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Home and away: the role of intraspecific behavioural variation in biological invasion

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ABSTRACT

Invasive populations cause adverse impacts on ecosystems, agriculture, and economic activities. Advancing understanding of how populations respond to environmental changes and develop their invasive status will enable improved prediction, prevention, and management of ecological invasions. Here, we review recent literature and find that behavioural shifts within species across native and invasive populations are common during invasion. We collate examples which demonstrate how behaviours associated with invasion can be an outcome of plastic, pre-adaptive, and/or post-adaptive processes. However, we find that research investigating the molecular basis of observed behavioural shifts associated with invasion is limited. Important research (but perhaps the most challenging to conduct), is the long-term study of ongoing invasions that track species' behaviour and genetic change throughout the stages of the invasion process. Additionally, future research should aim to establish whether behavioural shifts originate from plasticity, microevolutionary processes, or a combination of both. Common garden experiments (using distinct populations grown under shared conditions), carried out in conjunction with genetic studies that track changes at the molecular level, could aid this endeavour.

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Introduction

Ecosystems around the globe are faced with a multitude of challenges, one of the most significant being the establishment and spread of exotic species in areas beyond their natural ranges. Biological invaders are widespread (Vitousek et al. 1997) and present significant threats to agriculture, public health, and other human activities (Hulme 2009). Invasive species can drive population declines and extinctions and place considerable stress on native biodiversity through predation, competition for resources, and introduction of foreign diseases (Clavero and García-Berthou 2005; Mooney et al. 2013; Bellard et al. 2016). Moreover, the risks presented by invasive species are only increasing, as climate change creates opportunities for organisms adapted to warmer temperatures

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to expand their ranges, and invading species consequently reduce the resilience of native ecosystems (Mainka and Howard 2010).

Although invasion is common, only a small proportion of species that colonise new environments proliferate and expand their range (Williamson and Brown 1986) – but those that do present major challenges to invasion biologists, biosecurity managers, and environmental protection agencies. Key to the management and prevention of these ecological incursions is the identification of characteristics that correlate with invasiveness (Holway and Suarez 1999; Fogarty et al. 2011; Chapple et al. 2012a). If we can improve our understanding of how species respond to environmental changes and subsequently found and develop as invasive populations, we will be better placed to predict future incursions, map the ongoing development of existing invasions (Chapple et al. 2012a), prevent new ones, forecast their effects, and mitigate their damaging impacts on native communities (Holway and Suarez 1999; Kolar and Lodge 2001; Cassey et al. 2004; Puth and Post 2005).

Studies at the species level have shown that invasive taxa commonly excel at one or more convergent traits, with some invasive species arriving ‘pre-adapted’ to a new area – i.e. in possession of a range of genetic (e.g. high number of genes, Zhao et al. 2023), morphological (e.g. smaller body size, Mahoney et al. 2015), life history (e.g. generation time, number of offspring, reproductive output, Forsyth et al. 2004; Capellini et al. 2015), physiological (e.g. growth rate, heat tolerance, Bates et al. 2013), and behavioural traits that increase their invasive potential – while others rapidly evolve beneficial characteristics after the invasion event. Among these invasive traits are often behaviours that augment survival, functioning, and/or dispersal in new habitats, and also increase the invasive species’ environmental impact. For example, increased sociability, boldness/risk-taking, dispersal tendency, aggression, exploration, neophilia, learning ability, conspecific tolerance, foraging activity, and general activity levels (for example see Rehage and Sih 2004; and Pintor et al. 2008;) are all considered important behaviours across the four stages of invasion (including uptake onto transport vectors, introduction, establishment, and spread; Figure 1). However, data on behaviour is often absent from studies on invasion, having received less consideration than other characteristics that may explain invasion success (Holway and Suarez 1999), likely because such data can be extremely challenging to collect in natural systems.

Where invasive behaviour has been the subject of research, the scientific literature is dominated by comparisons made at the species level, rather than at the population level, or within an invasive metapopulation. However, different invasive species are likely to possess numerous trait differences aside from those suspected to influence invasion, making it difficult to determine which trait(s) result in greater invasiveness. Drawing intraspecies comparisons (i.e. between native and invasive populations of the same species) can conversely increase our understanding of how behaviour rapidly changes throughout the invasion process as a direct result of the invasion itself. Obtaining such knowledge will help environmental managers predict the possible trajectories of new incursions and, where possible, act to manipulate external pressures on invasive populations to mitigate their speed and/or impact.

Our aim was to review the role of intraspecific post-invasion behavioural change. To achieve this, we undertook a systematic review of peer-reviewed sources from the Web of Science. We assessed 490 publications that appeared in a search using the term ‘(behavio* OR personalit* OR plastic* OR syndrome*) AND (dispers* OR invas* OR non-invas* OR native OR foreign OR alien OR introduced OR introduction* OR non-native OR

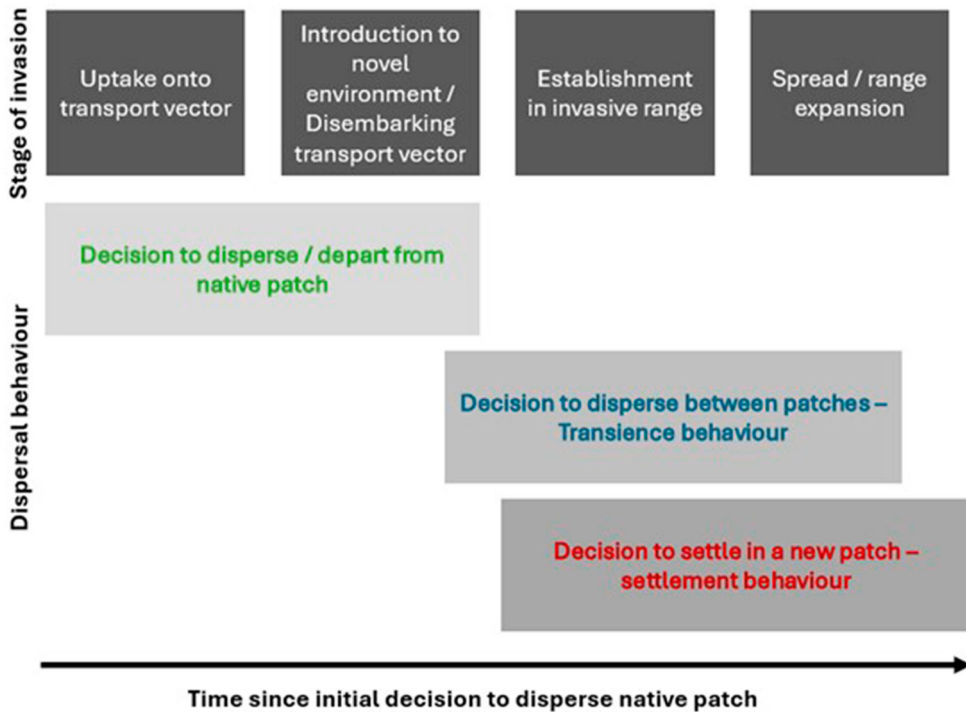


Figure 1. The invasion sequence and parallel dispersal behaviour over time (Clobert et al. 2009). The figure depicts the role of dispersal behaviour in invasion, however, other elements of behaviour (i.e. foraging behaviour, nest site choice) are also important, although not represented.

‘invasion front’ OR ‘range edge’ OR novel OR ‘range expansion’) AND (population* OR specie* OR colon* OR evolution)*. The titles of all 490 resources were reviewed for eligibility (e.g. publications from microbiology, cancer research, and metallurgy were excluded, as was research on plant behaviour). Abstracts from the remaining papers were then screened and included in the full literature review if they examined intraspecific behavioural variation between native and invasive ranges and/or between range cores and range edges in the invasive range. This resulted in 48 papers, which we combined with 22 additional publications that we identified during our wider reading and review of reference lists. Synthesising this research, we discuss mechanisms for behavioural change, highlighting case studies, summarising common findings and inconsistencies, and detailing directions for future research. Our review revealed that the literature is skewed towards post-invasion processes, therefore these form the balance of our focus. Our review is limited to the investigation of animal invasions, with studies of invasive plants, microbes, and fungi considered outside the scope.

Behaviours on the move: behavioural variation and invasion

A developing body of work shows that behavioural traits can rapidly shift upon introduction to a new environment, and that these post-invasion behavioural modifications could correlate with enhanced invasion success (Chapple et al. 2012b). For example, changes in

specific behavioural attributes, such as aggression (Pintor et al. 2008), feeding behaviour (Martin and Fitzgerald 2005; Pintor and Sih 2009; Carbonell et al. 2021), danger responses (Daniels et al. 2004; Levri et al. 2017), predator avoidance behaviour (Levri and Clark 2015; Reisinger et al. 2017; Johnston and Smith 2018), dispersal tendency (Levri and Clark 2015), social behaviour (Robertson and Rosenblum 2010), sexual behaviour (Westrick et al. 2019), daily or seasonal activity patterns (Fortes Silva et al. 2019; Poláčková et al. 2022), and neophilia (Candler and Bernal 2015) have all been detected in invasive populations when compared with their native counterparts (Figure 2).

In some instances, the co-occurrence of changes in multiple invasive behavioural traits have provided evidence for ‘invasive personality’ types facilitating invasion (Figure 2). For example, low risk-prone personalities (i.e. with a combination of higher exploratory, active, and bold tendencies) have been shown to be over-represented in invasive populations compared with conspecifics in natural ranges. This is evident in invasive crayfish (Pintor et al. 2008), fish (Rehage and Sih 2004; Myles-Gonzalez et al. 2015; Thorlacius et al. 2015), lizards (Short and Petren 2008; Damas-Moreira et al. 2019), amphibians (Baxter-Gilbert et al. 2021), and rodents (Malange et al. 2016). Similarly, studies investigating the role of personality types in the population dynamics of invasive fishes have suggested that dispersal may be led by individuals exhibiting an asocial personality

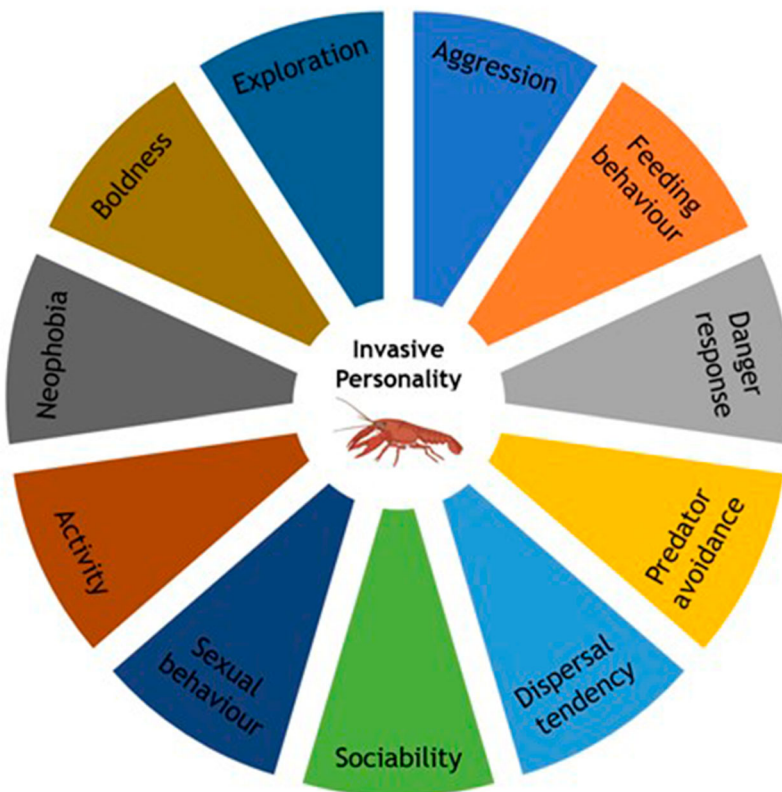


Figure 2. Changes in specific behaviours have been recorded in invasive populations when compared with counterparts in the native range. The co-occurrence of changes in multiple behavioural traits are indicative of an ‘invasive personality type’.

type (i.e. being more likely to avoid / disperse away from high density sites and to preferentially settle in low-density sites; Cote et al. 2011). For example, Cote et al. (2011) suggested that the invasion front of the invasive mosquito fish (*Gambusia affinis*; Figure 3) may be dominated by asocial individuals. Thorlacius et al. (2015) also

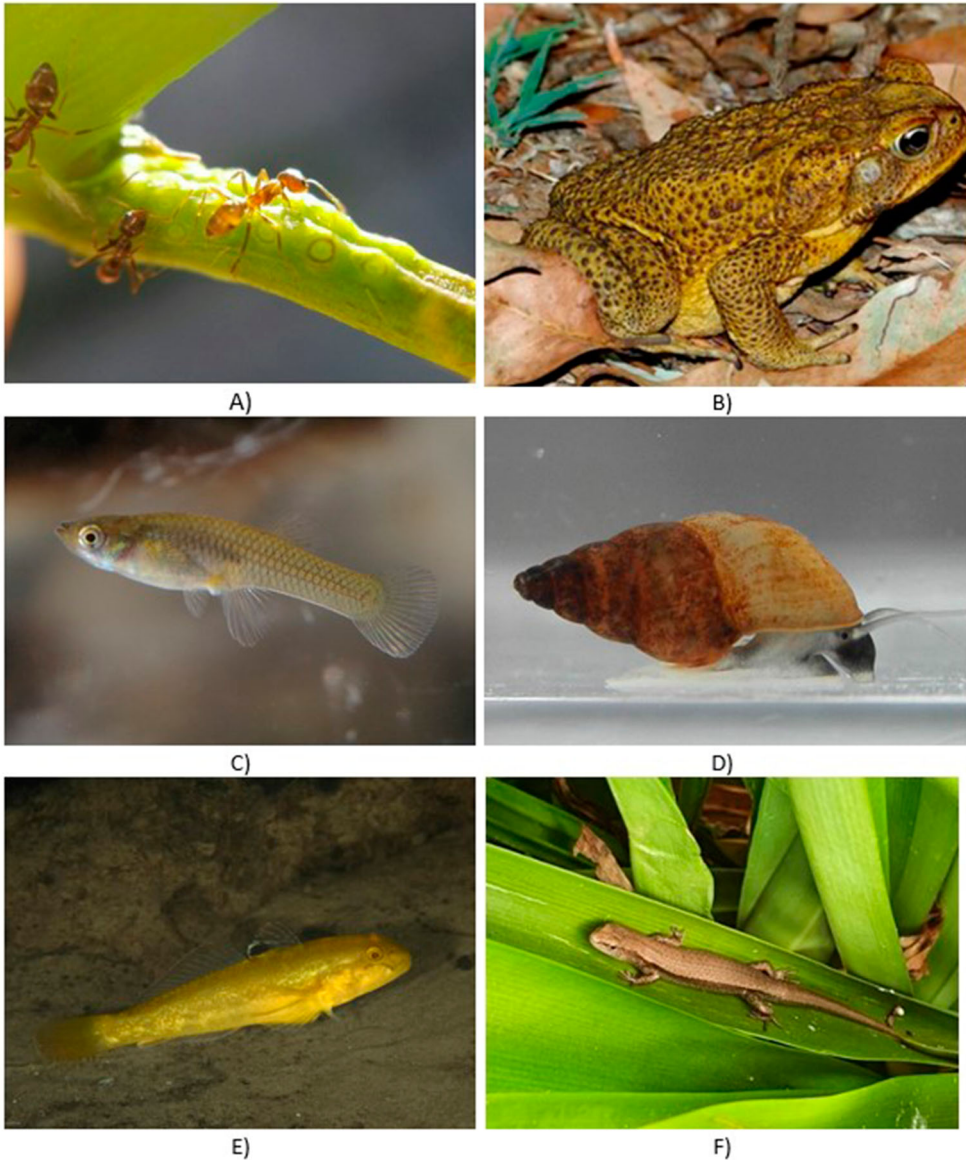


Figure 3. Key invasive species that have been the subject of behavioural research: **A**, Argentine ant (*Linepithema humile*), **B**, cane toad (*Rhinella marina*), **C**, mosquito fish (*Gambusia affinis*), **D**, New Zealand mud snail (*Potamopyrgus antipodarum*), **E**, round goby (*Neogobius melanostomus*), and **F**, plague skink (*Lampropholis delicata*). Photo credits: A, José Luis Barberán, ArgentiNat, B, Steve Kerr, iNaturalist NZ, C, NOZO, Wikimedia Commons, D, Michal Manas, Wikimedia Commons, E, Rob Dutch, iNaturalist, F, Michael Lambert, iNaturalist NZ.

demonstrated that populations of the invasive round goby (*Neogobius melanostomus*; Figure 3) vary in expression of personality traits, with individuals in newly-established invasive populations shown to be more asocial than older populations.

As well as invasive versus native range comparisons, individuals or populations at the invasion front (range-edge) can be compared to established invasive populations at the range core to provide useful insights into how certain behaviours may be up- or down-regulated at different stages of the invasive process (Duckworth and Badyaev 2007; Groen et al. 2012; Thorlacius et al. 2015). For example, relative to range-core counterparts, range-edge populations of expanding species can differ in dispersal tendency or ability, aggression, boldness, activity, and sociability. One of the consequences of this is that an invasive population can develop a continually accelerating dispersal rate (Hudina et al. 2014), as has been observed in the Australian cane toad (*Rhinella marina*; Figure 3), whose yearly rate of expansion has increased almost fivefold since first being introduced (Shine et al. 2006).

The ecological success of ants has made them globally abundant, yet notable differences in the social structure and behaviour of invasive and native populations has been repeatedly recorded across ant species, providing a compelling case study. In the native range, intraspecific competition between colonies generally constrains nest density. However, the formation of large supercolonies that lack intraspecific aggression between sub-colonies has been recorded in numerous invasive ant species (Kjeldgaard et al. 2022). These supercolonies often spread over thousands of kilometres and can contain substantial polydomous (occupying two or more spatially separated nests) and polygynous (males have more than one mate) colonies constructed from connected nests that liberally exchange individuals (Holway et al. 2002; Eyer and Vargo 2021), whereas such associations are generally absent in the native range. This social organisation requires an easing of colony boundaries and no, or significantly reduced, intraspecific aggression among colonies through a loss of nest mate recognition and a lack of aggression toward non-nest mates (Helanterä et al. 2009). Conferring dominance over resources (Tsutsui et al. 2000) and removing costs associated with intraspecific competition and territorial conflicts, this behavioural shift has resulted in populations that are ecologically dominant and outcompete native species, altogether inflating their environmental impact (Holway et al. 1998; Tsutsui et al. 2000; Holway et al. 2002). It can also work in concert with other behavioural modifications to further promote invasiveness. For example, alongside reduced aggression in the invasive range, Argentine ant (*Linepithema humile*; Figure 3) workers in Europe (introduced range) have a higher tendency to explore novel environments and scatter larvae, are more active and aggressive interspecifically, discover food resources more rapidly, and dominate more space than workers in the native range (Blight et al. 2017).

Beyond borders: mechanisms of post-invasion behavioural change

Despite increasing evidence that behavioural variation occurs between populations in their native and invasive ranges, the underlying mechanisms for these behavioural shifts are not well-understood (Phillips and Suarez 2012). However, there are two broad processes at play: (1) Swift changes in heritable behaviours and associated genotypes driven by the selective pressures imposed by a new environment (i.e. adaptation);

and (2) Behavioural plasticity induced by new environments experienced and, perhaps associated with, differences among individuals in regard to past experiences (i.e. learning) (Phillips and Suarez 2012; Gruber et al. 2017b). Understanding the mechanisms that enable behavioural change is key, as these can influence both the speed and impact of invasive species (e.g. on native species) (Ruland et al. 2020). For example, behavioural learning can dissipate through a population more rapidly than genetic changes (Zuk et al. 2014). The two mechanisms also likely operate in combination. For example, the capacity for behavioural plasticity may evolve during the process of range expansion or biological invasion (Stamps and Groothuis 2010; Diamond and Martin 2016; Reisinger et al. 2017), and behavioural plasticity may create non-heritable variation in the invading population that becomes genetically assimilated in later descendant populations (Huey Raymond et al. 2003; Badyaev 2005; Ghalambor et al. 2007; Foster 2013). In this section, we first cover processes that are genetic in nature (i.e. evolutionary processes), then follow with processes that are not genetically fixed (i.e. plastic processes). However, we recognise that these processes sometimes cannot be teased apart or discretely grouped.

Variation in dispersal behaviour

Successful biological invasions rely intimately on dispersal behaviour (Phillips and Suarez 2012), encompassing departure from the initial (native) patch, movement between patches (transience), and settlement in a new patch (Bowler and Benton 2005; Clobert et al. 2009) (Figure 1). Dispersing individuals often encounter dramatic ecological changes throughout the invasion process. As a result, the benefits conferred from the expression of different behaviours will vary depending on which stage of the invasion process a population is presently experiencing, with each stage potentially acting as a selective filter on traits related to invasion success (Carrete et al. 2012; Chapple et al. 2012a). For example, different behaviours may predispose individuals to capture during transport, or they may enhance dispersal upon arrival to the new habitat.

Dispersal behaviour has been shown to be highly variable among individuals (Clobert et al. 2009), suggesting that dispersers are not a random subsample of a population. In fact, non-random dispersal may be the rule, rather than the exception. Exemplifying this, asocial individuals are more likely to disperse when population density is high and may also be more likely to disperse further than their social conspecifics (Cote and Clobert 2007; Cote et al. 2010), which could potentially result in invasive populations that display more asocial behaviours than their native-range counterparts (i.e., socially-biased dispersal acting as a selective filter; Cote et al. 2010; Cote et al. 2011).

Bold, risk-taking, exploratory, active, individuals may be more likely to find their way onto transport vectors (Blackburn and Duncan 2001; Briski et al. 2018; Chapple et al. 2022). Once introduced, these individuals may be more likely to disperse further, more quickly, and discover more appropriate habitats and resources, resulting in an over-representation of such behaviour at the invasion front (Cote et al. 2011; Groen et al. 2012; Liebl and Martin 2012; Chapple et al. 2022). However, it can be difficult to determine whether these behaviours are the result of personality-dependent dispersal, or whether a random set of individuals has dispersed to the new range and those that have a bold, active, and asocial personality are the ones that survive and reproduce. It

is also possible that both processes operate and reinforce each other. Regardless, invasive populations often consist of more exploratory, active, and bold individuals than native-range populations (Lapiedra et al. 2017; Chapple et al. 2022), and the higher proportion of these individuals at invasion fronts likely facilitates the further dispersal and rapid expansion of invasive populations (Myles-Gonzalez et al. 2015).

Individuals that are more dispersive also tend to be the first to newly establish a population (Hanski et al. 2004; Shine et al. 2006; Hughes et al. 2007; Duckworth Renée 2008). When more aggressive, faster-dispersing individuals continue to expand the range front/edge, selection there will likely favour traits that increase dispersal ability further (Phillips Benjamin et al. 2008; Alford et al. 2009; Léotard et al. 2009) in a process known as ‘spatial sorting’ or the ‘Olympic Village effect’ (i.e. assortative mating or inbreeding of individuals at the range-front) (Shine et al. 2011). As a result, extremely aggressive, highly dispersive characteristics are expected to consistently evolve upwards during range expansion (Burton et al. 2010) permitting animals at the invasion front to infiltrate uncolonised areas several times faster than in the earlier stages of invasion (Alford et al. 2009).

Disperser-dependent founder effects can also occur during invasion when bolder, more exploratory individuals colonise new areas by chance. The ongoing expansion of the cane toad’s range in Australia is considered an example of this, with more bold individuals stochastically dispersing to the range-front to create new founding populations with a bold behavioural phenotype (Gruber et al. 2017b). Similarly, heritable differences in tadpole boldness between mainland and invasive island populations of common frogs (*Rana temporaria*) is thought to have resulted from more exploratory adults by chance being the colonisers of new islands as they rose above sea level approximately 350–800 years ago (Brodin et al. 2013).

Selective pressures on behaviours, such as aggression (Duckworth and Badyaev 2007; Duckworth Renée 2008; Groen et al. 2012; Michelangeli et al. 2017) and tendency to disperse, are expected to differ at the invasion front and range interior (Phillips Benjamin et al. 2008), as well as between the former and the native range. However, behavioural adaptations for increased dispersal should only exist in a population for a short time after colonisation as the adaptive value of dispersing declines and selection instead favours other trait combinations that confer advantages in higher density populations with increased competition for resources (Thorlaciuss et al. 2015). This pattern has been observed in the highly successful invasive cane toad (Phillips et al. 2007), where toads at the invasion front show an amplified dispersal ability compared with toads in range-core populations (Urban Mark et al. 2008), but become less exploratory and risk-taking with time (Gruber et al. 2017a). Similarly, in western bluebirds (*Sialia mexicana*), aggressive individuals dominated populations at the invasion front for a few generations, but aggression waned after a competitor (mountain bluebirds, *Sialia currucoides*) had been excluded (Duckworth and Badyaev 2007). These examples demonstrate how selection can favour different traits depending on the invasion stage and associated spatial sorting and population density (Cote et al. 2011; Fogarty et al. 2011).

Evolutionary processes

Evolutionary processes, such as genetic drift (including bottlenecks and founder effects, where demographic changes associated with invasion of a small number of individuals

reduces genetic diversity), and adaptive evolution, can operate at multiple stages of the invasion process, and can ultimately lead to genetic divergence from conspecifics in the natural range (Holway et al. 2002; Pintor and Sih 2009; Blight et al. 2017).

Genetic drift

Low genetic diversity in the invasive range following population foundation is common (Rollins et al. 2015), with bottlenecks generally predicted to inhibit population growth due to inbreeding depression, increased fixation of deleterious alleles by genetic drift, and reduced evolutionary potential to respond to new selection pressures (Schrieber and Lachmuth 2017). However, many introduced populations do not appear to be challenged by these problems in a phenomenon known as the ‘genetic paradox of invasion’ (Estoup et al. 2016). Theory suggests that such populations may benefit from multiple introduction events from genetically diverse source populations (Facon et al. 2006), while a temporary or permanent release from stress in invaded habitats may also alleviate the problems associated with reduced genetic diversity (i.e., the ‘enemy release hypothesis’; Roy et al. 2011; Sarabeev et al. 2017; Antonini et al. 2019; Michelan et al. 2023). Moreover, interactions between inbreeding and the novel environment may actually facilitate rapid evolution and contribute to adaptation even under conditions of reduced genetic diversity (Schrieber and Lachmuth 2017).

Adaptive selection

Following invasion, populations may be subjected to new selective pressures that result in rapid adaptation of behavioural traits. For example, invasive populations of invasive plague skinks (*Lampropholis delicata*; Figure 3) were significantly more exploratory and, in some instances, bolder than their native range counterparts in a manner consistent with selective processes over and above founder effects (Chapple et al. 2022). The authors argued that, under a pure founder effects framework, the directionality of trait differences between native and invasive populations should be random, while they instead discovered consistent differences in exploratory behaviour across three discrete invasive lineages. One of these lineages – the invasive Lord Howe Island population – experienced recurrent introductions but showed no evidence that the associated genetic admixture from divergent source populations had countered or reduced any founder or other drift effects, providing further support that selective forces promoted risk-prone behaviour types in these skinks (Chapple et al. 2022). Other studies, including common garden experiments (i.e., in which organisms from different populations are reared together under the same environmental conditions to determine the influence of the environment vs. heritability; de Villemeireuil et al. 2016; Berend et al. 2019), have also supported heritable behavioural shifts in invasive populations as the outcome of rapid evolution in the new habitat (e.g. Gruber et al. 2017b; Stuart et al. 2019).

Founder/bottleneck effects and natural selection can, of course, operate in concert to promote invasion. An excellent example comes from the invasive *Potamopyrgus antipodarum* (Figure 3) – a New Zealand mud snail that can reproduce sexually, but for which invasive populations derive from different clones so that individuals within populations are genetically identical but different populations are genetically distinct (Alonso and Castro-Diez 2012). These snails have provided new insights into evolutionary processes associated with behavioural shifts during invasion, with certain invasive clonal

populations more invasive than others and their associated behaviours differing from each other but matching their relevant source populations, suggesting population, and possibly genotypic, effects on behaviour (Levri and Clark 2015). Levri and Clark (2015) showed that the most invasive clonal population of the snail exhibited behaviours that increased survival, reproduction, and spread, suggesting that particular clones may be more likely to establish and spread as a result of founder effects and adaptive selection operating in concert. Later research showed that two invasive populations of the snail responded behaviourally to the odour of an unfamiliar predator, while a non-invasive American population did not, though it was unclear whether predator avoidance evolved rapidly post-invasion in different populations, or was brought into new habitats by founder individuals and subsequently refined (Levri et al. 2017).

Another example of selection operating rapidly on behavioural traits is seen in the pond slater (*Asellus aquaticus*) following invasion of a novel stonewort habitat. Here, researchers compared the invading population with an ancestral reed population and found that boldness in the two populations diverged, forming two distinct ecotypes (Karlsson Green et al. 2016). The authors used a combination of common garden experiments and modelling analyses to investigate selection for trait combinations to determine the heritability of these behavioural differences. They showed that genetic correlations among some traits decreased or disappeared following colonisation, while one new correlation arose in the stonewort population. This was taken as evidence that behavioural characteristics had become decoupled in the short time (< 40 years) since colonisation of the new environment (Hargeby et al. 2004). Thus, genetic correlations among behavioural traits can change to optimise fitness even within short time frames, and may reflect adaptive processes post-invasion (Roff and Fairbairn 2012).

Pre-adaptation: the AIAI hypothesis

Pre-adaptation is an important feature of invasion success, and recent evidence suggests that urbanisation may facilitate this when species have adapted to urban environments in their native range before being introduced to a similar environment in the invasive range (Hufbauer et al. 2012; Borden and Flory 2021). For example, urban populations in both the native and invasive range of the guttural toad in Durban, South Africa were significantly bolder than their rural counterparts, providing a considerable advantage during invasion of new urban environments in both Mauritius and Réunion Islands (Baxter-Gilbert et al. 2021). Such behavioural modification could occur via behavioural flexibility (Hudson et al. 2017), developmental plasticity (Brodin et al. 2013; Gruber et al. 2017b; Mühlenhaupt et al. 2022), or rapid localised adaptation (Whitney and Gabler 2008; Baxter-Gilbert et al. 2019), and supports the ‘anthropogenically induced adaptation to invade’ (AIAI) hypothesis (that species adapting to human-modified settings can increase their invasive potential through the development of adaptive phenotypes that offer advantages in anthropogenic habitats; Hufbauer et al. 2012). Under the AIAI hypothesis, urban areas can be seen as ‘sorting grounds’ for many invasive species, selecting successful establishers for future invasion (Hufbauer et al. 2012).

While Baxter-Gilbert et al.’s (2021) study provided support for the AIAI hypothesis and showed a clear divergence in behaviour among adult populations of guttural toads, common garden experiments to determine whether the observed behavioural shifts were heritable adaptations or examples of behavioural plasticity were inconclusive

(Mühlenhaupt et al. 2022). This highlights the difficulty of conclusively determining the mechanisms behind behavioural change, and many of the studies discussed above were similarly unable to infer the evolutionary processes that may have produced the observed behavioural patterns. Further molecular and common garden experiments (de Villemer-euil et al. 2016; Berend et al. 2019) are required to elucidate the mechanistic drivers behind behavioural shifts that accompany invasion.

Behavioural plasticity

Behavioural plasticity refers to the capacity of a single genotype to produce different behavioural phenotypes in response to a range of environments and ecological conditions (Roff 1999). Behavioural plasticity may buffer animals against the novel selection pressures they face within a new range by allowing them to rapidly adjust their behaviour to the new environmental conditions. Therefore, behavioural plasticity is considered particularly important for invasive processes, as it allows immediate within-individual changes in response to new conditions without the requirement for genetic adaptation (Robinson and Holmes 1982; Robinson and Dukas 1999; Ghalambor et al. 2007; Lande 2009; Ruland et al. 2020). In fact, plasticity may even be a requirement for survival during the initial stage of colonisation, allowing individual modification to occur as a first response before adaptive processes (that may require changes in morphological, physiological, or life history traits; West-Eberhard 2020) can operate (Lande 2009; Chevin et al. 2010).

Behavioural plasticity is commonly invoked as a major mechanism that facilitates the expansion of a population's geographic range and the colonisation of novel environments (Roughgarden 1972; Holway and Suarez 1999; Ghalambor et al. 2007) for two main reasons. First, plasticity may allow more colonising individuals to initially survive and persist so that the population can later adapt to new environmental conditions via directional selection (Ghalambor et al. 2007; Crispo 2008; Foster 2013; Levis and Pfennig 2016). Thus, plasticity may promote evolution by creating non-heritable variation in the invading population that is later genetically assimilated (Huey Raymond et al. 2003; Badyaev 2005; Ghalambor et al. 2007; Foster 2013) – a process that may be especially critical in invasive populations that have low genetic diversity (Robinson and Dukas 1999). However, a key condition is that individuals must be able to behaviourally respond to new selective pressures operating on the invading population if new habitats are ecologically, but not evolutionarily, novel (Ghalambor et al. 2007; Crispo 2008; Foster 2013; Levis and Pfennig 2016). This is because lineages may retain the proximate physiological mechanisms that generate adaptive plasticity, even if the environmental factors that induce phenotypic shifts have not occurred in that lineage for extended periods of evolutionary time (West-Eberhard 2020). Invasive populations of guttural toads provide evidence that beneficial behavioural traits can be preserved in populations and re-expressed post-invasion (Baxter-Gilbert et al. 2021). Second, plasticity might evolve rapidly in the initial colonising generations to facilitate local adaptation (Wcislo 1989; Price et al. 2003; Schlichting 2008; Foster 2013). However, despite a large amount of theory, there is no direct evidence that plasticity is positively selected during colonisation (West-Eberhard 2005; Chevin et al. 2010; Lande 2015). Therefore, further research is needed, and native/invasive range comparisons

will be critical for assessing relevant hypotheses (van Kleunen and Fischer 2005), such as that species become more plastic in their invasive range. Moreover, longitudinal studies will be essential for enhancing knowledge of the role of behavioural plasticity throughout the invasive process. To our knowledge, no such studies currently exist, most likely due to the difficulties associated with the rapid collection of genetic and ecological behavioural information once an invasion has been detected.

Behavioural plasticity enables swift responses to environmental change either by innovation or through social learning of new behaviours. At the individual level, plasticity may result from individual learning, in which an individual devises a new behaviour or modifies an existing one ('innovation') (Laland and Reader 2003), or through social learning, in which an individual learns a new behavioural variant displayed by others (Boyd and Richerson 1985). Behavioural plasticity through either form of learning is predicted to be advantageous when environments change, although social learning may be less useful when conditions fluctuate swiftly (Dawkins 1980). Individual and social learning differ in their propensity to introduce new behavioural variants into the repertoire populations. Individual learning can generate innovative behaviours that enhance the behavioural diversity of the population, while social learning can lead to the establishment of learned behaviours that may displace those attained by individual innovation, thus leading to a general decrease in the number of behavioural variants expressed by individuals in the population (Laland and Reader 2003). Therefore, individuals from invasive populations may adjust the degree to which they express behavioural plasticity in an adaptive manner during the different stages of invasion. This is a key prediction of the 'adaptive flexibility hypothesis' (Wright et al. 2010). As it relates to biological invasion, this hypothesis predicts that the expression of behavioural flexibility, and thus the diversity of behaviours observed in a population, will rapidly increase throughout colonisation and the early stages of establishment, due to innovation and the need to shift to a new optimal phenotype in response to new environmental conditions. An associated prediction is that evolution will favour higher plasticity initially in a novel environment, with this then expected to decline during the establishment and growth phases of invasion as a result of social learning of successful behavioural traits (Wright et al. 2010; Lande 2015; Westrick et al. 2019). In particular, Huang et al. (2015) suggested that large costs and minor benefits may constrain the evolution of greater plasticity in the native range, but reduced costs and increased benefits of plasticity may promote such evolution in the introduced range. These authors also suggested that, as invasive populations are often released from natural enemies, they may more easily afford the costs associated with evolving greater plasticity than native populations (Huang et al. 2015). Therefore, behavioural flexibility may promote stability and persistence during the early stages of invasion when invasions are characterised by small populations that are susceptible to environmental and demographic stochasticity, but become disadvantageous as the population becomes established, causing plasticity to decrease towards native-range levels (Lande 2015). As such, behavioural plasticity may itself evolve over time, resulting in changes in the genetic mechanisms underlying the way or degree to which animals respond to environmental cues (Ghalambor et al. 2007; Shaw et al. 2007; Foster 2013; Levis and Pfennig 2016). A fundamental assumption underlying this theory is that there is genetic variation for plasticity, such that selection has the opportunity to act on its expression (Scheiner 1993).

A consequence of fluctuating behavioural plasticity is that the point in the invasion process at which a population is surveyed for plasticity has serious implications for determining whether it is adaptive or not (Agrawal 2001; Pigliucci and Murren 2003). Few empirical studies comparing native and invasive patterns of behavioural plasticity exist (Handelsman et al. 2013). However, female guppies (*Poecilia reticulata*) from introduced populations are less responsive to males when reared without predator cues but return to a high-predation phenotype when reared with predator cues (Westrick et al. 2019). This pattern was evident across introduced populations from different ranges but absent from the native range where females consistently experience high predation pressure, suggesting it is likely to have evolved in the invaded range rather than to have resulted from drift or founder effects and/or adaptive plasticity in the native range (Westrick et al. 2019). Plague skinks showed more plastic exploratory behaviour, activity, and boldness than their native counterparts, with the greatest differences in the most recently-established populations (Chapple et al. 2022). Chapple et al. (2022) argued that this increased behavioural plasticity may be one way in which organisms cope with changing environmental conditions during biological invasions, however they could not determine whether it represented a pre – versus post-invasion adaptation (Chapple et al. 2022).

Research suggests that invasive species may use plastic behavioural responses to kairomones – allelochemicals released by one species that benefit another – to evade predation by new predators (Hazlett et al. 2003). In fact, plasticity in anti-predator responses is assumed to be one of the key ecological forces enabling the survival and rapid evolution of prey that face new predators in the invasive range (Pujol-Buxó et al. 2013). However, empirical evidence in support of behavioural plasticity to kairomones in invasive populations is weak. For example, Levri et al.'s (2017) experiments on New Zealand mud snail clones revealed that genetically distinct invasive clonal populations responded differently to novel predators, though this may reflect founder effects and selective forces (as discussed above).

Closely related to behavioural plasticity is the ability to alter behaviour in response to learned patterns, and this is likely a contributing factor to the success of invasive species. For example, invasive cane toads use spatial memory of experiences with an environment to alter their exploratory and foraging behaviours in order to increase foraging efficiency (Miller et al. 2018). This is consistent with anecdotal information on cane toad foraging behaviour in urban environments (Alexander 1965) and aligns with similar research on colonising rats, which decrease their exploratory behaviour over time to stay close to known areas (Russell et al. 2010). Similar to behavioural plasticity, Miller et al. (2018) noted that the adaptive value of spatial learning is likely highest at the initial stages of introduction and is expected to decrease as individuals spread.

The molecular basis for behavioural change

An objective in current animal personality research is to identify the molecular basis of measured behavioural variation (Laine and van Oers 2017). While many quantitative genetic studies of animal personality have reported moderate to high estimates of heritability (Stirling et al. 2002; Dochtermann et al. 2015; Dochtermann et al. 2019), few studies have investigated the molecular basis for this observed heritability, and research on the relationship between genes and behaviour is in its infancy. Laine and van Oers

(2017) provided an overview of quantitative and molecular genetics approaches in the field of animal personality and Bubac et al. (2020) reviewed the scientific literature investigating the molecular basis of behavioural traits in natural populations. Both reviews revealed that few studies have attempted to determine the genetic basis of behavioural phenotypes in natural populations and there is a need to integrate molecular and quantitative genetic methods. Similarly, many of the studies discussed so far have used behavioural assays, common garden experiments, and the tracking of behavioural patterns to theorise the mechanisms behind behavioural shifts in invasive species. However, the molecular mechanisms that may underpin these behavioural changes are less-studied and poorly understood despite the fact that elucidating their genetic basis is a key step towards understanding the evolutionary potential and limitations of the invader.

Fortunately, high-throughput nucleotide sequencing and other technological advances are now increasing our ability to examine the genomic basis for the functional shifts associated with biological invasions (Rius et al. 2015). In a notable study, Mueller et al. (2014) identified SNPs associated with neophilic behaviour and activity level in two invasive populations of the yellow-crowned bishop (*Euplectes afer*) and proposed that these alleles were likely introduced from the native population. The short invasion history (c. 30 years) and assumed small original population size(s) of the birds were used to suggest that the behaviour-associated SNPs were unlikely to have established from new mutations that arose after the invasion. However, the study lacked a comparison of allele frequencies between the invasive and native populations and did not compare invasive populations of different ages to track genetic changes over time (Carrete et al. 2012; Edelaar and Bolnick 2012). More recently, Yagound et al. (2022) used RNA sequencing to investigate brain transcriptomes of cane toads from Hawai'i (the native population) and nine invasive populations along an east to west transect across the Australian invasive range that reflects the timeline of the cane toad invasion. These authors found extensive differences in brain gene expression profiles between Hawai'i and Australian populations for key genes with functions putatively associated with dispersal behaviour, while more modest differences were seen across the Australian transect (Brown et al. 2015). These genes may therefore play an important role in the behavioural changes associated with the introduction of invasive Australian cane toads (Yagound et al. 2022). However, teasing apart the effects of rapid evolution and environmentally-induced variation (i.e., phenotypic plasticity), or the adaptive evolution of phenotypic plasticity itself, is difficult (Ghalambor et al. 2007) and common garden experiments that measure dispersal-related behaviour alongside gene expression in the identified genes will be required to elucidate the heritability, and thus evolvability, of the observed behavioural and transcriptomic changes (Yagound et al. 2022).

As noted above, ants provide a compelling case study for behavioural studies. The most touted theory explaining the lack of, or limited aggression among, invasive ants is that individuals in invasive colonies are genetically alike (via a founder effect) and thus have similar or identical heritable recognition cues (Tsutsui et al. 2000; Tsutsui et al. 2003). In supercolonies of invasive Argentine ants, many populations exhibit low levels of genetic variation, even at a transcontinental scale, though others exhibit considerable genetic variation between populations (Tsutsui et al. 2000; Sunamura et al. 2009). Reduced variation in loci relating to cuticular hydrocarbon production ('CHC') – chemicals used in kin mate recognition in ants (Pirk et al. 2001; Giraud et al. 2002) – has garnered much

interest. In fact, supercoloniality appears to be coupled with a reduced number of, or low variability in, these recognition-related compounds for several invasive ant species (Errard et al. 2005; Cremer et al. 2008; Brandt et al. 2009), suggesting a potential mechanism for the rise of supercoloniality whereby a loss of polymorphism at CHC loci may have decreased the ability of workers to discriminate between nest mates and non-nest mates (Tsutsui et al. 2000; Giraud et al. 2002; Tsutsui et al. 2003). To gain further insight into the molecular basis of variation in the Argentine ant's behaviour across its native and introduced ranges, Felden et al. (2019) measured variation in the expression of genes associated with key biogenic amine neural pathways. Various behavioural traits (such as foraging and inter- and intraspecific aggression) are regulated by biogenic amines in social insects (Liang et al. 2012; Kamhi and Traniello 2013; Kamhi et al. 2017), thus Felden et al. (2019) theorised that range-specific behavioural differences would also display range-specific expression profiles at the molecular level. Indeed, these authors found that ten of 14 gene receptors were expressed at significantly higher levels in the native versus introduced range (Felden et al. 2019), providing evidence for variation in the molecular basis of behavioural differences between the ranges. Further clarification of the underlying causes of variation in gene expression between native and introduced ranges will require additional studies that quantify genetic variation in functional or regulatory loci related to the relevant signaling pathways for long-term replicate populations from independent introduction events.

New horizons: conclusions and future research

With global invasion rates escalating (Huang et al. 2015), much work remains to explain intraspecific behavioural variability between native and invasive populations, and between range edges and range cores in the invaded environment. Indeed, we found an overall paucity of information on this topic, despite its key implications for the effective management of invasive species – including the potential for better identification of threats prior to establishment and for enhanced understanding of dispersal behaviours and adaptive shifts during the invasive process.

Based on our review, future research should prioritise increasing our understanding of how behavioural changes among frontier populations arise, as it is at the range edge that 'invasiveness' (e.g. dispersal tendency) accelerates to expand a species' range and worsen its impact. Another marked gap we noted is the lack of research that uncovers the evolutionary (including genetic and molecular) processes that underlie behavioural shifts in invasive species. While the theories concerning the role and evolution of behavioural plasticity in biological invasion are well-developed, empirical studies are necessary to determine which processes are important and how they may interact. Future common garden experiments and molecular genetic studies will help to establish whether behavioural shifts originate from plasticity, microevolutionary processes, or a combination of both. Finally, perhaps the most important research, but also the most challenging to conduct, are long-term studies of ongoing invasions that track species' behaviour and genetics throughout the stages of the invasion process. This will require systems and processes to be established that enable the rapid mobilisation of funding and resources as soon as incursions are detected to forecast range-expansion trajectories and best inform invasion management.

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