





Expanding insect pollinators in the Anthropocene

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ABSTRACT

Global changes are severely affecting pollinator insect communities worldwide, resulting in repeated patterns of species extirpations and extinctions. Whilst negative population trends within this functional group have understandably received much attention in recent decades, another facet of global changes has been overshadowed: species undergoing expansion. Here, we review the factors and traits that have allowed a fraction of the pollinating entomofauna to take advantage of global environmental change. Sufficient mobility, high resistance to acute heat stress, and inherent adaptation to warmer climates appear to be key traits that allow pollinators to persist and even expand in the face of climate change. An overall flexibility in dietary and nesting requirements is common in expanding species, although niche specialization can also drive expansion under specific contexts. The numerous consequences of wild and domesticated pollinator expansions, including competition for resources, pathogen spread, and hybridization with native wildlife, are also discussed. Overall, we show that the traits and factors involved in the success stories of expanding pollinators are mostly species specific and context dependent, rendering generalizations of ‘winning traits’ complicated. This work illustrates the increasing need to consider expansion and its numerous consequences as significant facets of global changes and encourages efforts to monitor the impacts of expanding insect pollinators, particularly exotic species, on natural ecosystems.

Key words: invasive species, exotic species, expansion, global change, conservation, butterflies, bees, bumblebees

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I. INTRODUCTION

The development of human societies has profoundly impacted global biogeochemical systems to such a degree that the period of time in which we now live has been dubbed the Anthropocene (Lewis & Maslin, 2018; Sage, 2020). From the point of view of biodiversity, this epoch has been marked by a global wave of species extinctions, population extirpations, and negative population trends leading to a significant shift in ecosystem composition (Dirzo *et al.*, 2014). Although species declines have understandably received much attention, this has overshadowed another facet of global change: species undergoing expansion. This latter phenomenon comprises either an increase in the total area of a species' distribution or a shift from its original distribution, implying expansion into new territories along with the loss of part of their historical range. In both cases, the resulting distribution encompasses new locations with potential consequences for native wildlife (Tomuolo & Ward, 2018).

Three main factors predominantly account for how a subset of species undergo expansion (McGeoch & Latombe, 2016). First, species can respond positively to successful interventions in their habitats that were planned to avoid their extinction (Willis *et al.*, 2009; Neel *et al.*, 2012). Second, steadily increasing evidence shows that populations and species can expand along at least one margin of their distribution range following global changes in temperature and habitats (e.g. Hiddink, Burrows & Molinos, 2015). Third, species can reach new localities and establish inside or outside their native range through human transport (Aizen *et al.*, 2020). While increases in relative abundance, range shifts, and expansions of species as a result of global change are often well documented, the *traits* of species that allow them to expand and establish new and/or bigger populations are less well understood. Key combinations of life-history traits are known at least partly to explain such expansions under global changes (Estrada *et al.*, 2016; MacLean & Beissinger, 2017). For example, taxa with a higher dispersal ability are more likely to reach suitable habitats (Travis *et al.*, 2013) and undergo larger range shifts (Buckley & Kingsolver, 2012). Consequently, larger body size, often positively correlated with dispersal ability, shows a high potential to be associated with species demonstrating a geographical range expansion (Lyons, Wagner & Dzikiewicz, 2010; but see Angert *et al.*, 2011). Niche generalism, specifically dietary breadth and range of habitats used, can also affect the ability

of an organism to establish in new locations (Braschler & Hill, 2007; Angert *et al.*, 2011), and indeed these two traits are often intercorrelated (Lurgi, López & Montoya, 2012). Other life-history traits such as a high fecundity, or early and frequent reproduction can also favour the ability of a species to colonize, establish viable populations, and persist in areas beyond its historic distribution (Angert *et al.*, 2011). Although such traits may be important individually, they can present contradictory effects and thus may be counterbalanced. For instance, organisms with larger body size tend to have a lower reproduction rate, leading to antagonistic effects on range expansion (Lurgi *et al.*, 2012).

Given their high species diversity (>5.5 million species; Stork, 2018) and considerable economic importance (almost \$60 billion a year in the USA; Losey & Vaughan, 2006), insects represent excellent models to investigate the context-dependent importance of such traits following ecological disruptions (Halsch *et al.*, 2021). The ongoing shifts of global entomofauna are variable in space, time and intensity at the community, species and population levels, with impacts on natural (e.g. emerging patterns of introgressive hybridization, speciation and extinction) and anthropogenic (e.g. spread of pest species and disease vectors, loss of ecosystem services) biomes. In particular, the response of insect pollinators, mainly bees, butterflies, hoverflies, moths and pollinating wasps, to global changes has garnered much attention due to their role in facilitating the sexual reproduction of both wild plants and crops (Potts *et al.*, 2010; Ollerton, 2017). More than 80% of the world's flowering plants are dependent on insects for pollination (Ollerton, Winfree & Tarrant, 2011), including ~75% of all crops (Vanbergen & The Insect Pollinators Initiative, 2013; Kremen, 2018). Although pollinating insects are widely reported to have experienced drastic population declines (e.g. Settele *et al.*, 2008; Goulson *et al.*, 2015; Kerr *et al.*, 2015; Agrawal & Inamine, 2018; Wagner, 2020; Zattara & Aizen, 2021), a non-negligible number of species are increasing their abundance, shifting their original distribution area towards new territories, and consequently expanding from their historical distribution ranges (e.g. Duchenne *et al.*, 2020).

In the current context of a global biodiversity crisis, highlighting the factors and the traits that jointly allow a subset of species to benefit from global changes is a fundamental step towards better understanding and predicting the numerous consequences of ongoing global changes. In this context,

we aim to review the current understanding of the various factors (Fig. 1) and traits (Table 1) associated with expansions of pollinators. Finally, we discuss the impacts of such expansions on native wildlife.

II. POLLINATORS BENEFITING FROM CLIMATE CHANGE

(1) Global impact of climate change on pollinators

Both acute as well as gradual changes in temperature can impact species distributions and population dynamics, and a possible response to these pressures is a shift in distribution across elevation and latitude towards regions that were previously too cool prior to climate warming (Pecl *et al.*, 2017). Climatic conditions directly impact pollinator population dynamics through the modulation of survival (Crozier, 2004; Martinet *et al.*, 2021a), development (WallisDeVries & van Swaay, 2006; Vanderplanck *et al.*, 2019), fertility (Martinet *et al.*, 2021b), and dispersal (Parmesan *et al.*, 1999; Hill, Hastings & Botsford, 2002). Moreover, climate partly constrains pollinator distribution based on their thermal requirements (e.g. thermal minima and maxima) (Oyen *et al.*, 2016; Ghisbain *et al.*, 2020). Considering climatic variables independently from other confounding variables is however understandably complex, as climate also impacts pollinators indirectly through environmental changes.

Importantly, climatic variation impacts plant–pollinator interactions by altering the quality and the quantity of plant resources (i.e. pollen and nectar; Carnell, Hulse & Hughes, 2020) or mismatches in the spatio-temporal distributions of mutualistic partners (Thomson, 2016; Gérard *et al.*, 2020b). Water stresses (e.g. droughts, floods) are examples of extreme events that are likely to increase in frequency, duration and severity (Dai, 2013; EEA, 2017), and which have numerous effects on plant–pollinator interactions, including modifications in plant and flower size, inflorescence number, floral longevity, and scent (Thomson, 2016; Lambrecht, Morrow & Hussey, 2017; Campbell, Sosenski & Raguso, 2019; Kahl, Lenhard & Joshi, 2019; Descamps, Quinet & Jacquemart, 2020). The food supply for pollinator populations is expected to be altered as these extreme phenomena increase (reviewed in Descamps *et al.*, 2020).

(2) Dealing with the heat or tracking the cold

Several empirical studies have shown strong correlations between global warming (i.e. change in mean temperature) and spatial shift in butterflies (e.g. Parmesan *et al.*, 1999; Breed *et al.*, 2012; Au & Bonebrake, 2019), with more than 60% of studied butterfly species extending their distributions northwards by 35–240 km during the 20th century (Parmesan *et al.*, 1999). Although ~80% of butterfly species included in a more recent study underwent southern range

declines, many species with southerly centred ranges showed population growth and shifted their distributions northwards (Breed *et al.*, 2012). This phenomenon is well established in countries like Great Britain, where several studies have demonstrated a temperature-related shift towards northern regions (e.g. Asher *et al.*, 2001; Pateman *et al.*, 2012). Climate warming has also been proposed as a driving factor behind the colonization of subtropical areas by a diverse array of butterfly and moth species (Chan *et al.*, 2011; Cheng *et al.*, 2019). A key trait involved in these range shifts is that a high proportion of these newcomers are of tropical origin that follow the increasing suitability of subtropical areas for tropical species (Au & Bonebrake, 2019). Such range expansion that is at least partly due to climate change can occur particularly rapidly, as shown for the Indian native butterfly *Acraea terpsicore* that has colonized new territories of Southeast Asia at an estimated rate of 200 km/year over the last 30 years (Noor *et al.*, 2017).

Amongst the variables involved in expansion, seasonal warming has increasingly been shown to trigger significant effects on range shifts in certain insect pollinators through the expansion of their potential climatic niche. Milder winters, subsequent warmer overwintering conditions, and warmer months during the emergence of queens, have been correlated with the rapid westward colonization of the bumblebee *Bombus haematurus* by 20% in about 40 years without evidence of dietary niche shift (Biella *et al.*, 2020). Similarly, some heat-adapted carpenter bees (Apidae, *Xylocopa*) are expanding their distributions, this expansion being correlated with higher temperature in both winter and summer (Tripodi & Szalanski, 2011; Vickruck & Richards, 2017; Banaszak *et al.*, 2019). Possible mechanistic explanations for these trends might be decreased mortality in a critical phase of an insect's life cycle, as warmer winters could act as a prerequisite for range expansion by increasing larval survivorship (in butterflies, see Crozier, 2003, 2004) or queen success in overwintering (in bumblebees, see Biella *et al.*, 2020). Other life-history variables can also explain expansion trends, with some butterfly species that do not overwinter as eggs or unfed neonate larvae, as well as multivoltine species, being more prone to show range expansion (Breed *et al.*, 2012). As a result of milder winters, some bumblebee populations have been observed throughout the cold season feeding on under-exploited flowering plants from urban parks and gardens (Stelzer *et al.*, 2010). Although winter-foraging could be seen as a favourable adaptive strategy to avoid interspecific competition with other pollinators, such changes in phenology might only be physiologically feasible for pollinators that are able to forage at lower temperatures (e.g. close to 0°C), such as bumblebees (Heinrich, 1979). In species that are already multivoltine however, warmer temperatures during larval development are expected to lead to an additional generation(s) each year (Kiritani, 2006; Gomi *et al.*, 2007). Since 1980 in Europe, a significant proportion of multivoltine butterfly species showed increased frequency of second and subsequent

generations, and others even augmented the overall number of generations (Altermatt, 2010).

In Europe and North America, both range shifts and range expansions have only been shown in a minority of the predominantly cold-adapted bumblebees (Apidae, *Bombus*) (Kerr *et al.*, 2015; Martinet *et al.*, 2015; Rasmont *et al.*, 2015), while many other members of the genus are regressing (Cameron & Sadd, 2020). A recent study supports the hypothesis that climate (in conjunction with land-use change and floral availability) has driven an elevation shift in both bumblebees and plants in the mountains of south-western Europe (Marshall *et al.*, 2020). The observed concurrent changes were however asymmetrical, with plants having shifted on average 100 m higher than bumblebees. High-elevation habitats are expected to become critically important for cold-adapted pollinators, as they can act as cold-temperature refugia from habitats that may no longer exist at lower elevations (Rasmont *et al.*, 2015; Penado, Rebelo & Goulson, 2016). In other species of bumblebees, expansion with retention of the original range (e.g. *Bombus haematurus*, *B. schrencki*) could partly be explained by a greater inherent adaptation to acute heat stress during extreme

climatic events (i.e. higher critical thermal limit and/or longer time before heat stupor), as suggested by thermal stresses applied to bumblebees under laboratory conditions (Zambra *et al.*, 2020; Martinet *et al.*, 2021a). Higher resistance to heat stress can ultimately be associated with a higher survival rate that may allow persistence in areas experiencing an increased incidence of heat waves (Martinet *et al.*, 2021a). Alternatively, the observed retention of their original range could be due to (i) these localities acting as temporary climatic refugia, with the possibility that these relictual populations will die out following further climatic changes, and (ii) a lack of overall sampling in some parts of their range preventing an accurate quantification of their actual regression (Rasmont *et al.*, 2015).

Overall, both gradually increasing average temperatures and the greater frequency of extreme climatic events constitute key factors that can benefit species exhibiting key physiological or ecological traits, such as an inherent adaptation to hotter areas or resilience to heat waves, involved in reducing mortality during critical phases of the pollinator life cycle (Table 1). Although we are not aware of studies explicitly demonstrating positive effects of change in precipitation on the expansion of

Table 1. Traits associated with range expansion in pollinators and context in which the trait is beneficial

Candidate winning trait	Context in which the trait is efficient	References
Global warming		
Sufficient mobility to: (i) track colder areas (ii) follow warming areas	Gradual, localized warming Green network to reach higher latitudes or altitudes (i.e. no biotic or abiotic insurmountable obstacles)	Biella <i>et al.</i> (2020); Martinet <i>et al.</i> (2015); Rasmont <i>et al.</i> (2015); Kerr <i>et al.</i> (2015); Au & Bonebrake (2019); Parmesan <i>et al.</i> (1999); Breed, Stichter & Crone (2012); Pateman <i>et al.</i> (2012); Banaszak, Cibicka & Twerd (2019); Crozier (2003)
Plasticity to extreme temperatures	Sudden climatic events, heat waves but with a moderate duration	Zambra <i>et al.</i> (2020); Martinet <i>et al.</i> (2021a,b); see also Oyen, Giri & Dillon (2016)
Inherent association with warmer climates (e.g. tropical, Mediterranean)	Gradual global temperature rise Warmer winters	Biella <i>et al.</i> (2020); Martinet <i>et al.</i> (2015); Rasmont <i>et al.</i> (2015); Au & Bonebrake (2019); Banaszak <i>et al.</i> (2019); Noor <i>et al.</i> (2017)
Global habitat change		
Flexibility in nesting material Ability to use human structures for nesting Above-ground nesting	Increased anthropic material in ecosystems Increased frequency of impervious surfaces	Prÿs-Jones, Kristjánsson & Ólafsson (2016); Prÿs-Jones (2019); Ballare & Jha (2020); Geslin <i>et al.</i> (2020)
Generalized diet and resource use Flexible diet and opportunism (e.g. nectar robbing) High metabolic performance	Landscape homogenization Increased spatio-temporal plant–pollinator mismatches	Moerman <i>et al.</i> (2016); Vanderplanck <i>et al.</i> (2014); Braby <i>et al.</i> (2014)
Specialized diet on expanding host plants	Host is ornamental Host is a crop Host is itself expanding	Halsch <i>et al.</i> (2021); López-Urbe <i>et al.</i> (2016); Ryan <i>et al.</i> (2019); Betzholtz <i>et al.</i> (2013); Vane-Wright (1993)
Association with open habitats	Deforestation	Noor <i>et al.</i> (2017)
Association with woody habitats	Increased forested areas	Betzholtz <i>et al.</i> (2013)
Larger body size (increased dispersal ability)	Increase in habitat fragmentation	Gérard <i>et al.</i> (2020a); Pöyry <i>et al.</i> (2009); Freedman <i>et al.</i> (2020)

(Continues)

Table 1. (Cont.)

Candidate winning trait	Context in which the trait is efficient	References
Human facilitation		
Expected high efficiency as a crop pollinator	Increasing need for pollination services (e.g. growing human population, lack of natural pollination services)	Geslin <i>et al.</i> (2017) and references therein; Aizen <i>et al.</i> (2020) and references therein; Schweiger <i>et al.</i> (2010)
Easy to manage (e.g. eusociality)	Social species more likely to be chosen for domestication and exportation	
Flexibility in phenology	Global trade of wood and other goods by air/sea	Cane (2003); Fortel <i>et al.</i> (2016); Okabe <i>et al.</i> (2010) and references therein; Sheffield, Heron & Musetti (2020) and references therein
Wood nesting, cavity nesting	Palletized system of global trade	
Other facilitating ‘universal’ traits (can apply when the species has already expanded)		
Territoriality and aggression	Poorly competitive natives	Aizen <i>et al.</i> (2020) and references therein; Geslin <i>et al.</i> (2017) and references therein
Competitive advantage for resources	Regions lacking these behaviours with a ‘naive’ local fauna	
Parthenogenic, polyandrous reproduction system	Could apply without restriction	Magnacca & King (2013)

pollinators, further research is encouraged to investigate whether such events could be responsible for shifting success as a result of physiological adaptation to precipitation regimes.

III. POLLINATORS SURVIVING IN ANTHROPOGENICALLY MODIFIED HABITATS

(1) Thriving inside and outside cities: impact of habitat modification on pollinators

Urbanization leads to the creation of novel ecosystems, including a higher proportion of impervious surfaces, habitat fragmentation and isolation, and a high percentage of exotic plants and novel nesting material (Buchholz & Egerer, 2020). Outside cities, other anthropogenically modified habitats include the use of pesticides, which can impact mortality and behaviour (Henry *et al.*, 2012; Woodcock *et al.*, 2016), fragmentation impacting habitat quality (Senapathi *et al.*, 2015) or loss of floral and nesting resources for insect pollinators (Kleijn & Raemakers, 2008). Globally, habitat destruction and fragmentation, mostly associated with the intensification of agriculture and the consequent eutrophication (Carvalho *et al.*, 2020), is a leading factor driving the decline of pollinators (Powney *et al.*, 2019; Duchenne *et al.*, 2020) and insects in general (Wagner, 2020).

(2) New habitats, new opportunities

While anthropogenically induced land-use and land-cover change is well known to accelerate rates of extinction in many taxa (Ellis *et al.*, 2010), it can also create new opportunities for a subset of species. Depending on the nature of habitat modification, the identity and composition of the pollinator communities that will be favoured can vary strongly. The creation of novel open habitats helped, for

instance, the butterfly *Acraea terpsicore* expand its range by 7000 km² across large-scale palm-oil and *Acacia* plantations across Southeast Asia over a 30-year period (Noor *et al.*, 2017). By contrast, where forest cover has remained stable, such as in Northern Europe, forest species show greater range expansions than species associated with open habitats (Betzholtz *et al.*, 2013). Similarly in southern and eastern Europe, where reforestation occurred following the abandonment of agricultural lands due to socio-economic changes (Lasanta *et al.*, 2017), species strongly associated with woodlands are favoured (Jenič, Gogala & Grad, 2010).

(3) Dealing with fragmentation

Regardless of habitat modification, fragmentation impacts the number of suitable patches, their shape complexity, their isolation, as well as the proportion of edges (Didham, 2010). The increasing distance between patches of suitable habitats has been suggested to select for larger body size in pollinators, because larger body size can imply higher dispersal capability. In Finland, larger butterflies have been able to shift further distances than smaller ones (Pöyry *et al.*, 2009). In a context of large-scale migrations, a recent analysis revealed that initial monarch (*Danaus plexippus*) founders presented large and elongated forewings and were therefore well suited for long-distance movements, in contrast with populations that ceased migration after establishment (Freedman *et al.*, 2020). In several European countries, bumblebee queen body size has increased over the last century, possibly in response to increased habitat fragmentation (Gérard *et al.*, 2020a). This pattern has also been observed spatially, with some species of solitary bees displaying a larger body size in more fragmented agricultural landscapes (Warzecha *et al.*, 2016). Alternatively, highly agricultural landscapes

can also be associated with lower resource quality and quantity, two factors that negatively impact body size (Roulston & Cane, 2002; Gérard *et al.*, 2018). Moreover, smaller body size can lead to higher overall fitness in these landscapes as smaller offspring require fewer resources in absolute terms to reproduce (Renauld *et al.*, 2016).

(4) Nest opportunists

Landscape changes, particularly urbanization, have made available a completely new array of potential nesting locations for some insect pollinators. Given the mostly impervious nature of soils in cities, above-ground nesting pollinators are more likely to be selected in urban areas. In Europe, the bumblebee *Bombus hypnorum* nests in above-ground cavities, mainly in trees, but frequently takes advantage of human structures such as bird nest boxes, holes in walls, and roofing tiles (Prÿs-Jones, 2019). This ability, combined with increased forest coverage after 1945 and the urbanization of Europe after 1900, has probably allowed it drastically to increase its abundance, range, and density, including in new countries where it can be the most common species in urban areas (Prÿs-Jones *et al.*, 2016; BWARS, 2017; Prÿs-Jones, 2019). In North America, the carpenter bee *Xylocopa virginica* also benefits from anthropogenic modifications of habitats, this large bee nesting almost exclusively in structures built from milled lumber such as spruce and pine (Ballare & Jha, 2020). In cities, the increasing popularity of bee hotels in public parks also provides new nesting opportunities for bees. These structures have, however, been shown largely to favour the expansion of exotic species, as demonstrated in the South of France where the most common species that emerged from bee hotels was the invasive *Megachile sculpturalis* (Geslin *et al.*, 2020). A similar pattern has been observed from a survey of almost 600 bee hotels in Canada, in which introduced bees represented nearly half of all bees recorded (MacIvor & Packer, 2015).

(5) Host-plant opportunists

Some pollinator expansions can be related to the expansion of their respective host plants, either because these hosts are associated with horticultural practices (e.g. domestication of the host plants as ornamental plants), agricultural practices (e.g. domestication of the host plants as crops; selection/support of the wild host plants) and invasion, or because the hosts are themselves expanding following climate changes. For example, the Gulf fritillary butterfly (*Agraulis vanillae*) has expanded its range in the Western USA in the past 100 years (Shapiro & Manolis, 2007) partly following the use of its host *Passiflora* as a popular ornamental garden plant (Halsch *et al.*, 2021). Specialization on one specific agricultural crop explains range expansion in the North American squash bee *Peponapis pruinosa*, a strict pollen specialist of the plant genus *Cucurbita*. The bee is currently found far beyond the distribution of its ancestral wild host (*Cucurbita foetidissima*), in these areas relying entirely on domesticated

Cucurbita pepo used in commercial and domestic agriculture. Thanks to this anthropogenic facilitation, *P. pruinosa* has attained one of the largest geographical ranges of North American native bees (López-Urbe *et al.*, 2016). Similarly, although at a much broader scale, the cabbage white butterfly *Pieris rapae*, an agricultural pest, has undergone a dramatic expansion following the global use of brassicaceous crops on which its larvae feed (e.g. cabbage, canola, bok choy, turnips). The species is believed to have originated in Europe and to have started expanding ~1200 years ago following the diversification of brassicaceous crops and the development of human trade routes such as the Silk Road (Hiura, 1968; Fukano *et al.*, 2012). Over the last 160 years, *P. rapae* successfully continued its global invasion through multiple independent introductions and is now present on all continents except South America and Antarctica (Ryan *et al.*, 2019). Another consequence of agricultural expansion has been increased fertilizer use that has favoured plant species associated with nitrogen-rich habitats, a potentially important driver of range expansion in butterfly species with a nitrogen-favoured larval diet (Betzholtz *et al.*, 2013). An index assessing the level at which nitrogen-rich habitats can impact butterflies has been developed and could be used to forecast which species could benefit from anthropogenic habitats (WallisDeVries & van Swaay, 2017). Away from agriculture, climate-driven expansion of key host plants partly explains the dramatic northern expansion of the specialist giant swallowtail butterfly (*Papilio cresphontes*) by 180 km per decade in North America, an expansion that is also associated with warmer, wetter climate conditions in both overwintering and active flight stages of this pollinator (Wilson *et al.*, 2021).

In general, an inherently broader diet is likely best for facilitating species expansion, as the ability to consume a wider variety of available resources will allow dietary shifts depending on resource availability (Roger *et al.*, 2017). In Europe, the large majority of strongly expanding bee species are generalists, while specialized species are mostly stable or decreasing (Rasmont *et al.*, 2015; Scheper *et al.*, 2015). Among Australian butterflies, several species have expanded their ranges since 1970 (Peters, Smithers & Rushworth, 2010) and a common trait was the ability of the larvae to forage on non-native larval food plants (Braby *et al.*, 2014). Similarly, Nymphalinae butterflies showing a greater dietary breadth (i.e. with a more diverse host-plant use) are naturally more widespread than butterflies with narrower host-plant use (Slove & Janz, 2011). Whether a broader dietary breadth is a cause or a consequence of range expansion in such pollinators could be contextual. An increasing dietary breadth could lead to a range expansion if the range of the pollinator was originally restricted by the range of its host plant (Janz & Nylin, 2008). Alternatively, if the original range of a species is constricted by a factor other than diet (e.g. isotherms), a range expansion caused by an external factor (e.g. a temperature rise) can put the pollinator in contact with novel resources that could ultimately be used through ecological fitting (Agosta & Klemens, 2008). However, if the inherent

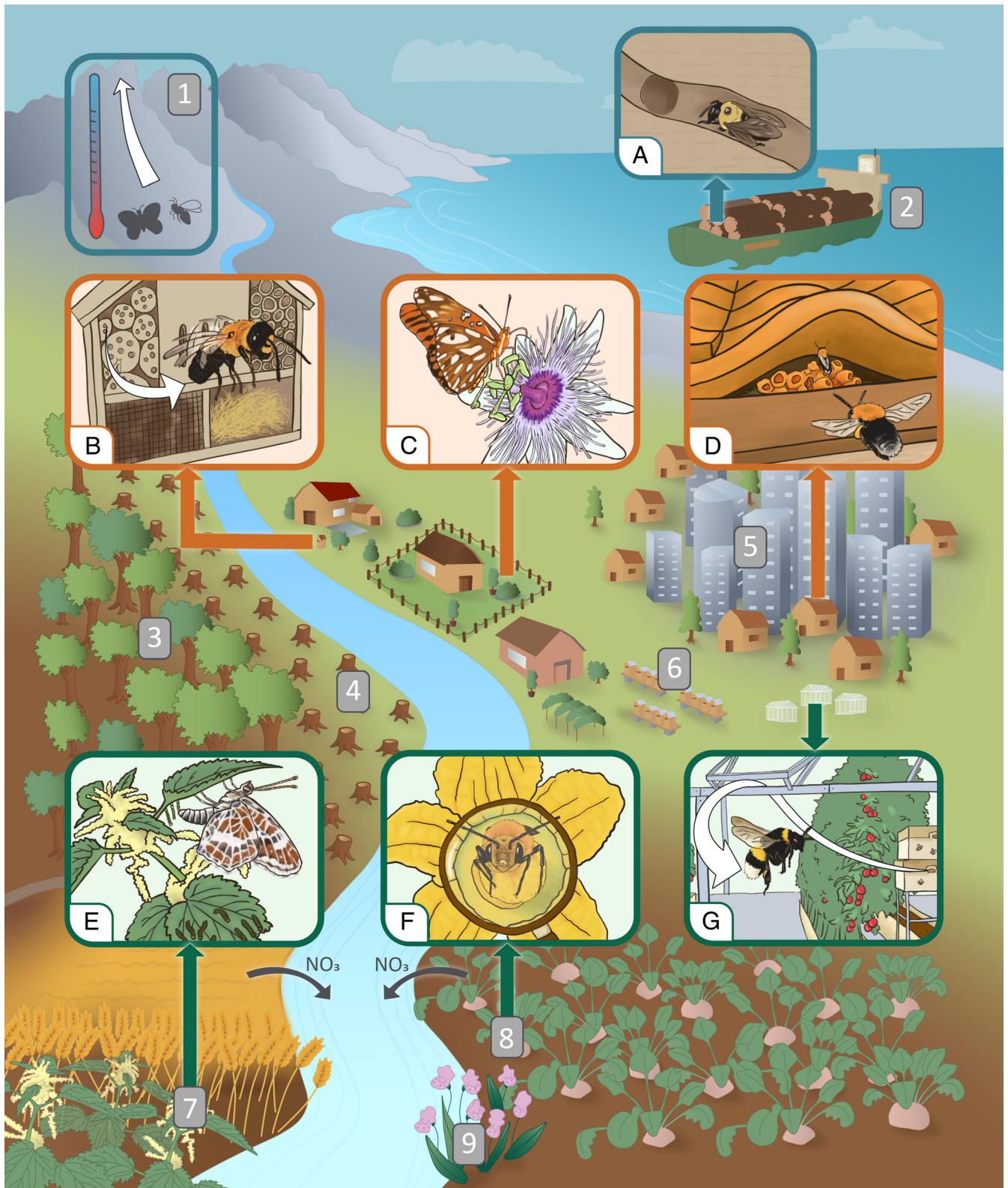


Fig 1. Visual representation of the factors involved in range expansion in pollinators in the Anthropocene: 1, climate change; 2, anthropogenic transport; 3, reforestation; 4, deforestation; 5, urbanization; 6, pollinator domestication; 7, eutrophication; 8, agricultural intensification; 9, plant invasion. A, carpenter bee moved through wood transport; B, invasive megachilid bee benefiting from bee hotels; C, butterfly co-expanding with its ornamental host; D, bumblebee nesting in a roof; E, butterfly co-
(Figure legend continues on next page.)

dietary flexibility of the species is too low, host switching is unlikely to occur, as dietary shifts generally occur over evolutionary time (Larkin, Neff & Simpson, 2008; Dellicour *et al.*, 2014).

Regardless of dietary breadth, the introduction of non-native plants into ecosystems can promote the expansion of non-native pollinators and *vice versa*. This phenomenon, reported as invasive mutualism or alien mutualism, can strongly erode native pollination networks by modifying the strength of interactions and distributions of asymmetries to the advantage of ‘super-generalist’ alien species during invasion (Aizen, Morales & Morales, 2008). The invasive mutualism of non-native honeybees and the exotic yellow star thistle (*Centaurea solstitialis*), both introduced to the western USA in the 1800s, is a key factor that allowed the expansion of both aliens (Barthell *et al.*, 2001). Similarly, human-driven colonization by milkweeds (*Asclepias* spp.) in non-native locations has aided the dramatic expansion of the highly mobile monarch butterfly across both the Pacific and Atlantic oceans in the 19th century (Vane-Wright, 1993; Pierce *et al.*, 2014).

Finally, an inherent physiological ability to perform well on a wide variety of diets or on novel diets is a key factor in range shifts, as is the case for the globally expanding generalist bumblebee species *Bombus terrestris* (Moerman *et al.*, 2016; see Section IV.2). More studies investigating and comparing the metabolic performance of pollinators under stressful conditions (e.g. heat stress; Tomlinson *et al.*, 2015) could provide key insights into the mechanisms allowing expanding species to arrive and establish in new areas. In contrast to bees, the majority of butterfly species are generally much more tightly bound to specific host plants (Forister *et al.*, 2015), although instances of host-plant shifts have attracted much recent attention (e.g. Chaturvedi *et al.*, 2018; Singer & Parmesan, 2019). Given that larval diet in butterflies is directly related not only to larval performance (Couture, Serbin & Townsend, 2015) but also to forewing characteristics and flight abilities in adults (Johnson *et al.*, 2014; Reim *et al.*, 2019), subsequent impacts are expected on adult migration, especially in a context of climate warming (Soule, Decker & Hunter, 2020).

IV. POLLINATORS BENEFITTING FROM HUMAN INTRODUCTION

(1) Expansion and invasion in human-introduced pollinators

Human introductions of pollinating insects can be deliberate (e.g. domestication followed by intentional introduction to

new areas), although most are accidental and caused by the international transport of goods (Russo, 2016). This introduction of non-native pollinator species to new geographical areas can subsequently lead to their establishment (Braby *et al.*, 2014) and therefore expansion from their original range. This phenomenon is mostly observed on islands where non-native pollinators can become the most abundant pollinator species, but invasions can also occur on the mainland (Russo, 2016). At the global scale, introduction of managed pollinators to improve pollination services has predominantly involved bees. The two most abundant and widespread introduced bee species are the buff-tailed bumblebee (*Bombus terrestris*) (see Section IV.2) and the Western honey bee, *Apis mellifera*, both eusocial species (Goulson, 2003; Garibaldi *et al.*, 2013; Kleijn *et al.*, 2015). With the notable exception of *Megachile rotundata* (Pittsinger & Cane, 2011), solitary bees have been introduced less extensively (e.g. the megachilid *Osmia ribifloris* for blueberry pollination from the west to the east coast of the USA, or the halictid *Nomia melanderi* for alfalfa pollination from North America to New Zealand) (Stubbs, Drummond & Osgood, 1994; Howlett & Donovan, 2010). Overall, most human-introduced pollinators are found within two families, Megachilidae (33 non-native species) and Apidae (30 non-native species) (Russo, 2016).

Some species are seen as ‘tramp’ species, meaning they are particularly prone to anthropogenic dispersal due to inherent combinations of traits that appear beneficial in particular contexts. Of the 30 non-native bee species that have established themselves in North America (Cane, 2003; Gibbs & Sheffield, 2009), most share two key traits: they are cavity-nesters and non-parasitic. While the former trait can directly facilitate establishment in exotic species (see example of *Megachile sculpturalis* in Section III.4), the latter is mainly due to non-parasitic pollinators having the advantage of not depending on a host for survival. Noticeable examples of species in which cavity-nesting is an advantage for range expansions include carpenter bees (*Xylocopa*), a genus of wood-nesting species that are commonly found outside their original ranges accompanying the global trade of wood (e.g. Okabe *et al.*, 2010). Short travel times of driftwood logs in oceans could also promote short-distance dispersal in these wood-nesting bees (Sheffield *et al.*, 2020).

Reproductive strategy can also be an important factor associated with expansion, as proposed for *Ceratina dentipes*, a bee originating from Southeast Asia and now rapidly spreading across Hawaii and the South Pacific (Groom *et al.*, 2017; Shell & Rehan, 2019). Because to date only females have been caught in Hawaii, the species is thought

(Figure legend continued from previous page.)

expanding with nitrophilous host; F, squash bee co-expanding with crop host; G, bumblebee benefitting from domestication. Blue outlines correspond to climate change and anthropogenic transport, orange outlines to novel anthropogenic habitats and green outlines to agricultural intensification and its consequences. Illustrator: Morgane Goyens.

to be capable of parthenogenic reproduction, a trait that could help facilitate invasion, as a population could be founded by a single mated female (Magnacca & King, 2013). Another way populations can be buffered against the challenge of colonizing new environments is through female multiple mating or polyandry, which can facilitate colonization by protecting against inbreeding, reducing the costs of mating with infertile or incompatible males (Lewis *et al.*, 2020).

Several other behavioural and morphological characteristics are likely to facilitate expansion in human-introduced pollinators, such as the aggressive territorial behaviour displayed by the males of *Anthidium manicatum*, a species native to Europe and northern Africa now established in Asia, North America, South America, New Zealand and the Azores (e.g. Strange *et al.*, 2011; Soper & Beggs, 2013). A major consequence of this aggressive behavior (Colla, 2016) is the exclusion of native bumble bees from floral resources in invaded sites (Graham *et al.*, 2019). In the Caribbean, aggressive Africanized honeybees fully replaced the European honeybee, followed by subsequent loss of aggressive behaviour (Rivera-Marchand, Oskay & Giray, 2012; Ackerman, 2021). Finally, aggressive behaviour could have acted as a facilitating trait for the spread of the Asian-native bee *Megachile sculpturalis* in both the USA and Europe, notably through evictions of native species and subsequent occupation of their nests (Roulston & Malfi, 2012; Le Feon *et al.*, 2018; Geslin *et al.*, 2020). Among other factors, this rapid expansion may be due to both its polylectic diet and its ability to nest in a wide range of cavities (see Section III.4), facilitating survival in a wide variety of habitats (Fortel *et al.*, 2016). Wasp pollinators in Vespidae have also frequently been mistakenly introduced into new areas, with some species becoming invasive and threatening native species (Beggs *et al.*, 2011). Their success is likely due to more efficient social and foraging behaviours, a generalist predatory lifestyle, and their aggression (Gamboa, Greig & Thom, 2002; Armstrong & Stamp, 2003).

Records of invasions following human introduction in other pollinators such as butterflies and hoverflies seem less common. For instance, while more than 10 exotic butterfly species have been introduced to Australia, only three have become established (Braby *et al.*, 2014). Finally, although many hoverfly species have also been actively introduced globally for pest management, this family is far less studied and no examples are readily available (Hardy, 1964).

(2) Case study of a winner: the worldwide success story of the recently domesticated buff-tailed bumblebee

One of the most famous cases of a pollinator expanding its range due to human facilitation is the bumblebee *Bombus terrestris*. Since the late 1980s, this species, native to the western Palearctic, has been exported across the globe for pollination of greenhouse crops, particularly tomatoes (Velthuis &

Van Doorn, 2006). However, the species rapidly showed invasive characteristics and now raises major conservation concerns where it has been imported (Geslin & Morales, 2015; Aizen *et al.*, 2020; Cameron & Sadd, 2020).

The global success of *B. terrestris* can be explained by an array of ecological and physiological features that make it highly adaptable, facilitating its survival and reproduction in a wide variety of habitats. First, *B. terrestris* has a large and highly flexible diet (Rasmont *et al.*, 2008; Boustani *et al.*, 2020), even in areas outside its native range where it is able to use indigenous plants (Hingston *et al.*, 2002; Goulson, 2003). It demonstrates the ability to rob nectar from plants, allowing (i) carbohydrate intake without the need to expend energy and time in handling flowers with complex morphologies (as suggested in *A. mellifera*; Dedej & Delaplane, 2005), and (ii) consumption of nectar from plants with nectaries otherwise inaccessible to its short tongue. This ability has been observed outside of its native range and is reported to decrease nectar availability for other pollinators (Sáez *et al.*, 2017). Under laboratory conditions, this species produces larger pupae than other bumblebees even on resources of lower quality (Vanderplanck *et al.*, 2014; Moerman *et al.*, 2016). They also have some degree of tolerance to pathogens that may have spilled over from this species detrimentally to infect native bees not previously exposed to these pathogens in areas of introduction (Arbetman *et al.*, 2013).

In addition to these characteristics, *B. terrestris* copes well with a variable climate. The species shows a high tolerance to a sudden and lasting hyperthermic stress, the major consequence of heat waves (Zambra *et al.*, 2020; Martinet *et al.*, 2021a) and has also been able to expand its range during recent increases in annual mean temperature (Martinet *et al.*, 2015). In addition to its physiological resilience to climate and diet, *B. terrestris* is a comparatively early-emerging bee, enabling it to benefit from spring resources to found a nest and initiate its colony before its competitors. Unlike most declining bumblebee species, its phenology is bivoltine (i.e. with two generations per year) or even winter active in suitable locations, allowing it to benefit from a larger array of floral resources throughout the year (Stelzer *et al.*, 2010). Consequently, social generalist bees with broad diets such as *B. terrestris* (but also *A. mellifera*) may suffer less from both temporal and spatial mismatches than solitary, univoltine and specialized bees which are generally restricted to narrower activity periods in which the host plants are available (Schweiger *et al.*, 2010). In addition, the large number of workers in social bee species optimizes egg production and food intake, contrasting with the lifestyle of solitary bee species (Stevens, Hogenboom & Schwarz, 2007).

With its combination of climatic tolerance, dietary flexibility, and strong dispersal ability, coupled with advantageous life-history traits such as a long phenology and sociality, *Bombus terrestris* provides key insights into our understanding of 'winning traits' for a pollinator in the context of global change.

V. CONSEQUENCES OF RANGE EXPANSION ON NATIVE ECOSYSTEMS

(1) Competition with native pollinators

There is surprisingly little evidence for competition between native species and expanding non-managed species for floral and nesting resources, although some cases have been reported (e.g. Portman, Tepedino & Tripodi, 2019). Many cases of expansions concern pollinators using resources with very low levels of competition, an element that could facilitate the expansion of such species. Documented examples of competition for nesting resources between non-managed exotic and native bees include the wood-nesting exotic bee *Lithurgus chrysurus* and the native *Megachile* spp. in North America (Rust *et al.*, 2004), and *M. sculpturalis* (see Section III.4).

On the other hand, competition between native species and massively introduced managed species (MIMS) has raised much interest, notably when MIMS integrate into native plant–pollinator networks (Geslin *et al.*, 2017). During recent decades, the use of MIMS has become more prevalent following the increased dependency of agriculture on managed insect pollination in ecosystems (Aizen *et al.*, 2008; Lautenbach *et al.*, 2012). The main consequence of the introduction of MIMS seems to be exploitative competition for floral resources (Stout & Morales, 2009; but see Nishikawa *et al.*, 2019; Iwasaki *et al.*, 2018). Such an overlap can trigger a cascade of effects on wild pollinators including a decrease in fitness (Elbgami *et al.*, 2014), in visitation frequency to specific plants (Shavit, Dafni & Ne'eman, 2009), and in shifts towards alternative plants (Walther-Hellwig *et al.*, 2006). In addition to potential spatio-temporal overlaps in floral choices, competition and exclusion of native pollinators from nest sites by introduced MIMS have been increasingly suggested as significant impacts, notably in bumblebees (Matsumura, Yokoyama & Washitani, 2004; Inoue, Yokoyama & Washitani, 2008; Inoue & Yokoyama, 2010).

(2) Co-expansion with exotic host plants

Introduction of non-native pollinator species may promote the spread or co-expansion of non-native plant species as the introduced bees could mainly forage on exotic flowers, potentially increasing their seed set and therefore fitness (Stout, Kells & Goulson, 2002; Morales & Aizen, 2006). For example, more than 80% of plants visited by the invasive *Anthidium manicatum* in New Zealand are exotic species (Lamiaceae and Plantaginaceae), although it also visits native plants (Soper & Beggs, 2013). Such non-native mutualisms can lead to the formation of ‘invasion complexes’, in which non-native pollinators disproportionately visit non-native plants for their resources, thereby promoting their reproduction (Morales & Aizen, 2002, 2006). However, range expansion into anthropogenic habitats could also potentially rescue

native plant species when wild native pollinators are scarce (Sanguinetti & Singer, 2014).

(3) Transmission of diseases and pathogens

Invader species can displace the resident fauna if they are tolerant to diseases that they vector, and that have detrimental effects on native species (Holt & Bonsall, 2017). Transmission of pathogens is increasingly discussed in the context of global expansion of managed insect pollinators, with growing evidence showing that they can be transmitted to wild species (Gisder & Genersch, 2017). Again, the most documented examples come from the intensely managed bumblebees. Data also show that non-native solitary bee species can transmit parasites to closely related indigenous species (Bosch, 1992; McKinney & Park, 2013; Hedtke *et al.*, 2015) and such pathogen transmissions may result in distribution shifts in native species. In Sweden, the northward expansion of the butterfly *Araschnia levana* has induced shifts in resident species distributions, with a possible explanation being parasitoid-driven competition generating significant mortality in the native species (Audusseau *et al.*, 2017, 2020).

Honeybees and more recently bumblebees have been intensely domesticated for the purposes of crop pollination, to such an extent that hundreds of thousands of colonies are now moved across countries on an annual basis. In particular, the recent globalization in the commercial use of bumblebees has caused a huge expansion of their range, raising concerns due to suspected impacts on the pathogenosphere of indigenous species. Growing evidence shows that parasite transmission by these anthropogenically expanding species, i.e. managed species, could be correlated with the decline of native species (Cameron *et al.*, 2011). Evidence supports the hypothesis that pathogen spillover to native communities occurs in the proximity of greenhouses in which commercial colonies are installed (Graystock, Goulson & Hughes, 2014). In practice, a large number of foragers escape from greenhouses and share floral resources with wild indigenous bees, with the potential for transmission of pathogens to wild populations *via* contact with flowers (Colla *et al.*, 2006). At the continental scale, there is growing evidence that European bumblebee colonies have carried at least two pathogens (*Apicystis bombi* and *Crithidia bombi*) to the Americas and parts of Asia (Cameron & Sadd, 2020). European strains of parasites have been found in Eastern Asia, highlighting the massive parasite migration that has accompanied the expansion of commercialized bumblebees globally (Goka, Okabe & Yoneda, 2006). The case of South America is particularly alarming, since the timing of the geographic expansion of domesticated *B. terrestris* appears to be congruent with the decline of the endemic Patagonian *Bombus dahlbomii*, which is now known to host at least one of the invader's pathogens (Arbetman *et al.*, 2013).

Domesticated pollinators can therefore facilitate the spread of non-native diseases to wild populations, triggering epidemics that could eventually affect both community structure and pollination services. Much work is still required to

understand fully the consequences of the global pollinator trade on pathogen prevalence and its consequences on wild pollinator faunas (Aizen *et al.*, 2020).

(4) Impacting crop yield

Non-native pollinators such as honey bees that outcompete native species, have been found to be less-efficient pollinators that can result in poorer fruit set and quality than pollination by native bees for some crop plants (see Winfree *et al.*, 2007; Garibaldi *et al.*, 2013). In extreme cases of invasion (e.g. by MIMS), a high abundance of non-native pollinators can translate into excessively frequent pollinator visits per flower, exacerbating costs to the plant (e.g. nectar robbing or flower damage; Sáez *et al.*, 2018). An oversaturation of pollination services, although not strictly limited to contexts in which exotic pollinators are present, is increasingly recognized as detrimental for fruit production and may even diminish yields of pollinator-dependent crops (reviewed in Aizen *et al.*, 2020). Apart from harmful effects of pollinators on plants during visits or during the pollination process itself, the global expansion of crop pests also negatively impacts crop yields, such as the butterfly *Pieris rapae* (McKinlay, 1992; Ryan *et al.*, 2019).

(5) Mating with native taxa

In addition to range expansions perturbing community interactions, introduced species can also impact local populations by creating novel points of contact among closely related species that were previously geographically isolated. When close relatives interact, introgression may occur (Bartomeus *et al.*, 2020; Cejas *et al.*, 2020). This can challenge the integrity of species, potentially threatening rare species (Rhymer & Simberloff, 1996), subspecies distinctions (Lecocq *et al.*, 2016), and species' fitness (Barton & Hewitt, 1989). Commercial introduction of the European bumble bee *B. terrestris* to Japan has led to reports of high levels of mating with the closely related endemic species *B. hypocrita*, resulting in reduced fertility (Kanbe *et al.*, 2008; Tsuchida *et al.*, 2019), and introduction of the eastern North American species *B. impatiens* into the range of its sister species in Mexico (*B. ephippiatus*) has raised similar concerns (Duennes *et al.*, 2017). Similarly, increased overlap of range limits of swallowtail butterflies *Papilio glaucus* and *P. canadensis* as a result of range expansions with climate change are thought to have generated hybrids with differing phenology and potentially host use (Mercader, Aardema & Scriber, 2009). Introgression also can lead to selective transfer of advantageous alleles between resident and introduced lineages that can enhance the ability of an introduced species to survive in its environment, enabling it to expand its range further. Such adaptive introgression has been demonstrated in mimetic neotropical *Heliconius* butterflies. Study of loci driving wing patterns has revealed that some of these butterfly species have acquired their mimetic phenotypes through introgression with other mimetic species (Dasmahapatra

et al., 2012; Kronforst, 2012). Once alleles for these color patterns were transferred to the new species, they became immediately adaptive, enabling the species to expand into new mimicry zones. Through similar processes, as alleles are shared among related pollinators as a consequence of range expansion, adaptive alleles may be transferred both within and across species that facilitate improved fitness in their newly occupied ranges, thus leading to further range expansion (Pfennig, Kelly & Pierce, 2016).

Overall, a substantial range of effects can be expected on native plant–pollinator systems following the expansion of insect pollinators. Two major issues must, however, be clearly separated: MIMS and non-managed pollinators. This separation is crucial because regulatory authorities have much more control on the former, and are responsible for the uncontrolled invasions that have occurred where regulations have been lacking (Aizen *et al.*, 2020; Bartomeus *et al.*, 2020). Although a few facilitative interactive effects of MIMS have been suggested (namely a spillover of shared plant resources and transfer of social information to optimize foraging, see Geslin *et al.*, 2017), these cases are not likely to compensate for the ecological disruptions caused by MIMS. The second case of expansion (non-managed pollinators) is much more difficult to control as it results from a combination of biotic (e.g. species traits) and abiotic (e.g. climate change) conditions that are much harder to predict (Fig. 1, Table 1). In this particular case, the role of governments predominantly lies in controlling and mitigating the anthropogenic factors that mostly *cause* the expansions, namely global warming and habitat destruction.

VI. CONCLUSIONS

- (1) While much has been written in recent decades about the threats and ecological traits associated with global biodiversity declines, the scientific literature contains significantly fewer syntheses focused on the characteristics of expanding species. Here, we reviewed the traits (Table 1) and factors (Fig. 1) that have facilitated the expansions of a fraction of the pollinating entomofauna, allowing this group to take advantage of what are generally deleterious global environmental changes.
- (2) Although the characteristics allowing species to expand are mostly taxon specific and context dependent, various traits including high mobility, high resistance to acute heat stress, and inherent adaptations to warmer climates appear to be important in allowing pollinators to persist and even expand in the face of climate change. Similarly, an overall level of flexibility regarding resource requirements is common in expanding species, although dietary niche specialization can also be involved in range expansion under specific contexts.

- (3) Importantly, expansion of wild and domesticated species can show diverse impacts on indigenous wildlife, including resource competition, co-expansion with exotic plants, pathogen spread, detrimental impacts on crop yield, and hybridization with indigenous wildlife.
- (4) The context-dependent nature of each of these success stories renders generalizations towards ultimate candidate ‘winning traits’ complicated. Similarly, the consequences of these expansions appear hard to predict and to disentangle from confounding biotic or abiotic disruptions.
- (5) There has been no global evaluation of how the combined patterns of decline and expansion of pollinators will affect our ecosystems and food security in the near future. What is clear however is that our current reliance on massively introduced pollinators is far from sustainable and must be considered a serious issue for the conservation of global ecosystems.
- (6) Further standardized work gathering quantitative data to reveal the rates and magnitude of range shifts is strongly encouraged to investigate the spatial and temporal aspects of expansions. In addition, further work investigating specific traits such as species fecundity and individual mobility are needed to understand population shifts better across space and time.
- (7) Continuously monitoring populations and identifying the relative contributions of both traits and factors involved with increases in range size and abundance remain crucial aspects of our understanding of how species react to environmental changes globally. Most importantly, these efforts need to be made at a much larger geographic scale than is presently the case, given that our global knowledge on insect conservation is derived predominantly from Europe and North America.
- (8) Considering patterns of both decline and expansion is fundamental to assess accurately current biodiversity changes at a global level. The present review underlines the importance for ecologists to understand how wildlife reacts to global changes, and we hope it will encourage future work on our understanding of patterns of species expansions worldwide.

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