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The evolutionary role of affordances: ecological psychology, niche construction, and natural selection

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Abstract
This paper aims to examine the evolutionary role of affordances, that is, the possibilities for action available in our environments. There are two allegedly competing views for explaining the evolutionary role of affordances: the first is based on natural selection; the second is based on niche construction. According to the first, affordances are resources that exert selection pressure. The second view claims that affordances are ecological inheritances in the organism's niche that are the product of a previous alteration of the environment. While there seems to be a mutually exclusive definition of affordances in each of these views, I argue in this paper that the views are not competing but, rather, complementary. In this sense, affordances play the role of either resources or ecological inheritances depending on the temporal stage of the evolutionary process. I make this argument by analyzing how natural selection and niche construction affect each other even when they function independently from each other. In this light, if these two evolutionary mechanisms exert their power in parallel but at two different stages in the evolutionary history of a given econiche, then there is room to claim that affordances can be understood as both resources and ecological inheritances. This dual aspect of affordances shows their evolutionary role.

Keywords Affordances · Evolution · Niche construction · Natural selection

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Introduction

Affordances are the possibilities for acting in our environment: objects of a certain size are graspable, floors are walkable, obstacles are avoidable, etc. These affordances are the main object of study of ecological psychology, a branch of psychology pioneered by James and Eleanor Gibson. The main aim of this paper is to show how we should understand the evolutionary role of affordances. To that end, some arguments are offered in favor of the compatibility of affordances with two different evolutionary mechanisms, namely, niche construction and natural selection.

Theorists of the ecological approach often claim that their view is linked to evolution and biology (Gibson 1979/2015, Michaels and Carello 1981, Reed 1996, Withagen and Chemero 2009). This has been a constant of the ecological approach, which is apparent in classical contributions like the following:

> Ecological theories not only assume that organisms exist in a rich sea of information about their environments, but also that they evolved in a rich sea of information. Consequently, it is supposed that the structure and function of the perceptual systems have become tailored to the available information. (Michaels and Carello 1981: 15)

Ecological psychologists assume that organisms evolve thanks to ecological information and affordances, but how exactly do affordances play a role in their evolutionary history? Here, I aim to reunite key contributions in the literature, mainly that of Reed (1996), with a picture according to which affordances are understood as elements of niche construction processes. This reuniting is possible because ecological psychology and niche construction share the organismal level of analysis and the idea that organisms are active beings that modify their environments. However, my proposal would be incomplete if natural selection, considered by many as the major evolutionary mechanism, were missing from this picture. There have been previous attempts to relate niche construction and affordances (Magnani and Bardone 2010; Withagen and van Wermeskerken 2010; Heras-Escribano and De Pinedo-García 2018; Heras-Escribano and De Jesus 2018, Heras-Escribano 2019). This paper intensifies this line of research and proposes the introduction of natural selection into the picture. The main effort to relate affordances and natural selection has been offered by Reed (1991, 1996). This article inherits and expands some of Reed's main ideas by relating them to niche construction processes in order to illuminate the role of affordances within evolutionary processes. In sum, I propose an approach in which affordances acquire their evolutionary role thanks to two different mechanisms (niche construction and natural selection). Thus, I aim to show that, in addition to their important role in our cognitive lives, affordances also play a role in our evolutionary history.

The combination of these two evolutionary mechanisms in a single picture seems to be problematic for some authors, especially with respect to their different approaches to the relation between organism and environment. Reed claimed that affordances should be understood as environmental resources exerting selection pressure and that the role of organisms in this picture is to compete for those resources (Reed 1996: 26–27). Hence, Reed was a selectionist who claimed that there is an asymmetry between organism and environment in which the environment is much more relevant for the organism than the organism for the environment (ibid.). In this view, natural selection is the main driver in the evolutionary process, and the role of the organism is minimized with respect to that of the environment. Affordances would be purely environmental resources that do not depend on animals for their existence, which has been criticized by authors such as Chemero (2009: 146), who claimed that Reed's picture fails to do justice to the mutuality of animal and environment at the basis of the original Gibsonian proposal (see also Withagen and van Wermeskerken 2010: 495).[1] In line with Chemero's criticism, authors such as Walsh (2014) claim that the introduction of affordances into the evolutionary picture necessarily implies a change in our ways of conceiving evolution and the environment, because an environment composed of affordances "is constantly shifting with changes in organismal form" (Walsh 2014: 223). In particular, compatible with certain views on niche construction theory[2] is the idea that affordances play a key role in the evolution of the organism because affordances offer a picture in which the organism-environment reciprocity is taken as central (Withagen and van Wermeskerken 2010: 504). Withagen and van Wermeskerken share Walsh's view on the mutual shifting of organism and environment in evolution; they claim that Reed's selectionism is unsatisfactory regarding the role of affordances in evolution since "the niche construction perspective suggests *alternative roles* [to the one offered by Reed] for affordances in evolutionary dynamics" (Withagen and van Wermeskerken 2010: 497, emphasis added). In this view, affordances would be aspects of niches that have been ecologically inherited by ancestors that modified the niche (Withagen and van Wesmerkerken 2010; Heras-Escribano and De Pinedo-García 2018). So, authors such as Withagen and van Wesmerkerken call for a new, alternative definition of the evolutionary role of affordances. This call shows that the definition of affordances as resources within natural selection processes and the definition of affordances as aspects within niche construction processes are incompatible according to some authors.

[1] A further analysis on the principles of ecological psychology will be offered in "Ecological psychology and affordances" section.

[2] Walsh proposes an affordance landscape in which the environment is shifting with changes in the organismal form (a symmetrical view in which both aspects affect each other) as opposed to an environment in which the organism is a passive subject constantly affected by natural selection (an asymmetrical view in which only the environment affects the organism). Walsh (2014) also claims that niche construction endorses a view of the environment that aligns with the latter view rather than with the former. However, the idea of the affordance landscape that he offers has been proposed to be compatible with niche construction theory, because niche construction theory holds that "organism and environment reciprocally affect each other in their mutual development, and those affections are always determined by the previous ones, which makes every interaction constitutive or formative of the following affection" (Heras-Escribano and De Pinedo-García 2018: 12). For a further discussion of the compatibility of Walsh's affordance landscape and niche construction theory, see Heras-Escribano and De Pinedo-García (2018).

Thus, the role of affordances in evolution is understood in two very different ways: from Reed's point of view, which is based on natural selection, they are mere resources that preexist and exert selection pressure on the animals that take them; from the point of view of those that support the compatibility of niche construction and affordances, affordances are ecological inheritances that emphasize the reciprocity of organism and environment as a necessary starting point for understanding evolution, which introduces a certain symmetry into the picture. Supporters of each view take both to be incompatible. The (apparent) incompatibility of both views is based on two main aspects: first, the role of the environment; second, the contributions of the organism in the environment. According to the selectionist view endorsed by Reed, neither the environment nor affordances depend upon the animal to exist. This asymmetry between organism and environment, giving priority to the environment in this case, is key for illustrating the incompatibilities of both views. Reed summarized his view as follows:

> [P]articular instances of an affordance may be realized (literally, made real) by an animal, as when a seagull drops shells on a rock to split them. But the affordance is a feature of the environment of all animals (in this case, all the sufficiently large and hard surfaces available to any gull) and *exists* independently of the particular animal even when it is not being used. An affordance is only a relation when an animal perceives or uses it (…) Affordances in the animal's niche are not relations; they are resources (…) (Reed 1996: 26, emphasis in the original)

Against those who take affordances as relations between environmental aspects and organismal properties (Chemero 2009), Reed claims that affordances are purely environmental aspects that enter into a relation as such when they are perceived or taken. This subtle difference leads to unexpected consequences, because those who accept that affordances are relations are more inclined to relate affordances to niche construction rather than to Reed's view (Withagen and van Wesmerkerken 2010). The main source of the (apparent) incompatibility between Reed's view and the niche construction view is that the latter view, unlike Reed's, accepts that the organism creates the environment. A clear antecedent of niche construction is *The Dialectical Biologist* (Laland et al. 2016), in which Levins and Lewontin claim that "[t]he organism influences its own evolution, by being both the object of natural selection and the *creator* of the conditions of that selection" (Lewontin 1985: 106, emphasis added). Reed totally rejected this view and, against Lewontin's view, claims that "it is true that birds, beavers, and humans significantly alter the landscape (…), but it is false that we *create* the landscape" (Reed 1996: 27, emphasis in the original). In this sense, Reed's view seems totally opposed to that of Lewontin, which inspired niche construction theory. Nevertheless, I think that this dispute is merely semantic because, despite the use of the word "creation" or "alteration," Lewontin and Reed share a conceptual core.

My aim in this paper is to show that this opposition between affordances as inheritances and affordances as resources is merely apparent. For this reason, I propose that the combination of niche construction and natural selection within a single picture does not necessarily alter the regular functioning of either mechanism. In my view, affordances exert selective pressure at t_1, and then these same affordances are inherited by the offspring at t_2. Once these affordances are inherited, they exert selective pressures regarding the configuration of the niche. I propose to show that affordances are *both* resources *and* ecological inheritances, although they function as either resources or inheritances depending on the moment of the evolutionary process in a given niche. This picture allows for the compatibility of both definitions of affordances (as both resources and ecological inheritances), which are accommodated as two different roles of affordances within a diachronic explanation of the evolutionary process.

The paper progresses as follows: first, in "Ecological psychology and affordances" section, I introduce ecological psychology, which is an embodied, situated, and informational approach to cognition based on the perception of affordances, that is, the possibilities for action in our environment. Then, in "The extended evolutionary synthesis and niche construction theory" section, I introduce the main aspects of niche construction theory. Niche construction is a process by which organisms modify their environments, and some of these modifications facilitate their adaptation. "Affordances, niche construction, and natural selection" section shows how affordances are compatible with niche construction and natural selection. I propose a unifying picture of how these key evolutionary mechanisms can be combined, and I emphasize the importance of affordances in that unified picture so as to reveal that they fulfill a different role at different stages of the evolutionary process (either as resources or as ecological inheritances).

Ecological psychology and affordances

Ecological psychology is an approach to perception and perceptual learning pioneered by Gibson and Gibson (Gibson 1979/2015, Gibson and Pick 2000). Ecological psychology was conceived as a third path in psychology beyond behaviorism and cognitivism. Ecological psychology rejects the cognitivist approach (according to which cognition is a matter of computing or manipulating representations according to certain rules) on the basis that cognition is itself a capacity of the organism-as-a-whole rather than the functioning of inner abstract processes. At the same time, it also rejects the stimulus–response view of behaviorism since this view takes the organism as a passive being that merely reacts against certain worldly impingements. The starting point of the ecological approach is that, because the organism is an agent (an active explorer of its environment), we cannot explain how an organism perceives and acts if we do not appeal to the history of interactions established between that organism and its environment. In this sense, ecological psychology is a clear antecedent of the embodied, situated, and anti-cognitivist approaches to perception and action that are now gaining momentum in the cognitive sciences (Gibson 1979/2015, Richardson et al. 2008).

The first idea that motivates the ecological approach is that perception is continuous with action. This means that we cannot differentiate perception and action because they are two sides of the same cyclical process: in fact, organisms explore their surroundings and, thanks to this exploration, perceive aspects that cannot be perceived otherwise (Richardson et al. 2008). These aspects, in turn, guide the behavior of the organisms, allowing them to continue exploring and starting this process over and over again. In this sense, we perceive because we act, and our action determines the way in which we perceive. This idea comes from the pragmatist tradition in which the sensory capacities cannot be differentiated from our active skills (Dewey 1896). Thus, organisms are taken as active agents rather than passive beings that merely react to stimuli.

The second idea that motivates the ecological approach is situatedness: since perception and action always occur in a given place and time, the main unit of analysis according to ecological psychology should not be restricted to the neural system; on the contrary, the suitable level of analysis should include the organism and its environment, which means that explaining perception is explaining the interaction or coupling of organism and environment. For this reason, the main unit of analysis is the organism-environment system (O–E system). It is important to remark that Gibson's idea of environment differs from the idea of world inasmuch as the environment is the surroundings of the organism described in relation to organisms' capacities, whereas the world is a description of the surroundings of the animal described in terms of particles and forces (Gibson 1979/2015: 4–11). For this reason, the ecological approach includes a series of terms ("O–E system," "ecological information," "specificity," and "affordance") that aim to do justice to how the organism couples with the environment, this coupling being a starting point for a new means of understanding psychology. When we explain cognition from this perspective, we are postulating an *ecological scale*, that is, a methodological framework that works as the proper level for understanding cognition from an ecological standpoint.

The ecological approach emphasizes that the organism-environment coupling forms a system, which in turn is the main unit of analysis of psychological processes. But how is this reciprocity achieved? What is the organism seeking in its exploratory activity, and what does it find to maintain its own activity? According to ecological psychology, this reciprocity is established through *ecological information*. This kind of information is the way in which we describe the energies of the environment in relation to the bodies and capacities of the organisms that perceive them (Heras-Escribano and De Pinedo 2018: 575). A peculiar aspect of this kind of information is that it allows us to perceive the environment in a direct way. In this sense, ecological psychology reacts against "indirect" approaches to cognition like cognitivism (Gibson 1979/2015). Cognitivism states that the stimulation of sensory receptors is sufficient for achieving perception, while the ecological approach claims otherwise. Imagine a human inside a densely fog-filled room. In this example, light stimulates that person's retina, but she would be unable to perceive her surroundings. The organism cannot perceive the surroundings of the room because light does not reverberate; hence, it does not offer any kind of information about the available affordances (Gibson 1979/2015: 46, Chemero 2009: 107–8). Once the fog is removed, light can reflect and reverberate on the surfaces, thus gaining its structure and finally showing the human the possibilities for acting (Glotzbach and Heft 1982: 111). In this case, light is informative. This is how ecological information is formed. The person in the room detects this information because she is an agent, that is, because she acts in order to discover the different affordances available in the room. As she explores her environment, she detects or picks up the ecological variables that provide information about the room's affordances, which amounts to saying she discovers what she can and can't do. Unlike cognitivism, there is no need to postulate inner representations: behavior can be accounted for solely in terms of the organism-environment coupling. There is no need to postulate representations of the outer world to make sense of perception because ecological information is a description of how the outer world *is related to our capacities*; it shows how the distribution of energy arrays is disposed in relation to the agent's movement: "[t]he optical disturbances created by an approaching car, for example, do not resemble the car; rather they uniquely specify it and its path of locomotion in relation to oneself" (Gibson and Pick 2000: 18). The expression "in relation to oneself" is key for stressing that we do not represent the world as a static picture: rather, we perceive the world from a concrete spatiotemporal location and always in relation to our bodily constitution. For all these reasons, according to the ecological approach, "perception is a direct—noninferential, noncomputational—process, in which information is gathered or picked up in active exploration of the environment" (Chemero 2009: 106; see also Michaels and Carello 1981).

A typical example of an ecologically-informational variable is tau or time-to-contact (Lee 2009). This variable consists in "the ratio of the optical size [of the approaching object] to the rate of optical expansion [of the same object during time]" (Jacobs and Michaels 2007: 324); in other words, when something (an object, an organism) is approaching you, that object or organism progressively expands in your visual field. The relation between the expansion and the approximation gives information about the time-to-contact between the perceiver and the object or organism that is perceived. This example shows how the environment consists in the surroundings as they relate to the organism, since time-to-contact is an agent-related metric that helps the organism anticipate when collision will happen. This is not expressed in neutral, agent-unrelated metrics like meters per second. Agency is key in this picture, and this implies that the metrics of what happens in the environment relate to the action and position of the agent-perceiver. Needless to say, time-to-contact suffices for guiding behavior, since the optical expansion in each moment reveals the available affordances for the perceiver: avoidance, collision, climbing, vaulting, crawling, grasping, etc.

As we can see, ecological information shows or reveals the available affordances. In the terminology of ecological psychology, this means that ecological information specifies the available possibilities for each agent's actions. *Specificity* is a term that refers to the one-to-one correspondence of ecological information and affordance perception: the detection of certain ecological variable corresponds to the perception of affordances and vice versa (Chemero 2009: 111). As Käufer and Chemero (2015) claim, specificity works in such a way that the presence of ecological information guarantees the presence of affordances. This concept is the bedrock upon which the scientific character of ecological psychology is built, because it establishes a lawful correspondence and regularity between ecological information and affordances (Jacobs and Michaels 2002: 129, Richardson et al. 2008: 177). This lawful regularity is understood in a very particular way within the ecological approach: "Ecological information is lawful not in the Newtonian sense of being universal in space and time, but in an ecological sense of being regular within an ecological context of constraint" (Warren 2005: 342–343). This lawful regularity shows why ecological information such as time-to-contact specifies or guarantees the presence of certain affordances, and these affordances change depending on the spatiotemporal coordinates in which they are perceived: for example, given a particular rate of expansion in our visual field we can perceive not only the possibility of avoidance but also the possibility of grasping or collision depending on the moment and the circumstances. Now we can fully understand the nature of the main objects of perception for ecological psychology: affordances.

Affordances are possibilities for action that are available in the environment for a particular kind of organism. Affordances are, then, aspects of the environment that are considered in relation to the bodily constitution and capacities of the agents that perceive them. The perception of the available opportunities for action is dependent on the detection or picking-up of ecological information: objects are graspable for agents with posable thumbs, steps are climbable for those who can raise their legs at a certain length, etc. These objects of perception are quite intuitive, therefore, and we are constantly surrounded by affordances in our daily lives. Nevertheless, their philosophical status is still in dispute, and this is because they are challenging for traditional philosophical categories. On the one hand, affordances are not mind-independent aspects of the environment; on the other hand, they are not purely subjective aspects. They escape the objective-subjective dichotomy because they are environmental aspects *relative to* the bodily constitution and abilities of their perceivers (Gibson 1979/2015: 120–1). The coupling or reciprocity of organism and environment is challenging for standard dichotomies in philosophy, and this is why affordances and the ecological standpoint that takes the O–E system as a main unit of analysis are innovative conceptual frameworks that allow us to understand cognition form an innovative perspective.

This coupling between organism and environment is the key aspect that connects ecological psychology and niche construction.[3] As we have seen, affordances play the role of illustrating the reciprocity of organism and environment at the cognitive level, but the ecological study of affordances can also play the role of illuminating how we can understand evolution better under the principles of niche construction. Affordances are aspects of the environment related to bodily features or traits of the organism that the organism encounters when exploring the environment; these affordances exert a feedback function to the organism that guides its behavior, and this function can be described in dynamical systems. This influence of environmental information working as a feedback mechanism for exploring the environment is key for our developmental processes and perceptual learning, as it has been proved with empirical evidence by ecological psychology (Gibson and Pick 2000; Jacobs and Michaels 2007). This is the very idea that underlies niche construction: modifications in the environment lead to an alteration in the evolutionary dynamics of the population that cause it. In this sense, the dynamics established by the interaction with the affordances of the environment can exert an influence in the evolutionary

[3] I thank an anonymous reviewer for urging me to comment upon this idea.

dynamics as well: if the processes of niche construction lead to a certain modification of the environment and the creation of new affordances, these affordances play a role in both the cognitive and the evolutionary history of the population that will benefit from perceiving and using them. Thus, this well-established psychological study of perceptual learning can serve as an illustration to emphasize the importance of these feedback relations between organism and environment. For these reasons, affordances are an example of how important niche construction processes are for making sense of evolution beyond the typical examples at a genetic level. In order to understand this in more detail, we have to describe the principles of niche construction and how it fits within the extended evolutionary synthesis.

The extended evolutionary synthesis and niche construction theory

Niche construction theory is often presented as one of the main theories that conforms to what has been called the extended evolutionary synthesis (EES), a view that challenges the traditional approach to evolution, also known as the Modern Synthesis.

The Modern Synthesis (MS) is considered the mainstream approach in evolution; it consists in the combination of Darwinian natural selection with Mendelian genetics (Huxley 1942). The viewpoint of the MS focuses on the role of genes and genetic inheritance, and this insistence on genetic inheritance as a cornerstone of evolution has often been called the gene's view or the gene-centered view (Fisher 1930; Williams 1966; Maynard Smith 1998; Dawkins 1976). According to this view, the explanation of evolutionary change and adaptation relies on the role and functioning of genes.[4] From this perspective, adaptation is taken as a process guided by natural selection, which is the only (external) force that drives evolution by acting like a filter by which populations with the suitable genetic pool fit their particular environmental circumstances. Random genetic mutations of some organisms are essential for increasing their chance to reproduce against hostile environmental conditions and, if successful, those organisms transmit their genes to their offspring (Maynard Smith 1998: 10). In this sense, only genes transmit the essential elements that provide the adaptation to the environment. The main reason to choose genes instead of other aspects as the main units, or to choose the organisms' genotype (the unobservable genetic aspects that determine the observable features) rather than the organisms' phenotype (the observable features or traits), is that phenotypes, unlike genotypes, are extremely contingent and temporary combinations of how genes are expressed and how the environment is disposed (Williams 1966: 22–23). This allows for dramatic variations in short periods of time that do now allow one to quantify

[4] The gene-centered view is understood here as centered on individual genes as opposed to genomes or whole organism phenotypes. This view is compatible with Dawkins's view of organisms as survival machines of genes, as well as with orthodox views in the Modern Synthesis cited above. To show the intricacies of the idea and its relation to phenotypic variation, I offer a comparison of niche construction within the Extended Synthesis and Dawkins's extended phenotype within the Modern Synthesis at the end of this section. I thank an anonymous reviewer for urging me to clarify this idea here.

and analyze the real impact of adaptation and evolution. This is an asymmetric process in which an external force acts upon a particular population and in which we know whether or not adaptation is achieved by merely looking at the genetic level. This is because "the environment is largely autonomous with respect to the organisms," and for this reason it works "according to its own intrinsic dynamics" (Godfrey-Smith 2001: 254). There is no coupling or significant mutual affection between organism and environment. The environment exerts selection pressure and does so basically via natural selection.

A this point we can see how the MS usually adopts a gene-centered view, and this general picture offers three main consequences regarding evolution and adaptation: first, the main (and maybe only) driving force in evolution is natural selection; second, genetic inheritance is the main (and maybe only) kind of inheritance that matters for evolution and adaptation; third, organisms are receptacles in which genes are transmitted generation by generation. This latter idea leads Dawkins (1976) to define organisms as "survival machines" of genes.

Despite the influence of the MS and the gene-centered view, a new and emerging approach to evolution has been gaining momentum in recent years: the extended evolutionary synthesis (EES). It is a new view that aims to expand the claims of the MS by incorporating different evolutionary mechanisms neglected or not sufficiently emphasized in the previous years. In particular, the EES rescues the importance of developmental processes for evolution, as well as the reciprocal causation and co-determination of organism and environment (Oyama 1984; Lewontin 2000; Jablonka and Lamb 2014; Pigliucci and Muller 2010; Laland et al. 2015). Proponents of the EES argue against a restrictive view of the MS by claiming that there are means of inheriting beyond the genetic level, and they question the primacy of natural selection as the sole force driving evolution. In this sense, the EES aims to gather some processes, phenomena, and mechanisms beyond natural selection (such as developmental processes, epigenetics, niche construction, or ecological inheritances) so as to enrich and expand the main ideas of the MS. In this sense, these often neglected aspects or mechanisms play the role of a bias in the drift of selection. According to the picture offered by the EES, natural selection still works as a major force in evolution, but it is not the only one. In the same vein, new forms of inheritance beyond genetic inheritance are also considered relevant for making sense of evolutionary drift.

According to these authors, a key example of a neglected evolutionary mechanism is niche construction (Odling-Smee et al. 2003). Niche construction is an evolutionary mechanism by which organisms alter or modify their environments in a way that is beneficial to them and their offspring since those alterations increase their chance of reproduction and survival (Lewontin 1985; Odling-Smee et al. 2003; Laland et al. 2015). Niche construction analyzes the ways in which the environment is shaped by the organisms that inhabit it. In this sense, changes in the environment can be divided in two main kinds: first, inceptive perturbations, that is, the changes in the organism's behavior that physically alter environmental aspects (such as the emission of detritus, dairy farming, or the construction of dams[5]); second, inceptive relocations or the migrations of organisms to new habitats in which those organisms encounter new environmental aspects or variables (Odling-Smee et al. 2003: 47). In these inceptive perturbations and relocations, the organisms are the drivers of environmental change, and they act in an exploratory way, but there are also counteractive approaches to perturbations and relocations: counteractive perturbations are those actions in which organisms respond to or compensate a drastic environmental change by modifying their environments (like the thermo-regulation of bird nests against a drastic change in temperature), and counteractive relocations provoke migrations to other places due to environmental changes (like the seasonal migrations of some birds). In sum, organisms find certain cues that guide their exploration and allow them to expand their behavioral repertoire in order to survive, reproduce, and thrive, compensating disturbances in the environment and finding new habitats with resources that will benefit them. They seek these cues in order to succeed in their goals. For this reason, according to both defenders and opponents of this view, "niche construction is guided by (genetic or acquired) information" (Scott-Phillips et al. 2014: 1234).

From the point of view of niche construction, inceptive perturbations play the role of a bias in the direction of selection, which means that apparently innocuous alterations of the environment might generate a changing output on a larger scale that modifies the spatiotemporal dynamics of the niche. If we analyze some of the examples provided above, dams alter the environment not only in a way that is beneficial for their builders (humans, beavers); they also affect different aspects of the environment that were not taken into account by their builders. For example, drastic changes in the current of rivers may help the reproduction of microorganisms that could not reproduce otherwise, leading to new diseases or parasitic relations between species in that habitat. In the same vein, stopping the current of a river with a dam might create a habitat suitable for birds to stop during their migration process, and this could also attract certain predators. In this sense, altering the environment not only serves the purpose of benefiting the organisms that make those alterations; they also trigger unexpected changes in the dynamics of the niche. Hence, if the activity of the organisms produces alterations in habitats that benefit their fitness and that also provoke unexpected changes in their niche that bias their evolutionary drift, they are not simply receptacles of genes subject to changes in their habitats.

There are physical consequences that are produced by these alterations. And sometimes those physical consequences are objects that become part of the habitat, like the previously mentioned example of the dam. When these objects are

5 It should be highlighted that not all alterations in the environment produced by the organism are goal-directed and adaptive. Dairy farming in humans is clearly a goal-directed action, but the emission of detritus in populations of squirrels is not necessarily a goal-directed action. Despite this difference, the alterations of both inceptive perturbations can produce an equally significant alteration in their particular ecosystems. The same goes for the adaptive role: not all such alterations are beneficial in adaptive terms, although they equally change the evolutionary dynamics even without an adaptive impact. In this sense, I focus here on affordance perception and affordance taking as an example of goal-directed action, but not all aspects of niche construction processes involve this kind of aspect. I thank an anonymous reviewer for inviting me to highlight this point.

inherited by the offspring of those who altered their environment, they are categorized as ecological inheritances. Ecological inheritances are defined as the physical or material consequences of niche construction processes (Odling-Smee et al. 2003). There are multiple kinds of ecological inheritances that range from cultural practices like dairy farming to artifacts, buildings, tools, etc. Biological inheritances expand beyond genetic inheritance, since those material consequences determine the development of organisms and their habitats. This counters the claim that genetic inheritance is the only kind of biological inheritance. Within the EES there are non-genetic mechanisms that contribute to inheritance, such as parent–offspring transmission of objects that alter the environment in a way that benefits their fitness. Ecological inheritances also alter the genetic expression of phenotypes in the development of organisms (Donohue 2005). In this sense, the material consequences of previous alterations of the environment are inherited, which means the benefit obtained by the alteration is transmitted and modifies the evolutionary history of populations in ways that were unexpected before the alteration.

In sum, the EES expands the main ideas and claims of the MS regarding evolution and adaptation, offering a richer view of the phenomena that take into account processes and mechanisms usually neglected. At the same time, the introduction of these mechanisms and processes supposes a challenge to the gene-centered view that includes certain theoretical changes in our way of understanding adaptation, evolution, and biology in general.

The main theoretical consequences of MS and the gene-centered view are the following: organisms are receptacles of genes, and the only force that drives evolution is natural selection, which means the only kind of inheritance is genetic inheritance. At the same time, defenders of niche construction claim that organism-environment coupling establishes certain dynamics that bias the direction of evolution. These alterations favor their survival and reproduction, and the material consequences of those changes are inherited by their offspring. These material consequences show that there is inheritance beyond genetic inheritance. All these aspects in combination reveal that adaptation is not conceived within the EES as an asymmetric process by which biological features evolve in response to environmental selective pressures. In this view, adaptation is partially constituted by the (voluntary or involuntary) activity of organisms, because they bias their evolutionary drift at the same time that they are affected by other selective mechanisms. This mutual affection of organism and environment emphasizes the importance of the organismal level for explaining the causal role of these kinds of process, moving from the asymmetrical picture of the MS to a symmetrical picture (Walsh 2014: 216).

One might think that the MS's emphasis on the role of genes leaves aside the importance of organisms' active capacities and that, in turn, these capacities are taken into account within the EES view (particularly in niche construction). Nevertheless, a more cautious treatment of how the MS understands the activity of organisms reveals that this picture is not accurate. In particular, a supporter of the MS view would claim that gene distributions only have selective consequences through the activity of organisms. In this sense, the role of organismal activity is rather essential in the traditional view. Thus, the differences between both views do not rely on the active powers of organisms but, rather, on other aspects.

An example is the significantly different ways in which the MS and the EES understand development and the conceptual relation among variation, differential fitness, and heredity (Uller and Helanterä 2019). Variation, differential fitness, and heredity are taken as autonomous concepts and quasi-independent processes within the MS (Walsh 2015). Variation (random mutation) is explained independently. At the same time, the variable rates of survival among individuals determine the features that will be present in the offspring. Nevertheless, these processes do not directly affect the process of inheritance, which is explained by independent Mendelian rules. Each element provides the materials for the next step, but every step is explained by appealing to its own dynamics or rules (Uller and Helanterä 2019). It is important to note that development has a reduced role in this view, because the only evolutionary causes related to development are those that pass through the filter of natural selection and are inherited (Walsh 2015). Development, then, is separate from the mechanisms that explain the content transmitted trans-generationally (the genes), and it only affects the environmental context in which the content is expressed (Uller and Helanterä 2019). However, there are authors who claim that this quasi-independence should not be taken literally, since the developmental processes that produce recurrent phenotypic expressions are closely related to processes that produce recurrent selection insofar as the way organisms respond to certain disturbances during their ontogenetic development shapes their environment and their adaptation to it; furthermore, these responses will affect the way in which their offspring will treat the already modified environment, favoring survival and reproduction (Uller and Helanterä 2019; Sultan 2015). In this sense, the EES does not take biological processes as quasi-independent. The emphasis on development and the intertwinement of development and fitness is another clear difference between the MS and the EES, which aggravates the differences between both syntheses and helps to offer a different picture of the role of the organismal level in adaptation.

These differences establish different views regarding the status of certain evolutionary processes in evolutionary biology, a discussion carried out between supporters of niche construction theory and defenders of the MS. These discussions emphasize the role of niche construction in evolution. There are biologists who claim that the MS can accommodate the main contributions of niche construction, mainly because they think that phenomena such as niche construction do not necessitate rethinking evolutionary theory as it is conceived within the MS (Laland et al. 2014). Niche construction processes in this view, according to Laland et al. (2014), are reduced to mere feedback relations between organism and environment, and these feedback relations, although they play a part in evolution by altering it, are not essential for it (the only essential aspects are—according to these authors—natural selection, drift, mutation, recombination, and gene flow). Some authors might claim that niche construction resembles well-established ideas in the literature that do not need to appeal to mechanisms beyond natural selection, such as Dawkins's extended phenotype. Although overlaps exist between the idea of extended phenotype and niche construction, there are differences: first, the extended phenotype only focuses on selective feedback from environmental modification to the genes responsible for those modifications, but niche construction takes into account other environmental aspects that are potentially unrelated to those genes; second, unlike the extended phenotype, niche construction theory emphasizes the legacy of modifications that remain beyond the modifiers as inheritances; third, again unlike the extended phenotype, niche construction does not require traits to have a strong genetic basis or a strong association with fitness since niche construction processes include or acquire characters that generate selective feedback even without being extended phenotypes (Laland et al. 2016). Thus, the idea of extended phenotype is a narrower concept compared to niche construction, which includes phenomena that go beyond well-established ideas in the MS and that play a relevant role in the alteration of evolutionary dynamics. Niche construction theorists are among the advocates of the EES who claim that MS is insufficient and should be enriched, but the relation between the EES and the MS varies depending on each author. For example, while some authors claim that evolutionary theory should be expanded (Kauffman 1993) or urgently rethought (Laland et al. 2014) on the basis of new evidence so as to create a new synthesis, other authors think that the MS should be replaced because it no longer offers a satisfactory framework for evolutionary biology (Jablonka and Lamb 2008). The proposal offered here aligns with the views of authors such as Odling-Smee et al. (2003), who emphasize the role of certain environmental aspects in altering the evolutionary dynamics of a particular population, and I hold that affordances contribute significantly to these alterations.

Affordances, niche construction, and natural selection

Affordances and niche construction

There are various similarities and complementarities between niche construction and ecological psychology. In particular, the ideas of agency and information are key in both approaches. Furthermore, the way both concepts are depicted in each theory shows that there is room for a certain compatibility inasmuch as we accept that cognitive or psychological processes play a certain role in biological aspects such as development and adaptation.

First of all, both theories emphasize the role of organismal activity. As we have seen, although some examples of NC involve active "psychological" agents behaving in ways that are aimed at modifying the environment, other examples imply that the modifications on the environment are fortuitous. Thus, many cases of niche construction do not involve any behavior or agency at all (e.g., chemical changes in the soil produced by bacterial detritus). Given that I aim to reconcile niche construction and ecological psychology, and given that ecological psychology implies volition and agency, the niche construction processes to which I am appealing that can be explained by the principles of ecological psychology and ecological information are very few. Nevertheless, it could be claimed that, in these specific cases, organisms are active explorers and modifiers of their habitats and that some of those changes are produced in their favor, increasing their chances of survival and reproductive success. The offspring of that population will find those previous alterations in their environment from their very beginning, increasing as well their chances of survival and reproduction. In this sense, the action of organisms is essential for their survival and fitness from a niche construction perspective, since their capacity for altering the environment has a direct effect on these aspects. By contrast, organisms are considered active explorers within the ecological approach because the organism acts in order to perceive the available affordances of the environment. Action is so crucial for the ecological approach that Gibson's main book claims that motion or action is the criterion for dividing the cognitive from the non-cognitive, the animate from the inanimate (Gibson 1979/2015: 3). Thus, niche construction and ecological psychology focus on the idea of organism as an active agent that explores the environment in search of opportunities for action (affordances) that play the role of resources for adapting to the environment.

Another source for similarities between the ecological approach and NC is the emphasis on information. This is what guides niche construction and perception–action processes. As argued by both niche construction theorists and their opponents, "niche construction is guided by (genetic or acquired) information" (Scott-Phillips et al. 2014: 1234). Leaving aside genetic information, if we analyze the kind of information we can find at the organismal level, it seems that niche construction endorses the idea that organismal behavior is guided by some kind of acquired information that results from the coupling of organism and environment, which is sometimes produced by the organism's alteration of its own habitat. In the same sense, ecological psychology claims that the organism-environment coupling is achieved thanks to ecological information, which is formed by ecological or higher-order variables that result from the interaction between energy arrays and the action of agents. For this reason, some authors point to the idea that ecological information can be conceived as one kind of acquired information that guides niche construction processes, proposing a continuity of cognitive and evolutionary processes from an organismal and informational perspective (Heras-Escribano and De Pinedo-García 2018; Heras-Escribano and De Jesus 2018).

The final aspect shared by both the extended synthesis and ecological psychology is the emphasis on development or the ontogenetic history of organisms adapting to their environments. As already shown, developmental processes play a crucial role within the EES since the experience of the organism during its own development is crucial for compensating for the disturbances of the environment. In this sense, the responses developed by the organism to facilitate its own adaptation to the environment and survival will have a direct impact on its offspring, because the offspring will enter into an environment or habitat that has been already modified for increasing the probability of its own survival and adaptation (Uller and Helanterä, 2019; Sultan, 2015). One of the major branches of the theory since its birth, development is also very important within ecological psychology. E. J. Gibson focused on the importance of ontogenetic processes and perceptual learning, thereby developing a line of research parallel to that of J. J. Gibson focused on perception (Gibson 1969; Gibson and Pick 2000; Rader 2018; Read and Szokolszky 2018). The main innovation of this approach is Jacobs and Michaels's (2007) direct learning theory, which proves that participants evolve from novice to expert performers of a certain task because they tend to pick up the specific ecological variables over the non-specific ones. The ecological approach to perceptual learning shows how organisms make use of specific ecological information available in their environments: organisms attune to their environments when they seek the most convenient information in order to perform a task, and for this reason they need to calibrate or adjust their behavior to the already-found informational variable (Lobo et al. 2018a).

These similarities show that there are sufficient conceptual compatibilities between niche construction and ecological psychology so as to consider affordances as aspects in the niche construction process[6] (at least as aspects that play a role for niche construction in cases when niche construction implies active agency). As a result, the material consequences of niche construction processes are not restricted to the physical objects that are inherited: the social function and the affordances of those objects are also inherited (Heras-Escribano and De Pinedo-García 2018). For example, any kind of device that we use in our society (a pair of glasses, typewriters, keys, chairs, etc.) are inherited as physical objects, but we inherit them along with the ways in which we should deal with them. These ways of dealing with the objects are twofold: first of all, there is the way in which we deal with them from an individual point of view, that is, as an individual organism dealing with the environment and aiming to satisfy its purposes and needs by perceiving the affordances of objects; secondly, we deal with the environment as social beings, that is, as members of a community of shared practices in which we are instructed and trained, and as social beings we aim to follow the norms and behavioral patterns because they help us modulate how we take the affordances of objects in different ways[7](Heras-Escribano and De Pinedo 2018: 486–587). In this sense, our niche contains not only the physical structures of those objects as such but also their affordances (which is the way in which those objects relate to our bodily skills and capacities) and the behavioral patterns that are socially enacted and serve to deal with those objects in an organized manner benefitting the community. This implies that human nature at an organismal level establishes a double dialectics: the reciprocal interplay of organism and environment on the one hand and, on the other, that of the individual and the community of sociocultural practices (Reed 1993, 1996; Heft 2007, 2018; Ingold 2001/2011).

[6] As suggested by an anonymous reviewer, it is worth highlighting that niche construction theory applies to all organisms, including those that are not traditionally conceived as perceivers (though they do detect things), behavers (in most senses of the term), or fast (animated) movers. This is important to avoid equating the words "organism" and "cognizer" and giving the false impression that niche construction processes are only triggered by cognitive organisms. In the case of chordates, action capacities are well-developed so as to act in a fast way and develop a certain plasticity and flexibility that increase their cognitive capacities (Settleworth 2010), and niche construction processes are triggered thanks to these capacities. In this sense, organisms that do not possess these capacities are also capable of producing alterations in their environments, which trigger niche construction processes (Odling-Smee et al. 2003). Nevertheless, there are also organisms that are usually categorized as non-cognitive but, as recent empirical studies prove, show cognitive capacities in ecological terms, as happens in the field of plant cognition, which is gaining momentum in the cognitive sciences (see, for example, Heras-Escribano and Calvo 2019).

[7] Based on how it is written, it might seem that a greater capacity for social sharing of information is always advantageous. However, sometimes it is not, since such capacities also carry costs that vary according to the ecological situation of the organism. I thank an anonymous reviewer for asking me to point this idea out.

The affordances of our human environment are aspects of our environment shaped by our activity, but they are also at the same time environmental resources that modulate our activity and, in addition, exert selection pressure on the behavior of organisms (Reed 1996: 18). For this reason, the affordances that exert selection pressure and that remain as ecological inheritances in our niches (because they increase our and our offspring's chances of survival and reproduction) contribute to the systematic bias exerted by our alterations, thereby conditioning our evolutionary drift in a direction that could not have been achieved otherwise. This is because the behavioral patterns acquired by social interaction teach us how to deal with affordances in a way that is beneficial for our adaptation and that of our offspring.

Some authors could claim that affordances do not offer substantial contributions to the explanation of evolution in terms of niche construction.[8] As shown earlier, supporters of niche construction do not need the concept of affordance to make their central point, although this per se does not preclude affordance from entering into the picture of their central point. Yet, can affordances make a genuine contribution to niche construction? As we have seen, genetic or acquired information guides niche construction processes (Scott-Phillips et al. 2014). If so, then ecological information is one of the kinds of acquired information that help us guide niche construction processes in the realm of perception and action (Heras-Escribano and De Pinedo-García 2018; Heras-Escribano and De Jesus 2018). According to the ecological approach, the direct perception of affordances amounts to the detection of ecological information, and perceiving affordances helps us navigate the environment. This idea is canonical and lies at the very core of the ecological approach (Gibson 1979; Michaels and Carello 1981; Turvey et al. 1981; Reed 1996; Chemero 2009; Heft 2001). In this sense, ecological information is a special kind of information of which we are aware in our navigation of the environment; this information is useful for us since it guides and constraints our range of behaviors when we explore our surroundings. We can also modify the environment and alter the available affordances while retaining others as we please. In this sense, perceiving and taking affordances via the detection of ecological information can be taken as a key process in our cognitive lives, since we are constantly detecting ecological information that allows us to explore the environment in an efficient way. The acceptance of ecological information as a kind of acquired information that plays a decisive role in niche construction processes implies the acceptance of affordances as a key aspect not only of our cognitive lives but also of our evolutionary process.

In conclusion, it can be argued that affordances and niche construction share the same organismal level of analysis; they share the ideas that organisms are agents, that development is crucial for perceptual learning and adaptation, and that our dealings with the environment are guided by information of all kinds, including ecological information for affordances. In this sense, the ecological approach to perception and action can be understood as an approach that shares the main commitments and premises of niche construction. This shows that there are cognitive processes of

[8] Thanks to an anonymous reviewer for making me aware of this idea.

affordance perception and taking that can be inserted within such evolutionary processes as niche construction located at an organismal level.

At the end of "Ecological psychology and affordances" section, I emphasized the importance of ecological psychology for niche construction theory, and some words must be now added to emphasize the importance of niche construction to ecological psychology.[9] As shown in the introductory section, most ecological psychologists agree that affordances are tightly related to our evolutionary processes, although few systematic proposals have been offered to date. Niche construction can illuminate the evolutionary impact of affordances and also various other aspects within the ecological approach like effectivities. This is because niche construction can explain how affordances can modify phenotypes: according to the Connecticut School in ecological psychology (Lobo et al. 2018b), the complementary aspects of affordances are animals' effectivities, that is, properties of the organism related to affordances. Although a well-established aspect in this tradition, not much has been said about effectivities and its evolutionary role, but niche construction can illuminate how effectivities can change and how they can serve to create new affordances in the environment. This is because, if we understand affordances as key environmental aspects within niche construction processes, there is a tradeoff between phenotypic plasticity and niche construction in which the environment induces changes in the phenotype and, at the same time, these changes in the phenotype may involve adaptive specializations that might in turn lead to changes in the environment, which is why plasticity is a major source of niche construction that could trigger changes within species (Laland et al. 2016: 196). For this reason, understanding affordances from a niche construction perspective and trying to combine niche construction and ecological psychology are quite helpful gestures for understanding not only the evolutionary role of affordances but also different aspects of the ecological approach (such as effectivities) from an evolutionary perspective.

Introducing natural selection

The previous subsection shows that cognitive processes of perceiving and taking affordances are compatible with a general scheme of evolution as portrayed by niche construction processes. In this subsection, I aim to integrate natural selection—the most influential evolutionary mechanism to date—into the picture offered above. As a consequence, I offer here a rich view relating two evolutionary mechanisms to affordances and highlighting the evolutionary role of these objects of perception.

Natural selection is an evolutionary mechanism that causally connects heritable variation to differential ability to survive and reproduce in a given population. Spontaneous mutations of genes and their phenotypic expression can be either beneficial or punitive depending on the external circumstances. If the organisms with that genetic material and its correspondently developed phenotypic expression survive

[9] Thanks to an anonymous reviewer for urging me to comment this idea.

the external circumstances, then they will pass their genes to their offspring. This means that those individual differences are beneficial for survival and, hence, preserved and transmitted to future generations. Those traits and genes are then selected, and the organisms that possess them are said to be adapted to the environment. As Darwin wrote, "[t]his preservation of favorable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest" (Darwin 1876/2009: 63). In this sense, natural selection is the combination of three different principles that correspond to the three quasi-autonomous processes presented in "Ecological psychology and affordances" section above. Each process produces the materials that are available for the functioning of the rest of the processes. They are summarized as follows:

1. There is variation in morphological, physiological, and behavioral traits among members of a species (the principle of variation).
2. The variation is in part heritable, so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, offspring resemble their parents (the principle of heredity).
3. Different variants leave different numbers of offspring either in immediate or remote generations (the principle of differential fitness).

   (…) All three conditions are necessary as well as sufficient conditions for evolution by natural selection (Lewontin 1985: 70).

As such, natural selection is a mechanism that works at a population level since evolution and adaptation focuses on which genes are successfully transmitted to the next generation and thereby preserve their presence in a given population, as seen in "Ecological psychology and affordances" section above. The distinction between an organismal and a sub-organismal level with their own evolutionary mechanisms implies that niche construction and natural selection are not incompatible processes. In this sense, certain genes that allow for developing particular behavioral strategies for detecting ecological information can be inherited, provoking certain differential fitness in the offspring. This is the way in which natural selection is related to ecological information and affordances as environmental resources that exert selective pressure, and this is the way in which Reed's approach (1991, 1996) actualizes Michaels and Carello's claim according to which "it is supposed that the structure and function of the perceptual systems have become tailored to the available information" (Michaels and Carello 1981: 15).

Reed (1991, 1996) proposed a means to relate the ecological approach and evolution by natural selection by emphasizing the role of ecological information. As Reed claimed, organisms that are differentially sensitive to ecological information compete in an environment where that information is a relevant resource[10] that improves the possibilities of survival and reproduction (Reed 1991: 193). In this sense, as Reed claims, all forms of behavior are modes of competition for the use of some resource and have therefore evolved thanks to natural selection (Reed 1985: 359). Thus, the behavioral, physiological, and genetic variation allows for a certain degree of sensitivity to ecological information, and this variability is what allows for competition among organisms. These informational resources work in the same sense as other resources in nature: Organisms with greater sensitivity to that kind of information outcompete those with lesser sensitivity. This is why organisms that develop more efficient behaviors for exploiting those resources are more likely to survive and reproduce than those that do not. This greater sensitivity is partially achieved by the organism thanks to different environmental influences during its development. And this is when a niche construction process enters the scene.

Unifying natural selection, niche construction, and affordances in a single picture

In the picture I offer, there are two evolutionary mechanisms working at the same time. First of all, processes at the sub-organismal level such as spontaneous mutations in the genotype lead to certain (morphological, physiological, and behavioral) variation, which is expressed in the phenotype. This process goes in a bottom-up direction, as the expression of the genotype is also affected by developmental processes and the configuration of the (ecological and social) environment at the same time. If those traits are beneficial for survival (that is, if those traits can deal with the available affordances of the environment), they are transmitted to the following generation, and this is why natural selection preserves that genetic pool. Meanwhile, organisms alter their environments in beneficial ways through niche construction processes. As such, the offspring of those organisms will benefit from those environmental alterations, as we have seen in "Ecological psychology and affordances" section. Thus, we have two mechanisms working in parallel.

At this point a pertinent question arises: are these two mechanisms totally isolated from each other? I do not think so. In the case of ecological information, the "greater sensitivity" to which Reed refers may be either the product of a spontaneous

[10] An anonymous reviewer urges me to explain Reed's emphasis on the idea of resources in his approach to affordances. Reed defines affordances as resources for behavior in his book *Encountering the World*. The idea of resource plays a key role in the definition of affordance, and it is defined as an environmental aspect that exerts selective pressure and that gives an evolutionary advantage to the organisms that take them. The author does not refer to a particular tradition or author in the literature on evolutionary biology from which he takes the concept. As the anonymous reviewer claims, a justification this paper's recourse to Reed's idiosyncratic way of thinking must be provided. The reason is primarily that Reed's contribution provides the first attempt to relate evolutionary biology and ecological psychology systematically, thereby offering a milestone in the history of ecological psychology and pioneering new paths for understanding the connection between non-representational, non-cognitivist psychology and evolutionary biology, a research line that has been deepened in the latest years (see, for example, Stotz 2014). In this sense, Reed's understanding may be rather idiosyncratic, as the reviewer claims, but his contributions are sufficient to include his views as one key approach to take into account when discussing the relation between evolutionary biology and affordances.

mutation that can be taken as favorable for detecting that information, or the product of training to detect it during the ontogenetic development of different agents. In the latter case, elements like the presence of ecological inheritances or the education of attention taught by mates in a particular niche of a given organism during its development critically improve the possibility of developing a special sensitivity to detect ecological information, as happens in the case of humans (Gibson 1950: 155; Costall 1995: 477; Ingold 2001/2011: 36). Hence, the configuration of the niche in general and the importance of the education of attention as a decisive factor for detecting ecological information in particular have been emphasized by theories of perceptual learning from an ecological perspective (see "Affordances and niche construction" section above). Consequently, those agents that inhabit a niche filled with social mediation and instruction are favored when they compete against other organisms for the same resources (in this sense, ecological information is a resource for perception according to Reed). This is the way in which niche construction processes and natural selection relate with regard to the evolutionary role of affordances. In fact, supporters of niche construction appeal to these two mechanisms as working continuously and affecting each other. This is why they claim that, "[w]hen such modifications [of the niche] alter natural selection pressures, evolution by niche construction is a possible outcome" (Laland et al. 2016: 192). In this sense, modifications occur and give rise to alterations, but these new alterations also exert selective pressure as well.

As these two evolutionary mechanisms exert their power in parallel, it would not be strange to assume that the modifications of the environment produced in niche construction processes make a difference in the way in which natural selection preserves a certain genetic pool, as we can expect in the case in which humans educate their offspring to detect ecological information as a resource that they can find in their environments.

As I recalled earlier, there are authors that hold the environment to be autonomous with respect to organisms, which means that it has its own intrinsic dynamics (Godfrey-Smith 2001: 254). Yet, if we conflate natural selection and niche construction in the same picture, the alterations of the environment made by agents at the organismal level drastically change the alleged "intrinsic dynamics" of the so-called "autonomous" environment, and consequently the effects of niche construction processes at the organismal level have an impact on the very functioning of natural selection, because those environmental alterations increase the chances of survival and reproduction of agents, which has an indirect impact at the sub-organismal level because it facilitates the preservation of the genotype of organisms. In this picture, the environment has no fully autonomous dynamics, at least if "autonomous dynamics" is understood in the minimal sense that the action of organisms does not affect how environmental pressures will be exerted. For example, an environment full of negative affordances (those that are injurious—see Gibson 1979/2015: 128–129) that minimize the probability of survival and reproduction can be restructured by agents (willingly or unwillingly) so as to become beneficial for them and their offspring. In this sense, it seems far from obvious that the environment possesses dynamics isolated from the effect of the organism. This is also reflected, for example, in aspects that involve development. In this sense, while it is true that what happens at the sub-organismal, genetic level is partially autonomous from what happens at the phenotypic, organismal level (because the principles of variation, fitness, and heredity imply their own functioning), if we accept that developmental processes and environmental conditions affect the expression of genes (as they usually do—see Reed 1985: 366; Hunter 2005; Lobo 2008; Ralston and Shaw 2008) and that alterations made at an organismal level may facilitate the work of preserving a certain genetic pool at a sub-organismal level, then we should not conceive the environment as having intrinsic dynamics independent of the dynamics of organisms, as supporters of the gene-centered view claim. If the previous claim is on the right track, some symmetry should be included in the evolutionary picture (Walsh 2015) once we aim to start offering a view that combines niche construction and natural selection together (which seems the most plausible and reasonable approach, given the scientific evidence in favor of both mechanisms). In this view, symmetry is achieved because organisms constantly modify their environment, thereby altering their pre-existing affordances so as to make a more habitable and protective habitat, which in turn affects organisms back not only at the organismal level (via niche construction) but also at a sub-organismal level (via natural selection).

This previous reflection leads us to the main tension introduced in Sect. 1. Namely, focusing on different mechanisms leads to different understandings of the role of organisms, environments, and affordances in evolution. As seen previously, both evolutionary mechanisms are related, which invites one to think that it is not entirely clear that environments and organisms are totally independent, as some authors suggest. At the same time, the allegedly contrasting views of affordances do not seem to be irreconcilable. There is a tight connection between niche construction and natural selection because, as seen earlier, modifications in the niche lead to alterations in natural selection pressures, which may result in niche construction as a possible outcome (Laland et al. 2016: 192). Nevertheless, even when those modifications alter the already existing pressures, there will be others that result from this alteration of the niche, so the alteration of the niche does not inhibit the functioning of natural selection. This shows that there are not really two isolated mechanisms working in parallel; rather, there are two mechanisms that are continuous or connected, but they function in parallel at two different times or moments. This is quite illuminating for understanding the role of affordances, because this shows that the allegedly competing views are not really competing. As one will recall, Reed's selectionist view defines affordances as resources for regulating the organism's relation to the environment (Reed 1996:17), whereas supporters of niche construction understand affordances as ecological inheritances that maximize the offspring's chances of survival (Withagen and van Wesmerkerken 2010: 505; Heras-Escribano and De Pinedo-García 2018: 10–11). This leads some supporters of the latter view to claim that "the niche construction perspective suggests alternative roles [to the one offered by Reed] for affordances in evolutionary dynamics" (Withagen and van Wesmerkerken 2010: 497). Whence the alleged incompatibility. However, if one pays attention to the point made earlier concerning the relation between niche construction and natural selection (Laland et al. 2016: 192), then one can claim that there affordances play a double role in evolution: first, they work as a resource that, in Reed's sense, apply selective pressure; second, after seizing the affordance and

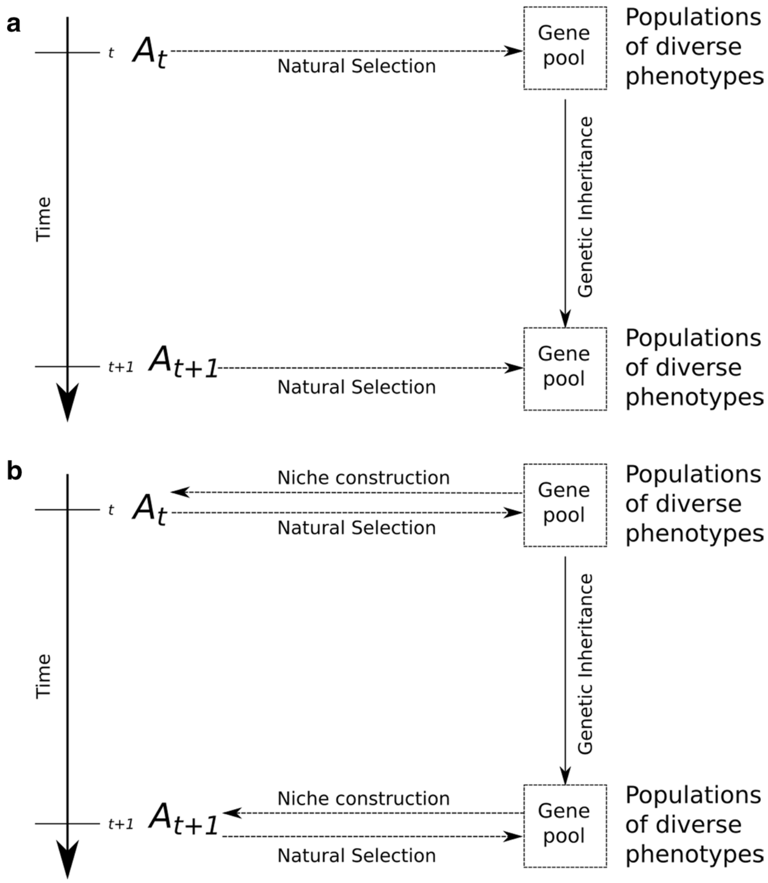

Fig. 1 Adaptation from Figure 1.3 in Odling-Smee et al. (2003: 14). While **a** is the standard evolutionary perspective of the MS in which organisms transmit their genes from generation t to generation t + 1, **b** represents the EES view in which niche construction processes are included in the picture, where organisms modify their environments by taking or giving rise to affordances in their environment (A). Each generation ecologically inherits from their ancestors the affordances that were previously perceived, taken, or that emerged thanks to their ancestors' modifications of the environment within niche construction processes

after proof of its selective advantage, affordances can work as ecological inheritances from one generation to the next (offering the same selective pressure), and so on. In this light, Withagen and van Wesmerkerken's (2010: 497) point should be understood while taking into account that the alternative roles for which they call are still compatible with the view offered by Reed (1996). Thus, affordances can be understood as ecological inheritances of an already modified environment that, at a different time, played the role of resources exerting selection pressure in the new environment produced by the alteration effected by organisms in the niche construction process: first, they exert selective pressure at stage t_1, and then the same affordances work as inheritances for the offspring at stage t_2. In this sense, the evolutionary role of affordances is dual: they are both resources and inheritances. Adapted from Odling-Smee et al. (2003), the following Fig. 1 diagram exemplifies this idea:

The reader may note that the adaptation of the diagram originally designed by Odling-Smee, Laland, and Feldman is not fortuitous. As we have seen in previous sections, there are different ways to understand the extended synthesis and, given this variety, affordances are either accepted or rejected as key aspects in the niche construction processes. In this paper, I argue in favor of the view propounded by Odling-Smee, Laland, and Feldman and according to which the metabolism and action of organisms in their ecosystem lead to unexpected consequences in the direction, rate, and dynamics of the evolutionary process. For ecological information is pervasive in our everyday lives, and affordances are common objects of perception for every human being. Because they are so common, they must have a role in our evolutionary history, and I propose that they are related to the two main evolutionary mechanisms: natural selection and niche construction. Nevertheless, although natural selection and niche construction are two different mechanisms, they do not have to be taken as completely discrete and isolated from each other.[11] This point is emphasized in the idea that, according to these authors, the alteration of selection pressures leads to niche construction processes as a possible outcome (Laland et al. 2016: 192) and in the idea that niche construction processes of ancestors modifies the selection of offspring (Odling-Smee et al. 2003: 11), which shows that these two mechanisms are not as isolated as one might at first think. For this reason, the idea that natural selection and niche construction are isolated from each other makes no sense in light of the approach to niche construction endorsed by authors such as Odling-Smee and Laland. The discreetness of both mechanisms is also criticized by other supporters of the extended synthesis (Uller and Helanterä 2019). The idea of affordances casts considerable doubt on the discreetness of both mechanisms, in addition, because they help emphasize the intertwinement of both mechanisms in different moments of evolutionary history, playing one role at one moment (as pressure) and another at a different moment (inheritance). Regarding this last point, affordances may serve a greater purpose than showing the intimate connection between natural selection and niche construction. As such, affordances are aspects that, given their "dual" role in the evolutionary process (as pressures and as inheritances), have the power to make more visible the impact of niche construction process and the potential to re-configure niche construction theory in the life sciences completely.[12]

Thus, affordances are key aspects of the niche construction process (Heras-Escribano and De Pinedo-García 2018), but they are also environmental aspects that exert selection pressure (Reed 1991, 1996). At this point it becomes clear that affordances possess an evolutionary role that cannot be avoided and, at the same time, that this biological aspect of affordances opens the door to conceive a more organismal-centered, agential, and informational approach to evolution.

[11] Thanks to an anonymous reviewer for making me aware of the importance of this idea.

[12] Thanks to an anonymous reviewer for inviting me to highlight this consequence.

Conclusion

In this paper, I have offered a general attempt to explain the evolutionary role of affordances. For this reason, I have delved into former views on the evolutionary role of affordances (the selectionist view and the niche construction view), and I have analyzed the consequences of understanding affordances in each. According to the selectionist view (Reed 1996), affordances are mere resources that exert selection pressure, whereas they are ecological inheritances in the niche construction process according to the niche construction view (Withagen and van Wesmerkerken 2010; Heras-Escribano and De Pinedo-García 2018). According to some authors (Withagen and van Wesmerkerken 2010), there seems to be a tension in which two different views on evolution lead to two different views on affordances. Nevertheless, I have shown how the allegedly incompatible views on affordances reconcile. These views on affordances are complementary because niche construction and natural selection are two different mechanisms that are connected, although one does not alter the functioning of the other (Laland et al. 2016). The alterations of the environment in the niche construction process alters the selective pressure of different aspects of the environment, but even these alterations lead to a new configuration of the environment the elements of which will also exert selective pressure: in this scenario, this means that affordances (if they remain without alteration) exert selective pressure at stage t_1, and then these affordances are inherited by the offspring as ecological inheritances at stage t_2, thereby exerting selective pressures as well depending on the configuration of the niche. In this sense, affordances are both resources and ecological inheritances, although they function as one or the other depending on the moment in the evolutionary process. This dual nature of affordances shows their evolutionary role.

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