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The importance of eco-evolutionary dynamics for predicting and managing insect range shifts

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Evolutionary change impacts the rate at which insect pests, pollinators, or disease vectors expand or contract their geographic ranges. Although evolutionary changes, and their ecological feedbacks, strongly affect these risks and associated ecological and economic consequences, they are often underappreciated in management efforts. Greater rigor and scope in study design, coupled with innovative technologies and approaches, facilitates our understanding of the causes and consequences of eco-evolutionary dynamics in insect range shifts. Future efforts need to ensure that forecasts allow for demographic and evolutionary change and that management strategies will maximize (or minimize) the adaptive potential of range-shifting insects, with benefits for biodiversity and ecosystem services.

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Introduction

Insect range expansions and contractions in response to human activities are widespread and are reshaping entire food webs and altering ecosystem functions and services [1•,2•]. Practical consequences of range shifts include the rescue of species from degraded habitats, more robust populations with expanded ranges, and increases in local biodiversity. While such consequences can often be favorable, negative impacts are also observed, if range-shifting species include agricultural pests and vectors of human and agricultural diseases, or disrupt native communities and ecosystem services [3,4]. Because both ecological and economic consequences of insect range shifts are important, it is a priority to understand what drives some insects, but not others, to undergo rapid range shifts, and to further understand drivers of variation. Until recently, however, forecasting models have mostly considered ecological drivers such as colonization, biotic interactions, and abundance shifts, without taking into account rapid evolution associated with range shifting, which can affect all of these ecological parameters. Rapid evolution commonly occurs during range shifts; this phenomenon was first shown in insects [5•], and is clearly a dominant phenomenon in this group, facilitated by their sensitivities to environmental change and by their short life cycles and large population sizes. These characteristics can facilitate rapid transgenerational genetic or epigenetic change [6,7•] Strong ll life-history trade-offs in insects can further help to maintain

evolutionary variability, and therefore, perhaps counter-intuitively, can increase fitness when encountering novel environments during range expansions [8].

Range shifts are ecological processes, so when they involve evolution they invoke eco-evolutionary dynamics, i.e. interactions between evolutionary change and ecological outcomes. For example, insect range expansions can both drive evolution of dietary niche breadth [9•] and be facilitated by it [5•,10]. There is well-established theoretical understanding of eco-evolutionary dynamic feedbacks between microevolutionary change and demographic shifts during colonization of novel environments [11]. However, empirical evidence lags behind theoretical developments. This omission is largely due to a lack of established approaches for discovering, diagnosing and monitoring eco-evolutionary processes in wild systems. Lack of data to test models therefore makes it difficult to predict evolutionary responses and their relationship to ecological patterns and processes. This is unfortunate, given that conservation and management actions depend on a robust prediction of range shift trajectories. To increase awareness of this gap between theory and data, we (1) highlight opportunities that insects offer for identifying the eco-evolutionary basis of range shifts and their applied relevance; (2) discuss recent advances in our understanding of eco-evolutionary dynamics of insect range shifts; and (3) identify critical avenues for robustly assessing the temporal and spatial scale of those dynamics to improve predictions of range shifts and their impacts on biodiversity.

The importance of studying eco-evolutionary dynamics during insect range expansions

Insects are among the most rapidly range-expanding of all terrestrial taxa [12•]. Range-shifting insects have a large impact on the assembly of resident biotas [13], on pollinator networks [4] and other ecosystem services [14•]. Life histories of range-expanding insects are often distinct from resident communities in that they exhibit increased resilience to stressors, ecological generalism, or competitive ability [15]. These observations have been used to suggest that colonizing species are those already with ecological traits that enable rapid spread. However, this conclusion rests on the assumption that ecological and evolutionary processes occur on different time scales, where the evolution of the traits that confer the capacity for ecological disruption is thought to occur in advance of geographical expansion. However, we argue that this assumption is often unlikely to be true, in part because attempts to discover traits predisposing range expansions have failed or detected only weak effects (reviewed in [16•]). Instead, we suggest that traits conferring colonization ability most likely evolve *during* range expansions (see also: [17•]; Figure 1). Conversely, traits and processes likely to arise during range contraction may potentially confer enhanced sensitivity to further declines, although evolutionary processes during range contraction are even less well characterized than those associated with expansion.

Insects further offer ideal opportunities for detailed studies of range shifts. Data on insect distributional shifts is increasing in volume owing to technological advances in rapid insect surveying methods [18], such as remote sensing and techniques that exploit frequencies of solar radiation to track individuals and their microclimates [19•]. These advances offer more in-depth insight into the densities, distributions and dispersal behavior of flying insects. However, such data are highly biased towards terrestrial insect communities, which are unlikely to be representative of aquatic species and the important ecosystem services they provide. Increasing research on the eco-evolutionary dynamics of range shifting pest species and disease vectors [20] is particularly needed, given their relevance for food sustainability and human health.

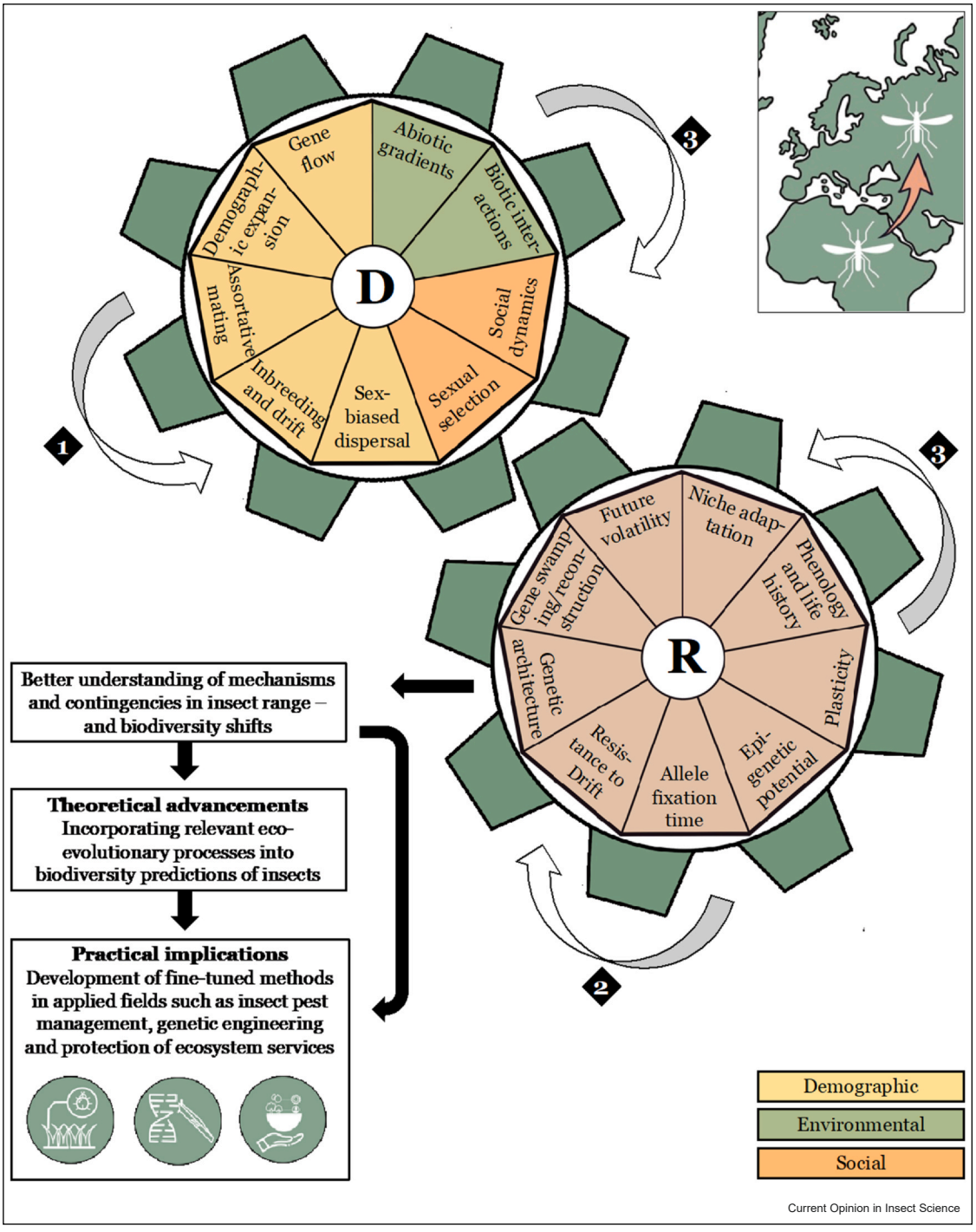
Eco-evolutionary dynamics during insect range shifts

Many studies of evolution during range shifts in insects have focused on changes in physiological traits, such as thermal tolerances, shaped under ecological selection in the new part of the range (e.g. [21–23]). However, novel demographic conditions arising from range expansion can also impose selection on characteristics such as enhanced dispersal or resistance to inbreeding, and on life history traits such as reduced generation time, voltinism and diapause that can speed up the expansion itself [24]. In addition, gene flow from the historic range and genetic drift further shape genetic variation and, thus alter evolutionary dynamics [25]. Neutral, rather than adaptive processes, can dominate evolutionary changes during colonization events, making it difficult to predict range shift outcomes. Nonetheless, certain anticipatory responses may also evolve, for example, serial colonization at the leading edge of range shifts can select for indiscriminate individuals that are more likely to accept marginal habitat conditions [26].

Recent studies highlight the importance of trait plasticity for insect adaptation during range shifts [23,27]. In particular, increased learning ability may be important for insects to cope with environmental heterogeneity and unpredictability during colonization events [28,29] Evolutionary ioncreases in learning ability, as in any form of plasticity, can further facilitate environmental adaptation by allowing persistence in a novel environment until genetic accommodation has occurred [30].

Dispersal evolution is often part of eco-evolutionary feedback loops, both as a driver and response [31]. In addition to being favored during serial colonization [24],

Figure 1



Mechanistic, simplified representation of eco-evolutionary dynamics during insect range shifts and their importance for (applied) research. The gear wheels can move in the direction indicated by the arrows, such that the exemplary selection of demographic, environmental and social drivers (D) (see color legend on bottom right) may individually, or in combination, (1) evoke evolutionary responses (e.g. epigenetic, or genetic) (R) in range expanding insect populations on contemporary time scales (2). Understanding the rates and strengths of these processes will be crucial for theoretical advancements and practical implications of insect range shifts (see boxes on bottom left). Moreover, responses can induce new driving forces (3), resulting in positive or negative eco-evolutionary feedbacks and feedback loops, for example, an increase in a driving process A induces a genetic response that further increases versus decreases trait A, thus accelerating or dampening the dynamic and resulting range shift trajectory.

high or low population densities at the range limit may further facilitate changes in dispersal propensity [32]. Evolutionary impacts of range shift-induced dispersal traits may not evolve independently from other traits, meaning that changes in dispersal will impact correlated traits, further modifying eco-evolutionary dynamics [33•,34•]. Furthermore, insect dispersal traits are often temperature-sensitive, suggesting that the interplay between shifts in environmental plasticity and dispersal needs to be considered together to predict likely evolutionary dynamics [35].

Social dynamics also evolve readily during range shifts, influencing adaptive potential to both expand and to resist contraction. This may occur for instance if sexual or other socially-mediated selection differs between the range core and the range edge [36], due to changes in fragmentation, relatedness, or density conditions at fluctuating range edges that impact reproductive and competitive opportunities. Novel social dynamics at range margins can feed back to impact individual phenotypes and fitness, for example, via invoking generalized stress responses that also confer fitness in novel environments [37]. Another consequence of range shifts may be skewed sex ratios, particularly where sexes differ in dispersal, meaning the more dispersive sex reaches the range limit in higher numbers. The resulting skew can impact mating systems or the strength of sexual selection (e.g. in damselflies: [7•]).

An understudied area is the complex, interactive effect of eco-evolutionary change on community dynamics during insect range shifts. For example, novel plant-insect interactions caused by unequal rates of range shifting likely impact both plant and insect biodiversity, population sizes, and evolutionary potential, with shifts in pollinator and pest communities impacting food security. In particular, encountering novel resources during range shifts can trigger diet evolution (e.g. increase or reduction in Lepidopteran host breadth: [9•,38•,39•]). Moreover, shifts in plasticity, physiology, life history and dispersal associated with range shifts can further impact future community dynamics: colonizing lineages, which have already adapted to spatial variability, may then have an evolutionary advantage over existing residents when future environments become more variable or less predictable [40]. To take into account the evolution of interactions among species and environments, an approach that includes multiple drivers and responses is needed to detect how biotic interactions affect and are impacted by eco-evolutionary processes during range shifts (Figure 1).

Advances in the study of eco-evolutionary dynamics

To advance our understanding of eco-evolutionary dynamics, a temporal approach is needed to quantify the nature, rate and magnitude of population changes along range expansion trajectories. However, due to practical constraints, most studies assess range shift dynamics across only one or a few generations. Improving temporal resolution may be accomplished via judicious use of historical records or genetic inference of past demography and adaptation, to make links between previous or ongoing population processes and resulting demographic characteristics or trait values [7•,39]. Statistical approaches that account for abiotic and biotic factors that can bias range estimates are also developing rapidly to enable more accurate modeling of past and current range dynamics [41••].

Recent advances in genomic sequencing approaches and computational improvements further present the opportunity to track historical eco-evolutionary processes using a greatly expanded set of 'omic' markers. Spatial genomic datasets allow for high-powered tests for dispersal and demographic processes that influence genetic connectivity, and provide insight into spatial and temporal dynamics of neutral and adaptive genomic variation [42,43]. Likewise, transcriptomic approaches can test the relationships between environment, gene expression, and phenotype in insect populations impacted by range shifting, providing insight into how the genetic basis of traits, and their plasticities, may evolve [44,45•]. Epigenomics, the study of DNA modifications that impact gene expression, is another growing field that identifies how insects can rapidly respond to a changing climate [6], with accumulating evidence suggesting that modifications can have significant transgenerational impact [46]. One interesting idea is that the evolution of 'epigenetic potential' (i.e. proportion of the genome available for new epigenetic modifications) may be an important mechanism of plasticity evolution during range shifts [47], a hypothesis that remains untested in insects.

Effective use of these techniques depends on careful experimental design to allow for generalizations about the role of eco-evolutionary dynamics in the likelihood, rate, and outcomes of range shifts. For instance, effective design may include careful sampling over time within the range as well as at the edge, repeated sampling across multiple range shift transects within a species, or comparing outcomes across range-shifting versus nonshifting species along a shared spatial gradient [48]. Meta-analyses adopting this latter approach have recently revealed that *only range-shifting insects* exhibit classical latitudinal gradients in dietary and thermal niche breadth. This work suggests that rapid niche evolution during range shifts is an important cause of macroecological patterns [9•,49]. In addition, replicated assessment of trait or distribution outcomes across independent expansion trajectories within a species, such as in [38], are crucial to understand what patterns are due to stochastic versus general responses of populations.

Appropriate application of 'omic approaches often requires a mechanistic understanding of how genetic variation links to relevant traits, which in turn impact demography and adaptation. Wetherefore advocate for combining wild studies with laboratory or field experiments to robustly corroborate these links. Experimental approaches may involve evolution of replicate laboratory populations under range shift conditions, and adopting an 'evolve and resequence' approach to track how genetic and phenotypic (co)variation respond to experimentally altered patterns of demography and environmental variation [50]. Alternatively, common garden or reciprocal transplant studies can be used to establish causality. Such common garden studies can also be combined with more complex breeding designs coupled to sequencing, to experimentally disentangle and quantify genetic and environmental factors [51].

Increased collaborative efforts are also essential. Extending the temporal and spatial scales of study requires investment and prioritization at multi-institutional, and in many cases, multi-national levels. A multidisciplinary approach is also critical for integrating data from environmental, physiological, demographic, genetic, and epigenetic data sources. Effectively combining this information will be essential for modeling evolutionary trajectories and feedbacks that facilitate or hinder range shifts. Such models are still in their infancy. However, recent work suggests that incorporation of data on genetic variation improves species distribution models and forecasts [52], and the development of genetically explicit process-based models is increasing at a rapid pace [53,54]. Inverse fitting of process-based forecasting models parameterized from rigorous empirical demographic and genomic data represents the next stage in forecasting sophistication [55].

Conclusions

Accurate forecasting of which insect species will or will not range-shift or adapt is urgently needed. Insect range shifts are already impacting biodiversity, human disease risk, agriculture, and forestry, with severe economic consequences [3]. Providing the needed empirical data to understand and model the eco-evolutionary processes that underpin range shifts demands multidisciplinary insights e.g. from 'omic' approaches, and combinations of wild and laboratory studies at the appropriate temporal and ecological scale. Once we understand the biological processes limiting or enhancing insect range shifts, species and communities identified as being at risk can be targeted to support their ecological and adaptive potentials.

Conflict of interest statement

The authors declare no conflict of interest.

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