

# The role of aggression in range expansion and biological invasions

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**Abstract** Traits that aid in the invasion process should exhibit a gradient across the expansion range in response to changing selection pressures. Aggression has been repeatedly associated with invasion success in many taxa, as it may help invaders to wrestle the resources from other species which enhances their success in a novel environment. However, aggression primarily allows individuals to overcome conspecific rivals, providing advantages in competition over resources. Agonistic prowess could therefore increase fitness at both ends of the expansion gradient. Here we review the role of aggression in range expansion of invasive species, and its potential role as a driver of range expansion. We analyze how these different mechanisms could affect trait variation in expanding and invasive populations. Specifically, we look at how aggression could help dilate the edges of a population through niche competition, as well as lead to exclusion from the center (i.e. areas of high population density) by the conspecifics. Both of these processes will result in a characteristic spatial distribution of phenotypes related to aggression that could provide insights into the ecological pressures and dynamics of expanding populations, potentially providing clues to their success as niche competitors and invasive species [*Current Zoology* 60 (3): 401–409, 2014].

**Keywords** Aggression, Trait variation, Invasion success, Invasive species

## 1 Introduction

Biological invasions represent a major aspect of human-induced rapid environmental change (Sih et al., 2011, Simberloff et al., 2013), contributing to the biodiversity loss, degradation of ecosystem structure and impairment of ecosystem services worldwide (Pyšek and Richardson, 2010). A tiny subset of introduced species passes successfully through all stages of invasion process to become invasive (cf. Williamson, 1996; Lockwood et al., 2007). Even so, the establishment and spread of invasive species exerts adverse environmental or economic impacts worldwide (e.g. Pimentel et al., 2001; Pyšek et al., 2008). Given such high variability in establishment success between different non-indigenous species and their potentially adverse impacts on native communities, prediction and identification of successful invaders has become a one of the most urgent challenges for invasion biology and invasive species management (Holway and Suarez, 1999; Marchetti et al., 2004). Frequently studied determinants of invasion success include introduction history (i.e. propagule pressure: Lockwood et al., 2005; Simberloff et al., 2009), ecological and evolutionary processes within the

recipient environment (cf. Alpert et al., 2000; van Kleunen et al., 2010) and species traits (i.e. Kolar and Lodge, 2001). Benefits of specific traits are often context-dependent, as their effects on invasion success may differ across different stages of invasion (Kolar and Lodge, 2001, Moyle and Marchetti, 2006) and conditions at the invaded ecosystem (Fogarty et al., 2011). Establishing the exact mechanisms of range expansion is therefore a complex problem which limits our ability to predict the dynamics of biological invasions and manage them successfully.

In addition to ecological and physiological advantages, behavioral traits can play an integral role in range expansion and with it the invasion success of animal populations. Behavior mediates species' interactions with their environment, and plays an integral role in the success of their transition through multiple stages of invasion process (i.e. Chapple et al., 2012; Holway and Suarez, 1999; Weis, 2010; Blackburn et al., 2009). Aggression is a behavioral attribute which has been frequently associated with the success of invasive species, mostly in establishment and post-establishment phase (Holway and Suarez, 1999; Duckworth and Badyaev,

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2007; Weis, 2010; Chapple et al., 2012). Along with other morphological, life-history and behavioral traits, aggression has also been shown to exhibit variation in expanding populations (Table 1), suggesting its plasticity and context dependence. The primary role of aggression is competition with conspecifics over scarce resources. Aggression usually translates to dominance in direct agonistic interactions, and is considered an important fitness determinant since it usually brings immediate benefits to the winner through priority of access to limited resources (Wilson, 1975). This is beneficial for individuals in established populations in the species' native range, and increases in importance as density increases in introduced populations as well. In addition to its roles in conspecific contexts, aggression may also help invaders to wrestle the resources from other species which enhances their competitiveness in a novel environment against unfamiliar niche competitors (cf. Weis, 2010; Chapple et al., 2012; Groen et al., 2012). In particular, relative advantages that elevated aggression provides to more aggressive individuals can translate to

selective advantages, priming certain phenotypes to be more successful in expanding the population's (cf. Shine et al., 2011). Elevated aggression can therefore equally benefit colonization of new areas and maintenance of population dynamics in established populations, and consequently increase fitness at both ends of the expansion gradient. Here we review the role of aggression in active range expansion as well as an endogenous mechanism that drives populations to expand. We i) compare the role of aggression as a driver of range expansion and invasion that allows successful niche competition and redistribution of individuals in space, ii) discuss the potential mechanisms how aggression can affect the range expansion processes and iii) examine the importance of ecological and social context of both departing and recipient environment. The resulting spatial structuring at different stages of range expansion could aid in our understanding of the dynamics of biological invasions, as well as lead to more robust predictions of invasiveness and associated management actions.

**Table 1** Variation in behavioral and morphological and life-history traits between two distributional extremes in invasive range: Invasion front (F) and established, core populations (C), and between native and invaded range.

Invasive Species	Front (F) vs. Established or Core (C) population/individuals	Introduced (I) or Dispersal (D) vs. Native range (N) or Resident (R) population/individuals	Taxa code-References (A-Amphibians, B-Birds, C-Crayfish, F-Fish, I-Insects, M-Mammals)
<b>Behavioral traits</b>			
Boldness	F=C (F6, F11)	I>N (C13) D>R (F3)	F3-Cote et al., 2011, C13-Pintor et al., 2008. F6-Groen et al., 2012, F11-Lopez et al., 2012.
Dispersal tendency	F>C (A1, A10, I18) C=F (F11)	~	A1-Alford et al., 2009, F11-Lopez et al., 2012. A10-Llewelyn et al., 2010, I18 – Lombaert et al., 2014.
Activity/Foraging/ Exploratory behavior	~	I>N (C13, C14) D>R (F3)	F3-Cote et al., 2011, C13-Pintor et al., 2008. C14-Pintor and Sih, 2009.
Intraspecific aggression	F>C (F6)	I>N (C13), D<R (M15 <sup>+</sup> ) I<N (I8, I17), D>R (B4*)	B4-Duckworth and Badyaev, 2007, I8-Holway et al., 1998, F6-Groen et al., 2012, I17-Suarez et al., 1999, C13-Pintor et al., 2008, M15-Pocock et al., 2005.
Interspecific aggression	~	I>N (C14) D>R (B4*)	B4-Duckworth and Badyaev, 2007, C14-Pintor and Sih, 2009.
<b>Morphological &amp; life-history traits</b>			
Body size	F>C (F2, F7, F21) F<C (F19)	~	F2-Brandner et al., 2013, F21-Bøhn et al., 2004. F7-Gutowsky and Fox 2011, F19 -Brownscombe and Fox 2012.
Growth rate	F>C (A12, F20)	I>N (F9, C14)	F9-Grabowska et al., 2011, C14-Pintor and Sih, 2009, A12-Phillips 2009, F20 – Carol et al. 2009.
Reproductive investment	F>C (F11, C16) F<C (F2)	I>N (F5, F9)	F2-Brandner et al., 2013, C16-Rebrina et al., 2013, F5-Fox et al., 2007, F9-Grabowska et al., 2011, F11-Lopez et al., 2012.
Body condition	F>C (F2, F11, C16, F20, F21)	~	F2-Brandner et al. 2013, C16-Rebrina et al. 2013, F11-Lopez et al., 2012, F21-Bøhn et al. 2004, F20-Carol et al., 2009.
Age at maturity	~	I<N (F5, F9)	F5-Fox et al., 2007, F9-Grabowska et al., 2011.

'>' depicts increase in trait expression compared to respective population, '<' an decreased in expression and '=' no significant differences between compared populations. '\*' depicts range expansion of native species, while '+' its dispersal.

## 2 Aggression Driving Range Expansion through Dilation of Population Edges

Aggressive success translates into advantage over competitors (i.e. Holway and Suarez, 1999; Snyder and Evans, 2006; Gherardi and Cioni, 2004; Hudina et al., 2011), and increases the probability of resource acquisition in both intraspecific and interspecific contests (e.g. Enquist and Leimar, 1987; Morell et al., 2005; Hudina et al., 2011). Resource acquisition and monopolization can lead to increased growth, survival and reproduction and overall improved fitness of the dominant competitor. For example, study by Hudina et al. (2011) demonstrated the benefits of higher aggression in competition between two successful crayfish invaders. Higher aggression of the signal crayfish *Pacifastacus leniusculus* allowed it to dominate the contests with the spiny-cheek crayfish *Orconectes limosus*, led to its dominance in shelter competition, and also resulted in decreased fitness (weight loss and higher injury frequency) in the inferior *O. limosus* competitors in group-scale experiments (Hudina et al., 2011). Due to its potential fitness benefits to species undergoing range expansion where it may face other native or introduced rivals, it is intuitive to consider that highly aggressive individuals will be more likely to disperse and consequently accumulate at the population edge or invasion front (Duckworth and Badyaev, 2007; cf. Groen et al., 2012).

Besides its direct benefits in dominance over niche competitors, aggression could also be integrated with other traits which generate advantages to the expanding individuals into behavioral syndromes. Behavioral syndromes are defined as consistent individual differences, i.e. consistent correlation between certain behavioral traits, across ecological contexts and time (Sih et al., 2004 a, b; 2012; Cote et al. 2010; Fogarty et al., 2011). Aggression, boldness, foraging activity and dispersal tendency have all been identified as traits comprising a behavioral syndrome (Pintor et al., 2008; 2009; Sih et al., 2004a, b; Cote et al., 2010; 2011). Integration of traits can provide additional advantages to individuals, enabling them to face multiple challenges imposed by the novel situations and environment, with certain combinations then contributing to successful dispersal. Behavioral syndromes can therefore provide an advantage for colonization of new areas, which has been recognized in personality dependent dispersal studies (Clobert et al., 2009; Cote et al., 2010; 2011). For instance, Duckworth and Badyaev (2007) examined the apparent coupling of aggression and dispersal tenden-

cies during range expansion of western bluebirds *Sialia mexicana*. Dispersal of western bluebirds was driven by highly aggressive males, resulting in their accumulation at distribution edges and their competitive advantage and subsequent displacement of congener species, mountain bluebird *Sialia currucoides*.

Heightened aggression could also be elevated in expanding population simply due to its co-occurrence with other traits within a behavioral syndrome that actually help a species overcome the constraints of the low conspecific density in recipient environment. For example, increased activity and exploratory behavior could potentially help species overcome potential Allee effects that impart reduced survival/reproductive success at low densities in novel environment (Lockwood et al., 2007). Since bold and active individuals are often selected for during dispersal (i.e. Johnson and Sih, 2007; Pintor et al., 2009; Cote et al., 2010; Fraser et al., 2001; Rehage and Sih, 2004), and with boldness and aggression being positively correlated in many taxa (Bell, 2005; Johnson and Sih, 2007; Moretz et al., 2007; Pintor et al., 2009), individuals at the expanding population edge would also tend to be more aggressive as an indirect consequence of such behavioral syndrome. Thus, in addition to its potential direct advantages during range expansion in direct competition, aggression could also become more prevalent at the edge of an expanding population through integration within a specific behavioral syndrome that provides benefits and is selected for during dispersal.

## 3 Spatial Patterns of Aggression as A Consequence of Edge Dilation

Both direct and indirect selection of aggression dilating population edges may result in specific pattern of spatial distribution in the expanding population. If aggression represents direct competitive advantage and is selected for during dispersal, more aggressive individuals would become prevalent at invasion fronts or population edges. Due to non-random dispersal (Cote et al., 2010), fast dispersing individuals could become increasingly prevalent at expanding range edges (Phillips et al., 2010; Shine et al., 2011). This spatial sorting by dispersal ability could lead to further evolutionary increase in dispersal rates over next generations and ultimately contribute to the emergence of new dispersive phenotypes (Phillips et al., 2006, 2008; Shine et al., 2011; Shine, 2012). Furthermore, due to established links between aggression and personality-dependent dispersal, as demonstrated in the behavioral syndromes

context (cf. Sih et al., 2012), increase in aggression towards population edges could occur indirectly through its integration with other traits beneficial for dispersal. In both cases, spatial pattern involving the increase of aggression at population edges in comparison to core population areas would occur, with the emergence of a spatial pattern in which more aggressive individuals are more frequent at the edge of the expanding range.

#### 4 Aggression Driving Range Expansion through Exclusion from Population Center

While it can help in niche competition, the primary role of aggression is competition against conspecifics over scarce resources (cf. Harper, 1982; Maynard Smith, 1982; Tokeshi, 1999; Eccard and Yonlen, 2002; Gherardi and Cioni, 2004). The importance of aggression increases as resources become limited (Enquist and Leimar, 1987). High population density usually results in relative scarcity of resources, which increases the perceived resource value and consequently raises the intensity of resource competition (Maynard Smith, 1982; Enquist and Leimar, 1987; Bowler and Benton, 2005; Morell et al., 2005). While competition intensity would continue to rise with progressively fewer opportunities to obtain resources, leading to extreme fighting strategies (Grafen, 1987; Enquist and Leimar, 1990; Innocent et al., 2012), it also gives rise to ritualized fighting with sequential assessment (Enquist and Leimar, 1983). Ritualized fighting offsets such pressures by decreasing the immediate fighting cost when great asymmetries exist, but also allows individuals to retain fighting and wrestle resources from closely matched opponents. While frequent opportunities create more ritualized and therefore less overtly aggressive agonistic interactions to reduce the costs of fighting (cf. Maynard Smith, 1982), such individuals still need to retain a greater tendency to escalate in conflicts. Therefore, elevated aggression will be favored in high population densities as it translates to dominance in direct competitive interactions (cf. Fero et al., 2007) which is an important predictor of access to key resources (Wilson, 1975).

Even if aggressive interactions become ritualized, a spatial displacement of losing individuals and their exclusion from resources can lead to spatial heterogeneity in distribution of phenotypes. Numerous experimental studies demonstrated that the propensity for dispersal increases with density (reviewed by Bowler and Benton, 2005). As aggression can translate into success in in-

tense competition for scarce resources, in such conditions less aggressive individuals may also become displaced through competitive exclusion by the dominant conspecifics (Hamilton, 1971; Holecamp and Smale, 1998; Schradin and Lamprecht, 2002; Pockok et al., 2005; Guerra and Pollack, 2010; reviewed in Cote et al., 2010; Hudina et al., 2013). In such circumstances, less aggressive individuals will gradually become prevalent at the edge of the population (as in selfish herd model; Hamilton, 1971). Individuals excluded from high density areas of established populations will then also end up being in a position of leading the range expansion (i.e. Schradin and Lamprecht, 2002; Hudina et al., 2013). This has been documented in an endemic cichlid fish *Neolamprologus multifasciatus*, where the least aggressive females also had the smallest breeding territories and emigrated (Schradin and Lamprecht, 2002). Thus, exclusion from optimal breeding territories by the more aggressive females led to dispersal of less aggressive individuals within a population. Similarly, in experimental studies on invasive signal crayfish, males from invasion fronts consistently displayed lower levels of aggression compared to individuals from established populations at core populations, which indicated their displacement from core populations by the more aggressive males which remained resident (Hudina et al., 2013). Range expansion could thus be driven outwards from established populations by the growing competitive pressure within a population, rather than by highly aggressive dispersive individuals.

In addition, reduced aggression at the edges of expanding population could also benefit population growth at distribution edge indirectly through other population dynamics processes. In a classic concept that subordinate individuals are forced to disperse by the dominant competitors (reviewed by Bowler and Benton, 2005), differences in population characteristics could occur in expanding and invasive populations. For example, if subdominant and less competitive individuals are squeezed out by more successful competitors and pushed to habitats on population edges, reduced aggressiveness could allow such invaders to reach high densities and outnumber native populations. The benefits of decreased aggression in an invasion process have been demonstrated for Argentine ant, which exhibits significantly reduced aggression at any spatial scale in its invasive range in California and Chile compared to its native range (Holway et al., 1998; Suarez et al., 1999; Holway and Suarez, 1999). Such loss of aggression and territoriality were identified as important factors con-

tributing to its high population densities and its success in competition with native species (Holway and Suarez, 1999). Furthermore, due to potential asymmetries in aggression and costs of dispersal between sexes (i.e. Bowler and Benton, 2005; Brandner et al., 2013), sex-biased dispersal may occur (cf. Bowler and Benton, 2005; Chaput-Bardy et al., 2010; Hudina et al., 2012; Gutowsky and Fox, 2011; Brandner et al., 2013), resulting in differences in sex ratios between established populations and expanding invasion fronts. Sex ratios skewed towards females are thought to promote population establishment and growth (Brandner et al., 2013), while male-biased sex ratios may promote reproductive interference and the replacement of native congeners (Soderback, 1994). Asymmetries could also occur in characteristics which influence resource holding potential of an individual (i.e. its ability to gain/ maintain access to limited resources; Parker, 1974), such as larger body size, experience or larger weaponry (reviewed in Schroeder and Huber, 2001). The subordinate, usually smaller, less experienced individuals will be forced to the population edges and end up dispersing into new environments. For example, in the common shrew *Sorex araneus*, dispersing individuals were smaller than resident individuals which were also more competitive in experimental trials (Hanski et al., 1991). Similarly, as body size is one of the important determinants of agonistic success and social status in crayfish (Gherardi and Cioni, 2004), smaller individuals may disperse first and thus accumulate at invasion fronts (Hudina et al., 2011). Thus, spatial assortment by competitive ability may also result in spatial sorting of other traits which are directly or indirectly influenced by aggression.

## 5 Spatial Patterns of Aggression as A Consequence of Exclusion Effects

If aggression excludes poor competitors from high density areas of established populations, this could result in a specific spatial pattern of aggressive phenotypes. In this case, more aggressive individuals remain at the center of the population, while less aggressive individuals will end up being squeezed out to population edges and areas of low conspecific density. This pattern is similar to selfish herd model of social groups, in which individuals are assumed to reduce predation risk by placing other conspecifics between themselves and predators (Hamilton, 1971). This kind of dynamics therefore puts less aggressive individuals in position to disperse and expand the range of a population. Disper-

sive individuals may therefore be those with reduced aggression, but also with advantages such as higher reproductive rate or lower resource requirements. As with edge dilation, a specific spatial distribution of aggression phenotypes, as well as other characteristics, will emerge from the predominant social and ecological conditions experienced by the population during and after its establishment.

## 6 Temporal Prevalence of Aggression Patterns and Trade-Offs in Expanding Populations

As discussed in previous chapters, both edge and endogenous effects of aggression in range expansion would create a distinct spatial patterns of aggression and other related behavioral, morphological or life-history traits. Discerning such spatial patterns in the field offers a glimpse into expansion and invasion history, enables understanding of the mechanisms and selection pressures driving range expansions (Phillips et al., 2010; Shine et al., 2011), and may help in determining the role of aggression in range expansion and invasion success of specific invaders.

However, such patterns may sometimes be visible only a short period after dispersal to novel environment, since selection of dispersive phenotypes may sometimes be maladaptive (Travis et al., 2007) in post-dispersal period (i.e. population establishment and growth). Previous studies demonstrated that dispersive individuals may suffer higher predation and decreased reproduction rates, as well as develop morphological features that have significant negative effects on their fitness (reviewed by Shine, 2012). Similarly, elevated aggression at population edges could result in fitness drawbacks. Aggressive individuals are more prone to engage in aggressive interactions which imply injury risks and costly energetic investments since they deplete reserves that would be otherwise allocated to growth or reproduction (Sneddon et al., 1999; Rovero, 2000). Unless facing a strong challenge from niche competitors, increased frequency of such interactions in low density populations establishing at the edges may be counterproductive, since more aggressive individuals would spend much more time fighting than foraging (cf. Sih et al., 2012; Kolluru and Gether, 2005). Similarly, in the case of western bluebirds, aggressive males are poor parents (Duckworth, 2006), which negatively influences juvenile survival and ultimately the rate of population growth. Thus, in post-dispersal period the utility of in-

creased aggression could be significantly reduced at invasion fronts and could be quickly replaced by more beneficial behaviors/traits (i.e. Duckworth, 2008).

Similarly, in the case of spatial sorting by exclusion from population center, the presence of less aggressive phenotypes along with potentially more abundant resources at population edges could lead to fitness advantages. Several studies already demonstrated that individuals at expanding population fronts exhibit better body condition, higher reproductive fitness and sometimes larger size compared to the individuals from core populations (Gutowsky and Fox, 2011; Lopez et al., 2012; Brandner et al., 2013, Rebrina et al., 2013; Table 1). Such circumstances which improve the condition of individuals that actually expand the range may ultimately elevate the rates of population growth (Burton et al., 2010; Phillips et al., 2010) either through increase of individual growth rates which decrease the time needed to reach sexual maturity (Brandner et al., 2013) or through increased reproductive fitness which raises the capacity for reproductive investment (i.e. fecundity; Lopez et al., 2012; Rebrina et al., 2013). As rapid growth rates may result in larger average size of individuals at invasion front compared to core populations (Brandner et al., 2013), this indirectly increases their competitive ability and readiness to engage in aggressive contests (Groen et al., 2012), thus changing the initial spatial distribution of aggression. Therefore, as specific aggression patterns which arise due to spatial sorting may be lost over time, they are best identified in an actively expanding populations.

## 7 Conclusion

Rapid range expansion of invasive species is one the major attributes of their post-establishment success. Aggression helps shape and regulate species interactions and thus has an important role in expanding populations, however, this role is not straightforward. Both edge dilation and exclusion from centre elaborated in previous chapters may shape trait distribution due to specific and often dynamic ecological and social context both within the population and in the surrounding environment. Thus, the role of aggression in range expansion may be more complex than previously thought.

Different factors such as the pressures building within a population with increasing density as well as external factors such as the presence and challenge from niche competitors will create distinct patterns of distribution of aggression phenotypes. This offers a glimpse into the historical and current population dynamics of,

as well as ecological and evolutionary challenges faced by, expanding or invasive populations. Knowing these patterns can also contribute to the understanding of population processes that occur between introduction /establishment and range expansion. For example, a balance between the endogenous pressures stemming from population density and counteracting pressures from other populations or niche competitors could play an important role in invasion dynamics of introduced species. While at first a population may be prevented from expanding by external forces, a shift in favor of exclusion by conspecifics may lead to a release and active dispersal at the expense of native competitors. As such, this shift could represent one of the determinants of a lag between establishment and expansion of introduced species. Such insights could have important implications for management actions aimed at predicting and controlling expanding as well as currently stable populations of introduced species.

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