



Defining the niche for niche construction: evolutionary and ecological niches

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Abstract

Niche construction theory (NCT) aims to transform and unite evolutionary biology and ecology. Much of the debate about NCT has focused on construction. Less attention has been accorded to the niche: what is it, exactly, that organisms are constructing? In this paper I compare and contrast the definition of the niche used in NCT with ecological niche definitions. NCT's concept of the evolutionary niche is defined as the sum of selection pressures affecting a population. So defined, the evolutionary niche is narrower than the ecological niche. Moreover, when contrasted with a more restricted ecological niche concept, it has a slightly different extension. I point out three kinds of cases in which the evolutionary niche does not coincide with realized ecological niches: extreme habitat degradation, commensalism, and non-limiting or super-abundant resources. These conceptual differences affect the role of NCT in unifying ecology and evolutionary biology.

Keywords Niche construction · Ecological niche · Evolutionary niche · Habitat degradation · Commensalism

Introduction

The past thirty-odd years have seen the development of a new player in the field of evolutionary theory, niche construction theory (NCT). The general principle underlying NCT is that organisms can directly influence evolutionary processes by altering their environments. Specifically, niche construction is the process by which organisms make changes to the environment, relocate to a different environment, or in any other way alter the environment experienced by the focal organism, its conspecifics, or members of another species (Odling-Smee et al. 2003). Niche construction, it is argued, affects the direction and speed of evolutionary change and should

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therefore be considered alongside natural selection as an important evolutionary process.

Much of the debate about NCT has focused on the evolutionary significance of niche construction (Laland and Sterelny 2006; Laland et al. 2014; Scott-Phillips et al. 2014). In addition, recent theoretical work has considered what sorts of phenomena can count as niche construction and how different sorts of niche construction can be defined (Chiu and Gilbert 2015; Aaby and Ramsey 2019; Fabry 2021). In contrast, little attention has been accorded to the concept of niche used in NCT (though see Stotz 2017). This is despite the fact that the definition of niche employed in NCT is at least superficially distinct from standard definitions of the ecological niche.

Ecologists typically define the niche in terms of the environmental factors that are tolerated or required by individuals, populations or species (e.g., Begon et al. 2006, 31). In contrast, in NCT the niche is defined as the sum of selection pressures affecting a population (Odling-Smee et al. 2003, 40). Why does NCT not make use of a standard ecological niche definition? Is the NCT niche definition really just a simple translation from ecological to evolutionary terms, as its proponents suggest? Does the NCT niche definition make a difference for how niche construction is defined and understood?

One reason to ask these questions stems from an additional claim associated with NCT. According to its proponents, NCT will not only transform evolutionary theory, but may also help to integrate evolutionary biology and ecology (Odling-Smee et al. 2003, 26). This unifying potential is jeopardized by the use of ecological terms in non-standard ways. If there are not only superficial but also substantial differences between the NCT niche and the ecological niche, it may be that models, theories and empirical findings in one field cannot be directly transferred to the other without adjustments and exceptions. Hence, assessing the unificatory potential of NCT requires investigating the niche.

In this paper I critically examine NCT's definition of the niche and how it compares to standard ecological definitions. I focus on NCT as expounded by John Odling-Smee, Kevin Laland, and Marcus Feldman in their book *Niche Construction* (2003). There have been more recent theoretical developments. As I mention later in the paper, it would be an interesting project to determine what niche concepts are used in other accounts of niche construction and how they compare to both the *Niche Construction* evolutionary niche and the ecological niche. Nevertheless, *Niche Construction* continues to be regarded and used as a key resource in the field and therefore deserves investigation.

In the section "Niche Construction and the Evolutionary Niche", I introduce NCT's evolutionary niche and argue that it supports their claim that niche construction is significant for evolution. From there, I move in the section "Introducing the Ecological Niche" to develop a conception of the ecological niche. In "Contrasting Niches" I compare and contrast the evolutionary niche and ecological niche. Once the ecological niche is defined in a restricted way as the realized population niche, there is considerable overlap with the evolutionary niche. Nevertheless, some areas of non-coincidence remain. In the section "Three Cases of Non-Coincidence" I identify and provide examples of three sorts of non-coincidence: habitat destruction,

commensalism, and non-limiting resources. The evolutionary niche is therefore not a straightforward translation from ecology to evolution, since the extension shifts in the process to include some new instances of niches and exclude many others. I conclude in “Niche Construction Across the Conceptual Divide” by assessing what these differences in extension mean for niche construction. Any unificatory work between ecology and evolution, whether through NCT or another approach, must take into account the differences between the ecological and the evolutionary niche.

Niche construction and the evolutionary niche

Niche construction includes activities such as those when “organisms [...] take energy and resources from environments, make micro- and macrohabitat choices with respect to environments, construct artifacts, emit detritus and die in environments” (Odling-Smee et al. 2003, 1). Odling-Smee, Laland and Feldman identify two sorts of niche construction. First, perturbational niche construction occurs when organisms bring about changes in the environment. Second, relocational niche construction occurs when organisms change the environment with which they interact by moving to a new location or through selective interaction with certain environmental factors. Both perturbational and relocational niche construction share the consequence that the organism is exposed to a different environment.

In calling relocation and perturbation *niche* construction, NCT proponents stress the way that organisms alter not only their environment, but their niche. Odling-Smee, Laland and Feldman define the niche as such: “We will treat the niche of any population as the sum of all the natural selection pressures to which the population is exposed.” (Odling-Smee et al. 2003, 40) They call this the evolutionary niche.

Evolutionary Niche. The niche is the sum of the selection pressures affecting a population.

Alternative names include “selective niche” (Stotz 2017; Uller and Helanterä 2019), or “selective environment” (Jablonka 2011). Indeed, NCT’s evolutionary niche is remarkably similar to Robert Brandon’s concept of selective environment. Brandon defines the selective environment as an area where a population experiences a homogenous selection pressure (Brandon 1990). The selective environment is therefore defined in distinction to what Brandon calls an “ecological environment” (not to be confused with ecological niche), an area where organisms of a particular type have a homogenous absolute fitness even if their relative fitness varies in that area. Brandon’s concept of selective environment could be used to add greater precision to the evolutionary niche of NCT by clarifying which changes in the external environment count as changes in the selection pressures affecting a population. On the other hand, using the term “niche” emphasizes the proximity to ecological theories, a point to which I return later.

The definition of the evolutionary niche is pivotal for NCT. First, it has the consequence that not just any changes made to the environment count as niche construction. Only those environmental changes that also change the acting selection

pressures alter the evolutionary niche and hence are instances of niche construction. In addition, environmental modifications with wide-scale and long-term effects become especially important (Odling-Smee et al. 2003, 42). Changes in the environment that are inherited by future generations, so-called ecological inheritance, affect not just a particular individual's survival and reproduction but also that of individuals in generations to come. Niche construction with ecological inheritance is therefore more paradigmatic since it involves a noteworthy change in selection pressures.

Second, defining niche construction as a process of altering evolutionary niches is crucial for NCT's claims to evolutionary importance. Selection pressures are factors that lead to fitness differences within a population and thereby determine the direction, rate, and likely outcome of natural selection. In concert with other evolutionary processes such as drift and migration, natural selection determines the evolution of populations. It follows that niche construction, as an activity altering selection pressures, can change the direction, rate, and outcome of natural selection and hence affect evolution—provided other evolutionary processes aren't dominating. Add to this some empirical information about the prevalence of niche construction, and we can readily conclude that it is an important evolutionary process.

The evolutionary niche is therefore a primary element in the argument for the evolutionary significance of niche construction. Indeed, one might suspect that the evolutionary niche has been defined precisely to ensure that niche construction is an evolutionary process. This is, of course, not what NCT's proponents claim. They argue that the evolutionary niche is "a simple, pragmatic, and minimalist definition" derived by highlighting the evolutionary aspects of ecological definitions of the niche (Odling-Smee et al. 2003, 40). It is to this claim that I will turn for the remainder of the paper. First, however, we should briefly consider alternative characterizations of niche construction.

The conception of niche construction due to Odling-Smee, Laland and Feldman is broad, covering anything from respiration and digestion to building complex structures in the environment and even social and cultural processes. This has generated debate about whether all such activities should be labelled "construction" (Oka-sha 2005; Archetti 2015). Biologists often restrict niche construction to activities that cause changes in environmental factors or structures, such as building a dam or a nest. These cases are the most intuitive instances of niche construction, parallel to "construction" in the literal sense of building houses and roads.

On the other hand, some authors have argued that the term "niche construction" has an even wider scope, including not only perturbation and relocation but also alterations in an organism's phenotype, since any of these changes ultimately alter the niche (Lewontin 2000; Chiu and Gilbert 2015; Aaby and Ramsey 2019). In addition, evolutionary-developmental biologists recognize other ways in which an altered environment can affect evolutionary processes. For instance, changes in the environment can affect the sorts of variation available to be selected. As Karola Stotz (2017) argues, accounting for these elements of evolutionary processes requires distinguishing selective and developmental niche construction.

In this text I concentrate on the niche construction concept from Odling-Smee, Laland and Feldman, and thus on perturbation and relocation. This restriction is significant, because other accounts that exclude relocation, include phenotypic

changes, or distinguish different types of niche construction may be working with slightly different concepts of the niche. I return briefly to this below (see “Contrasting Niches”). For now, we can work with the evolutionary niche defined in terms of selection pressures and proceed to the comparison with the ecological niche.

Introducing the ecological niche

The ecological niche is itself subject to considerable debate. The concept has undergone a number of redefinitions since being coined at the start of the twentieth century (Griesemer 1992; Pocheville 2015). Discussions continue about how to understand and operationalize the niche, and even whether it is a useful concept at all (Mikkelsen 2005; Kearney 2006; Holt 2009; McInerney and Etienne 2012; Wennekes et al. 2012). There are nevertheless some fairly well accepted formulations of the niche which we can use for present purposes. In this section I develop a rough basic definition that can be specified and adjusted to generate more specific ecological niche concepts. This will allow us in the following section to begin a comparison to the evolutionary niche.

The simplest place to start is with textbooks. One widely used ecology textbook defines the niche as “the conditions and resources needed by an individual or a species in order to practice its way of life.” (Begon et al. 2006, 31) Another states that “the niche summarizes the environmental factors that influence the growth, survival, and reproduction of a species. In other words, a species’ niche consists of all the factors necessary for its existence—approximately when, where, and how a species makes its living.” (Molles 2015, 200) Generally, then, in textbooks the niche is defined by the requirements for a species, and perhaps also an individual, to live the way it typically does.

The textbook definitions focus on requirements, but other conceptualizations of the ecological niche include both conditions that organisms need as well as those they can tolerate. This is evident in what has become a theoretical standard for the ecological niche. In his “Concluding Remarks,” G. Evelyn Hutchinson defines the niche as “an n -dimensional hypervolume [...] every point in which corresponds to a state of the environment which would permit the species S_1 to exist indefinitely.” (Hutchinson 1957, 416) In essence, the niche includes the factors in the environment that allow a species to persist, represented as ranges along numerically defined niche dimensions. The factors that permit persistence cover conditions the species can tolerate, such as a specific temperature range, as well as resources they need to consume, such as a particular prey size. So far, this largely agrees with the textbook definitions, minus the references to ways of life and to individuals and adding tolerances as well as requirements.

Hutchinson introduced an additional distinction between the fundamental and the realized niche, a difference in modality. The fundamental niche is defined by the requirements and tolerances of a species regardless of where it actually lives, representing conditions under which the species *could* persist. The realized niche is the portion of the fundamental niche that the species actually realizes, given interspecific competition and dispersal limitations (Hutchinson 1957, 418–419). It therefore

represents only the conditions relevant to the species' *actual* persistence in the community.

Hutchinson's niche concept is decidedly complex—it includes *any* factors that affect where a species can or does persist. Its operationalization has required significant simplification. Typically, niches are modelled using one or at most a few dimensions at once. For instance, species distribution modelling or ecological niche modelling involves correlating the actual distribution of a species with values for readily measurable environmental conditions such as rainfall, temperature, light, or mineral abundance (Elith and Leathwick 2009). Well-constructed models can explain and predict species distributions, but they rarely include biotic interactions and hence do not represent the entirety of a species' niche (Araújo and Guisan 2006; Elith and Leathwick 2009; McNerny and Etienne 2012). Observations of resource use are another operationalization of the niche concept, this time with attention to biotic rather than abiotic factors (Feinsinger et al. 1981; Smith 1982; Schoener 1989). Finally, mechanistic niche models use information about organisms' physiology, morphology, and behavior in order to determine requirements and tolerance limits for factors such as temperature and humidity (Leibold 1995; Kearney 2006).

In standard operationalizations of the niche concept, the resource or environmental condition is construed as one dimension in the multi-dimensional niche space. If the actual resource use or tolerance is studied, for instance by gut content analysis or observation of distribution, the resulting graph corresponds to a dimension of the realized niche. In contrast, if the tolerances or requirements of the species are determined experimentally, for instance by growing a species under many different temperature regimes, this reveals a fundamental niche dimension.

In addition to its simplified operationalizations, there are a number of theoretical variations on Hutchinson's niche concept. For instance, ecologists have modified Hutchinson's definition to accommodate individuals having their own niches, so-called individual or individualized niches (Bolnick et al. 2003; Sargeant 2007; Violle et al. 2012; Layman et al. 2015). This development is reflected in the first textbook definition cited above, which referred to the conditions needed by individuals as well as species. Other extensions or modifications have also been proposed, such as the establishment niche, representing conditions allowing a population to first become established (Holt 2009), the developmental niche, representing conditions involved in reproducing the life cycle (Stotz 2017), and the social niche, representing only interactions with conspecifics (Saltz et al. 2016).

We have then a collection of definitions: textbook definitions, a theoretical standard, its operationalizations, and several extensions and modifications. To facilitate a comparison between ecological and evolutionary niches, I will propose a rough basic definition of an ecological niche.

Ecological Niche. The niche is the environmental conditions, both biotic and abiotic, that permit the continued existence of an individual, population or species.

Importantly, the requirements and tolerances of the individual, population or species determine which conditions permit continued existence. This rough definition can serve as a template for other, more specific and more complete,

definitions of the ecological niche. For instance, it can be specified into realized and fundamental niches by referring to conditions that permit *actual* continued existence or conditions that *could* permit continued existence, respectively. The definition can also be decomposed into individual, population and species niches. Finally, it is easy to modify the definition in order to refer just to social niches (where the environmental conditions only include interactions with conspecifics), establishment niches (by referring to establishment rather than continued existence), or developmental niches (development rather than continued existence). Some of these specifications, decompositions and modifications of the ecological niche will prove relevant in the comparison to evolutionary niches.

Contrasting niches

In introducing their definition of the evolutionary niche, Odling-Smee, Laland and Feldman say that it is a simple translation of the ecological concept into evolutionary terms. This translation, they write, involves taking the standard ecological definition of a niche and replacing the ecological factors—the conditions and resources which are tolerated or required—with selection pressures. Specifically, they state that their translation of Hutchinson's niche

[...] differs only in that the fundamental niche is now treated as a set of “n” natural selection pressures relative to its occupant, in addition to being a hypervolume of resources and tolerance limits relative to its occupant, the former being merely the evolutionary aspect of the latter. (Odling-Smee et al. 2003, 40)

In this section I argue that the evolutionary niche is not a simple translation of the ecological niche into ecological terms because the ecological niche is significantly broader in scope than the evolutionary niche.

Let us first see the two definitions together, using the basic definition of the ecological niche introduced above.

Evolutionary Niche. The niche is the sum of the selection pressures affecting a population.

Ecological Niche. The niche is the environmental conditions, both biotic and abiotic, that permit the continued existence of an individual, population or species.

There are some obvious disparities between these definitions. First, the evolutionary niche only refers to populations, whereas the ecological niche also allows individuals and species to have niches. This is perhaps unsurprising, since only Hutchinson's standard definition was cited as a source for the evolutionary niche, and Hutchinson focused on populations (though his later work does acknowledge that individual variation affects niches; Hutchinson 1978, 175–81). It is an interesting question whether an individualized evolutionary niche could be defined. I

will however postpone this consideration and questions about species niches, and instead limit the comparison to population ecological niches, thereby removing the first discrepancy.

The second major difference between the evolutionary and the ecological niche is in modality. The former is about the selection pressures *actually* affecting a population. The latter, as we are already aware, can be understood in terms of the realized niche or the fundamental niche. While the realized niche is also about actuality, the fundamental niche has a different modality: it involves environmental conditions under which a population *could* but may not actually persist. The evolutionary niche is therefore not identical to the fundamental niche, in contrast to the quote above from Odling-Smee, Laland and Feldman. Only when we restrict our attention to the realized ecological niche, which represents the environmental conditions permitting the population's actual persistence, do we have something closer in modality to the evolutionary niche.

The third divergence between evolutionary and ecological niches is that between selection pressures on the one hand and environmental factors permitting continued existence on the other. This difference remains even when we focus on the realized population ecological niche.

Evolutionary Niche. The niche is the sum of the selection pressures affecting a population.

Realized Population Ecological Niche. The niche is the environmental conditions, both biotic and abiotic, that permit the actual continued existence of a population.

Here we arrive at the crux of the comparison. How do selection pressures relate to environmental conditions which permit actual continued existence? Are the former simply the “evolutionary aspects” of the latter?

There is more similarity between selection pressures and environmental conditions permitting persistence than it might initially seem. As introduced earlier, selection pressures are factors that bring about fitness differences in a population. Fitness differences in a population occur as a result of variation in phenotypic traits in a specific environmental context, as well as—depending on one's definition of fitness—chance events that affect individuals' reproductive success. Yet NCT proponents classically focus only on the way that environmental factors are changed, not on how phenotypic changes alter selection pressures (though recall that phenotypic change has been included by some authors; Lewontin 2000; Chiu and Gilbert 2015; Aaby and Ramsey 2019). This focus on the environment fits with a standard, though contested, understanding of natural selection, according to which phenotypic features are selected and the factors doing the selecting are environmental. On this view, selection pressures are simplified to environmental factors that, given the phenotypes present in a population, lead to fitness differences in that population (Wells 2015, 555; Uller and Helanterä 2019, 353).

The externalist interpretation of the evolutionary niche not only accords with the concentration in NCT on environmental rather than phenotypic change, but also allows for a more straightforward comparison to the ecological niche. Now we can ask: are the environmental conditions which lead to fitness differences in

a population the same as the environmental conditions which permit population persistence?

Externalist Evolutionary Niche. The niche is the (sum of the) environmental factors that lead to fitness differences in a population.

Realized Population Ecological Niche. The niche is the environmental conditions, both biotic and abiotic, that permit the actual continued existence of a population.

Certainly, many conditions that lead to fitness differences also permit population persistence, and vice versa. From Darwin's finches in the Galápagos Islands to peppered moths in darkening industrial Britain, conditions that induce selection often still permit population persistence, albeit with a preference for particular types of individuals in the relevant population. Even examples relevant to niche construction usually coincide. The beaver building its dam, the earthworm shifting soil, or the bird making its nest: they alter both their selective environments and the resources they consume or the conditions they are tolerating. Many similar instances of overlap can be found amongst standard cases from evolutionary biology and ecology.

It is also not untoward to talk about fitness when explaining population persistence. Population persistence requires that the population does not consistently decline. Assuming no migration, population decline occurs when fewer offspring are produced than there are in the parental generation. In other words, population decline occurs when, over multiple generations, absolute fitness is on average lower than one. Population persistence therefore occurs when the average absolute fitness for individuals in the population is greater than or equal to one (Leibold 1995; Kearney 2019). Yet an average absolute fitness of one or more, the condition defining population persistence, is not identical to the existence of fitness differences, the condition defining selection pressures. Indeed, as I show below, factors that lead to an average fitness of one or more do not necessarily contribute to fitness differences, and vice versa.

Before moving to contrast the externalist evolutionary niche and the realized population ecological niche, we should take stock. We have already discovered some differences between the evolutionary and the ecological niche. First, the subjects differ: whereas the evolutionary niche is restricted to populations, the ecological niche also includes individuals and species. Second, the modality differs: evolutionary niches are actual, whereas ecological niches can refer to both actuality and possibility. Hence, the ecological niche is broader than the evolutionary niche. An interesting question is how a non-externalist definition of the evolutionary niche might compare to standard ecological niche definitions. There may be greater similarities, especially given that both non-externalist selection pressures and ecological requirements and tolerances are determined by phenotypic traits. This is an important point for further research. For now, we can examine the restricted contrast between the externalist evolutionary niche and the realized population ecological niche.

Three cases of non-coincidence

In this section I show that there are some instances where the two sorts of conditions—those that lead to fitness differences and those that permit population persistence—do not coincide. On the one hand, there are environmental conditions that lead to fitness differences but do not permit population persistence. The primary example I discuss is habitat degradation. On the other hand, there are environmental factors that permit population persistence but do not lead to differential fitness. I consider the examples of commensalism and non-limiting resources, but it may be that certain dimensions of developmental niches also fit the bill (Stotz 2017). These different sorts of non-coincidence are depicted in Fig. 1. I will discuss each in detail, illustrating them with empirical examples.

Case 1: Habitat degradation

The first example of non-coincidence involves conditions which lead to population decline. Environmental conditions that bring about population decline, especially rapid decline so that populations are threatened with extinction, certainly do not count as parts of the realized ecological niche. The ecological niche only includes those conditions that *permit* population persistence—conditions which the population requires or can tolerate—not those that threaten to end a population's continued existence. Yet conditions that bring about population decline often also bring about fitness differences, that is, they exert selection pressures; such conditions count as parts of the evolutionary niche. Organisms that create conditions which threaten their own population's persistence can therefore still be performing niche construction, even if they generate environmental conditions that lie outside their ecological niche. A good example of this sort of niche construction is habitat destruction.

Grazers and foragers are known for causing habitat destruction, as an example from a population of geese illustrates. Since the 1970s there has been a boom in numbers of lesser snow geese (*Chen caerulescens caerulescens*), caused primarily by increased availability of food in wintering and stopover areas due to agricultural

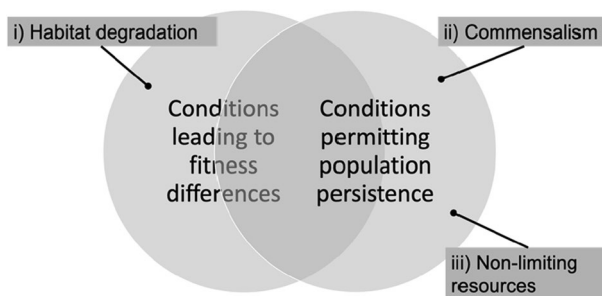


Fig. 1 Contrast between environmental conditions included in evolutionary and ecological niches. Although there is considerable overlap between environmental conditions that lead to fitness differences and those that permit population persistence, there are some exceptions. Three types of cases are identified here: (i) habitat degradation, (ii) commensalism, and (iii) non-limiting resources

changes (Peterson et al. 2013). This population increase has had dramatic effects on arctic salt marshes. Grazing and grubbing (digging for roots) by the over-abundant geese led to rapid and long-lasting degradation of the habitat driven by vegetation loss and salinification (Srivastava and Jefferies 1996). Most geese responded by moving to new areas where vegetation is intact, but habitat degradation has led to reduced fitness of geese still breeding in those areas (Aubry et al. 2013). At some point it is likely that the geese will exhaust the supply of new vegetated areas, especially given the changes in vegetation occurring with climate change (Aubry et al. 2013). At this point, their population would be threatened with extinction. Such effects have been witnessed in other systems more heavily influenced by humans, such as the aridification of the Sahel following overgrazing by livestock (van de Koppel et al. 1997; Hein and De Ridder 2006).

Depleted resources in an overgrazed area exert a selection pressure on a population that remains there and are hence part of the population's evolutionary niche. However, it is unlikely that a population can persist in the barren regions that were once salt marshes or grasslands. Since the environmental conditions in degraded habitats do not permit population persistence but rather endanger it, they are not part of the population's ecological niche. We have an example where the environmental and ecological niche do not overlap. In particular, overgrazing is a case of evolutionary niche construction that does not construct but rather destroys an ecological niche.

Odling-Smee, Laland and Feldman actually recognize this phenomenon when they speak of "negative niche construction" (2003, 47–48). They argue that most niche constructing activities can be expected to increase fitness, but that some activities, especially in the long run, might lead to an overall decrease in fitness. An example they provide is the buildup of pollution or detritus. Negative niche construction is still niche construction since it alters the evolutionary niche. However, negative niche construction can shift a population into an environment where it cannot persist, that is, shift it out of its ecological niche.

Case 2: Commensalism

The remaining examples of non-coincidence concern the other side of the contrast: cases of environmental factors which permit population persistence but do not lead to fitness differences. One primary example is commensalism. Commensalism is usually defined as a relationship between organisms of different species in which one species obtains a benefit from the other without causing it any benefit or harm (Casadevall and Pirofski 2000; Leung and Poulin 2008). Benefit and harm can be defined and measured in various ways, including tissue damage, immune responsiveness, metabolic rates, condition, behavior, and fitness (Casadevall and Pirofski 2000; Leung and Poulin 2008). For obvious reasons, I will focus on fitness effects.

The species which obtains the benefit from a commensal relationship represents a neutral environmental condition for its host. The commensal relationship does not exert any selective pressure on the hosts, since the hosts are neither harmed nor benefitted by the relationship. Commensal relationships are therefore not part of the

evolutionary niche. Commensalisms also tend not to be included in ecological niche models, where tolerances are often restricted to abiotic conditions. Yet they do permit population persistence, so they should count as part of the ecological niche. Specifically, commensalisms are non-constraining factors (Hurlbert 1981), that is, variables that in many cases are neglected in favor of more decisive factors determining resource use, species distribution and community composition.

Identifying whether a relationship is truly commensal is very difficult in practice (Leung and Poulin 2008). In particular, isolating fitness effects, or lack thereof, in experiments often does not reflect the complicated interactions between environmental factors that can occur in the field. An example from plant–insect interactions highlights the complexity of commensalism, chosen because of its clear causal structure.

Experimental studies have shown that wild tobacco (*Nicotiana attenuata*) fitness is not affected by infestation with the herbivorous *Tupiocoris notatus* mirid bug (Kessler and Baldwin 2004). This lack of effect is explained by the upregulation of photosynthesis in non-damaged tissue in response to mirid attack, compensating for loss of photosynthetic activity in damaged tissue (Halitschke et al. 2011). One might be tempted, as I was, to conclude that the presence of *T. notatus* is part of wild tobacco's ecological niche without exerting a selective pressure. However, the reaction to *T. notatus* simultaneously confers an increased resistance to other, more damaging, herbivorous insects, notably *Manduca* hornworms. Observed in the field, plants affected only by hornworms have a much lower fitness than those affected by both mirids and hornworms, due to the plant's defensive reaction to the mirid bugs (Kessler and Baldwin 2004). Hence, the presence of mirids together with hornworms exerts a selective pressure on wild tobacco, selecting for the traits that allow it to respond to mirids in a way that confers resistance to hornworms. Given that both mirids and hornworms are typically co-present (to varying degrees), this means the presence of *T. notatus* is part of both the realized ecological niche and the evolutionary niche of wild tobacco.

Mirid bugs are however not always mutualists. Another study of mirid bug effects on a different plant species that lacks wild tobacco's photosynthesis reaction identifies a commensal relationship. It has been shown that *T. notatus* infestation of the American perennial *Datura wrightii* do not lead to differences in fitness of affected plants (Hare and Elle 2002). In addition, no interaction effects were noted between *T. notatus* and other herbivores present on the affected plants. The authors take this as an indication that *T. notatus* does not exert a selective pressure on *D. wrightii*. This means, for instance, that *D. wrightii* morphs which are susceptible to *T. notatus* ("sticky" plants with glandular trichomes) are not selected against, at least not because of their increased susceptibility. The authors of the study suggest that this surprising result may be explained by the greater importance of the size and persistence of leaf canopies for fitness, traits which are not negatively affected by the piercing-sucking mirid bugs. Despite not leading to fitness differences, mirid bugs are certainly present in the native habitat of *D. wrightii*. Hence, assuming there are no other interactive effects that weren't measured in the study, we seem to have an example of an environmental condition that is part of *D. wrightii*'s realized ecological niche—it is tolerated by *D. wrightii* populations—but not its evolutionary niche.

For *D. wrightii*, mirid bugs are an example of a naturally occurring commensal. There are many more examples of commensal relationships, many of them far less surprising than fitness-neutral herbivores. The contributions made by host species to commensal relationships—in the plant case, giving up sap to mirid bugs—do not count as niche construction because they do not alter the host's evolutionary niche. But such activities can count as the species' contribution to its ecological niche, the conditions which permit its persistence in areas where the commensal partner is present.

Case 3: Non-limiting resources

Commensalisms are about what environmental conditions a species can *tolerate*, and it may be relatively unsurprising that there are tolerances which do not lead to fitness differences. There may also be some *requirements* which do not lead to fitness differences. An example that is theoretically quite suitable and has some empirical support can be found by looking at requirements for non-limiting or super-abundant resources.

Competition for resources is a well-known source of selective pressure. In competitive selection, competition for a resource brings about selection for the use of that resource the most efficiently (as long as efficient use does not lead to significant disadvantages in other realms). When a resource is non-limiting, organisms that use the resource do not have to compete for it. Assuming that there is some other factor limiting population growth, there will be enough of the non-limiting resource to go around. Thus, a non-limiting resource does not induce competition and therefore does not bring about selection for those organisms that can use that resource most efficiently. It is partly for this reason that strains grown in labs are kept under consistent favorable conditions with plentiful water and nutrients to avoid competition (e.g., Lomnicki and Jasienski 2000; Flynn et al. 2017).

However, a resource can still bring about fitness differences without competition. For example, limited water leads to selection for increased water-use efficiency (Dudley 1996; Donovan et al. 2007). When water is not limiting, plants with higher water-use efficiency should therefore not have higher fitness and not be selected for. Yet water-use efficiency is a complex trait that also affects the amount of photosynthesis a plant undertakes and the quantities of resources that can be taken up through the roots. As a result, plentiful water in combination with nutrient limitation (via the presence of intraspecific competitors) induces a selection pressure away from increased water use-efficiency, because water use-efficiency limits nutrient uptake (Campitelli et al. 2016).

We therefore need an additional assumption, namely that there is no fitness-relevant phenotypic variation that responds to the non-limiting resource—at least not at its current levels. It's not easy to find direct evidence for such non-limiting resources that do not induce selection pressures. For instance, during mast years of oak and beech trees, rodents that rely on these resources for food do not need to compete for access to seeds. In those years, food availability does not exert a selection pressure. However, rodent populations may still be under selection for traits such as efficiency

of gathering or storing seeds due to the regular occurrence of non-mast years where food resources are scarce (Stenseth et al. 2002).

A possible example is that of atmospheric carbon dioxide for plants. CO₂ is a necessary resource for all land plants, but current atmospheric levels are high enough that it is a non-limiting resource. Studies of plant respiration show that angiosperms differ from conifers and ferns in their response to higher CO₂ levels (Brodrribb et al. 2009). Specifically, the stomata of angiosperms close in response to higher levels of CO₂, a response absent in conifers and ferns. This CO₂ response is not fitness-relevant for angiosperms at current CO₂ levels because it's not exercised. But it may prove advantageous or disadvantageous as atmospheric CO₂ levels increase with climate change: since closing stomata prevents water loss, it is likely to be advantageous if the climate is drier, and disadvantageous if the climate is wetter. The same could be said if there is variation within a population (rather than between phyla) for the CO₂ response mechanism: some individuals might have higher or lower fitness depending on how fast or efficient their CO₂ response mechanism is. But the current level of atmospheric CO₂ does not exert this selection pressure, since it does not trigger the mechanism.

Atmospheric CO₂ is thus an example of a non-limiting resource that at current levels does not affect any variable fitness-relevant traits in plant populations. Atmospheric CO₂ is just one such resource; it seems likely that in many systems there will be other similar resources, though again evidence is difficult to locate. It is also important to recognize that such non-limiting factors will still be causally relevant to fitness. If we took the resource away or altered its abundance, this would affect the fitness of the organisms relying on the resource and may lead to some individuals being fitter than others. Nevertheless, absent such changes, the non-limiting resource does not bring about fitness differences in the population.

Non-limiting resources do little to help us predict species distribution or resource consumption. Nevertheless, Hutchinson's realized niche concept is defined in terms of which resources permit actual population persistence, and it cannot be denied that CO₂ levels make a positive contribution to the survival and reproduction of plant populations. In addition, CO₂ levels might actually play a role in modeling the effects of climate change on forest or agricultural systems, given the realistic expectations of increased CO₂ levels in the near future. It therefore makes good theoretical and practical sense to include CO₂ levels as a dimension of the ecological niches of land plants. Similar arguments can be made about other examples of non-limiting resources for other species, which may become relevant when a population is exposed to different environmental conditions due to climate change or when invading new areas.

If we accept this argument, we have an environmental factor that directly supports population persistence—rather than only being tolerated, it positively contributes to survival and reproduction of population members—that doesn't exert a selection pressure. In other words, non-limiting resources are another non-coincidence between the evolutionary and ecological niche. Moreover, this is an environmental factor that the populations in question, various species of land plants, can affect by respiration. Hence, we may be able to speak of a sort of niche construction that affects not the evolutionary but the ecological niche.

Niche construction across the conceptual divide

The contrast classes introduced above demonstrate that the evolutionary and ecological niches do not have exactly the same extension. Habitat degradation, commensalism, and non-limiting resources are points at which the realized ecological niche and the evolutionary niche come apart. Sometimes environmental conditions lead to fitness differences but do not permit population persistence, and sometimes they permit population persistence (both as tolerances and as requirements) but do not lead to fitness differences.

We might wonder how significant the cases of non-coincidence are. The evolutionary and realized population ecological niches still coincide to a large extent. Yet the conceptual differences should be taken seriously. First, there will likely be further examples of the contrast classes identified, and there may even be whole other kinds of non-coincidence between the evolutionary and ecological niche. That said, I do suspect that cases may be hard to identify in empirical research due to the practical and epistemological limitations on research into fitness-neutral or non-selective conditions and the difficulty of conducting large-scale, long-term field studies.

Second, recall the significant restrictions on the ecological niche necessary to even reach a sensible comparison. All the environmental conditions that are included in fundamental niches, as well as references to individualized and species niches, are excluded from the evolutionary niche. For instance, experimental research into environmental tolerances can provide information about a species' fundamental ecological niche but will not necessarily be relevant to its evolutionary niche, since the latter depends on how selection pressures play out in reality. To take another example, field research into intraspecific variation in resource use of a population, for instance through gut content analysis, reflect realized individualized and population ecological niches, but do not necessarily tell us anything about the fitness consequences of these differences and hence do not directly inform us about the evolutionary niche. Given all of these discrepancies, I conclude that the evolutionary niche is not a simple translation of the ecological niche: many things are lost in translation, and some things are gained.

There is also a difference in emphasis between ecological and evolutionary niches that is slightly more difficult to pinpoint but worth mentioning. Ecologists usually focus on factors that are positive or beneficial for a population, such as the resources or conditions that it needs in order to survive. In contrast, evolutionary biologists often look at factors which negatively affect a population, such as predation or resource limitations which select *against* certain types. This distinction between positive and negative influences is by no means hard and fast, and there is much overlap. But it does give a sense for differences in what sorts of conditions ecologists and evolutionary biologists might tend to focus on when investigating their respective niches, above and beyond the definitional discrepancies I have demonstrated in this paper.

I mentioned in the introduction that a motivation for comparing evolutionary and ecological niches is the claim that NCT might unify ecology and evolution.

NCT can still perform this role despite conceptual divergence. But any cross-disciplinary work has to bear in mind the differences between the ecological and the evolutionary niche. Ecological findings about niches cannot be directly imported into evolutionary work on NCT, nor vice versa. Changes to the ecological niche are not necessarily instances of evolutionary niche construction, but only if they involve changes in selection pressures. Hence, the claim that “with niche construction all [ecological] links become evolutionarily significant” (Odling-Smee et al. 2003, 209) must be treated with caution. In the other direction, a new evolutionary niche does not imply a new fundamental ecological niche, and perhaps not even a new realized ecological niche, depending on the viability of population persistence under those conditions.

Instead of direct transfer of theory and results between disciplines, cases should be assessed for which sort of niche is in focus and whether the example lies in the region of coincidence between evolutionary and ecological niches. Specifically, I have shown that the following elements must be considered: reference unit (individual, population, or species), modality (actual or possible), and relevant effect (population persistence or fitness differences, or other effects such as development, population establishment, survival, and so on). Only by assessing these aspects can elements from either discipline be considered relevant to and useful for the other. Such a considered approach to evolutionary and ecological niches should help to promote interdisciplinary work while avoiding and addressing some of the confusions that sometimes arise across disciplines. In particular, asking such questions will help to delineate a shared set of focal cases at the intersection of evolutionary niches and realized ecological niches.

Another implication of recognizing the differences between ecological and evolutionary niches is that we gain a great number of possible definitions of *ecological* niche construction. We might choose to talk about the construction of realized population niches, of fundamental individualized niches, of social niches, of establishment niches, and so on. All of these different concepts would introduce much needed nuance to research on organisms’ interactions with the great variety of factors in their environments. For instance, it would make it clear that so-called negative niche construction, such as habitat destruction, is a way to change evolutionary niches but might destroy a realized ecological niche altogether. Or as another example, it would become clear that phenotypic change can alter a fundamental ecological niche, and perhaps also an evolutionary niche, without necessarily changing the realized ecological niche. In addition, defining types of ecological niche construction would make it clear that altering selection pressures is just one way in which organisms can change their environment. In particular, the study of niche construction would be able to encompass further aspects of organisms’ interactions with environmental factors where fitness effects are either absent or unknown, such as the shaping of commensal relationships.

Broadening and subdividing niche construction in this way would therefore require revising the claims about the evolutionary significance of niche construction. Rather than a direct consequence of the definition of the niche, any evolutionary significance would have to be determined based on the observed effects of the changes that organisms make in interaction with their environments. This does not mean that

niche construction would lose its evolutionary significance altogether. The classic examples from NCT would remain as one sort of niche construction, and of course many further instances of niche construction would fall within the overlap between evolutionary and realized ecological niches. But once we accept not just an evolutionary but also an ecological niche construction, niche construction's evolutionary significance would not be a given.

Declarations

Conflicts of interest

The author does not have any competing interests.

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