# Niche construction: evolutionary implications for parasites and hosts

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Organisms can determine the environment they experience through the process of niche construction. This may have important evolutionary consequences by exposing them to new selection pressures, producing a faster response to selection, and building suites of coadapted traits. Traits of the parasite which influence the likelihood of encountering different host environments, or which change the host environment, can be regarded as niche construction traits, as can traits of the host which influence the likelihood of the host being infected by parasites. A niche construction perspective may provide new insights into the evolution of host/parasite interactions; this is illustrated with several examples from the viewpoint of both parasite and host traits.

## Parasites, hosts, and niche construction

Niche construction is the process by which the traits of an organism determine the biotic and abiotic environment in which it lives (see Glossary and Box 1). By actively or passively choosing where they live, or by modifying their surroundings, organisms alter their environment. If this altered environment persists to influence the phenotypic traits of subsequent generations, the evolutionary trajectory of a species might be substantially changed. In host/ parasite systems, niche construction can be viewed from the perspective of either the parasite (considering the host as part of the environment) or the host (considering the parasite as part of the environment). Microparasites have much shorter generation times than their hosts, and there has been some investigation of the potential role of niche construction in the evolutionary dynamics of bacterial [1] and viral [2] populations in a static host environment. There has been little consideration, however, of the possible evolutionary implications of niche construction in macroparasites - which may live for an appreciable fraction of their host's lifespan and which must usually leave the host to complete their life cycle. Nor has there been much consideration of how the evolutionary dynamics of hosts may be affected by the way in which their physiological and behavioural activities shape their parasite community.

This Opinion article considers how a niche construction perspective might provide new insights into genetic change by parasites in response to selection pressures exerted by hosts, and genetic change by hosts in response to selection pressures exerted by parasites. These considerations are speculative and are intended to suggest examples of host/ parasite interactions where a niche construction view may be productive. I take a quantitative genetic approach to evolutionary dynamics, in part because I believe that most traits which influence the interaction of hosts and parasites are polygenic in nature (Box 2), but also because the evolutionary implications of niche construction are most far-reaching for polygenic traits.

#### Niche construction may alter selection pressures

The most obvious way in which niche construction can influence evolutionary dynamics is by altering exposure to existing selection pressures or by exposing organisms to new selection pressures. This change in selection pressures may affect the evolution of any trait for which genetic variation exists in the population, and does not require genetic variation in the niche construction trait itself.

#### Glossary

Additive genetic variance: the extent to which phenotypic differences among individuals are due to differences in allelic composition. Correlational selection: selection which acts upon the covariance between two

traits, in other words, favours certain combinations of trait values.

**Ecosystem engineering:** modifications of the abiotic environment by an organism that create habitat for organisms of different species.

**Extended phenotype:** an adaptation of an organism which manifests outside of the body of the individual to affect the abiotic environment, conspecifics or other species.

**Genetic covariance (correlation):** the proportion of variance shared by two phenotypic traits due to genetic causes.

Genotype-environment correlation ( $r_{GE}$ ): occurs when particular genotypes are more likely to experience particular environmental conditions than expected by chance.

**Genotype–environment covariance (Cov**<sub>GE</sub>): non-random association between genetic and environmental effects on the phenotype.

Linkage disequilibrium: non-random association between alleles at different gene loci.

Niche construction: the process whereby organisms, through their choice of habitat, behaviour, or metabolic activities, influence the environment they experience.

Phenotypic plasticity: the capacity of a single genotype to exhibit a range of phenotypes in response to environmental variation.

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**Personality:** behavioural differences among individuals in a population which are consistent over time and in different contexts. The term 'behavioural syndrome' refers, strictly speaking, to correlations among personality traits measured at the population level, but is often used as a synonym for personality, as are the terms 'temperament' and 'coping style'.

**Positive assortative mating:** a pattern of sexual reproduction in which individuals with similar phenotypes (and/or genotypes) mate more often than would be expected by chance.

Reaction norm: the pattern of phenotypes expressed by a single genotype over a range of environmental values.

#### Box 1. Niche construction

Niche construction is 'the process whereby organisms, through their metabolism, their activities and their choices, modify their own and/or each other's niches' [55]. According to this broad definition. niche construction is any changes that organisms have on their environment; it is not limited only to those changes that are adaptive or that impact upon the niche constructing organism. Niche construction includes obvious examples, such as the construction of dams by beavers and webs by spiders, but also more subtle processes such as the choice of a particular habitat or alteration of the environment through metabolic activities. For example, the feeding activities of earthworms alter soil chemistry, structure, aeration, and drainage. This benefits plants, leading to increased plant growth, which in turn provides increased plant litter supply for earthworms. Both earthworms and plants now experience a different environment than did their ancestors, and this has shaped their evolutionary responses [55].

While this is a fairly straightforward concept, there has in recent years been a surge of interest in the ecological and evolutionary importance of niche construction (reviewed in [3,56]). There has also been much controversy over whether niche construction has been adequately accounted for in standard evolutionary theory [57]. Proponents of the niche construction perspective argue that the environment, because it is in effect manipulated by organisms, plays a much more active role in both micro- and macroevolution than is commonly believed. Critics argue that niche construction is often defined so broadly that it can be applied to almost any trait of an organism, and that concepts such as the extended phenotype and ecosystem engineering adequately account for any creative role that the environment plays during evolution.

A distinction should be made between the process of niche construction, of which there are a great number of interesting examples, and niche construction theory, which proposes niche construction as a fundamental cause of evolutionary change, equal in importance to natural selection [57]. A pragmatic approach is to consider whether viewing a trait from the perspective of niche construction provides novel insights into evolutionary and ecological processes, in other words whether a niche construction approach leads to lines of enquiry which would not otherwise have been followed.

There are, however, many examples of genetic variation in niche construction traits, in which case different genotypes may consistently experience different environments, a phenomenon known as gene–environment correlation ( $r_{GE}$ ); this can bias selection pressures, leading to different evolutionary trajectories for niche construction genotypes [3].

### Niche construction by the parasite

Hosts are essential for completion of the life cycle of a parasite and are therefore a predominant feature of the selective environment. From the viewpoint of the parasite, different hosts available to the same life-cycle stage represent alternative environments. Any trait which influences the likelihood of encountering different host genotypes or species can be regarded as a niche construction trait and may alter selection pressures on parasite traits which interact with the host environment. Genetic variation in niche construction traits may lead to  $r_{GE}$ , favouring the evolution of host-adapted races. The formation of host races has been studied most closely in phytophagous insects, starting with Walsh [4], who reported the shift of the apple maggot fly Rhagoletis pomonella from native hawthorn (Crataegus spp.) to introduced apple (Malus pumila) trees. There are now well-characterised host races in several species of phytophagous insects,

#### Box 2. Polygenic traits and quantitative genetic analysis

The evolutionary significance of niche construction does not depend on any particular genetic model. Laland *et al.* [58,59] used a Mendelian, two-locus population genetic model to analyse the evolution of a niche construction trait and an additional recipient trait whose selection depended on the environmental change caused by niche construction. This led to unexpected evolutionary dynamics, including momentum effects (continuing evolutionary dynamics, including momentum effects (continuing evolutionary change when selection has stopped), inertia (delayed response to selection), the fixation of otherwise deleterious alleles, and the maintenance of stable polymorphisms. More recent studies have considered the effect of niche construction on complex, polygenic traits, and suggested novel ways by which niche construction can influence evolution by affecting the genetic variance of these traits [3].

What is the appropriate approach for considering the evolutionary implications of niche construction for interactions between parasites and hosts? Initial models of parasite/host coevolution were largely based on single locus, two allele systems for the genetic determination of parasite infectivity and host resistance [60]. The empirical basis for these models came from interaction loci identified in plant/pathogen (mostly fungi) associations [61]. More recent theoretical and empirical studies, however, suggest that coevolutionary interactions between parasites and both animal and plant hosts are more often mediated, at least in part, by complex, polygenic traits (e.g., [62–70]).

The inheritance of polygenic traits has traditionally been analysed by the statistical techniques of quantitative genetics, which enable the observed phenotypic variance of the trait (V<sub>P</sub>) to be partitioned into components due to genetic (V<sub>G</sub>) and environmental (V<sub>E</sub>) effects: V<sub>P</sub> = V<sub>G</sub>+V<sub>E</sub>. V<sub>E</sub> is the phenotypic variation due to differences in environments among individuals and V<sub>G</sub> is the phenotypic variation due to differences in allelic composition among individuals (for simplicity I ignore non-heritable components of genetic variance due to dominance and epistatic interactions). A quantitative genetic approach to predicting the evolution of polygenic traits assumes that these traits are determined by a very large number of genes, each contributing infinitesimally small additive effects. In recent years genomic mapping studies have generally found that the infinitesimal model provides a good approximation to the inheritance of polygenic life-history traits [71,72].

many of which are consistent with a sympatric mode of divergence [5].

Phytophagous insects are able to actively choose their host. This may also be the case for parasites of animals, particularly ectoparasites and those with free-living stages. For example, infective stages of the parasitic copepods Lepeophtheirus thompsoni and L. europaensis preferentially colonise turbot (Psetta maxima) and brill (Scophthalmus rhombus), respectively, and these sympatric fishes are the hosts on which each species of copepod is found in the Western Mediterranean [6]. For many parasites of animals, however (and certainly many endoparasites), transmission is passive. Nevertheless, there are parasite traits which will influence host occurrence. Heritable differences have been found in cercarial emergence time between populations of Schistosoma mansoni infecting either humans or black rats (Rattus rattus) in Guadeloupe [7]. Genotypes with an early pattern of shedding are found more commonly in humans, whose activity is principally diurnal, while genotypes with a late pattern of shedding are found more commonly in rats, which are nocturnal. Genotypes which differ in cercarial emergence time will therefore be associated with different host environments and different selection pressures.

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