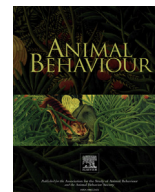




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## Special Issue: Cognitive Ecology

## Behaviour shapes environmental variation and selection on learning and plasticity: review of mechanisms and implications

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Biologists have long been interested in the factors that maintain variation in learning and plasticity within and between species, especially given the role of such flexibility in coping with novel and changing environments. A large body of theoretical and empirical work has established the role of environmental variation in selecting for learning and plasticity, suggesting that simple measures of such variation could serve as proxies for organismal flexibility. However, a wide range of behavioural and physiological traits can shape *how* organisms experience environmental variation, and thus how plasticity is shaped by selection. Given that these traits themselves can evolve, this sets up the potential for complex feedbacks in the evolution of learning and plasticity. We begin this review by first detailing the wide variety of behavioural traits that shape environmental variation, ranging from exploration and dispersal to sensory biases and habitat choice. We then review relevant theory that suggests how such behavioural traits can modify selection on learning and plasticity, often favouring the evolution of specialization in heterogeneous environments by reducing the variation that organisms experience. When models allow behavioural traits to jointly evolve with plasticity, model outcomes differ and complex evolutionary feedbacks may emerge. We suggest that further theoretical insights could be gained by incorporating more nuances of development and behaviour, such as variation in the developmental window of environmental sensitivity of traits or differences in exploratory periods prior to breeding. Finally, this review discusses implications of this perspective for understanding the maintenance of genetic variation in learning, differences in colonization and survival in novel environments and making predictions about how species will cope with environmental change.

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Biologists have long been fascinated with the question of why learning, cognition and plasticity vary both within and between species. Adaptive phenotypic plasticity – in behaviour, morphology and physiology – allows individuals and genotypes to adjust traits to local conditions and thus cope with novel and changing environments (Schlichting & Pigliucci, 1998; West-Eberhard, 2003). For instance, greater neural investment has been linked to innovative foraging behaviours and survival in novel environments (Maklakov, Immler, Gonzalez-Voyer, Ronn, & Kolm, 2011; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol, Timmermans, & Lefebvre, 2002). Such developmental plasticity in behaviour or learning can allow rapid adjustments to new conditions. In an age of human-induced environmental change, there has been interest in

developing broad predictors of variation in learning and plasticity (Sih, 2013).

For decades, environmental variation has been viewed as a major driver in the evolution of learning and phenotypic plasticity. For example, when genotypes experience intermediate levels of coarse-grained environmental variation, where the environment differs spatially or temporarily across generations, there is a benefit to adjusting the development and expression of traits depending on the environment an individual finds itself in and plasticity evolves (Gomulkiewicz & Kirkpatrick, 1992; Levins, 1968; Lively, 1986; Moran, 1992; Van Tienderen, 1991; Via & Lande, 1985). In models of the evolution of learning, moderate amounts of environmental variation – whether experienced within or between generations – favour the evolution of learning (Aoki & Feldman, 2014; Stephens, 1991). For very high rates of environmental variation, learning and plasticity are disfavoured as the benefits of plasticity are outweighed by the costs of constantly adjusting one's phenotype (Schlichting & Pigliucci, 1998; Stephens, 1991).

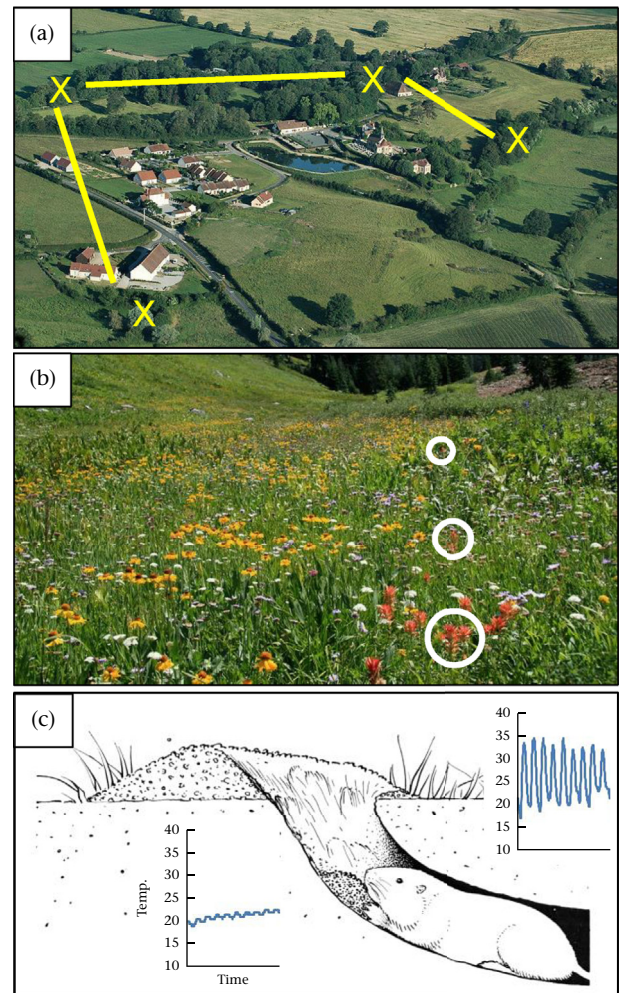
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The importance of environmental variation in the evolution of learning and plasticity suggests that if we can quantify environmental variation, then we can predict variation in organismal flexibility across species, for a given set of costs and constraints. This is straightforward in an experimental evolution context (Kassen, 2002), but it can be more challenging in natural environments. Despite this, a wide range of studies have linked the degree of abiotic environmental variation to the evolution of plasticity, including such variables as the probability of a pool drying (Cook & Johnson, 1968; Richter-Boix, Llorente, & Montori, 2006), spatial variation in soil chemistry (Baythavong, 2011), or latitudinal differences in temperature variation (Deutsch et al., 2008). Many components of biotic variation have also been linked to the evolution of plasticity, such as the degree of variability in the diet (Day, Pritchard, & Schluter, 1994), predation (Van Buskirk, 2002), herbivory (Karban & Nagasaka, 2004), sex ratio (Carroll & Corneli, 1995) or competition (Van Kleunen & Fischer, 2001). With respect to the evolution of behavioural flexibility, insect species that experience a greater range of diets tend to be better learners with greater neural plasticity (van Dijk, Janz, Schapers, Gamberale-Stille, & Carlsson, 2017; Hoedjes et al., 2011).

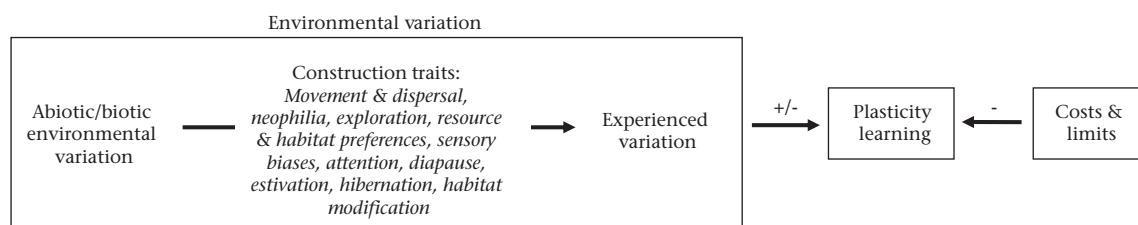
This range of theoretical and empirical studies has clearly implicated the importance of environmental variation, and the degree of such variability, in the evolution of plasticity and learning. However, biologists have long recognized that the levels of 'environmental variation' an organism experiences are not simply a measure of the external abiotic and biotic environmental variation. As further discussed below, patterns of individual movement, habitat choice and dispersal will influence how an organism experiences environmental variation and thus selection on learning and plasticity. While this seems an obvious point, such a perspective is important because as soon as aspects of environmental variation become an organismal property, there is a chance of genetic influences on that trait, resulting in complex evolutionary feedbacks. Individuals 'construct' environmental variation, which can select either for or against plasticity, depending on the circumstances. Such a niche constructionist view on environmental variation (Laland, Odling-Smee, & Feldman, 1999; Lewontin, 1978; Odling-Smee, Laland, & Feldman, 1996) offers insights on complex evolutionary feedbacks between behaviour, environmental variation and selection on learning and plasticity (Han, Li, Hui, & Zhang, 2006; Hui, Li, & Yue, 2004; Hui & Yue, 2005; Kylafis & Loreau, 2008; Silver & Di Paolo, 2006).

In this review, we first summarize mechanisms by which individual behaviour can both increase environmental variation, or more commonly, decrease environmental variation (Fig. 1). Second, we review theoretical expectations for how such behaviours shape the evolution of learning and plasticity through their effects on experienced environmental variation (e.g. 'experiential niches', Sultan, 2015). Here, we also highlight how more realistic models of development may offer additional theoretical insights on the



**Figure 2.** Examples of how behaviour can shape environmental variation. (a) A spatially heterogeneous environment can be simplified as a mobile individual moves through the landscape and chooses preferred patches (image: Wikimedia commons, Jean-Louis Zimmerman). (b) A diverse field of potential resources can be simplified through sensory biases, such as a bias for red colours (image: Wikimedia commons, Jane S. Richardson). (c) Active modification of the environment, such as through burrow construction, can create more predictable conditions. For instance, moving from the surface to 30 cm below ground can drastically reduce temperature variation (graphical insets modified from Snell-Rood et al., 2016; image: Wikimedia commons, Tracy I. Storer).

evolution of plasticity. Finally, we review implications of this perspective for maintenance of genetic variation in plasticity and predicting colonization of novel environments and resilience to environmental change. Overall, this discussion suggests that if we



**Figure 1.** Summary of behavioural traits that can modulate external environmental variation. Environmental variation selects for learning and plasticity, but the degree of variation experienced by an organism depends on a wide range of behavioural (and physiological) traits that can themselves evolve ('construction traits'). Behavioural traits can both increase (+) or decrease (–) selection on learning and plasticity, depending on the combination of traits in a particular environment. Costs and constraints can select against or inhibit the evolution of learning and plasticity.

wish to use measures of environmental variation as proxies of potential for plasticity, we will need to incorporate a range of other factors in our predictive models.

### BEHAVIOUR CAN INCREASE OR DECREASE EXPERIENCED ENVIRONMENTAL VARIATION

A wide range of behavioural traits, which may vary at the individual or species level, can affect the range of environments an organism experiences. Differences in movement, dispersal and exploration can in some cases increase the range of environments experienced. Species and individuals vary in personality or temperament traits such as boldness, neophilia and exploration (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), which can influence the chance they encounter a new habitat or experience a new resource or predator. Species of birds that are more generalist are more exploratory with novel objects and in novel environments relative to specialists (Greenberg, 1983, 1990; Mettke-Hofmann, Winkler, Hamel, & Greenberg, 2013; Tebbich, Fessl, & Blomqvist, 2009). Similarly, populations of birds in novel habitats are more exploratory and neophilic (Liebl & Martin, 2012; Sol, Griffin, Bartomeus, & Boyce, 2011), and resident species are more exploratory than migrant and nomadic species that move between predictable patches (Mettke-Hofmann, Ebert, Schmidt, Steiger, & Stieb, 2005; Mettke-Hofmann et al., 2013; Mettke-Hofmann, Winkler, & Leisler, 2005). Species or populations that are more exploratory or neophilic may experience a relatively greater range of environments, thus increasing environmental variation relative to less exploratory species or populations.

Although movement and dispersal can increase the range of environments experienced in some cases, in many other cases it can functionally decrease environmental variation, especially if movement is coupled with choice behaviour (Fig. 2a). For instance, a highly mobile individual can incorporate multiple preferred patches into a home range, turning what looks like a patchy and fragmented environment into a more predictable and homogenous habitat (Kotliar & Wiens, 1990; Rolstad, 1991). Similarly, migration between preferred regions can reduce climatic variation across seasons. Individuals that find themselves in less preferred habitats, for instance resource-poor or thermally stressful areas, can continue moving until preferred areas are found (Bartlam-Brooks, Beck, Bohrer, & Harris, 2013; Long et al., 2014). Thus, movement, coupled with preferences for preferred resources or habitats can effectively decrease environmental heterogeneity (Johnson, Wiens, Milne, & Crist, 1992; Wiens, 1989).

Nonrandom dispersal and movement across the landscape appear to be the norm; such dispersal that depends on an individuals' previous experiences or phenotype should effectively reduce environmental variation (Edelaar & Bolnick, 2012; Edelaar, Siepielski, & Clobert, 2008). For instance, it is commonly observed that individuals, from insects to mammals, prefer habitats that they experienced early in life – so called natal habitat preference induction (Davis & Stamps, 2004). For example, dispersing mice prefer to settle in habitats that resemble those experienced early in life (Mabry & Stamps, 2008a), and microhabitat feeding preferences learned early persist for life in some birds (Slagsvold & Wiebe, 2007). Natal habitat preference induction may occur in part because experiences in certain habitats have 'trained' individuals with respect to movement and foraging traits that excel in those environments (Stamps, 1995). For example, tiger snakes, *Notechis scutatus*, not only prefer to settle in habitats that they were reared in, but their locomotor performance in those habitats is higher because traits that developed in their natal habitats match their adult habitats (Aubret & Shine, 2008). Similarly, in anoles, habitat preference is influenced by relative limb length, which is in turn

influenced by perch rearing conditions (Dill, Sanger, Battles, & Johnson, 2013; Losos et al., 2000). Phenotypic variation that influences habitat preferences can stem from both genetic and plastic influences. For instance, grasshoppers (*Tetrix subulata*) prefer habitats to which they are colour matched (Karpestam, Wennersten, & Forsman, 2012) and this colour variation originates in part from genetic variation in coloration and also phenotypic plasticity based on rearing environment (Edelaar, Banos-Villalba, Escudero, & Rodríguez-Bernal, 2017). In stickleback fish (*Gasterosteus aculeatus*), lake and stream ecotypes, which stem from both genetic and environmental influences (Lohman, Stutz, & Bolnick, 2017; Moser, Kueng, & Berner, 2015; Oke et al., 2016), prefer their respective matching habitat type (Bolnick et al., 2009). While habitat choice based on an individuals' own phenotype often acts to reduce experienced variation, habitat choice based on social cues (Nocera, Forbes, & Giraldeau, 2006; Webster & Hart, 2006) could increase or decrease variation depending on whether conspecifics prefer a range of different habitats or exhibit rather conservative preferences, and whether social cues attract or repel conspecifics (Jaumann & Snell-Rood, 2017).

Movement coupled with sensory biases and preferences can also act to simplify a complex or variable environment on a finer scale of resource choice (Fig. 2b). For instance, more mobile species can cope with resource heterogeneity by increasing their encounter rate with preferred resources (Kareiva, 1982). Beyond simple preferences, any sensory adaptation that influences the detectability of an object can drastically alter a search process and thus the perception of environmental variation or environmental complexity. This idea has been particularly well studied with respect to opsins in visual systems, which are often adapted to their light environment in a way that influences the detectability of resources and sexual signals in those conditions (Price, 2017). For instance, the 'M' and 'L' cones in human visual systems have been hypothesized to be tuned in a manner to make fruit more detectable against a green leaf background (Regan et al., 2001); similar environment-specific tuning is seen in the visual system of fish and birds in different light environments (Bloch, 2015; Hofmann et al., 2009). Differential attention is another route to increasing the detectability of a signal. Attention to ultraviolet (UV) reflection or iridescence may allow individuals to more quickly and easily locate resources while moving through complex landscapes, effectively simplifying a search (Steck & Snell-Rood, 2018; Whitney, Reed, Rands, Chittka, & Glover, 2016). Increasing the detectability of a resource in a complex landscape may also occur by increasing attention towards cues associated with that resource (Hawkins et al., 1990; Vergheze, 2001) such that learning associated colours or shapes or some aspect of a search image alters how individuals experience the environment. Whether at coarse levels of variation (in choosing habitats) or at finer levels of variation (in choosing resources), behaviour can greatly modify experienced environmental variation.

While most of the present discussion has focused on how individual behaviour can modify the perception of spatial variation, physiological and behavioural processes can also modify the experience of temporal variation. Diapause, hibernation and estivation can all act to put an organism on hold until preferred or favourable conditions are present. In thinking broadly about plant 'behaviour' (e.g. Silvertown & Gordon, 1989), germination can act as a form of niche construction or habitat selection as such developmental decisions are responsive to environmental cues (Baskin & Baskin, 1998; Donohue, 2005; Donohue, Dorn, et al., 2005; Donohue, Polisetty, & Wender, 2005). Similarly, genetic variation across populations in diapause timing can result in individuals experiencing similar favourable conditions despite environmental differences across populations (Hairston & Olds,



1984; Schmidt & Conde, 2006). Timing of reproduction or life cycle transitions with local or global climate cues may reduce experienced year-to-year variation (Frederiksen, Harris, Daunt, Rothery, & Wanless, 2004). Movement can also modulate temporal variation, for instance, long-distance migration buffering seasonal variation (Shaw & Couzin, 2013) as in migratory species of birds.

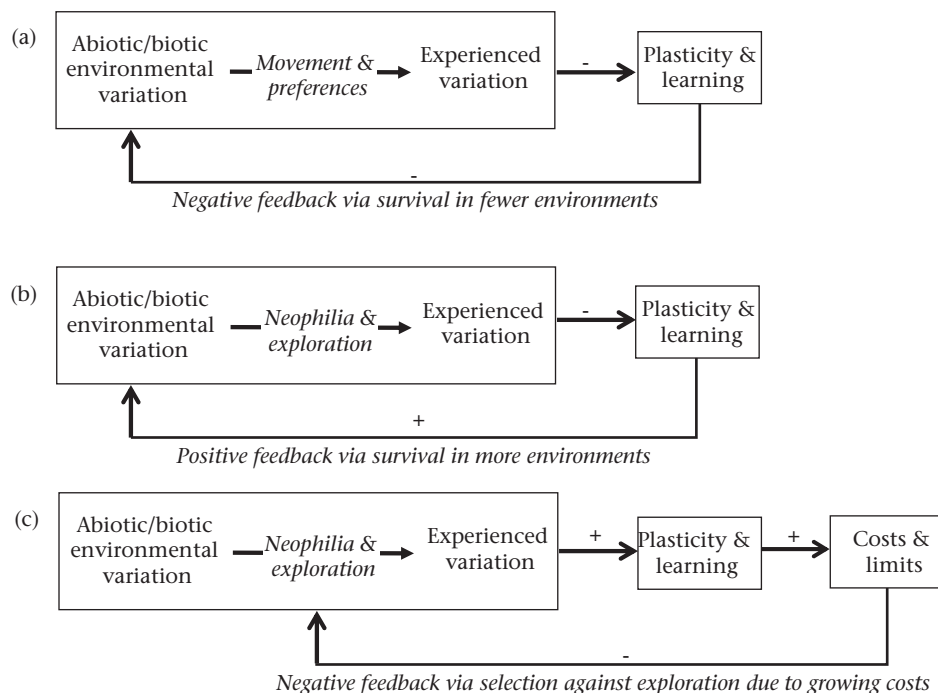
Finally, complex or variable environments can be simplified or homogenized through active habitat modification (Fig. 2c). Some species of tropical ants create monocultures of their preferred hosts by poisoning nonhosts with formic acid (Frederickson, Greene, & Gordon, 2005). Beavers can create their preferred pond habitat through construction of dams (Rosell, Bozser, Collen, & Parker, 2005), and dung beetles can decrease both nutritional and temperature variation for their offspring by constructing and burying dung balls (Snell-Rood, Burger, Hutton, & Moczek, 2016). Similarly, constructed shelters may protect individuals from desiccation (Gilbert, 2014) or predators (Fukui, 2001), resulting in more consistently favourable conditions. Such forms of ecosystem modification (Hastings et al., 2007; Jones, Lawton, & Shachak, 1994) represent an energetically costly, but effective, method by which organisms match their environment to their phenotype, by changing the environment itself. Humans, by creating climate-controlled buildings, predictable cityscapes and monocultures of agriculture, represent the most extreme form of such homogenization through ecosystem modification (Ellis & Ramankutty, 2008).

#### BEHAVIOUR MODULATES SELECTION ON PLASTICITY THROUGH ITS EFFECTS ON ENVIRONMENTAL VARIATION

Many of the behavioural traits reviewed above, such as habitat and resource selection, act to reduce the degree of environmental

variation an individual experiences throughout their lifetime, and potentially, across generations. Theoretical studies have long recognized that habitat selection can increase the probability of evolving specialization by reducing environmental variation and increasing the efficacy of selection on traits relevant to a specific environment (Brown, 1990; Brown & Pavlovic, 1992; Levins, 1963; Ravigne, Dieckmann, & Olivieri, 2009; Rosenzweig, 1987; Whitlock, 1996). Over time, this process can increase the probability of speciation (Bolnick et al., 2009; Maynard Smith, 1966), especially for natal habitat preference induction (Berner & Thibert-Plante, 2015). Thus, a seemingly complex or heterogeneous habitat does not necessarily select for cognition and plasticity – instead, behavioural traits that decrease the effects of environmental variation can favour specialization (e.g. Fig. 3a).

When behaviour determines environmental variation, the selective environment itself can evolve. In theoretical models, when behavioural traits, such as habitat selection and dispersal, can evolve, different outcomes and complex feedbacks result (Scheiner, 2016; Scheiner, Barfield, & Holt, 2012). For example, when habitat choice can evolve, specialization is a relatively more likely outcome than generalization (Ravigne et al., 2009). This recalls the more general observation that niche construction can result in complex evolutionary feedbacks (Kylafis & Loreau, 2008), including in cognitive evolution (Kerr, 2007; Kerr & Feldman, 2003). In the case of plasticity, there may be negative feedback loops when declines in experienced variation lead to lower selection on plasticity as the environment becomes more predictable (Fig. 3a). On the other hand, increases in exploratory behaviour and dispersal may select for greater plasticity, which leads to higher survival in novel environments and selects for further plasticity (Fig. 3b). If the costs of plasticity become too high, an evolutionary reduction in plasticity may occur through selection for reduced exploration or increased habitat selection (Fig. 3c).



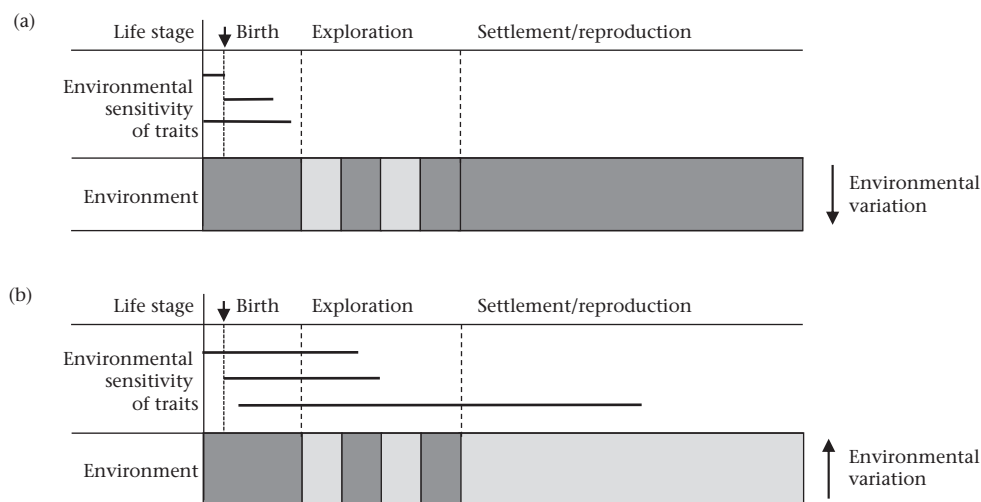
**Figure 3.** Examples of feedbacks in the evolution of plasticity. (a) Movement through space, coupled with preferences or sensory biases for specific habitats or resources, can decrease levels of experienced variation, resulting in selection for lower plasticity (more specialization). The resulting survival in fewer environments may result in a negative feedback loop as experienced variation decreases. (b) Neophilia and exploration may increase levels of experienced variation, resulting in selection for greater plasticity. Survival in a greater range of environments may result in a positive feedback loop as experienced variation increases. (c) As the costs of plasticity increase as plasticity increases, there may be selection for reduced plasticity via less exploration and more habitat selection.

Given the ubiquity of behavioural traits that reduce environmental variation, it might be somewhat surprising that generalization, plasticity and learning ever evolve, especially if there are associated costs. One solution to this question is the fact that there are limits to the ability to choose a matching habitat, such as the costs of searching and the availability of habitat (Ravigne et al., 2009). As the number of possible habitat types increases, models suggest a relative advantage of plasticity over habitat choice that matches a specialist to its environment (Edelaar, Jovani, & Gomez-Mestre, 2017). Environmental variation over time also favours plasticity: even if an individual can reduce spatial variation through habitat choice, temporal variation within that habitat may favour plasticity (or subsequent movement, Scheiner, 2016).

Further understanding how behaviour modulates selection on plasticity may require more realistic models of the development of behaviour and traits (Draghi & Whitlock, 2012; Panchanathan & Frankenhuys, 2016; Stamps & Frankenhuys, 2016). If developmental plasticity shapes later habitat choice as discussed above, then it may be important to incorporate such developmental windows into models of movement, habitat choice and the evolution of plasticity. Such developmental windows, coupled with patterns of dispersal and timing of reproduction, will affect how individual behaviour scales up to affect population-level experienced variation, and thus selection on plasticity, although recent models suggest that developmental timing may be less important than other factors (Edelaar, Jovani, et al., 2017). The developmental sensitivity of traits to the environment varies across developmental time, across traits, and across species. For instance, species often have traits that are sensitive to the environment during some life stages but not others (Fig. 4): the turnover of bone tissue declines with age, but the timing of bone ossification varies across species (Mitgutsch, Wimmer, Sanchez-Villagra, Hahnloser, & Schneider, 2011). The developmental process itself can evolve, as evidenced by the many examples of heterochronic shifts across species (Klingenberg, 1998; Smith, 2001), shifts between precocial and

altricial development across species (Starck & Ricklefs, 1998; Thomas & Székely, 2005), and biodiversity as a whole. Furthermore, the degree of behavioural exploration varies across development, with exploration and neophilia tending to peak in juveniles relative to adults (Delgado, Penteriani, Nams, & Campioni, 2009; Gopnik et al., 2017; Mettke-Hofmann, 2007; Miller, Bugnyar, Polzl, & Schwab, 2015; O'Hara et al., 2017; Pellis, 1981).

The timing of movement and exploration relative to developmental critical periods will shape how environmental variation is experienced at the individual and population levels, and thus selection on plasticity and learning (Fig. 4). Certain life cycles, developmental processes and choice behaviours may act to decrease environmental variation within the adult life of an individual while variation between generations increases. This increased coarse-grained variation should favour the evolution of developmental plasticity and learning, especially if there are costs to developmental reorganization later in life ('epiphenotype problem', e.g. DeWitt, Sih, & Wilson, 1998; Snell-Rood, Swanson, & Young, 2015). For example, many birds and mammals go through exploratory periods prior to choosing a breeding habitat, while they are within critical juvenile developmental periods. Dispersing brush mice explore 25–187 m from their natal nests, sampling from up to four habitat types before making a decision about where to breed (Mabry & Stamps, 2008a, 2008b). This exploratory period falls within the developmental critical period for aspects of neural and morphological development, including vision and jaw structures (Menegaz, Sublett, Figueroa, Hoffman, & Ravosa, 2009; Menegaz et al., 2010; Prusky & Douglas, 2003). Thus, if traits are sensitive to the environment during this exploratory phase, experiences during exploration could shape development and subsequent phenotype-dependent habitat preferences (Fig. 4b). Such timing of trait development may effectively increase experienced environmental variation. In contrast, if the timing of trait development occurs before exploration, for instance in precocial relative to altricial species (Fig. 4a), it may effectively reduce environmental



**Figure 4.** Developmental timing affects how plasticity influences habitat selection. In this figure, three traits (solid lines) vary in their sensitivity to the environment over development time and thus the extent to which their eventual form is influenced by the pre-natal environment (before the arrow), the natal habitat (after the arrow), areas experienced during any exploration phase, and/or their adult habitat. Thus, assuming that an individual's phenotype influences adult habitat choice, developmental timing of traits can play a major role in the type of generation-to-generation environmental variation (environments indicated by different shaded boxes) experienced by a genotype. For example, (A) demonstrates a situation where trait development is sensitive to the environment only prior to, or just following birth, such as a relatively more precocial species. Thus, only the natal habitat influences trait development, and individuals prefer to settle in habitats that match their natal habitat, thus potentially reducing environmental variation across generations. In contrast, (B) represents a species or genotype where trait development is sensitive to the environment after leaving the natal area, such as a relatively more altricial species. Here, trait-based habitat preferences may be influenced by the exploratory process, potentially increasing environmental variation experienced by that species. Note that each component of this incredibly simplified life cycle could potentially evolve – the stages of the cycle, the sensitivity of traits to the environment, the presence or details of an exploratory period – which will subsequently affect how behaviour shapes environmental variation and selection on plasticity.

variation. If early developmental experiences shape trait expression and subsequent habitat and resource preferences, generalist species may often end up being composed of specialized individuals (reviewed in Bolnick et al., 2003; Fox & Morrow, 1981; e.g. Estes, Riedman, Staedler, Tinker, & Lyon, 2003; Slagsvold & Wiebe, 2007).

## IMPLICATIONS OF BEHAVIOURAL MEDIATION OF ENVIRONMENTAL VARIATION

### *Maintenance of Genetic Variation in Learning and Plasticity*

Despite obvious fitness benefits, learning, and plasticity in general, are neither infinite nor ubiquitous, and vary within and between species (Bednekoff, Balda, Kamil, & Hile, 1997; Girvan & Braithwaite, 1998; Nelson, Marler, & Palleroni, 1995; Prokopy, Cooley, & Papaj, 1993; Raine & Chittka, 2008). While it is well established that differences in external levels of environmental variation, such as seasonality, may explain some of this variation, individual differences in the perception of environmental variation may also maintain genetic variation in learning and plasticity (Hollander, 2008; Parsons, 1997). In other words, some genotypes, populations or species may experience greater environmental variation than others, and thus stronger selection on learning and plasticity. Niche construction more broadly has been hypothesized to be an important factor in the maintenance of genetic variation (Han et al., 2006; Hui & Yue, 2005; Silver & Di Paolo, 2006).

The present discussion suggests that genetic variation in any 'construction trait' (Fig. 1) could result in the maintenance of variation in learning and plasticity. Thus, genetic variation within and between populations or species in resource and habitat preferences (Futuyma & Peterson, 1985), the degree of natal habitat preference induction (Davis, 2008; Petit et al., 2017), movement traits (e.g. in butterfly flight: Jones, 1977), sensory abilities (e.g. human olfaction, Hasin-Brumshtein, Lancet, & Olender, 2009) or other behaviours that affect the perception of environmental variation, could lead to maintenance of variation in learning within species, and potentially within populations. For example, genetic variation in the dopamine system has been linked to variation within species in novelty seeking and activity in vertebrates (Fidler et al., 2007; Gizer, Ficks, & Waldman, 2009; Korsten et al., 2010; Schinka, Letsch, & Crawford, 2002), which could potentially maintain variation in flexibility through differences in how individuals experience environmental variation. *Drosophila* genotypes with higher movement rates ('rovers') have poor long-term memory (Mery, Belay, So, Sokolowski, & Kawecki, 2007). Similarly, in butterflies, genetic variation in movement and attention to novel colours in host search has been tied to variation in learning (Snell-Rood & Steck, 2015). Such correlations could maintain variation in learning within populations as the high movement genotypes effectively increase their encounter rate with an expected resource and, in the end, locate as many resources as a low-moving genotype that learns to find locally abundant resources. The mechanisms driving these correlations are in need of further study, whether they are developmentally driven (e.g. Snell-Rood & Steck, 2015) or result from co-segregating alleles.

### *Predicting Colonization and Survival in Novel Environments*

Linking behaviour to selection on learning and plasticity can be relevant to predicting how organisms will colonize and survive in novel environments. Variation in movement and dispersal can determine which organisms track shifting habitats in the face of climate change and habitat destruction (Higgins & Richardson, 1999; Kotiaho, Kaitala, Komonen, & Paivinen, 2005; Poyry, Luoto, Heikkinen, Kuussaari, & Saarinen, 2009; Thomas et al., 2001).

Similarly, survival in novel environments is influenced by aspects of behaviour, personality and cognition (Chapple, Simmonds, & Wong, 2012), as well as correlations between behaviour and movement (Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Duckworth & Badyaev, 2007). Associations between movement and plasticity, and the underlying mechanism affecting such a correlation, will be particularly important as they should determine whether genotypes that colonize a new environment actually survive there, and subsequent evolutionary changes (e.g. Lande, 2009; Price, Qvarnström, & Irwin, 2003). Understanding the direction of correlations between movement and plasticity is important to predicting colonization of new patches, whether at range edges (Angert et al., 2011; Morin & Thuiller, 2009) or representing invasions in novel environments (Sol, Bacher, Reader, & Lefebvre, 2008; Sol et al., 2005).

While the phenotypic plasticity literature sometimes suggests there should be positive associations between movement and phenotypic plasticity (Hollander, 2008; Scheiner & Holt, 2012), there are many studies that show negative correlations between movement and behavioural flexibility, which is not surprising given the complexities discussed above. Bold individuals are generally slower to adjust their behaviour in response to an environmental change (e.g. in great tits, *Parus major*: Exnerova, Svadova, Fucikova, Drent, & Stys, 2010). Similar negative correlations are also seen in butterflies (*Pieris rapae*: Snell-Rood & Steck, 2015) and humans, such as attention deficit hyperactivity disorder (Biederman, Newcorn, & Sprich, 1991; Bickel, 1996; Furnham, Monsen, & Ahmetoglu, 2009; Rosenthal & Allen, 1978). These studies suggest that, in some cases, bold genotypes with rapid or long-distance dispersal may be the most likely to colonize a novel environment, but the least likely to adjust their behaviour to deal with novel conditions or resources within that environment. The combination of movement traits with exploration, attention and sensory biases should determine whether high-dispersing individuals are experiencing greater or lesser environmental variation, and thus are more or less likely to be highly plastic and flexible. As mentioned above, the mechanisms underlying such correlations may vary (e.g. genetic correlation, pleiotropy, developmental conditions), and will also play a role in how these correlations affect evolutionary processes in new environments.

### *Predicting Responses to Anthropogenic Change*

Rapid human-induced environmental change has spurred biologists to develop theories for predicting responses of diverse species to environmental change and novel environments, from niche models to evolutionary rescue (Carlson, Cunningham, & Westley, 2014; Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009). Learning and plasticity play a major role in models predicting population persistence in novel environments (Chevin, Lande, & Mace, 2010; Sol et al., 2005). In translating such models to real conservation questions, there is a huge interest in proxies of plasticity and learning that are relevant to predicting population declines in real time, and some progress has been made with measures such as brain size (Maklakov et al., 2011; Shultz, Bradbury, Evans, Gregory, & Blackburn, 2005). Because environmental variation is such an important driver of plasticity, can we just use some easy-to-quantify measure of environmental variation such as temperature variation as a proxy for plasticity? Given the importance of behaviour in shaping how environmental variation is experienced, the answer seems to be, unfortunately, 'No'. Two species may coexist in the same highly variable and complex environment, but experience it very differently based on patterns of diapause or resource choice.



If we are interested in predicting variation in learning and plasticity, we may need a more direct measure of ‘experienced’ environmental variation, or a suite of traits that together may interact to determine how an organism experiences variation. For instance, measures of specialization and generalization, which likely more directly measure the degree of environmental variation a species experiences, are often tied to modern-day population trends (Devictor, Julliard, & Jiguet, 2008; Siriwardena et al., 1998). Models that combine such measures of resource use with other factors reviewed here, such as dispersal or migratory tendencies (Both et al., 2010), should be even more powerful predictors of population declines (Forister, Jahner, Casner, Wilson, & Shapiro, 2011; Warren et al., 2001). This review of traits underscores the fact that there is more than one way to thrive in a changing world, from moving around until an individual locates an environment to which they are adapted, to producing lots of genetically variable offspring, to plastically adjusting to whatever conditions arise.

The role of behaviour in shaping environmental variation and selection has been recognized in the theoretical literature for decades (e.g. Levins, 1963; MacArthur & Levins, 1964) across dozens of models (reviewed in Ravigne et al., 2009). From a theoretical perspective, we may still have insights to be gained by incorporating more behavioural and developmental realism into our models (Fig. 4; e.g. Draghi & Whitlock, 2012; Stamps & Frankenhuis, 2016). For instance, how might matching habitat choice and the evolution of plasticity change as the window of environmental sensitivity for trait development varies (Panchanathan & Frankenhuis, 2016)? As components of environmental variation can evolve, how do models of evolutionary processes change in terms of feedbacks and complexity? Over the last three decades, there has been an increasing call for incorporating development and behaviour into evolutionary models (Pigliucci, 2007; West-Eberhard, 2003), and, as we do just that, we are beginning to learn just how much biological realism is necessary for a more predictive theory of evolution. Regardless, the diversity of behavioural mechanisms that affect experienced environmental variation results in the potential for complex and variable environments to select both for and against learning and plasticity.

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