# Developmental Niche Construction

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Abstract

Niche construction is the modification of components in an environment through an organism's activities. Humans modify their environments mainly through ontogenetic and cultural processes, and it is this reliance on learning, plasticity and culture that lends human niche construction a special potency. In this paper we aim to facilitate discussion between researchers interested in niche construction and those interested in human development by highlighting some of the related processes. We discuss the transmission of culturally relevant information, how the human mind is a symbol-generating and artefact-devising system, and how these processes are bi-directional, with infants and children both being directed, and directing, their own development. We reflect on these in the light of four approaches: natural pedagogy, activity theory, distributed cognition and situated learning. Throughout, we highlight pertinent examples in non-humans that parallel or further explicate the processes discussed. Finally we offer three future directions; two involving the use of new techniques in the realms of neuroscience and modelling, and the third suggesting exploration of changes in the affects of niche construction across the lifespan.

Keywords: niche construction, pedagogy, activity theory, distributed cognition, situated learning, cultural evolution

## 1. Niche Construction Theory

Niche construction refers to the modification of both living and non-living components in environments through the metabolic, physiological and behavioural activities of organisms, as well as through their choices. For example, many species of animals manufacture nests, burrows, holes, webs, and pupal cases; algae and plants change levels of atmospheric redox states, and influence energy and matter flows by modifying nutrient cycles; fungi and bacteria decompose organic matter; bacteria also fix nutrients and excrete compounds that alter environments.

The niche-construction perspective in evolutionary biology explicitly recognizes environmental modification by organisms ('niche construction'), and its legacy over time (henceforth 'ecological inheritance'), to be *evolutionary processes*: that is, they cause evolutionary change by acting as sources of modified selection, as well as of modified phenotypes (Lewontin, 1983; Odling-Smee, Laland & Feldman, 2003). This stance can be contrasted with the more tacit recognition of organisms' environmental impacts in standard evolutionary accounts.

From the niche-construction perspective, environmental modification is regarded as an evolutionarily significant process, and not just a product of other recognized evolutionary processes; as a cause, rather than an effect. This extension has produced a body of conceptual and formal theory, known as 'niche construction theory' (henceforth 'NCT'), which explores the ecological and evolutionary ramifications of niche construction (Boni & Feldman, 2005; Kendal, Tehrani & Odling-Smee, 2011; Kylafis & Loreau, 2008; Laland, Odling-Smee & Feldman, 1996, 1999, 2010; Lehmann, 2008; Odling-Smee et al., 2003; Post & Palkovacs, 2009; Silver & DiPaolo, 2006). These insights from mathematical evolutionary theory provide unambiguous evidence that niche construction is likely to be of considerable ecological and evolutionary importance, and suggest that NCT may have implications for adjacent disciplines.

Here we consider some of the ramifications of NCT for one such academic field – developmental psychology. The opportunities for a fruitful bi-directional transfer of knowledge between these two fields of enquiry are rich. This fertile exchange is underpinned by a long, and largely independent, tradition of 'constructivist' thinking in developmental psychology that resonates with the arguments inherent in NCT. For instance, Daniel Lehrman (1953, 1970) stressed how the animal mind does not consist of pre-specified programmes, but is built via a constant interplay between the individual and its environment. Likewise, the developmental biologist Conrad Waddington (1959, p1636) anticipated many of the key aspects of NCT, writing that 'the animal by its behaviour contributes in a most important way to the nature and intensity of the selective pressures which will be exerted on it'. For Lehrman and Waddington, like many other developmentally-minded psychologists and biologists since (including Schneirla, Gottlieb, Bateson, Oyama, Gray, amongst others), individuals are construed to play an active role in shaping the conditions of their own development.

In the sections below we review this tradition and then attempt to draw out some commonalities between it and NCT, as well as opportunities for useful exchange and future directions. We begin by introducing NCT, describing how niche construction can both result from multiple processes, including developmental processes, and trigger feedback at a variety of levels, including at levels of analysis relevant to developmental psychologists.

### *1.1 What is niche construction?*

The conventional view of evolution is that, through the action of natural selection, species have come to exhibit those characteristics that best enable them to survive and reproduce in their environments. Organisms are generally perceived as being moulded by selection to become suited to their world (Figure 1a). The niche construction perspective in evolutionary biology contrasts with the conventional perspective by placing emphasis on the capacity of organisms to modify environmental states. In doing so, organisms co-direct their own evolution, often but not exclusively in a manner that suits their genotypes, in the process modifying patterns of selection acting back on themselves, as well as on other species that inhabit their environment (Figure 1b). Organisms and environments are treated by NCT as engaged in reciprocally caused relationships (Laland & Sterelny, 2006; Laland, Sterelny, Odling-Smee, Hoppitt & Uller, 2011), that are negotiated over both ontogenetic and phylogenetic timescales, entwined in, to coin a very apt phrase from developmental systems theory, ‘cycles of contingency’ (Oyama, Griffiths & Gray, 2001).

In recent years this feedback from organisms’ activities has been subject to intense investigation through mathematical population-genetic analyses. It is now well established that the selection modified by niche construction can be evolutionarily important, and can generate rich microevolutionary dynamics. By modifying selection, niche construction can create new evolutionary outcomes, affect the stability of equilibria, generate timelagged effects (e.g., populations continue to evolve after selection has stopped), facilitate range expansion, generate self-perpetuating, acceleratory niche-constructing capabilities (Kylafis & Loreau, 2008; Laland et al., 1996, 1999; Odling-Smee et al., 2003; Silver & DiPaolo, 2006), as well as many other important consequences. In other words, the feedback that niche construction generates in evolution makes a difference to how organisms evolve.

One implication of NCT is that, because organisms are recognized to modify selection pressures in their own and in other species' environments, and in the process to introduce feedback to both ontogenetic and evolutionary processes, niche-constructing organisms cannot be viewed as merely 'vehicles' for their genes (Dawkins, 1976), or as passive victims of selection. Many researchers have suggested that this active, constructive conception of the role of organisms in evolution, and indeed in ontogeny, fits better with conceptualisations of human agency that are widespread within the human sciences (Bickerton, 2009; Gottlieb 1998, 2000, 2002; Kendal et al., 2011; Laland et al., 2000; Layton, 2010; O'Brien & Laland, in press; Odling-Smee et al., 2003; Oyama et al., 2001; Plotkin, 2010).

A second implication is that there is no requirement for niche construction to result directly from genetic variation in order for it to modify natural selection. Humans can and do modify their environments mainly through ontogenetic and cultural processes, and it is this reliance on learning, plasticity and culture that lends human niche construction a special potency (Kendal, in press; Kendal et al., 2011; O'Brien & Laland, in press; Smith, 2007). However, humans are far from unique in engaging in niche construction. Niche construction is a very general process, exhibited by *all* living organisms (Odling-Smee et al., 2003), and species do not require advanced intellect or sophisticated technology to change their world (Cuddington et al., 2010; Jones, Lawton & Shachak, 1994, 1997; Odling-Smee et al., 2003). Nonetheless, largely because of its reliance on culture, human niche construction is unusually potent – so much so that our species has been characterized as 'the ultimate niche constructors' (Smith, 2007, p. 188).

While the niche construction perspective is growing rapidly in followers, articles and recognition, it is not yet a mainstream view within evolutionary biology, and remains the source of some controversy (Laland, Odling-Smee & Feldman, 2004; Laland et al., 2011; Laland & Sterelny, 2006; see http://www.nicheconstruction.com/ for a discussion of some of the issues). Yet, there are reasons to anticipate that NCT might be regarded as less contentious, and of more overt immediate utility, to researchers studying human behaviour than elsewhere. That is partly because of the self-apparent potency of human niche construction. There can be no doubt that human culture, expressed in our tools, our engineering and our technology, has massively changed human environments. That fact, combined with the comparatively reduced role of genetic variation in causing human behavioural variation, means that human niche construction cannot be fully explained by prior natural selection. There are already many signs that evolutionarily-minded human scientists, including philosophers, archaeologists, anthropologists, psychologists, and primatologists are finding NCT useful (see Kendal et al., 2011 for an overview), and one message of our article is that there are likely to be similar opportunities for developmental psychologists.

*1.2 Multiple processes of niche construction*

Odling-Smee et al. (2003) describe how humans can acquire the knowledge that is expressed in niche construction through a set of information-acquiring processes operating at three different levels – population genetic, developmental and cultural (Figure 2). The three levels are distinct but interconnected with each interacting with, but not completely determined by, the others.

All organisms inherit genetic information from their ancestors, and this is the most fundamental source of information that underpins niche construction. However, some factors in the environment can potentially change many times within the typical lifespan of the animal concerned, and natural selection has selected for processes allowing individuals to adjust on a within-lifetime basis, some of which are adaptations for acquiring knowledge. These secondary sources of information are complementary to the first; for instance, learning allows individual organisms to fine tune their behaviour.

Learning and development can be of considerable importance to evolution because learned knowledge can guide niche construction, the consequences of which can be inherited through ecological inheritance. This highlights one of the major differences that niche construction makes to the evolutionary process: acquired characteristics can play a role in evolution through their influence on the selective environment. In humans this ability is facilitated by a further set of processes, such as language, teaching, and prosociality that collectively underlie cultural processes, enhancing the efficacy of knowledge transfer (Boyd, Richerson & Henrich, 2011; Dean, Kendal, Schapiro, Thierry & Laland, 2012; Moll & Tomasello, 2009). Much of human niche construction is guided by socially learned knowledge and cultural inheritance, but the transmission and acquisition of this knowledge is itself dependent on pre-existing information acquired through genetic evolution, complex ontogenetic processes, or prior social learning (see Figure 2).

### *1.3 Feedback at multiple levels*

Niche construction modifies selection not only at the genetic level, but also at the ontogenetic and cultural levels as well, to facilitate learning and mediate cultural traditions, with consequences that not only feed back to the constructor population, but modify selection for other organisms too. For instance, the construction of towns and cities created new health hazards associated with large-scale human aggregation, such as the spread of epidemics (Diamond, 1997). Humans may either respond to this novel selection pressure, exclusively or in combination (*i*) through biological evolution, with the selection of resistant genotypes, (*ii*) at the ontogenetic level, by developing antibodies that confer some immunity, or (*iii*) 'cultural evolution', for instance by creating hospitals, medicines and vaccines (Laland et al., 2000; Laland & Brown, 2006; Odling-Smee et al., 2003).

Where a culturally transmitted response to human niche construction is not possible, perhaps because the population lacks the requisite knowledge or technology, then a genetic response may occur. An example is the coevolution of dairy farming and the allele for adult lactose absorption, where several lines of evidence now support the hypothesis that dairy farming created the selection pressures that favoured this allele in pastoralist populations (Burger, Kirchner, Bramanti, Haak & Thomas, 2007; Durham 1991; Holden & Mace, 1997; Myles et al., 2005; Simoons, 1970). Cultural niche construction can also generate selection on other species, most obviously the domesticates. Beja-Pereira et al. (2003) established that the spread of dairy farming also affected geographical variation in milk protein genes in European cattle breeds, which covary with present day patterns of lactose tolerance in humans.

Humans are massive constructors of developmental environments. By modifying the world, human niche construction creates artefacts and other externally inherited resources that not only act as sources of biological selection on human genes but shape the learning opportunities and developmental trajectories of recipient organisms. Wheeler and Clark (2008, p. 3564) describe as 'cognitive niche construction' the fact that 'animals build physical structures that transform problem spaces in ways that aid (or sometimes impede) thinking and reasoning about some target domain or domains', and these physical and informational legacies 'make possible whole new forms of thought and reason'. We see this also in non-human animals. For instance, Fragaszy (in press) describes how capuchin monkeys create learning environments for youngsters, by transforming the environment in a manner that scaffolds their learning, and channels it towards established traditions (we discuss this further below). Social transmission maintained through inadvertent, or less commonly advertent, modification of the local environment is surprisingly common: it is known to underlie pine cone opening in black rats (Terkel, 1996), milk-bottle opening in various birds (Sherry & Galef, 1984), the learning of food sites through pheromone trails in ants (Denny, Wright & Grief, 2001), mate-choice copying in egg-dumping fishes (Goldsmidt, Bakker & Feuth-de Bruijn, 1993), and food preference learning through excretory products in rats (Laland & Plotkin, 1991, 1993). This facilitation of learning through the construction of developmental environments reaches its zenith in humans (Kendal, in press; Sterelny, 2012), as we detail in subsequent sections.

## 2. Developmental Niche Construction

In 2000, psychologist, Mary Gauvain, commented in support of Laland et al.'s (2000) niche construction review, but warned that amalgamation of biological and human social sciences 'will not be met unless the biological and evolutionary approaches are better integrated with theory and research in human psychological development' (Gauvain, 2000, p. 153). She pointed out that it is not coincidental that there is a strong assimilation of humanity's biological capabilities and their social and cultural context of development as this is essential for survival. Similarly, Boyd et al. (2011) argue that humanity's 'cultural niche' has allowed our species to settle in all corners of the world, through the transmission of cultural information necessary for building shelters, sourcing food and staying safe and healthy in even the most inhospitable environments. Without cultural information and the resulting niche that is developed over generations, it is unlikely that humans would survive in hostile environments. This point is illustrated well by the unfortunate fate of extensively resourced explorers, Sir John Franklin and Robert Burke, who perished in the Arctic and Australian outback, respectively, despite both locations being inhabited by natives relying on cultural niche construction to live in these harsh environments (Henrich & McElreath, 2003).

In the following section, we present an illustrative set of examples of human psychological development in relation to developmental niche construction: we discuss the transmission of culturally relevant information between individuals, how the human mind is a symbol-generating and artefact-devising system, and how these processes are bi-directional, with infants and children being directed, and directing, their development. We also highlight pertinent examples in non-humans that parallel or further explicate the processes we discuss.

Before a baby is born, behavioural indices of differences in heart rate and leg kicking show that during the final trimester, a foetus can discriminate different sounds, languages, forms of music, and voices (Hepper, 1989, 1991). Simultaneously, parents are typically structuring an environment for their imminent arrival that, unparalleled in any other species, facilitates the baby's rapid cognitive development and the acquisition of cultural information. A premise for much work by developmental psychologists is that this relationship between cognitive development and the constructed environment is dynamic. Here we present four processes, *natural pedagogy*, *activity theory*, *distributed cognition* and *situated learning*, in which we focus on how the construction of a learning environment by culturally knowledgeable others affects the acquisition of beliefs and practices by novices, and consider how cultural novices are active participants in this process. Our aim is to provide an illustration of possible interfaces between NCT and developmental psychology, in the hope of facilitating discussion between the two.

*2.1 Natural Pedagogy*

Typically, infants are born into cultural environments ('niches') and are surrounded by individuals performing cultural behaviour. A critical question is how cultural novices acquire this information? Gergely and Csibra (in press) argue that for a naïve learner to acquire cultural information solely through observational learning would be extremely arduous. First, cultural behaviour is often cognitively opaque, such that it is not obvious why an action is performed in a specific manner, nor which action to copy. Second, cultural information can be generic, involving a behaviour that can be generalised across a group of similar artefacts or contexts, and so an infant needs to extrapolate what she has learnt from the immediate context to related situations.

In order to acquire cultural behaviour, Gergely and Csibra (in press) propose that humans have a social communicative learning mechanism, 'natural pedagogy', in which culturally knowledgeable individuals (usually adults) assist novices in acquiring cultural behaviour through ostensive-referential demonstrations of the relevant aspects of the behaviour. Infants' preferences for eye contact, infant-directed speech and infant-directed contingent reactivity (that is behaviour made in response to an infant's behaviour) show that the proposed ostensive cues are relevant to infants from a young age (Csibra, 2010). These attention-gaining cues then allow gaze-following of a knowledgeable individual's focus to a referential target and their actions upon it (Senju & Csibra, 2008; Senju, Csibra & Johnson, 2008).

According to Gergely and Csibra (in press), what makes their proposal unique is that infants encode the information they receive from an ostensive-referential communication qualitatively differently than if acquired in a non-communicative situation. Ostensive-referential communication allows infants to learn referenced features of an object more quickly than non-referenced features (Yoon, Johnson & Csibra, 2008), to encode the demonstrated functional property of an artefact-kind (Futó, Téglás, Csibra & Gergely, 2010), and to learn novel means-end actions despite their apparent cognitive opacity (Gergely, Bekkering & Kiraly, 2002). Thus, ostensive-referential information presented by culturally knowledgeable others allows cultural novices to learn and apply referenced features to their own behaviour rapidly.

Natural pedagogy suggests that cultural experts construct a cultural niche, facilitating the acquisition of cultural knowledge by the novice by gaining their attention, through processes such as motionese (Brand, Baldwin & Ashburn, 2002), motherese (Newport, 1977), calling their name, and use of ostensive cues to highlight relevant aspects of the behaviour. As the term 'natural pedagogy' suggests, the predisposition to employ such cues is assumed to be universal amongst humans, yet the manifestation of these cues and the learning environment to which the recipient is exposed may be culturally variant. Variability in natural pedagogy across cultures is expected as cultures differ in many features including their child-rearing practices, the means deployed to allow transmission of culturally relevant behaviour, and the extent of cognitive opacity of local traditions and artefacts.

In contrast, chimpanzees and orangutans do not appear to understand the intention of another to impart useful information through pointing and/or gaze alternation between the 'learner' and referential target (Hare & Tomasello, 2004; Hermann, Call, Hernández-Lloreda, Hare & Tomasello, 2007; Tomasello, Call & Gluckman, 1997), whereas even pre-linguistic children do (Behne, Carpenter & Tomasello, 2005). Indeed, the human-specific propensity for developmental niche construction is likely to go far beyond the role of pedagogy. For instance, Tomasello, Carpenter, Call, Behne and Moll (2005) describe how humans engage in species-unique forms of cultural cognition and evolution, enabling everything from the creation and use of linguistic symbols to the construction of social norms and individual beliefs to the establishment of social institutions. This encompasses a species-unique motivation to share emotions, experience, and activities with other persons, greatly enriching what West, King and Arberg (1988) term, the *ontogenetic niche*. Cultural niche construction theory can coalesce our understanding of developmental mechanisms affecting the constructed learning environments and the influence of evolutionary dynamics on such environments. The developmental outcome is children's ability to construct dialogic cognitive representations, which enable them to participate in collective human cognition, a topic discussed below.

### *2.2 Activity Theory*

Within activity theory, which derives from the work of twentieth century Soviet psychologists, particularly Vygotsky and Leont'ev, an 'active' learner is placed within a wide social, historical and political context (Vygotsky 1962, 1978), that is, a cultural-historical niche. This bears some resemblance to the perspective of those primatologists influenced by ecological psychology, who view organism and environment as a combined whole or integrated system (Gibson 1979, 1986), and who suggest that an understanding of how behavioural traditions are maintained across generations requires, ‘a dynamic conception of the individual as *engaged* with its world, both social and asocial elements, in ongoing commerce’ (Fragaszy & Visallberghi, 2001, p.84, italics added).

As we will see for distributed cognition, activity theory transcends an actor’s boundary and investigates change both within and between individuals. It considers behaviour to be goal directed, and both for development to be mediated by social and cultural history and visa-versa; thus the unit of analysis is the socially organized activity (Leont’ev, 1981). This approach is pertinent to NCT, where elements of the socially-constructed niche such as tools, norms, schooling practices are culturally or ecologically inherited, influencing the learner’s activities and, at a population level, affecting cultural selection.

Similarly, in the animal kingdom the activities of others alter the learner’s relation with objects in their environment. For instance, Fragaszy (in press) describes how capuchin monkeys (*Cebus spp*.) create learning environments for youngsters through enduring alterations of the physical environment. The discarded palm nut shells and stone hammers (Ottoni & Izar, 2008), ripped bamboo canes resulting from extraction of beetle larvae (Gunst, Boinski & Fragaszy, 2008) or spilt traces of juice (Crast, Hardy & Fragaszy, 2010) are attractive to young monkeys and act as key artefacts which support persistent practice thus facilitating the acquisition of the extractive foraging behaviour. Likewise Leca, Gunst and Huffman (2010) report that piles of stones resulting from stone-handling activities in Japanese macaques are attractive to others, supporting re-use and even transport of such ‘favoured’ stones by group members. In these examples, learning is thereby stimulated and channelled towards established behavioural traditions even without direct observation of the behaviour.

In some cases, children may achieve the same end point, such as being able to undertake mathematical transformations through division and multiplication, but the specifics of their social environment may mean they learn and express these skills through different activities. For example, Brazilian street children are able to complete complex arithmetic calculations when presented in the familiar context of selling sweets/candy but when similar problems are presented in a more formalized manner, they fail to do so (Carraher, Carraher & Schliemann, 1985). Thus the learning and execution of a skill needs to be seen in context, as being constructed within, and supported by, a culturally-constructed niche.

The relation between activity theory and niche construction is illustrated by the ‘mediational triangle’ (Cole & Engeström, 2001, Figure 3, published in relation to *Distributed Cognition* which we discuss next, but relevant to the point we wish to make here), which expresses the complex relation between artefacts, norms, communities, objects and subjects. For example, mediation through cultural practices and understanding alters the ‘intramental plane’, that is the participant’s relation with an object. An example of cultural (and historical) mediation of the intramental plane, used by Leont’ev (1981), is the disparity in the way traders and geologists learn to view gem-stones, with one seeing them as valuable assets, and the other viewing them in terms of their geological properties. Thus, in relation to the intramental plane, 'collective activity shapes the object and possible responses to it' (recounted by Edwards, 2005, p. 4).

Cases of social learning in non-humans may be consistent with the activity theorists' notion of culturally specific mediation on the so-called intramental plane. For instance, Gruber, Muller, Reynolds, Wrangham and Zuberbühler (2011) show that two populations of chimpanzee (*Pan troglodytes Schweinfurthii*), react differently to the affordances of a multi-functional leafy-twig tool, such that chimpanzees from Sonso (who have a leaf technology) found the leaves most salient while chimpanzees from Kanywara (who have a probing technology) focussed on the stick part.

Vygotsky's work is particularly useful as he developed measurable concepts to capture the effect of mediation on learning; specifically, the Zone of Proximal Development (ZPD), defined as *'the distance between the actual* developmental level as determined by independent problem solving and the level of potential development as determined through problem solving under adult guidance or in collaboration with *more capable peers*' (Vygotsky, 1978, p. 86, emphasis in the original). The intention was that this concept could be applied to learning across a variety of contexts, and relate to qualitative changes in the learner's cognitive development (Chaiklin, 2003).

In line with the concept of the ZPD, adults frequently attempt to structure a child's learning environment, providing a learning niche for them, as described by Wood (1998, p. 97):

> When we help a child solve a problem, we are providing conditions in which he can begin to perceive regularities and structure in his experience. Where, left alone, the child is overcome by uncertainty and

> does not know what to attend to or what to do, instruction can help in a number of ways. When we point things out to the child, we help to highlight what he should attend to. By reminding children we are helping them to bring to mind and exploit those aspects of their past experience that we (as experts) but not they (as novices) know to be relevant to what they are currently trying to do.

Through his work using The Tower of Nottingham, (ToN; see Figure 4) Wood and colleagues have investigated tutoring and learning situations (Wood, Bruner & Ross, 1976; Wood, Wood & Middleton, 1978). Children younger than seven years could not build the ToN without help, but, after instruction from an adult, children as young as three years were able to complete the ToN alone. Adults scaffolded the children's learning experience by highlighting the mechanics of specific aspects of the task, selecting pertinent pieces, orienting objects so its pertinent parts were easily viewed and removing elements not critical to learning at that time. Yet, some forms of tutoring, such as demonstrating full assembly of the ToN or providing complex verbal instructions, were not successful as they overloaded the learner. Accordingly, Wood and colleagues coined the concept of 'contingent tutoring' as the most effective form of instruction, relying on two rules: when a learner is in difficulty provide more assistance, and when a learner is succeeding provide less.

Although advertent social learning, or teaching, is extremely rare in non-humans and its distribution likely linked to cooperative breeding rather than taxonomic affinity to humans (see Hoppitt, Brown, Kendal, Rendell, Thornton, Webster and Laland, 2008) one case merits discussion regarding 'contingent tutoring'. Thornton and McAuliffe (2006) elegantly demonstrated that in meerkats

(*Suricata suricatta*) non-productive 'helpers' teach young pups how to handle aggressive and toxic scorpions which form part of their diet. The behaviour of the tutor helpers appears to be contingent in that, upon provisioning a scorpion, they monitor the pup and nudge the scorpion with their paws or nose if the pup fails to attempt to handle it; a behaviour which seemingly attracts the pups attention and enhances consumption success. Likewise the provision of increasingly intact (and thus difficult/dangerous to handle) scorpions to pups as they increase in age would also appear contingent. However, it was found (Thornton & McAuliffe, 2006) that here the behaviour of the tutor was contingent upon the vocal cue of age-related changes in pup begging calls rather than the pups' changing competence. This situation perhaps being reminiscent of formal education being largely age, rather than performance, based in humans.

Two important points that are particularly evident in human populations are that children are not passive recipients of an adult's instruction and that instructors are not always adults. In relation to the former, in naturalistic settings it is often the child, not the adult, who initiates interactions and sets the goal (Carew, 1980; Wells, 1981). Thus, to a degree, and consistent with NCT, children direct their own learning by shaping their own learning environment**.** Also in natural settings, children often learn from other children (see Dean et al., 2012; Flynn & Whiten, 2010; Whiten & Flynn, 2010). For instance, Wood and colleagues extended their investigation to children's peer tutoring, finding that the rate of contingent tutoring increases with age from 3 to 7 years (Wood et al., 1995) and it appears that different forms of social learning (e.g. observational learning or reasoning regarding the intentions of tutors) may be pertinent at different ages (Ellis & Gauvain 1992; Flynn, 2008; Selman 1980; Whiten & Flynn, 2010). A child's cognitive development will, in part, influence the type of interaction most pertinent to their learning; cognitive development informs the learning niche that a child experiences.

Recent research has investigated the bi-directional relation between cognitive development and social learning. Theory and evidence suggest that more sophisticated mental state understanding leads to more effective peer tutoring (Flynn, 2010; Strauss, Ziv & Stein, 2002; Tomasello, Kruger & Ratner, 1993). Yet the reverse is also true; more sophisticated interactions lead to more complex mental state understanding, as well as more refined skills in other areas, such as executive functioning. For example, contact with adults or older siblings appears to have a positive effect on theory of mind development (Lewis, Freeman, Kyriadidou, Maridaki-Kassotaki & Berridge, 1996; Ruffman, Perner, Naito, Parkin, & Clements, 1998). Similarly, wider cultural norms of a society can affect cognitive development. For instance, Japanese children have been shown to pass theory of mind tasks later than their Western counterparts (Naito, 2003), a trend that may be due to a cultural focus on social rules, and less on mental states, in Japanese society (Naito & Koyama, 2006). In contrast, Asian children perform better than North American or British children on tests of executive functioning (Chen et al., 1998; Sabbagh, Xu, Carlson, Moses & Lee, 2006), perhaps due to differing cultural emphases on control of behaviour in social settings.

*2.3 Distributed Cognition*

While cognition is generally seen as a process that occurs within an individual, albeit with theoretical positions suggesting that environmental factors may facilitate this context, distributed cognition (DC) emphasises the dispersed nature of cognitive phenomena across individuals, artefacts and internal and external representations. In this respect it resembles the cognitive niche construction of Wheeler and Clark (2008). Cultural processes transcend the boundaries of the individual and so need to be understood in context with the single or multiple actor's/s' interactions with the artefacts being used within the given activity. Distributed cognition is critical in developmental niche construction as it allows children to work with others to learn, undertake and develop cultural practices, relying on coordination across a group.

Developmental systems theory strongly contradicts a purely 'genocentric account of heredity' (Griffiths & Gray, 2001) as many resources persist across successive generations and are part of the explanation for heredity. Likewise, NCT includes the notion that an inherited 'niche' constitutes an organism-environment relationship, which can consist of the inheritance of resource and semantic information both internal and external to the organism (Odling-Smee et al., 2003). These perspectives allows us to understand how people learn to design and use artefacts that have evolved through the process of cumulative culture and also how individuals learn to participate in cultural activities that require collaboration and cooperation (e.g. flying an aeroplane, Hutchins & Klausen, 1996).

One cognitive function that facilitates distributed cognition, and has been a recent focus of research in developmental and comparative psychology, is 'we-intentionality' (Plotkin, 2003) or shared intentionality (Tomasello & Carpenter, 2007). In this regard, Moll and Tomasello (2007, p. 1) coined the Vygotskian Intelligence Hypothesis, noting 'that the unique aspects of human cognition - the cognitive skills needed to create complex technologies, cultural institutions and systems of symbols, for example - were driven by, or even constituted by, social cooperation.' Thus social cooperation most likely provides a key component of the mediation process and the construction of a distributed niche. In contrast, non-human primates would appear to lack the same degree of pro-sociality (Dean et al., 2012) and typically fail in tasks that require coordinated collaboration, whether the goal is 'social' (Warneken, Chen & Tomasello, 2006) or a food-based reward (Jensen, Hare, Call & Tomasello, 2006; Silk et al., 2005).

Symbolic representation systems often form critical components of culturally constructed learning environments. For instance, the Sapir-Whorf hypothesis concerns the degree to which cognitive development is constrained by language (Whorf, 1956). Miller, Smith, Zhu and Zhang (1995) and Miller and Stigler (1987) investigated the acquisition of learning of mathematical notation for Chinese and American children. No difference was found for the acquisition of the numbers from 0 to 10; however, from 11 to 20 American children performed relatively poorly. It is thought that this is due to the relative irregularity of the number system (from 11 to 20) for English speakers. However, the language of a culture is entwined with other cultural practices, thus it would be premature to conclude that differences in thought are due entirely to the form of symbolic representation used. Furthermore, the distinction of ontogenetic and culturally specific cognitive, emotional, and identity-related characteristics can, themselves, be reflected and retained in linguistic cognates (Malik, 2000). In this context, NCT provides a framework to examine explicit relationships between the cultural evolution of symbolic representation systems and cognitive development. Crucially, NCT draws attention to the effect of the ecological inheritance of both information and resources on development.

The field of distributed cognition considers cognition in terms of the change in relational structures, including components that are internal and external to the mind. Hence, the focus is on the interaction of people and artefacts, rather than just assessing individual cognition 'within the head' (Nardi, 1996). Hutchins (1995) criticizes the cognitive sciences for not incorporating the cultural process, which generates artefacts, in their understanding of the individual. He asserts that this can lead to the over-attribution of intelligence (or aspects of cognitive facility) to the mind in order to explain observed behaviour, which instead, should be considered properties of sociocultural systems that include both biotic and abiotic phenomena. For instance, Hutchins argues that computation that results from a mathematician manipulating symbols on a chalk board is not occurring inside the head of the mathematician, but rather as a consequence of interaction with the external symbols. Computational tools that automate these sequences of symbolic manipulation are models of a sociocultural system rather than cognition internal to the mathematician. On this basis, Hutchins (1995) criticizes cognitive scientists and artificial intelligence research that have attempted to use the computer as a model for the human mind. NCT can be used to examine the developmental and evolutionary feedback between internal mental facility and external resources that make up the sociocultural system.

Taking the position that the development of cognition is affected by learned rules or axioms in conjunction with artefactual symbolic representation in material culture is equivalent to developmental systems theorists' advocation of a *parity thesis* in biology, that 'the roles played by the many causal factors that affect development do not fall neatly into two kinds, one exclusively played by DNA elements the other exclusively played by non-DNA elements. . . . Instead, there are numerous important distinctions to be drawn amongst the causal roles played by developmental factors' (Griffiths & Gray, 2005, p. 420).

## *2.4 Situated Learning*

The niche into which we are born will, in part, dictate what we learn. The authors of this article do not know how to build an igloo, or cook the perfect spanakopita, but all of us have learnt the art of playing rounders (a common primary school game in the UK). Developmental niche construction may not only dictate what we learn through careful signalling, scaffolding or the presentation of culturally relevant tools, but also through the presentation of opportunities to learn activities through participation. In its simplest form, regarding the physical environment, even animals who provide no parental care (Stamps, 2003), select a natal habitat for their eggs which provides a broad range of environmental conditions which influence development from laying to hatching and, where individuals remain in their natal habitat for extended periods, throughout juvenile development (West & King, 1987). Such spatial ‘ecological inheritance’ has evolutionary consequences due to the feedback it generates; through ‘preference induction’ (Stamps, 2003) individuals who experienced a certain niche during development are themselves likely to select it as a natal habitat for their offspring – a form of extragenetic inheritance.

The social aspect of situated learning has been highlighted by Sterelny (2012) who illustrated the point with another example from the animal kingdom. Some dolphins in Shark Bay, Western Australia, forage with sponges over their snouts likely as protection but also to increase foraging efficiency (Mann & Sargeant, 2003). Although group differences in sponge use have been reported, Sterelny (2012) points out that dolphins who use sponges spend longer in deep channels than those exploiting shallow waters off beaches. As calves accompany their mothers while foraging, the calves of sponge-users experience different environments to calves of beach-exploiters. Thus, being exposed for longer to the deep channels (irrespective of witnessing any use of sponges) may support trial and error learning of sponge use, through encountering sponges and spending longer in environs where sponge use is a beneficial foraging technique.

There are other prominent examples in non-humans, where the inherited social niche influences individual's social skill development. Sapolsky and Share (2004) reported the establishment of an atypical 'pacific culture' in a wild group of olive baboons (*Papio anubis*) which experienced a complete loss of the most aggressive group males. The peaceable culture of the group was maintained for at least a decade, representing complete turnover of the original males who died/emigrated. This is thought to be due to the participation in group life of immigrant males (often adolescent) resulting in adoption of the group tradition of a relatively 'relaxed' dominance hierarchy. More commonly, within old world primates the inheritance of rank, through being born into a matriline (or lineage) of a specific relative rank, influences the rates and types of agonistic interactions individuals experience, which in turn through 'ontogenetic ritualization' (Tomasello & Call, 1997) influences development of their social skills. Finally, Flack et al. (2006) showed how, in captive pigtailed macaques (*Macaca nemestrina*), impartial intervention in conflicts ('policing') by a few dominant individuals, served to stabilise social groups allowing individuals to develop within, and construct their own, social niches in ways that enhance the advantages of group-living. For example, individuals were involved in social networks that were large, and diverse in terms of partners; circumstances thought to facilitate the emergence of cooperation and behavioural traditions (Flack et al. 2006; Hill et al. 2011).

Despite these examples, situated learning is normally a term reserved for human learning. Karmiloff-Smith (2009) highlights how parents alter the environment for children who have a developmental disorder compared to their typically developing siblings. She states (2009, p. 60) that:

> Informal observations of families who visit our lab reveal that parents of infants and toddlers with genetic syndromes find it difficult (compared to parents of typically developing children) to allow their atypically developing offspring to mouth objects freely and to crawl/walk uninhibited in order to fully explore their environment. This reticence is probably because of greater fear of potential danger and accidents, but it results in a less richly explored environment.

She illustrates her point further with the example of parents of children with developmental disorders who, by quickly correcting mistakes, inhibit the common overgeneralization in language acquisition seen in typical development. Such inhibition of this overgeneralisation may create the delayed category formation seen in some developmental disorders along with presenting less variation in linguistic input, shorter sentences, and in general a less richly varied environment. Thus, learning opportunities about culturally relevant behaviour may not only arise through natural pedagogy, contingent tutoring or distributed cognition and the use of tools, but simply by having certain learning opportunities, and not others, available.

Lave and Wenger (1991) describe the process of becoming mature members of a 'community of practice', or social formation of individuals engaged in a particular kind of activity, as 'legitimate peripheral participation'. Newcomers begin in a position that is not central to the learned practice within a community, and yet their participation is legitimate, meaning that the newcomers take on established or recognised activity within the community during the learning process. For instance, tailor apprentices typically start their legitimate peripheral participation with initial preparation work and finishing details on completed garments. Then, the apprentice slowly moves backwards through the production process as skills develop, before being given crucial cloth cutting jobs.

Lave and Wenger assert that learning through legitimate peripheral participation occurs *in situ*, through participation in the community activity, emphasising the acquisition of cultural knowledge through participation and involvement rather than ostensive teaching and instruction (see Rogoff et al., 2007 and Rogoff, Paradise, Mejía Arauz, Correa-Chávez and Angelillo, 2003, for a similar process which they label 'learning through intent community participation'). Thus the process is not concerned with a knowledgeable individual transmitting information to a less knowledgeable individual (as discussed above), rather, seeing both individuals as parts of a larger community, with artefacts, symbols and social norms which support the novice's development in a community of practice. For example, López, Correa-Chávez, Rogoff and Gutiérrez (2010) found that Mexican children with experience of indigenous practices paid more sustained attention than their American Mexican-heritage counterparts to the instructions being given to another child about how to make a toy. Learning environments can be structured through a dynamic apprenticeship process, and this processes may vary culturally, with some cultures being more attuned to paying attention to ongoing events (Indigenous / Indigenous-heritage communities of the Americas), while others (Europeans) tend to focus on one event at a time, seemingly unaware of other co-occurring events (Chavajay & Rogoff, 1999; Correa-Chávez, Rogoff & Mejía Arauz, 2005; Rogoff, Mistry, Goncu &

Mosier, 1993). Taking a cultural niche construction perspective in the context of situated learning, the behaviour of the community of practice provides the constructed learning environment, which affects, during legitimate peripheral participation, the cultural selection of normative expectations, habits and values adopted by the learner.

While situated learning is principally concerned with the developmental learning process, Lave and Wenger (1991) situate their descriptive model within what is the equivalent of an evolutionary context. The idea of ecological inheritance of an environment modified by niche construction is inferred by their observation that, ‘reproduction cycles . . . leave a historical trace of artefacts – physical, linguistic, and symbolic – and of social structures, which constitute and reconstitute the practice over time’, resulting in the ‘continuity of roles while displacement of individuals’ (1991, p. 59). However, they also recognize potential for the evolution of novel behaviour and change in the community of practice over time, referring to this as, ‘developmental cycles of communities of practice’ (p. 121). They note that this can result from a conflict of interest between master and apprentice, and a change in resources such as the technology used in a particular trade (e.g., dairy farming technology in French Alpine villages; Layton, 2000).

The situated learning perspective of the evolution of a community of practice would appear consistent with that of niche-construction theory and developmental systems theory. The latter argues that ‘evolution is change in the nature of populations of developmental systems. This change is driven both endogenously, through the modification by each generation of developmental systems of the resources inherited by future generations, and exogenously, through modifications of these resources by factors outside the developmental system’ (Griffiths & Gray, 2001, p. 207).

*3 Future Directions*

We offer three areas for future directions, two of these involve the use of new techniques (neuroscience and modelling) and the other exploring the niche across the lifespan.

*3.1 Neuroscience, Culture and Niche Construction*

The brain's plasticity means that it can be shaped by environmental input, and this plasticity is not simply available to the young (see Hertzog, Wilson, Kramer & Lindenberger, 2009; Li, 2003; Lövdén, Bäckman, Lindenberger, Schaefer & Schmiedek, 2010 for reviews). Recent technological developments, such as brain imaging, have allowed empirical investigation of the interplay between brain, behaviour and socio-cultural contexts (Miller & Kinsbourne, 2012). The work of Shu-Chen Li (2003, 2008, in press) has been central in understanding the biocultural co-construction of brain plasticity across the life-span. She presents development within three scales, human phylogeny, ontogeny and microgenetic times, and views these from social-cultural, behavioural, cognitive, neural and genetic perspectives.

Brain differences due to experience have been seen in the visual cortex in congenitally blind individuals who are skilled Braille readers (Pascual-Leone, Amedi, Fregni & Merabet, 2005), in the primary motor cortex and auditory cortical representations of expert musicians (Elbert, Pantev, Wienbruch, Rockstroh & Taub, 1995; Pantev et al., 1998), and in, the now famous study by Maguire et al. (2000) of an increase in the posterior hippocampi in individuals who have professions requiring navigating complex spatial environments. Although plasticity appears across the life course, there are periods of sensitivity, and the extent of plasticity in old age is reduced in comparison to young adults (Erickson et al., 2007). Cross-cultural studies have also supported a ‘use-it-or-lose it’ approach to cognitive aging (Park & Gutchess, 2006, p. 107). Gutchess, Welsh, Boduroglu and Park (2006) compared Chinese and American young adults on an object processing task, finding that American participants showed more engagement in the ventral visual cortex. Furthermore, by comparing elderly Singaporeans with American counterparts, it was found that this deficit increased more so for the Singaporeans (Chee et al., 2006). Gutchess et al. (2006) suggest that the difference seen in object processing of the two populations, Asian and America young adults, may be due to cultural differences such as the number of objects in the environment, arguing that as Eastern environments contain more objects than American environments the distinction between object and background may be less clear for the Chinese participants. Equally, differences may be due to cultural variability in the level of attendance made to different levels of information in one’s environment, as highlighted my López et al. (2010) above, in this case with Chinese participants attending more broadly to their environment.

As Li (in press, p. x) points out, ‘findings regarding socio-cultural influences on life-long neurocognitive development are still very limited and leave many gaps between the different domains of analyses’; we completely agree. Thus there is much potential to explore the inter-relations between the cultural niche and neurological underpinnings of behaviour across the lifespan within many domains. Such exploration is extremely fruitful in the light of an ageing population, many of whom will suffer from cognitive decline, which may be alleviated with an appropriately constructed niche.

### *3.2 Modelling*

Mathematical modelling and simulation can be used to explore the interaction between developmental and cultural-evolutionary dynamics. As we have emphasised, the developmental dynamics may often be heavily influenced by the socio-cultural environment. Niche construction models have already been developed to consider the affects of ecological inheritance and change in constructed resources on selection (Laland et al., 1996, 1999, 2000; Lehmann, 2008). In the current context, similar models can be used to account for the cultural inheritance of material culture and systems of symbolic representation on development (Fragaszy, in press; Hazelhurst & Hutchins, 1991; Kendal, in press). Of course, development affects individuals' behaviour and thus their contribution to the socio-cultural environment. Thus modelling is required to clarify how particular forms of ecological inheritance interact with mechanisms of cognitive development.

We have emphasised the role of a knowledgeable-other's behaviour, and not just the influence of material culture, in constructing a learning environment affecting development. We can also expect interesting interactions between developmental and cultural-evolutionary dynamics in these cases too, where for instance, scaffolding traditions of a master affect the learning end-state of an apprentice (van Geert, 1991; van Geert & Steenbeek, 2005), or where there is continuous interaction between the dynamic learner's cognitive state and the socio-cultural learning environment to which they contribute. Where appropriate, these models can account for the effects of differential survival and reproduction and of gene-culture coevolutionary dynamics.

### *3.3 Culture, Peer Interaction and Niche Construction Across the Life Span*

Differing social norms influence how an individual progresses within a niche. For example, in Western societies shyness is viewed as problematic, while in Chinese culture, shyness denotes a level of maturity and understanding (Chen, 2010). These norms manifest themselves in peer interactions, and result in differing temperamental dispositions being reflected in the social niche in which one finds oneself. Chen, DeSouza, Chen and Wang (2006) observed 4-year-olds in a free play setting in both Canada and China. In Canada when a shy peer initiated an interaction children ignored these advances or overtly refused them; however, in China children were more positive to advances from shy children. Similarly, shyness was associated with peer rejection in Canada, and peer acceptance in China (Chen, Rubin & Li, 1995). Thus, the value placed by society on behavioural tendencies is transmitted early to young children. As a result children's experiences in their social circle are very different, such that shy children in China grow in self-confidence (Chen, Chen, Li & Wang, 2009), while shy children in North America who cannot regulate their behaviour to improve their peer status experience frustration and distress. Thus, variation in formative attitudes to shyness can provide a constructed environment that influences emotional development.

Interestingly, and in line with the activity theory position in which development and learning must be placed within a societal, political and historical context, Chen (2012) points out that as China has shifted in recent years to a more competitive economy adapting more individualistic values (thus its cultural niche has changed), children's shyness has increasingly been associated with peer rejection. Equally, in Western societies, where autonomy is valued, as children reach early adolescence their desire for independence from the family increases (Rubin, Bukowski & Parker, 2006), with peer, as opposed to family, support becoming a significant aspect through which they gain self-worth (Sullivan, 1953). Thus the interplay between the socio-political environment, that contributes to the cultural niche, and dispositional factors, such as temperament, need to be investigated across the life span, as early factors will influence the differing cultural niches an individual progresses through during their life. Conversely, the activity and interaction of individuals contributes to the socio-political environment. NCT provides a framework to consider the dynamic interaction of psychological development and socio-cultural environment within and across generations.

## 4. Conclusions

Our aim in this paper has been to meet the challenge set by Gauvain (2000) to better integrate the biological and social sciences in terms of theory and research in human psychological development in the light of humans as the ultimate niche constructors. We agree with Li (2003, 2007, in press) that more work needs to consider the biocultural co-constructive influences on life-span cognitive and behavioural development. It has not been possible to include discussion of all the time scales and levels of analysis highlighted by Li (2003) but we have nonetheless reviewed some of the parallel lines of thinking across developmental psychology and NCT, and it is immediately apparent that these are extensive.

This reflection has considered niche construction in dyadic settings, in which culturally-knowledgeable others transmit information to culturally-naïve individuals (natural pedagogy and activity theory), thus teaching them how to survive and thrive within the niche. It has also considered group behaviour within a niche, reviewing work on distributed cognition and situated learning, demonstrating that human infants become part of a community (a niche) and can draw from many different sources (peers, adults, constructed opportunities within the environment, cultural tools such as books or artefacts) to become an active member of that community. Children (like adults) are not passive recipients of biological and cultural inheritance but active agents, influencing what is learnt through changes in their cognitive development, and their active pursuit of knowledge.

Of course, identifying like-minded researchers, or sympathetic bodies of theory, in other fields is one thing, and fertile exchange is another. In what ways could NCT be useful to developmental psychologists? Three points come to mind. NCT has heuristic value in drawing attention to the active agency of humans as a source of environmental and social change, as well as to the evolutionary, ecological, and social ramifications of human niche construction. By foregrounding niche construction, NCT both reduces the likelihood that it will be neglected (Laland & Sterelny, 2006) and provides theoretical justification to those who find their emphasis on that agency is under-appreciated. Second, NCT offers conceptual tools for understanding phenomena within the Human Sciences, including a variety of experimental and theoretical methods for establishing where niche construction is consequential and quantifying its impact (Odling-Smee et al., 2003). These tools also encompass an overarching conceptual framework that embraces evolutionary theory and sets human development in a comparative perspective, but at the same time is explicit in emphasizing the active agency of humans in constructing their world, and thereby shaping their development. Third, NCT offers theoretically and empirically derived insights into the dynamics of evolving systems under the influence of niche construction. Potentially scientists working in the human realm can draw from these established findings to understand better the complex dynamics of their own study systems. More generally, we suspect that there are likely to be many contemporary developmental psychologists who are unfamiliar with NCT but who nonetheless can be regarded as ‘kindred spirits’, and who we hope will find it useful to engage with and employ NCT in new inter-disciplinary endeavours (Kendal et al., 2011; Laland et al., 2011; O’Brien & Laland, in press).

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Figure legends

Figure 1. (*a*) *A conventional view of the process of adaptation through natural selection.* Causation is primarily linear: it starts with selection pressures stemming from the environment and ends with changes in the organism. Reciprocal causation is recognized only in some 'special cases' where the source of selection is biotic (e.g. sexual selection, predator-prey coevolution). (*b*) *The niche construction perspective.* Niche construction is explicitly recognized as an evolutionary process. The match between organism and environment results from interactions of natural selection pressures in environments and the niche-constructing activities of organisms. Inheritance is expanded to comprise both genetic and ecological components (i.e. legacies of selection pressures previously modified by niche construction). Causation is primarily reciprocal, with selective environments shaping organisms, and organisms shaping selective environments, either relative to themselves, or other organisms.

Figure 2. There is selective feedback at multiple levels from multiple niche-constructing processes.

Figure 3. The relation between activity theory and niche construction is illustrated by the 'mediational triangle' (Cole & Engström, 2001), which expresses the complex relation between artefacts, norms, communities, objects and subjects.

Figure 4 The Tower of Nottingham, a wooden block construction task made from 21 pieces and requiring a minimum of 20 moves to complete.

Figure 1a.

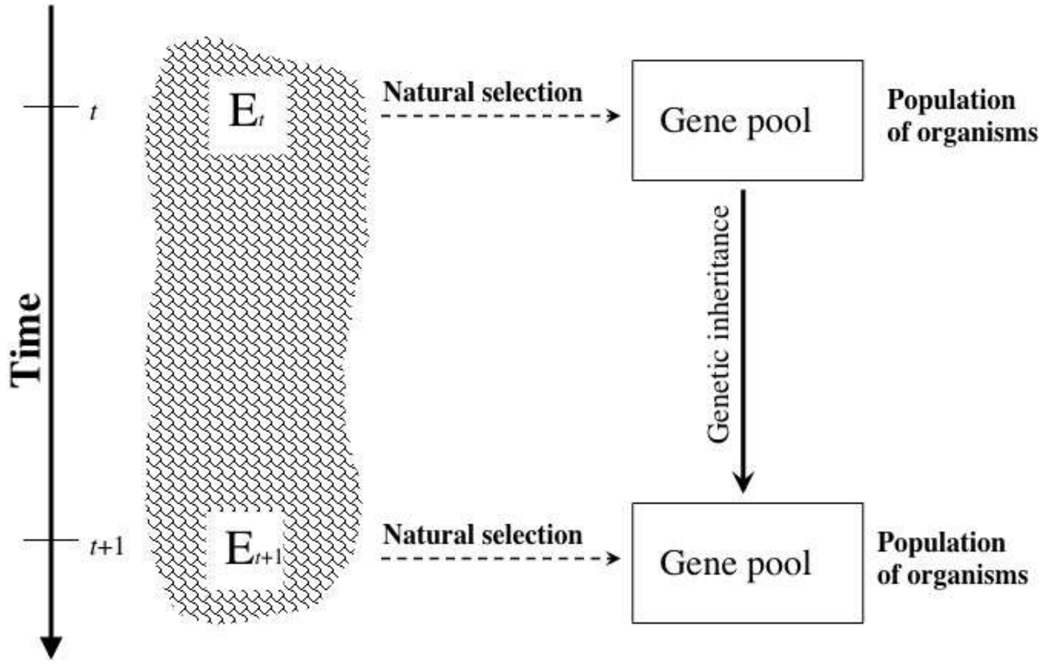



Figure 1b.

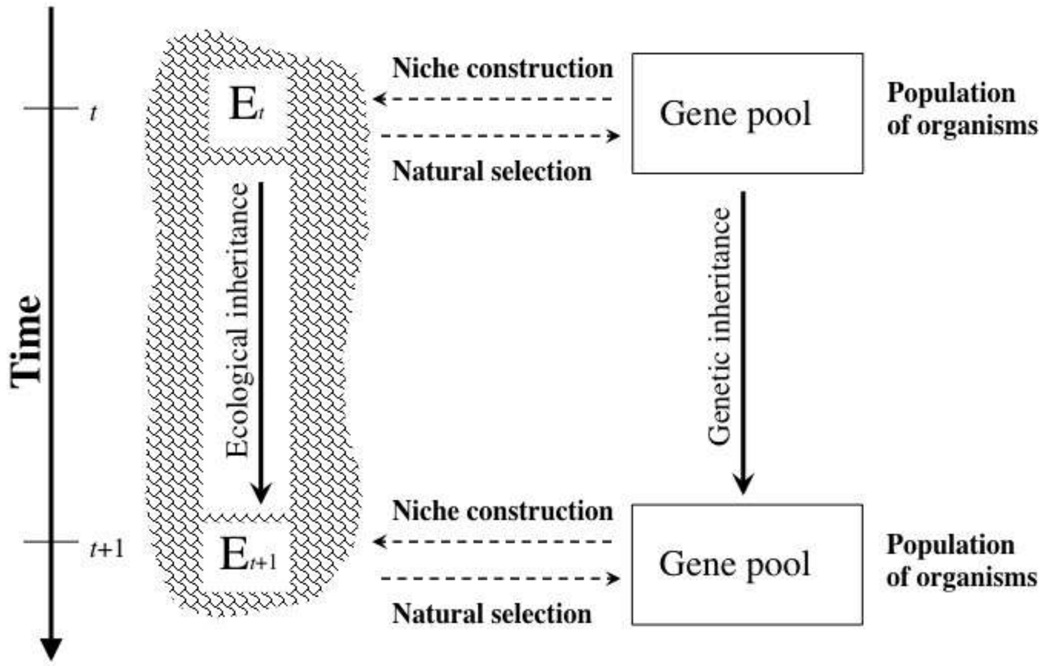
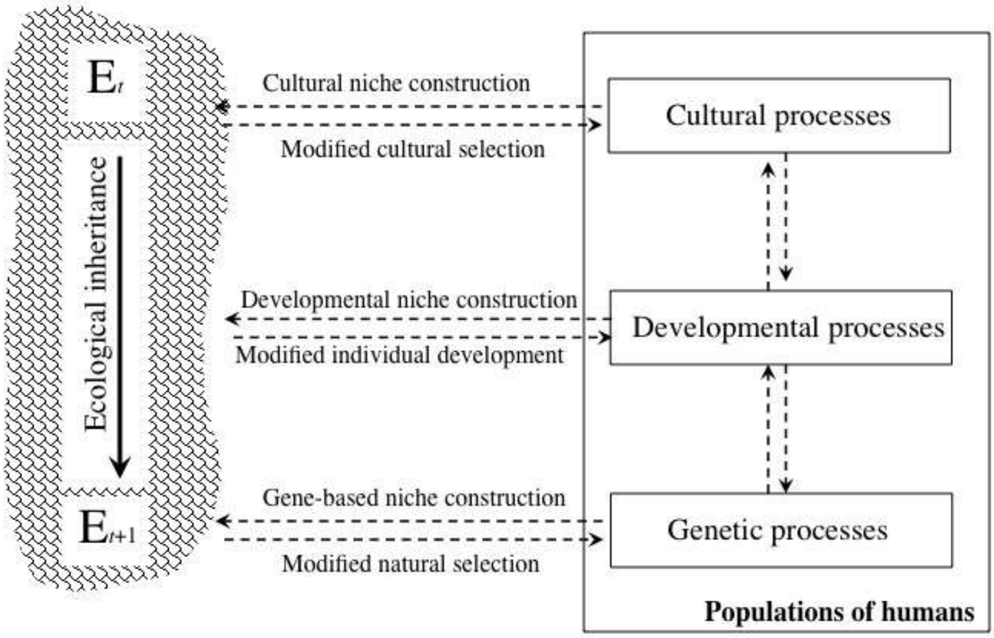


Figure 2.



E$_t$
Ecological inheritance
E$_{t+1}$
Cultural niche construction
Modified cultural selection
Developmental niche construction
Modified individual development
Gene-based niche construction
Modified natural selection
Cultural processes
Developmental processes
Genetic processes
Populations of humans

Figure 3

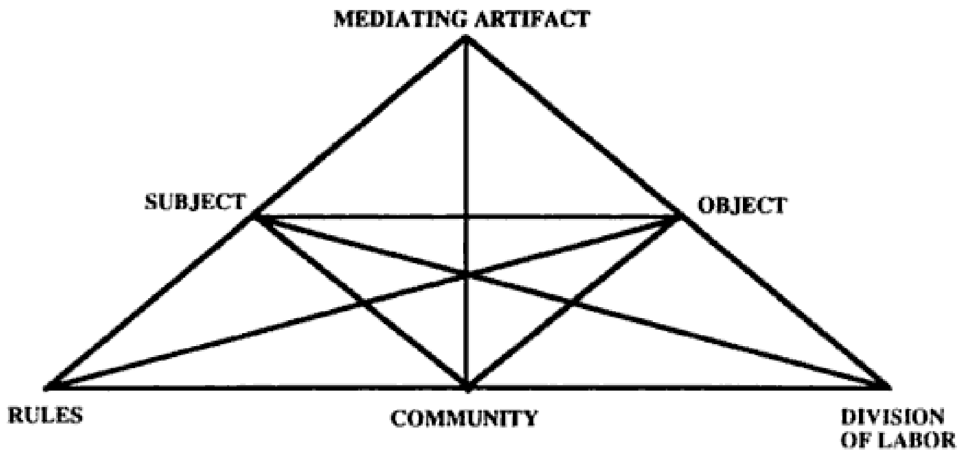



Figure 4