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# Annual Review of Entomology Environmental Adaptations, Ecological Filtering, and Dispersal Central to Insect Invasions

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## Keywords

biological invasions, dispersal syndromes, environmental stress, phenotypic plasticity, range expansion

#### Abstract

Insect invasions, the establishment and spread of nonnative insects in new regions, can have extensive economic and environmental consequences. Increased global connectivity accelerates rates of introductions, while climate change may decrease the barriers to invader species' spread. We follow an individual-level insect- and arachnid-centered perspective to assess how the process of invasion is influenced by phenotypic heterogeneity associated with dispersal and stress resistance, and their coupling, across the multiple steps of the invasion process. We also provide an overview and synthesis on the importance of environmental filters during the entire invasion process for the facilitation or inhibition of invasive insect population spread. Finally, we highlight important research gaps and the relevance and applicability of ongoing natural range expansions in the context of climate change to gain essential mechanistic insights into insect invasions.

### 1. DISTRIBUTION CHANGE IN INTRODUCED AND NATIVE INSECTS

Despite an increasing awareness of the ecological, economic, and sociological effects of humanmediated translocations of insects (176), the rate of alien introductions and establishment continues to rise considerably (151), with, for instance, a nearly twofold increase in the rate of establishment of alien insects in Europe over the past few decades (141). Introductions are defined as the translocation of organisms beyond their natural biogeographic barriers as a result of humanrelated transportation, intentionally or accidentally (47, 134) (see the sidebar titled Examples of Intentional and Accidental Introductions). Introduced insects that establish viable populations can further proliferate and diffuse away from the initial introduction point through repeated establishment and expansion events (**Figure 1**). This process is typically referred to as the invasive spread.

Contemporary climate change facilitates the establishment of introduced insect populations and can trigger the expansion of native species (**Figure 1**), as observed in the pine processionary moth, *Thaumetopoea pityocampa*, whose northward range expansion is often acknowledged as being causally and directly induced by climate change (7, 135, 145). Native species can therefore track climate windows or habitat modifications and shift their range by their own dispersal means (34, 37) and are referred to as range-expanding species.

The parallel between invasion and range expansion can provide insights into the mechanisms assisting geographic spread. In founder populations, the most extreme bottlenecks likely occur in invasive populations because of the relative scarcity of introduction events and reduced number of sampled propagules surviving through transportation. For instance, population genetics data suggest that the distinct invasions of the Asian yellow-legged hornet, *Vespa velutina*, in France and Korea followed the introduction of very few gravid females (2). In contrast, as native-range-expanding species do not have to breach geographical barriers like invasive species, gene flow with the nearby historic populations likely persists, at least partly, depending on the steepness of the selective gradients and on the fragmentation of edge populations (23). Yet, dispersal processes, which allow geographic spread, share several features in both native and introduced insects, whose individuals also consistently exhibit significant heterogeneity in dispersal ability.

The functional similarity of habitat conditions in native and invaded regions is key to invasion success and spread. However, geographic spread of invasive populations may occur in environments characterized by novel abiotic conditions and biological communities compared to the native range. For instance, the ground beetle *Merizodus soledadinus* naturally thrives in inland forest litter in Patagonia and Tierra del Fuego, whereas invasive individuals in South Georgia and the Kerguelen Islands primarily occur in intertidal habitats (64, 89). However, data supporting the expectation

## EXAMPLES OF INTENTIONAL AND ACCIDENTAL INTRODUCTIONS

Countless instances of accidental insect introductions exist, presumably mainly resulting from transportation with wood packaging and ornamental plants (84, 144). Notorious examples from recent years include the Asian longhorned beetle (*Anoplophora glabripennis*), the western conifer seed bug (*Leptoglossus occidentalis*), and the box tree moth (*Cydalima perspectalis*), all invasive to Europe (see 142, 144), as well as the winter moth (*Operophtera brumata*) (44) and the emerald ash borer (*Agrilus planipennis*), invasive to North America (142). Intentional introductions often result from the importation of biocontrol agents in new areas, such as the predatory harlequin ladybeetle (*Harmonia axyridis*) intentionally released in several countries to control hemipteran pests (142, 144). One of the most important and well-studied invasive pests worldwide, the gypsy moth (*Lymantria dispar*) lies between these two categories, as it was intentionally imported for breeding cultures and silk production in controlled conditions but was accidentally released in nature (98).



#### Figure 1

Main stages and barriers in the processes of biological invasion of an alien species (*red*) and range expansion of a native species (*purple*), adapted, with permission, from the unified framework for biological invasions proposed in Reference 12. The expansion stage of both biological invasions and native-range expansions is dependent not only on successful breaching of the barrier to dispersal but also on the environmental barrier because, owing to spatial autocorrelation, the more a species spreads, the more dissimilar environmental conditions it will face. As transportation and introduction stages select only a small pool of propagules in the native range, these stages specific to the invasion process are assumed to reduce gene flow, genetic diversity, and occurrence of natural enemies at the later stages of the invasion. Such changes are not expected in native-range expansions because the progressive and continuous expansion from the historic range does not readily disconnect pioneer populations from nearby core populations.

that invasive populations more often experience novel environmental conditions than native-range expanders is largely lacking. To better understand the success of invasions, we would need to simultaneously consider environmental conditions in the natal habitat and in the invasive range, in both successful and failed invasions. Unfortunately, evidence and insights on failed invasions are lacking, because alien populations are typically unnoticed until they become invasive (185).

After giving an insect-centered overview of the different phases of dispersal, we synthesize the existing knowledge on the main sources of heterogeneity in insect dispersal. In many situations, invasive insects face novel or nonanalog environmental conditions (see the sidebar titled What Are Novel and Nonanalog Environmental Conditions?), suggesting that invasion success should correlate with general stress resistance and dispersal. Therefore, we highlight the crucial role, so far poorly explored, of both adaptation to environmental stress in the native area and ecological filtering during transportation in driving the invasion success. A functional perspective incorporating individual variation in responses to novel conditions may provide the best insight into how environmental filters affect spatial spread in both contexts.

## 2. THE DIFFERENT PHASES OF DISPERSAL AND FURTHER SPREAD

Dispersal is the movement of individuals with potential consequences for gene flow (28, 139). Dispersal can be active or passive and can occur at the emergence of the imago (natal dispersal)

## WHAT ARE NOVEL AND NONANALOG ENVIRONMENTAL CONDITIONS?

Nonanalog conditions are defined as differences in community structure and climatic context that occur at temporal and/or spatial windows. Nonanalog communities describe the reshuffling of community structure (without necessarily extinction of species), resulting in new composition and interactions among species (179) without past equivalents. Similarly, nonanalog climatic conditions refer to changing climatic conditions, or disappearing climates, resulting in climates with no equivalent in the past (180). In the context of invasion, many introduced insects are confronted with combinations of species and climatic conditions that were not present in their native geographic region and may thrive in nonanalog habitats. Moreover, the establishment of invaders within communities can give rise to novel interactions and nonanalog communities, rendering the predictions of the future distribution of biodiversity particularly complex (48). Finally, novel environmental conditions refer to niche spaces present in the native and invaded ranges yet only experienced in the invaded range.

and/or between reproduction events (breeding dispersal). Dispersal is therefore distinguished from other types of movements functionally rather than by the scale of movement (**Table 1**).

The full process of dispersal has three component steps: departure, transience, and settlement (28, 139). Each of these will be influenced by the environmental context in which they occur, individual phenotype, and interactions between these factors (92). From a theoretical perspective, natural selection should favor dispersal in spatially subdivided populations that are spatiotemporally variable, be counter-selected in these populations if patch size is highly variable, and above all be counter-selected when dispersal costs increase, for instance in spatially subdivided populations with low connectivity among patches (139). Invasions may originate from single or multiple introduction paths, and selection may occur at each invasion stage. Translated to the population level, selection is thus anticipated to act on dispersal during emigration, transience (movement between habitat patches), and immigration and further spread (**Figure 2**).

Departure, the first stage of dispersal, is strongly influenced by environmental context, which either induces or impedes dispersal. Conditional responses (plasticity) are the main causes of heterogeneity in departure from natal/breeding patches. Departure decisions can include behavioral traits [e.g., how aggressive or sociable individuals are (32)] or morphological changes

Factors associated with	Routine/home range		
dispersal	movements	Dispersal	Migration
Spatial scale	Small (centimeters to kilometers)	Variable (meters to tens to hundreds of kilometers)	Large (typically hundreds of kilometers)
Temporal scale	Daily or periodic within a season	Occasional	Seasonal
Frequency across an individual lifetime	Frequent across a lifetime	Typically zero to infrequent across a lifetime	Variable; may occur once or annually across a lifetime
Associated with preparatory physiological changes?	Minimally (e.g., flight-muscle warm up)	Minimally to moderate (e.g., some energy storage)	Yes, strongly associated (e.g., large increases in fat stores, hormonal changes)
Associated with seasonal weather change?	Rarely	No	Yes, strongly
Effect on gene flow	None or minimal	Significant; primary driver of gene flow	Minimal for most species

Table 1 Differences between forms of insect movement



#### Figure 2

Spatial dimensions of selection during invasions. A species is moved from a stable native range (*orange*) toward new areas (*green*), where its range might either not expand and remain limited (*circles*) or expand (*arrows*). New areas serve as bridgehead populations (i.e., as sources for secondary introductions). Secondary introductions might induce admixture and proliferate genetic variation. Selection on dispersal occurs during emigration (E), transience (movement between habitat patches; T), and immigration (I) but also after immigration because of local selection (L).

[e.g., wing development in wing-dimorphic insects such as aphids that produce winged and nonwinged offspring (22, 187)] that permit or facilitate departure out of a habitat. Selection for initiating dispersal will act when organisms have some probability of increasing their fitness by colonizing new habitat, taking into account putative costs (109, 156). Low or declining habitat quality and higher population densities are both associated with higher departure rates (3, 38, 105). For example, backswimmers (*Notonecta undulata*) increase their rate of dispersal out of patches in response to both density and the presence of predators to avoid risky or low-quality habitat conditions (5).

Dispersal motivation has a genetic basis in many insects and arachnids (186), but it may be overridden by both density and relatedness (10, 38) and maternal and grand-maternal effects (11, 114). Overall, evidence indicates that the environmental context, especially weather conditions, microclimate, and habitat quality, prevails over social factors and individual phenotypes in determining departure decisions in insects and arachnids (13, 18, 75, 92). Community context, including interspecific competitors and predators, can also affect departure decisions (49). In particular, predation pressure intensity critically mediates both local densities and individual survival (129). The net effects of predators on dispersal depend on the relative strength of density and predation risk effects (62). Because such conditional responses evolve, spatiotemporal variation in resource quality and quantity, as well as antagonistic species interactions in native and novel environments, can affect the probability that individuals of an introduced species initiate dispersal and expand their range after the initial human-mediated introduction.

Transience is the movement (passive or active) through habitat that the individual either cannot or does not settle in following departure from the natal or breeding site (28, 139). Within the context of invasions, transience occurs during transportation that is human-mediated and during spread by the invader itself after introduction. Although some forms of human transport are quick and efficient (e.g., air transport), reducing transience costs and stressful conditions during human-assisted transportation (e.g., starvation, temperature, or water availability) is common. These conditions can result in high costs or strong filtering of species and phenotypes as a result of mortality or energetic expenditures directly resulting from movement (reviewed in 19). Importantly, the number of individuals that survive transportation has received little attention in the biological invasions literature (but see Reference 130, which simulated the effects of air transport of an insect pest, and Reference 181). During spread, habitat permeability is a critical factor for transience. Traits that promote more rapid transit in these environments [e.g., wing length (152) or wing loading (20) in flight-capable insects] enhance success during this phase of dispersal, including traits that are specific to facilitating movement through a given landscape context (113, 162).

During settlement, dispersers take up residence or leave offspring in a site. During spread, habitat settlement decisions determine the conditions offspring experience and favor habitat selection maximizing offspring success (72, 154). However, optimization of site selection will be limited by the costs of prospecting (40, 155). Settlement of invaders is expected to be primarily driven by the fitness differential imposed by the region of introduction, as possibilities for natal habitat selection should be low in unfamiliar environments. Nonetheless, even invading insects can make habitat selection choices among contrasting new environments, thereby improving their invasion success. For example, in choice trials involving two novel host plants, the fruit fly *Drosophila suzukii*, an invader in both Europe and North America, preferred the host that yielded higher fitness (42). Examples of female habitat selection that improve offspring performance are common, although not ubiquitous, in insects encountering novel host plants (reviewed in 52) and suggest habitat selection may play an important role in facilitating invasions.

The population and community context invaders encounter in a patch can influence settlement decisions. Competitive effects can result in a negative relationship between population density and the probability of settling in a patch when populations are well established. Yet, in newly established and expanding populations, the risks of settling in low-density patches (Allee effects, negative per capita population growth rates at small population sizes) may be greater than competitive effects (77), especially when demographic stochasticity is large. Invasive populations are typically vulnerable to Allee effects during the early phase of establishment, and these effects can limit the speed of species expansions by setting a minimal density threshold under which dispersal is inefficient because of high breeding failure (82, 99, 168).

## 3. SOURCES OF HETEROGENEITY IN DISPERSAL IN INSECTS AND ARACHNIDS

Dispersers are not a random subset of the population and exhibit a suite of morphological, physiological, and behavioral traits that offset dispersal costs and increase the probability of dispersal being successful. Below, we present the main factors generating heterogeneity in dispersal in insects and arachnids.

## 3.1. Causes of Dispersal

There is a long history of research on insect dispersal ecology (157, 187), particularly in those exhibiting wing dimorphism (136, 187). Studies have demonstrated selection on genotypes, with differential fitness under varying densities and environmental cues as important determinants of the induction of wing development during ontogeny (187). In macropterous specimens, both functional wing development (138, 171) and physiology related to flight performance have a genetic basis (177, 186). Genotype  $\times$  environment interactions are the basis of conditional responses under selection and are likely widespread among insects and arachnids. Most studies, however, report only on the importance of the environment, including low temperature, photoperiod, food

quality, and density dependence as parameters driving the development toward brachypterous or macropterous morphs (e.g., 22, 41).

Although the genetics of wing formation are well documented, the genetic background of dispersal in nondimorphic insects is largely unexplored because most studies to date focused either on morphological traits or on proxies related to movement ability. Such proxies are not strictly related to dispersal (but see 177). More research has focused on dispersal as a plastic decision-making process. Field studies documenting variation in movement, emigration, or dispersal-related morphology point at landscape structure, connectivity (110, 150), and population age as putative drivers of dispersal (21, 65, 173). Environmental conditions prevailed over social factors and individual phenotypes for dispersal movements in the large white butterfly, *Pieris brassicae* (92). Under field settings, temporal variation of dispersal propensity depends strongly on regional factors, including actual weather conditions (85) and climatic conditions experienced during development (18). Obviously, dispersal is typically stage-, age-, and gender-specific (38, 39, 169). Gender biases in dispersal capacity have been reported in moths (70), stink bugs (90), and beetles (8).

#### 3.2. Dispersal Syndromes

Because dispersal is central to range expansion, correlated phenotypic variance may accelerate or constrain these invasions. Individuals are by definition heterogeneous in their multivariate phenotypes, depending on the environmental and social conditions in which they developed (9). Dispersers are expected to exhibit trait values (i.e., dispersal syndromes) (140), thereby representing a nonrandom subset of the population (17) (see **Supplemental Materials S1** and **S2**). Dispersers are often characterized by increased metabolic rate (60, 117, 118), body condition such as energetic reserves and size (80), or explorative behavior, boldness, and sociability (32, 33), and variation in all these traits may be plastic and have a genetic basis. Theory focusing on intraspecific variation assumes that dispersing phenotypes are weak competitors (e.g., 95). In such cases, only invasions or range expansions in environments experiencing competitive release will be successful. Alternatively, some positive associations between competitive abilities and dispersal may evolve (15, 80, 115). For example, dispersing individuals in some spiders were found to be associated with traits favoring establishment in already occupied environments (16).

In contrast to the mixed evidence for competition-dispersal trade-offs in insects, there is abundant support in the literature for the existence of a trade-off between dispersal and reproductive capability in wing-dimorphic insects (58, 137). Flightless individuals have been shown to exhibit larger ovaries, earlier age of reproduction, and higher resultant fecundity (58, 187). In the codling moth, *Cydia pomonella*, the less mobile, sedentary individuals are characterized by larger body sizes, longer life spans, and higher lifetime egg production compared to dispersing morphs (57). Despite conflicting results for males, Zeng & Zhu (184) reported that males with lower dispersal abilities could have more copulations per day, probably resulting from the ability to allocate a higher amount of energy to mating than their dispersive counterparts.

Except for some wing-dimorphic insects—where wing formation definitively affects dispersal capacity but not, per definition, dispersal motivation—evidence for a genetic basis of dispersal syndromes and thus the presence of genetic correlations between dispersal and other traits is weak to nonexistent (14). Environmental conditions, especially, are known to affect the strength and direction of these dispersal correlations at the individual or population level (see, for example, 147). *Melitaea cinxia* and *D. melanogaster* are the only insect examples for which heterogeneity in dispersal could be attributed to molecular divergence, with allelic variation in *Pgi* affecting flight metabolism and dispersal rate in the former species (119) and association between a foraging allele and dispersal tendency in the latter one (43).

#### Supplemental Material

Recent experimental work using the large white butterfly showed that mobility-trait covariation did not emerge from genetic correlations but rather by sex-specific selection (91) and social and community context. In the dragonfly *Pachydiplax longipennis*, small males were more likely to disperse when large males were present (106), suggesting that dispersal in this species is a tactic adopted by social subordinates. In another aquatic insect, *N. undulata*, dispersal rate was positively correlated with the level of risk imposed by predators (5, 107) and in all cases correlated to body condition.

#### 3.3. Phenotypic Assortment During Range Expansion

Range expansion in itself imposes strong selection pressures on dispersal, and evolution may alter further consequences of invasions (46). Starting from a few founders, dispersal is known to strongly evolve through spatial sorting or spatial selection during range expansion (26, 121), because the most dispersive phenotypes inevitably accumulate at the expansion front, leading to assortative mating in these locations. In addition, the locally low densities below the carrying capacity at the leading edge will make vanguard individuals experience r selection rather than K selection. Both sorting and different ecological conditions at the range front are thus expected to affect the evolutionary trajectory of the individuals. Dispersal or dispersal-related traits have been observed to be selected for in edge compared to core regions in several arthropods (160, 166, 167), although few demonstrated a genetic basis for this rapid change. In the mite *Tetranychus urticae*, artificial selection on dispersal indicated a strong epigenetic process leading to divergence in dispersal during range expansions (172). Processes of selection additionally augment more rselected traits, like reproduction (165, 167), and may thus result in a positive genetic correlation at the population level. Multivariate selection of life history traits along gradients have been accompanied by extensive metabolomic changes in T. urticae (173), more specifically shifts related to a potential downregulation of metabolic pathways associated with protein synthesis. In an experimental system using the Chrysomelid beetle Callosobruchus maculatus as a model, heterosis was found to be an additional prominent genetic mechanism responsible for enhanced range expansion (174). Thus, it is suggested that admixture caused by multiple independent introductions could induce a so-called catapult effect leading to rapid expansion rates in invasive species. Such hybridization effects are anticipated to be less relevant in naturally expanding species because expanders are more likely to have a common origin.

## 4. BIOLOGICAL INVASIONS AND ADAPTATION TO ENVIRONMENTAL STRESS

As individuals must overcome several environmental filters, from sampling to establishment to invasion, pre-adaptations to environmental stress are likely key to successful invasion.

## 4.1. Environmental Conditions in the Native Range Contribute to Invasion Success

Environmental conditions of habitats (exogenous factors) can vary spatially and temporally; locally, the combination of abiotic and/or biotic parameters exposes insects to multiple stressors that can interact neutrally, synergistically, or antagonistically (127). To maintain functional homeostasis, phenotypic adjustments are conditionally expressed over the life history of the insect (**Figure 3**) and include a suite of responses within the lifetime of the individuals, ranging from physiological adjustments (163) to changes in phenology and range shifts (24, 27). At short timescales, microevolution may also occur in populations (88), but the effects of environmental



#### Figure 3

(a) Current (exposure to single and/or multiple stressors) and past (acclimation, hormesis) variability of environmental conditions affect phenotypes. (b) Individual scale: Exogenous and endogenous parameters and their interactions shape the phenotypes of insects. (c) Habitat and landscape scales: Local environmental characteristics, including diurnal, daily, and seasonal variations of environmental conditions, shape the phenotypes of individuals. Starting from a similar genetic background (T0), phenotypes of the insects from species A and B vary over time (top T+1 and T+2 highlighted in *blue*). Newly arriving species (native-range-expanding or invasive individuals) can progressively alter biotic interactions, modifying functional and phenotypic diversities (bottom T+1 and T+2 highlighted in *green*). Biotic characteristics and connectivity (larger arrow means stronger connectivity) of habitat patches affect phenotypes and, more particularly, dispersal evolution (see Section 3). This figure shows that, depending on the timing of the sampling and the habitat that is sampled, propagules of distinct genotypes and phenotypes will be collected (sampling shown in *orange circles*), which can have significant consequences for invasion success/failure.

characteristics in shaping genetic structure and diversity remain insufficiently studied (76). Therefore, the origin of the sampled propagules should be a strong determinant of their likelihood of passing through the succession of ecological filters (i.e., probability of being sampled, surviving transport, and establishing in recipient environments) (**Figure 1**).

Environmental heterogeneity experienced by populations is a strong determinant of their degree of adaptation to the varying abiotic parameters, as demonstrated in three sympatric *Drosophila*  species sampled from localities characterized by distinct thermal variabilities (103). During environmental fluctuations, functional homeostasis of insects can be maintained by trait canalization (i.e., there are no phenotypic changes despite organisms being exposed to small environmental variations) up to a certain threshold, after which phenotypic plasticity should take precedence over canalization. The lack of robustness beyond a certain limit may have an important role for insects thriving in variable environments. Ghalambor et al. (54, p. 399) proposed that "canalization for the most basic physiological and developmental processes to properly function is the best hope for increasing the likelihood of persistence in the new environment." Environmental variations within the native range likely shape the trade-off between robustness and plasticity. Highly variable environments may favor a more generalist phenotype capable of handling a wide range of conditions without plastic induction of alternative phenotypes. For instance, the metabolic rate of the butterfly Erynnis propertius was more robust (less sensitive) when individuals were subjected to increased temporal variability of thermal conditions (178). Experimental selection in the beetle C. maculatus revealed that individuals from stable thermal environments exhibited enhanced thermal plasticity (61), whereas those reared under fluctuating temperatures showed similar or decreased plasticity, suggesting enhanced canalization. Other studies revealed that the level of thermal plasticity remained similar when Drosophila flies were exposed to novel thermal regimes (102, 103), suggesting that changes in thermal plasticity may be evolutionarily constrained (59, 102).

Phenology in the native range is another flexible phenotypic trait that can affect invasion success. In the range-expanding pine processionary moth, *T. pityocampa*, populations from different bioclimatic regions show distinct phenologies despite univoltine development (143). The resulting allochronic difference leads to differential resistance to local seasonal stressors (135, 149) that can determine success in new areas. The rate of prolonged diapause is also known to vary greatly across populations of this species (53), and diapause has been shown to impact dispersal abilities in other insect species (25). For instance, the weevil *Curculio elephas* was characterized by variable dormancy duration and moderate flight capacities, whereas individuals of *Cu. glandium* exhibited little variation in dormancy duration but enhanced dispersal abilities (126).

## 4.2. Ecological Filtering During Sampling, Transportation, and Introduction

During sampling, traits of individuals are filtered on the basis of their locomotor activity, boldness, or phenology, but no nonrandom selection toward better stress resistance is expected at this stage (**Figure 4***a*). Ecological filtering during subsequent transportation and settlement should, analogous to costs endured during natural transfer (19), select individuals for better performance under stressful conditions—in other words, those exhibiting traits (syndromes) that enhance

#### Figure 4

<sup>(</sup>*a*) Theoretical scheme presenting phenotypic diversity of insects (shown as different *colored dots*) of a given species in its native region. The sampled phenotypes are circled in gray. Some of them cannot survive the transportation phase, and not all of them will survive after they are released into the area of introduction. These phases will contribute to selecting in a nonrandom way the phenotypes that are able to deal with the encountered restrictive (stressful) conditions. The existing level of variation before transportation and the average phenotype therein may depend on the time of the year and region within the native area (see **Figure 3**). Admixture and (micro-) evolution are conducive to the appearance of new genotypes (and thus phenotypes). (*b*) Performance curves of the organisms from the sampled population in their native geographic area (each line represents the performance curve of one individual). (*c*) Ecological filtering of the organisms according to the conditions encountered during transportation. Acclimation to environmental conditions during transport may displace the performance curve of each transported insect to maintain functional homeostasis as high as possible. Thus, the level of stress resistance of invasive insects highly depends on the pheno- and genotypic composition of the founder population (**Figure 3**), the ecological filters encountered during transportation and introduction, and the genetic diversity of establishing insects.



survival when encountering abiotic and biotic constraints (123, 146) (Figure 4b). The strength of this filtering is fairly important, as propagule size positively affects founding events as demonstrated in waterstriders (1) and in the whitefly *Bemisia tabaci* (69). Using data from past introductions of parasitoids for biological control purposes and mathematical models, Hopper & Roush (67) suggested that about 1,000 insects should be introduced for the successful establishment of a population. In parallel, genetic background reliably influences the establishment success and reproductive rates, as demonstrated in *B. tabaci* (69).

Surprisingly, comparisons of stress resistance between populations of insects from their native and introduced ranges are scarce. For thermal tolerance, contradictory results have been obtained, probably because of the interspecific nature of the investigations. Some authors reported lower thermal plasticity of invasive populations (108, 182), whereas others reported higher thermal plasticity compared to native insect populations (74, 120, 125). Winter survival is another key factor affecting invasion dynamics, and higher overwinter survival of invasive insect populations as compared with their native counterparts has been reported (71, 97).

Dry conditions represent another environmental filter for invasive insects. Walters & Mackay (175) reported that populations of Argentine ants invading South Australia prefer more humid conditions as compared with a native dominant ant species. Accordingly, relative humidity and water availability drove the survival success of the invasive carabid beetle *M. soledadinus* (124), whereas osmoregulatory constraints experienced by this insect in salted habitats were surmounted through behavioral and physiological plastic responses (64). These findings may be explained by the fact that desiccation resistance is often increased to the detriment of development time and egg production, as demonstrated in *D. melanogaster* (164).

Biotic factors can further drive stress resistance and invasion success (see the sidebar titled Biotic Interactions, Community Composition, and Establishment Success). For instance, native competitors can push invasive insects to marginal habitats, as suggested for *D. subobscura* when it competes with *D. pseudoobscura* in North America (55). Also, viruses may facilitate invasion, as reported for the invasive B biotype of the whitefly *B. tabaci*, whose performance and fecundity are boosted when they feed on plants infected by whitefly-transmitted begomoviruses, to the detriment of the native whiteflies (73). Although symbiotic bacterial communities may correlate with invasion success in insects (68), Lu et al. (100) reported that the invasion success and shifted diet of the Argentine ant, *Linepithema humile*, was not associated with changes in microbiome composition, as also reported in the aphid *Aphis glycines* (6).

#### 4.3. Surviving Environmental Heterogeneity in the Invaded Area

Environmental similarity of native and invaded areas can make environmental filters more permeable and increase invasion success (63). However, some invasive insects can develop on distinct resources or occupy new ecological niches and habitats (131), including potentially stressful conditions (124), compared to those in their native ranges. The ability to cope with a large panel of environmental stressors via general stress responses (see 83) and physiological plasticity likely play key roles for passing ecological filters (78), thereby reducing the mismatch between native and invaded areas.

The idea of shared responses elicited by insects exposed to a range of environmental stressors, also known as cross tolerance (153, 159), likely supports the invasion process. A master trait (i.e., a conserved physiological response shaping the phenotype of the individual across environmental stressors) has been reported in the invasive carabid *M. soledadinus*, which consistently accumulates compatible solutes (amino acids, polyols, or sugars) when adults are exposed to cold, desiccating, or saline conditions (64, 87, 124). Other master traits using distinct pathways (cross-talk) can be

## BIOTIC INTERACTIONS, COMMUNITY COMPOSITION, AND ESTABLISHMENT SUCCESS

Invasion success and the impact of invasions on native systems are both influenced by the community context that invaders encounter on arrival. At small geographic scales, functional composition, species richness, niche partitioning, and lack of community saturation are hypothesized to be important factors for the level of biotic resistance of communities to invasions (see review in 185). The phylogenetic relatedness of invasive populations to native ones has also been proposed as a possible explanatory variable affecting the invasion success of the invader in native communities. Much of this work has been done in plant systems and has, in some instances, resulted in conflicting conclusions (e.g., 96, 158). More closely related invaders are more likely to affect the native communities by a nonrandom loss of particular lineages (93). During invasions, the largest dispersal events (introductions) are anthropogenic rather than dependent on organismal dispersal, and rapid evolution during invasive range expansions may result in novel trait combination in which the dispersive invader is also a dominant competitor and can increase the potential for invasional meltdown.

triggered simultaneously, including synthesis of heat shock proteins (79) and the enhancement of antioxidant capacities (86).

Despite general stress responses, a small fraction of individuals often outperform others in stressed populations (35). This emphasizes the importance of considering individual variation in responses to novel conditions for a better understanding of the traits associated with establishment success and geographic expansion. In the invasive tenebrionid *Alphitobius diaperinus*, 8% of the insects exposed to 10°C survived about 92 days, whereas the median survival time of the population was around 48 days (133). The transcriptional and biochemical reprogramming of the individuals involve a stress-specific response, as demonstrated in *D. melanogaster* (56), and compensatory mechanisms likely incur energetic costs that cannot be supported by all individuals. Consistently, extreme survivors of cold stress in *A. diaperinus* were those individuals that best managed their body reserves (132). Energetic costs of the stress response are particularly evident when the conditions become favorable again (29), as metabolic rate is temporarily boosted during recovery from stress exposure (86).

Maintaining energy production across environmental heterogeneity is crucial, and many responses that have evolved for coping with stressful conditions also improve physiological resilience and insects' bioenergetics. For instance, fruit flies previously exposed to cold conditions maintained coupling to ATP hydrolysis better and could sustain higher ATP production than nonacclimated relatives (30). Therefore, we suggest that ecological filtering selects individuals according to their ability to cope with environmental stressors and according to the main characteristics (amplitude, width, flexibility) of their metabolic scope during each step of an invasion process (104).

Interestingly, enhanced stress resistance of invasive insects may have positive side effects on dispersal ability, and this aspect should be explored in future studies. For instance, thermal variations may have functional consequences equivalent to oxygen fluctuations and may generate increases in the production of reactive oxygen species (ROS), triggering enhanced antioxidant capacity. During dispersal, metabolic rate peaks, as demonstrated in the Glanville fritillary butterfly (118), and higher flying activity increases ROS production in the housefly *Musca domestica* (183) (but see Reference 101, which reports no difference in *D. melanogaster*).

Finally, increased phenotypic variability within single genotypes can be selected with bethedging strategies to spread fitness risks and avoid total offspring mortality when encountering unexpected conditions (i.e., diversifying risk spreading) (66). Flexible expression of duration of diapause is a striking example of within-generation risk spreading reported in the chestnut weevil, *Cu. elephas* (111, 112) and pupae of the pine processionary moth, *T. pityocampa* (148). In the latter species, pioneer populations far beyond the main expansion front are assumed to be founded by introduced pupae transported in the soil when ornamental mature trees are translocated (143), and prolonged pupal diapause should increase the probability of being transported through this pathway. However, firm evidence of bet hedging, in particular for risk spreading through spatial and temporal dispersal (i.e., the distribution of individuals into separate reproductive events) (25), remains scarce in the invasion literature.

#### 4.4. After the Introduction: Carry-Over Effects

Carry-over effects (i.e., the influence of previous individual experience/history on current organismal performance) (122) impact settlement success (128) and further spread (9). During invasions, poor habitat quality and lower carrying capacities, increased levels of kin competition, and increased population growth due to enemy release are expected to initially boost spread under nonequilibrium conditions through elevated dispersal. Populations originating from spatiotemporally variable metapopulations typically evolve high dispersal abilities that are then expected to facilitate range expansion in the introduced area. Likewise, stable populations established from a few founders or from highly isolated populations may evolve higher dispersal rates because of kin competition (51, 94), thereby enhancing spread after introductions. The evolutionary history from the native spatial structure will thus strongly impact spread in the introduced areas through genetic carry-over effects. For instance, if geographic spread of native or invasive insects contributes to selecting individuals with enhanced performance to cope with oxidative stress, this could have significant effects for reproductive success (101, 183), thereby further affecting population dynamics.

Genetic carry-over effects may be more cryptic than those following adaptive evolution. Neutral or maladaptive mutation surfing and subsequent drift in the expanding populations may lead to genetic divergence between edge and core populations, providing the necessary genetic background for adaptation to novel environmental pressures (45). So far, the only supporting evidence of this in range-expanding insects is the genomic signature of selection to novel habitat temperatures in the damselfly *Coenagrion scitulum* (161).

In contrast, short-term (ecological) carry-over effects can affect the initial settlement phase, thereby overcoming establishment costs and presetting conditions for further spread. As energy budgets are dynamic (81), natal habitat quality is an important determinant of body condition, which in turn constitutes a major driver of competitive outcomes (116). Unfortunately, relatively little data exist on carry-over effects in invaders and their consequences for invasion success. The importance of natal habitat characteristics on the subsequent performance of the competitive interactions of the dispersers as a function of the density dependence of the colonized habitat has been assessed (170). Low-quality habitat alters competition between *Tribolium confusum* and *T. castaneum*; the former dominates in low-quality conditions, whereas *T. castaneum* is more competitive when the landscape encompasses high-quality habitats (170). Carry-over effects of the energetic condition may directly impact further spread, with greater dispersal distances being attained by insects that can rely on body reserves. For example, flight distances covered by the beetle *Monochamus galloprovincialis* are influenced by the amount of energy reserves allocated to the thorax (36).

### 5. RESEARCH GAPS

The number and pace of invasions have increased to unprecedented levels over the past decades, without signs of saturation (144, 151). However, important gaps remain in our understanding of

the variables driving the success or failure in breaching each of the barriers in the invasion process (**Supplemental Materials S3** and **S4**). Overall, the selective filtering of phenotypes at each step of the invasion process has been poorly investigated, hampering our understanding of the invasion process and its predictability. Furthermore, the existence of phenotypic heterogeneity within populations makes the individual perspective key to understanding the multiple interacting factors acting during establishment and invasion processes. Invasion potential is consequently expected to differ dramatically on the basis of which individuals are sampled (i.e., when individuals become part of the propagule pool sent out from a region of origin), the propagule size, and the timing of the sampling. Dispersal capacities are not necessarily selected for until the stage of geographic expansion in a new range, whereas the ability to surmount abiotic characteristics of transportation and biotic factors during introduction are central to successful establishment. Consequently, the adaptive potential of the insects, set by the environmental conditions of native habitats, is pivotal for passing through filters during sampling, transportation, and introduction and ultimately for priming invasion.

Founder individuals surmounted filters during sampling and transportation, but the intensity of selection therein is expected to vary greatly among introduction pathways, limiting our insights into its importance. Environmental similarity and stress resistance represent first components determining introduction and establishment success and can boost further spread. However, evidence on environmental matching between novel invasions and natal habitat from an ecophysiological perspective at the individual level is missing. When dissimilarity is high, to what degree can informed dispersal compensate and maximize habitat matching? Where possible, fitness deviations should be measured and further linked with dispersal success. Our understanding of the role of phenotype-dependent dispersal (including syndromes) relies mostly on observations from ongoing invasions, but insight on phenotypic and ecological attributes in failed invasions is needed to make inferences on the deterministic drivers of invasion success.

Theory is progressing on how spread might proceed and be influenced by kin competition or informed dispersal (50), but we lack connection with real systems to move from tactic to predictive models. In addition, little is known about the forces affecting expansion beyond the initial introduction point, including how community context affects dispersal decisions (49) or what traits favor sustained expansion. If stress tolerance and dispersal are positively correlated, then best colonists are expected to perform better at both dispersing and establishing, which may lead to accelerating invasion dynamics. In contrast, if stress tolerance is traded for dispersal, then predicted invasion speed based on dispersal capacity may be overestimated. Moreover, invaders' immune responses are expected to vary (31) as a result of large variations in population density along invasion gradients, but this has rarely been investigated in insects (but see 4). Finally, we lack insights from theory and empirical observations on how evolutionary history under spatiotemporal characteristics of native habitats may eventually affect success in invaded habitats and how further evolutionary dynamics impact predictability of further spread processes (e.g., 46, 69).

#### **FUTURE ISSUES**

1. Identify the main spatiotemporal environmental variations of the habitat in the source range. This would allow an assessment of how much the origin of the sampled propagules is a determinant of their likelihood of passing through the succession of ecological filters (i.e., probability of being sampled, surviving transport, and establishing in the recipient area).

#### Supplemental Material

- 2. Describe the conditions encountered by the propagules during their transportation. These data would allow an evaluation of the nature of the selection imposed to the pool of individuals initially taken out of the native region and an estimate of which phenotypes eventually pass this filter.
- 3. Characterize the genetic and phenotypic pool of individuals in a newly established population. Genetic structure may be a strong driver of expansions owing to kin competition, but the connection to dispersal behavior is missing.
- 4. Identify the forces that elicit the expansion of invaders outside the initial area of establishment.
- 5. Determine whether there are associations between stress tolerance and dispersal abilities in successful invaders or whether there are trade-offs between stress tolerance and dispersal. If trade-offs exist, invasion speed may differ from predictions on the basis of dispersal capacity alone (changes in the success/failure rate of those individuals dispersing).

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