirements and potential effects shape the interactions that occur between these organisms, their reproductive success, and their populations' growth-rates. For simplicity, I set those more detailed aspects aside in the below discussion, but this does not mean that I do not recognize them as important.

[8] Introducing the potential niche concept to our conceptualization of ameliorative facilitation also enables us to distinguish the way in which it expands the geographical range under which a species is able to persist from that in which *source-sink dynamics* similarly expand such range (Pulliam 1988; Amarasekare and Nisbet 2001). Source-sink dynamics are the phenomenon whereby a *sink population*, that is, a subpopulation located in a poor habitat where its morality exceeds its reproduction, nevertheless persists at that location as a result of immigration from a *source population*, that is, a subpopulation located in a more plentiful habitat and whose reproduction exceeds its mortality. As I just mentioned, *ameliorative facilitation* expands the geographical range under which a species is able to persist by making available at a location some ecological factors that are part of its (abstract) fundamental niche—i.e. by increasing the size of its *potential niche*. In contrast, *source-sink dynamics* expand the geographical range under which a species is able to persist by making it able to persist at locations where factors that are part of its fundamental niche are not sufficiently instantiated for it to be able to maintain itself through reproduction alone—i.e. at locations that lie outside of its potential niche (and hence also lie outside of its fundamental niche). Hence, in short, ameliorative facilitation expands distribution through the construction of a potential niche, whereas source-sink dynamics expand distribution without the construction of a potential niche.

Hence, I submit that Jackson and Overpeck's (2000) *potential niche* concept provides an illuminating way to conceptualize how ameliorative facilitation can affect a species' realized niche and to contrast it with how competition and predation can do so. Competitors and predators reduce a species' *realized niche* by making the species (all else equal) able to exploit less of the niche space included in its *potential niche* than if the competitors and predators were absent. And conversely, the removal of some competitors and/or predators expands a species' realized niche by making the species (all else equal) able to exploit more of the niche space included in its potential niche than if the competitors and predators were present. These changes in a species' realized niche do not change the relationship between the species' *fundamental* and *potential niches*. The same subset of the species' fundamental niche remains instantiated in the environment (see fig. 4). In contrast, ameliorative facilitation expands a species' *realized niche* by making more of the niche space included in its fundamental niche instantiated in the environment. This (all else equal) makes the species able to exploit more of the niche space included in its *fundamental niche* than if ameliorative facilitation did not occur. And conversely, the removal of some ameliorative facilitator would reduce a species' realized niche by (all else equal) by making less of the niche space included in its fundamental niche instantiated in the environment. This, (all else equal) would make the species able to exploit less of the niche space included in its fundamental niche than if the ameliorative facilitators were present. Here, the changes in the species' realized niche ensue from changes in the relationship between its *fundamental* and *potential niches*. A larger or narrower subset of the species' fundamental niche becomes instantiated in the environment (see fig. 5). Thus, in short, competition and predation affect the difference between a species' realized niche and its fundamental niche *without* changing the difference between its potential and fundamental niches, whereas ameliorative facilitation affects the difference between a species' realized and fundamental niche *through* affecting the difference between its potential and fundamental niche. In neither case, however, the realized or potential niches can become larger than the fundamental niche.

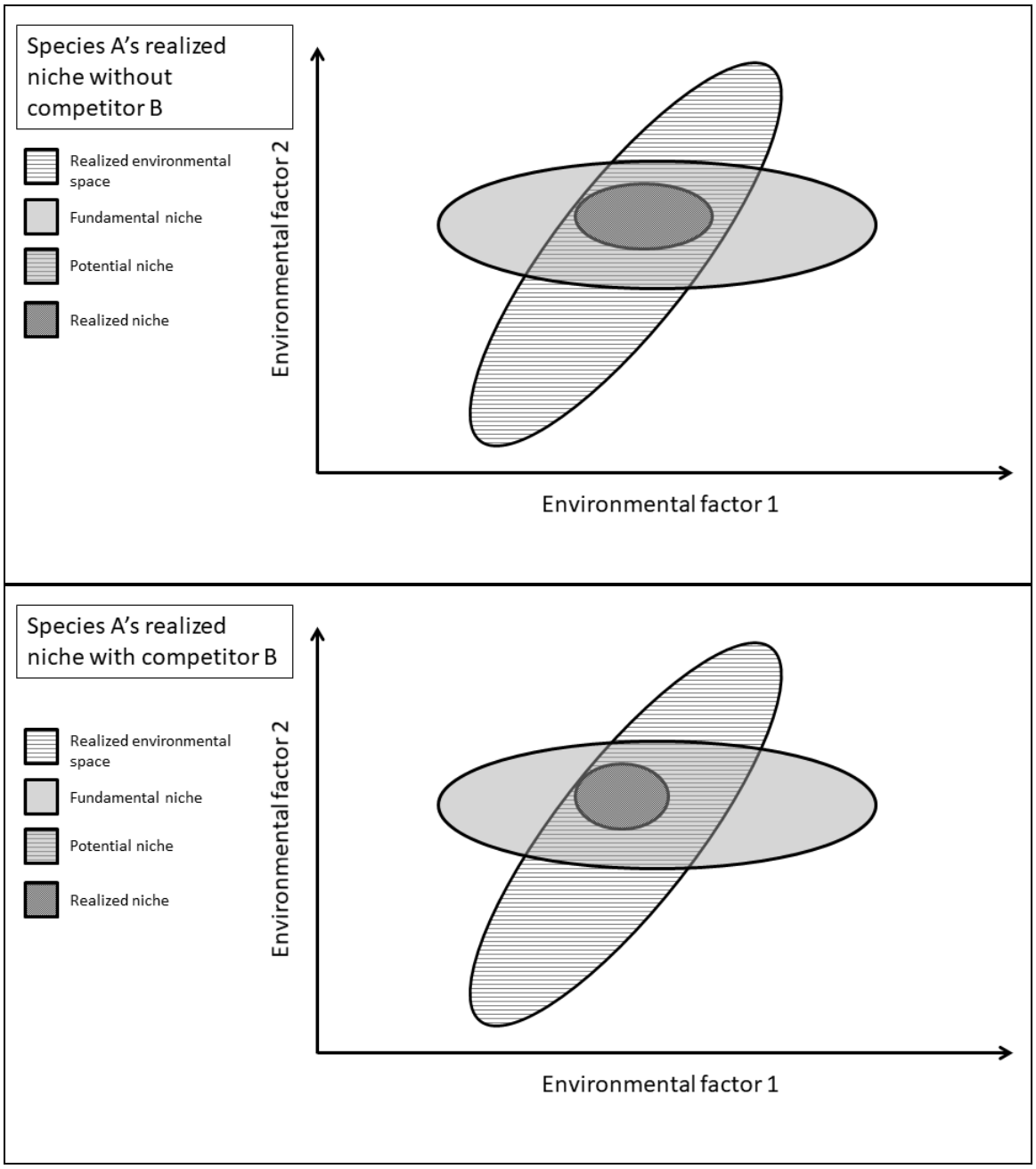

Figure 4: A species' realized niche without and with the presence of a competitor. The subset of the potential niche occupied by the species changes, but the size of the potential niche remains unchanged (the size of the fundamental niche also remains unchanged). Inspired from Jackson and Overpeck (2000, p. 197).

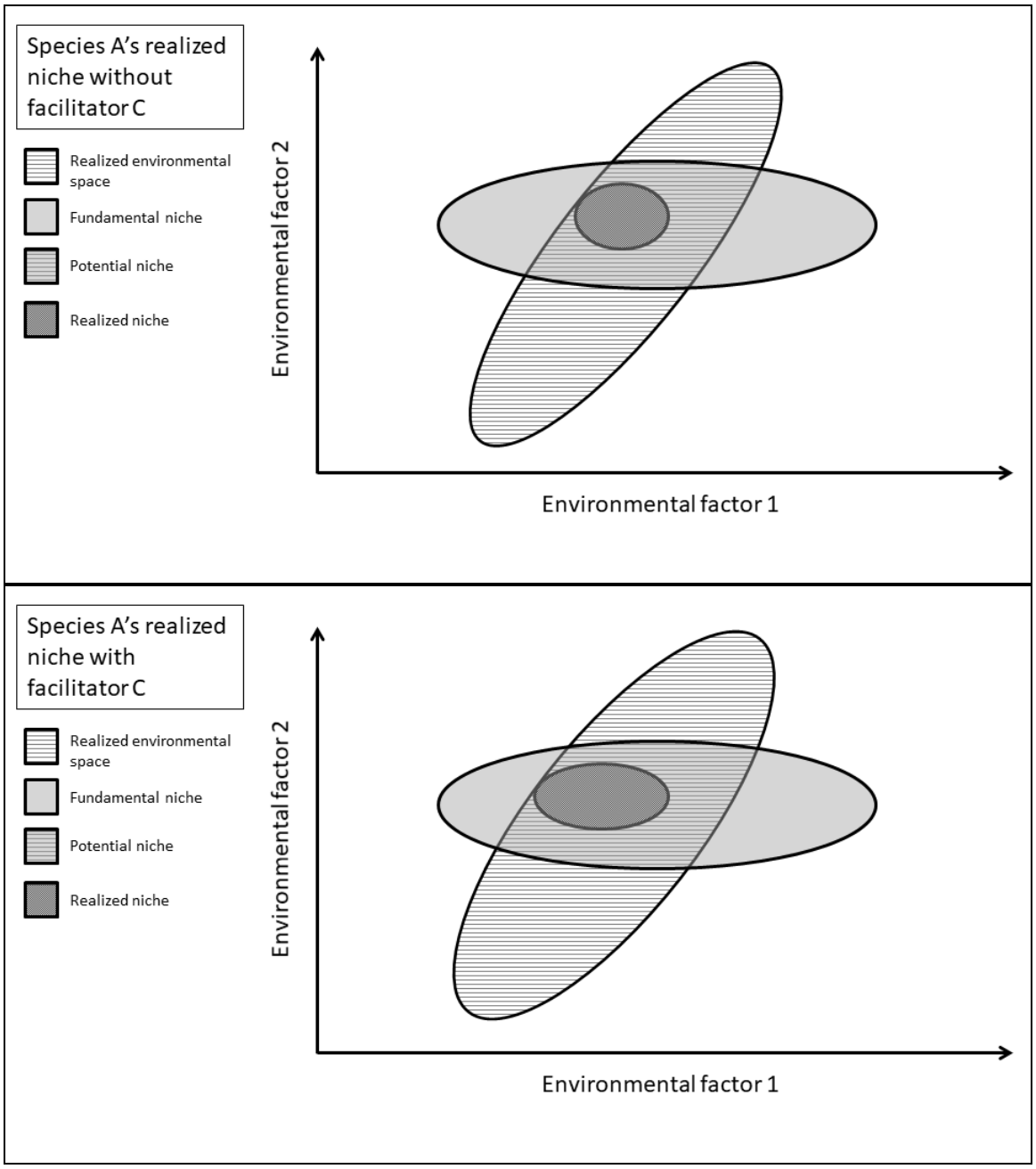

Figure 5: A species' realized niche without and with the presence of a facilitator. The size of the potential niche changes and this affects the size of the realized niche (the size of the fundamental niche also remains unchanged). Inspired from Jackson and Overpeck (2000, p. 197).

Supplementing Hutchinson's (1957, 1978, chap. 5) fundamental and realized niche concepts with Jackson and Overpeck's (2000) concept of the *potential niche* thus appears to offer a conceptually clean way to incorporate ameliorative facilitation into a niche-

based theoretical framework for studying ecological communities. In this supplemented framework, two types of interactions affecting a species' realized niche are recognized. First, interactions that (combined with abiotic processes) determine what subset of a species' fundamental niche will be instantiated in the environment—i.e. that affect the relationship between the species' fundamental and potential niches, and, by this mean, the relationship between its fundamental and realized niches. Those interactions will primarily be ameliorative facilitative ones. Second, this framework recognizes interactions that determine what subset of its potential niche that a species will be able to occupy—i.e. that affect the relationship between the species' potential and realized niches, and, by this mean, the relationship between fundamental and the realized niches. Those interactions will primarily be negative ones like competition and predation, but may, secondarily, be positive ones like mitigating facilitation.

This way to incorporate ameliorative facilitation into a niche-based framework for studying ecological communities does not have the drawbacks of Stachowicz's (2012) proposed reform which applies Hutchinson's realized/fundamental contrast to a spatial-geographical notion of the niche. It remains in line with standard uses of the Hutchinsonian terminology, and so does not require ecologists to introduce a new term to refer precisely to what Hutchinson's fundamental niche concept denoted. Instead, it introduces a new concept to denote what the Hutchinsonian conceptualization left in its dead angle, that is, the degree of instantiation in the environment of factors included in a species' fundamental niche.[9]

Hence, a unificatory niche-based framework that incorporates negative interactions, mitigating facilitation, *and* ameliorative facilitation, while retaining Hutchinson's abstract

[9] In an illuminating discussion of what they call "Hutchinson's duality," Colwell and Rangel (2009) show that Jackson and Overpeck's (2000) potential niche concept in fact aligns with the spirit of Hutchinson's use of the niche concept. They show that, although, for Hutchinson, the fundamental and realized niches existed in an abstract hyperspace, his method nevertheless paid significant attention to how and to what extent the dimensions represented in the niche space were instantiated in actual environments (which he conceptualized as the *biotope space*). Jackson and Overpeck's (2000) potential niche is thus not a fully new concept, though their conceptualization of it is.

construal of the fundamental niche, seems workable. Elaborating such a framework, however, requires us to *expand* rather than *reform* the Hutchinsonian conceptualization of the niche. The required expansion retains Hutchinson's abstract understanding of the fundamental niche, but supplements his realized/fundamental dyad with a new concept: the potential niche. This proposal aligns with Bruno et al. (2003) and Stachowicz's (2012) endeavor to expand niche theory so as to fully incorporate facilitation within it, but also heeds Rodriguez-Cabal et al.'s (2012) call for a more cautious use of the Hutchinsonian terminology.

5. Conclusion

This paper has proposed a way to incorporate facilitation into a niche-based conceptual framework for studying interactions within ecological communities. The proposed way consists in supplementing Hutchinson's realized and fundamental niche concepts with a third concept: the *potential niche*. This concept was introduced by Jackson and Overpeck (2000) to study the effects of environmental changes on species distributions, but it could also be used to study the effects of ameliorative facilitation on the environmental instantiation of factors that are part of a species' fundamental niche. The Hutchinsonian conceptualization of the relationship between the realized and fundamental niches sets ameliorative facilitation in its dead angle, but the *potential niche* concept provides a way to conceptualize its effects.

In comparison to Bruno et al. (2003) and Stachowicz's (2012) proposal to apply the realized/fundamental niche contrast to a spatial-geographical notion of the niche, this way to incorporate facilitation into a niche-based research approach has the advantage of remaining in line with standard uses of the Hutchinsonian conceptualization. It also does not require ecologists to introduce a new term to refer precisely to what Hutchinson's fundamental niche concept referred to. If, as many ecologists maintain, clean conceptualization fosters scientific progress, then ecologists looking for a unified understanding of how negative and facilitative interactions structure ecological communities should add Jackson and Overpeck's (2000) potential niche to their conceptual toolkit.

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