

The role of ecological interactions in determining species ranges and range changes

ALAN J. A. STEWART^{1,2*}, TRISTAN M. BANTOCK², BJÖRN C. BECKMANN³,
MARC S. BOTHAM³, DAVID HUBBLE⁴ and DAVID B. ROY³

¹*School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK*

²*101 Crouch Hill, London N8 9RD, UK*

³*Biological Records Centre, Centre for Ecology & Hydrology, Crowmarsh Gifford, Oxfordshire OX10 8BB, UK*

⁴*28 St Mary's Road, Bishopstoke, Eastleigh, Hampshire SO50 6BP, UK*

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Climate has been widely regarded as the main determinant of the geographical distribution of species. Biotic interactions between co-occurring species, however, are an important additional influence. We review the importance of interactions with food and nectar plants (as resources) in determining the distribution of phytophagous and pollinating insects (as consumers). We use biological recording datasets for seven taxonomic groups to quantify the relationship between the geographical distributions within Britain of 1265 phytophagous insects and their associated food plants, representing 9128 interactions in total. We find a consistent pattern across taxonomic groups in that individual phytophagous insect species rarely utilize the full range of their food plants and the relationship between the range sizes of insects and their food plants is not a simple linear one. For a small selection of phytophagous species where data are available, we highlight an association between changes in range and interactions with associated food plant species. Climate-driven range expansion may be constrained through disruption of trophic relationships between phytophagous insects and their food plants if they respond differently to abiotic drivers. By contrast, range expansion may be facilitated by temporary escape from natural enemies and/or exploitation of novel food plants that enable a broader set of habitats to be utilized. In a changing environment, some existing interactions will be disrupted but opportunities for novel interactions will also emerge, producing new assemblages and changes in distributions that will be dynamic yet hard to predict. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**, 647–663.

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INTRODUCTION

Ecologists have long been interested in answering the fundamental question of what determines the geographical distributions of species (Darwin, 1859; Elton, 1966). Ultimately, spatial distributions of species are limited by three broad groups of constraints: tolerance of physical environmental conditions (temperature, pH, humidity, etc.), including

plasticity and the ability to evolve in response to new conditions; the availability and spatial distribution of resources (food, nest sites, shelter, etc.); and interactions with other species, regardless of whether these are competitors, natural enemies or mutualists. History may also have an influence (e.g. where the location of an introduction or of refugia during previous range shifts determines the pattern of subsequent geographical spread). Some of these factors may serve to constrain the geographical distribution of a species more than others; thus, for example, the range dictated by food availability may be further restricted by interactions with natural enemies.

*Corresponding author. E-mail: a.j.a.stewart@sussex.ac.uk

Any strengthening or relaxation of any of these constraints (e.g. a change in mean temperature or a change in the distribution of a competitor) will have consequences for the ability of the species to maintain or expand its current distribution unless changes in other factors act to compensate. The ability of a species to shift or expand its range may be additionally constrained by major physical barriers (mountain ranges, watercourses, etc.) or breaks in the continuity of its habitat that exceed its maximum dispersal capability.

One approach to understanding distribution patterns in relation to key environmental parameters uses 'niche modelling' (Pearson & Dawson, 2003) to enable predictions to be made about how species distributions are likely to change in future. Niche models, commonly termed species distribution models (SDMs), rely on occurrence data collected over large spatial scales and often over long time periods. Species data for SDMs are typically derived from atlases of distribution (Hagemeijer & Blair, 1997; Mitchell-Jones *et al.*, 1999), collected as part of biological recording, itself a form of citizen science (Pocock *et al.*, 2015).

Biological recording data have been widely used to investigate the dynamics of species range changes, although analyses have rarely considered interactions between species. The traditional approach has been to focus largely on a single taxonomic group, for which records of species occurrences in space and time have been assembled specifically to map the geographical distributions of individual species. Analyses have tended to focus on explaining species distributions and range changes in relation to physical environmental factors and the distribution of major habitat types. Recent poleward shifts in the distributions of many species across diverse taxonomic groups, for example, have provided an accumulating body of evidence for the ecological effects of a warming climate (Mason, 2015). The prevailing view, however, that climate is the main driver of range changes is being questioned because of accumulating evidence showing that predictions need to take account of ecological interactions with co-occurring resource, competitor, mutualist or natural enemy species (Araújo & Luoto, 2007; Tylanakis *et al.*, 2008; Van der Putten, Macel & Visser, 2010; Wisz *et al.*, 2013; Svenning *et al.*, 2014). It has even been suggested that these interactions have been the proximate cause of more extinctions than the direct effects of climatic warming (Cahill *et al.*, 2013).

The present review explores how interspecific interactions influence the geographical ranges of species and the extent to which such interactions constrain or facilitate range changes in response to other factors such as climate change. We use phytophagous insects

as a model system to examine the fundamental relationship between the spatial distribution of primary consumers (phytophagous insects) and that of the primary resources that they exploit (their food plants). The spatial distributions of pollinators in relation to the geographical ranges of the plant species that they visit are also explored.

PHYTOPHAGOUS INSECTS AS MODEL ORGANISMS

Phytophagous insects make good subjects for examining the extent to which ecological interactions determine the geographical ranges of species and changes in those ranges over time. First, phytophagous insects and the plants on which they feed comprise a significant proportion of overall terrestrial macro-biodiversity (Strong *et al.* 1984) enabling us to examine the extent to which general patterns in interactions are consistent across a broad spectrum of taxonomic groups. Second, food plant species comprise the primary and most easily definable resource for phytophagous insects (Quinn, Gaston & Roy, 1997), although subtleties of food plant quality and condition will complicate the picture, as will the dependence on other resources such as nectar that may be required at other life-history stages. Third, the long tradition of biological recording in Britain has spawned a number of recording schemes (up to 20) focused substantially or entirely on phytophagous insects. These vary in size from small embryonic schemes with limited datasets in which most species are likely to be under-recorded, such as psyllids, to very large schemes with near-comprehensive coverage, such as the National Moth Recording Scheme with over 15 million records for 673 species over a 40-year period (Fox *et al.*, 2014). Finally, and perhaps most importantly in the context of ecological interactions, the food plant associations of many phytophagous insect groups in Britain are generally well documented. The Database of British Insects and their Foodplants (DBIF) holds a substantial body of published information on such interactions (Ward & Spalding, 1993; Smith & Roy, 2008). Cross-reference between this database and the extensive data on geographical distributions of species held by the associated national recording schemes enables us to address some fundamental questions about the factors controlling species ranges and changes therein.

Understanding interactions between phytophagous insects and their food plants is of more than academic interest. The ability to predict how such interactions will respond to future environmental change would also be of considerable applied value (e.g. in identifying which non-native species are likely to establish and become invasive in a new region into which they

have been introduced) (Roy *et al.*, 2015) or predicting the likelihood that native species will become invasive in response to a changing climate. It would also help to identify species that may become threatened by an inability to shift their distributions in response to a changing climate because of constraints imposed by interactions with other species (Gillingham *et al.*, 2015; Thomas *et al.*, 2015; Thomas & Gillingham, 2015). An understanding of how phytophagous insect ranges relate to those of their food plants could also help explain patterns of commonness and rarity across species. Under-recorded groups often lack sufficient information to enable meaningful statements to be made about the rarity status of (and threat to) individual species (Maes *et al.*, 2015). However, if it were possible to identify a threshold food plant range size below which associated phytophagous insects are likely to be rare, this would assist the selection of species that merit conservation action (Hopkins *et al.*, 2002).

TO WHAT EXTENT DO PLANT DISTRIBUTIONS DETERMINE THE RANGES OF THE PHYTOPHAGOUS INSECT SPECIES THAT FEED ON THEM?

Ultimately, the spatial distribution of a phytophagous insect species must be constrained by the distribution of the plant species on which it feeds. If the host plant resource is fully exploited, we would expect the geographical distribution of the insect to be exactly coincident with that of its host plant(s). Any discrepancy between the two, resulting in the insect not occupying the entire geographical range of its host plant, is likely to be the consequence of other constraints; these might be abiotic ones, the most likely of which are climatic limitations or physical barriers to historic dispersal, or biotic ones, including interactions with competitors, natural enemies or mutualists, or requirements for other resources.

Analyses both of macro-moths (Quinn *et al.*, 1997) and butterflies (Quinn, Gaston & Roy, 1998) in Britain have shown that the relationship between the range size of these insects and their food plants is positive but not a simple linear one. The relationship is approximately triangular, such that insects feeding on plants with small ranges necessarily have small ranges themselves, although those feeding on plants with large ranges may occupy a spectrum of range sizes from small to large. Minimum insect range size apparently does not increase with the range of the host, and so insects with limited geographical ranges feed on plant species that span range sizes from small to large. In general, the upper constraint on insect range size, defined by the range of the food plant, is

not closely followed. Monophagous species tend to feed on plants with large ranges but occupy a smaller proportion of that range compared to congeneric polyphagous species.

We tested the generality of the phytophagous insect–host plant range size relationship, previously documented for Lepidoptera. All analyses were performed at the 10-km square level. We firstly reanalyzed this relationship for 88 monophagous macro-moth species using a considerably more extensive dataset (distribution data for Britain based on 515 794 records since 1970) accumulated by the National Moth Recording Scheme (Fox *et al.*, 2014). Food plant information was taken from the DBIF, Skinner (2009), Waring, Townsend & Lewington (2009), Clancy, Top-Jensen & Fibiger (2012), and the UKMoths website (<http://ukmoths.org.uk>). Data on plant range sizes were extracted from the database used to produce the most recent national species distribution atlas (Preston, Pearman & Dines, 2002). Second, we investigated whether Lepidoptera are atypical in having such weak relationships between their range size and that of their food plants, perhaps because their more complex life cycle means that they require different sets of resources as adults compared to larvae. We therefore used data on 9040 insect–food plant associations in the DBIF combined with data from selected national recording schemes covering Britain to test the generality of the relationship for a total of 1177 species across six other phytophagous insect groups: two micro-lepidopteran groups with leaf-mining larvae (Pterophoridae/plume moths and Gelechiidae/twirler moths); two beetle families (Chrysomelidae/leaf beetles and Curculionidae/weevils); and two major hemipteran groups (Auchenorrhyncha/leafhoppers and related taxa, as well as Heteroptera/‘true’ bugs). The two beetle and hemipteran families, in which adults and immature stages generally exploit the same resource, might be expected to exhibit much tighter relationships with the geographical distribution of their food plants than is the case with the Lepidoptera.

None of the insect groups examined in the second analysis have geographical range data that are as comprehensive as for the macro-Lepidoptera, so certain measures were taken to allow for reduced recording effort. We excluded under-recorded squares by restricting the analyses to those in which a minimum of 1% of all species in the group had been recorded. For the 1757 plant species, this meant selecting from the 2885 squares that comprise the whole of Britain only those squares with at least 18 recorded species, thereby reducing the number of qualifying squares to 2808. The insect data (based on all available records since each recording scheme began) were subjected to the same 1% cut-off in an

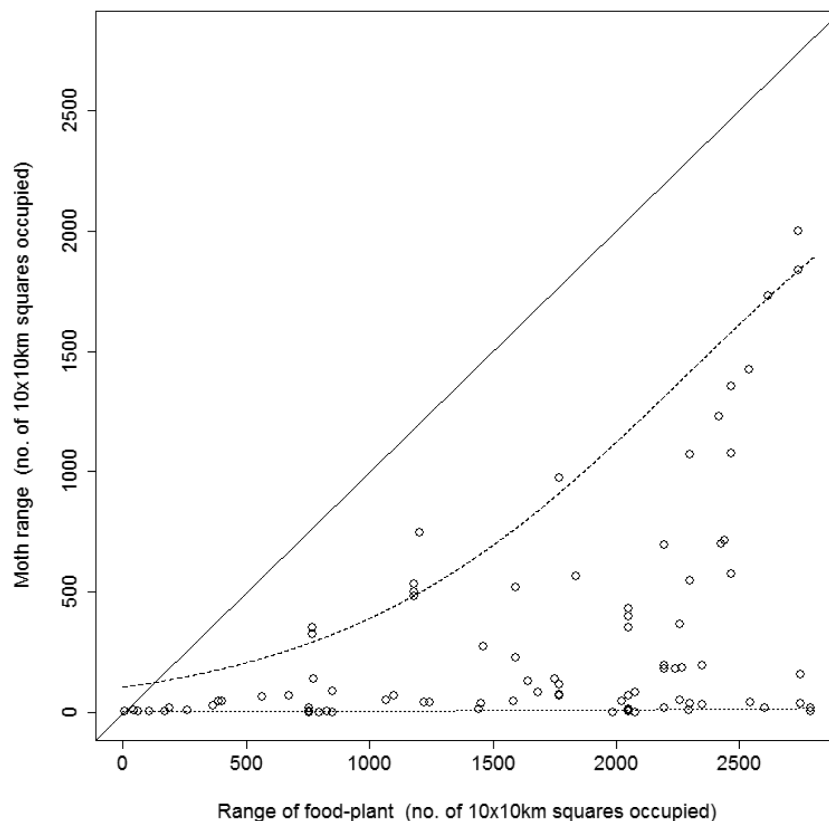


Figure 1. Relationship between the range size of monophagous macro-moth species and the range size of their food plants in Britain. Range size was measured as the number of 10-km squares occupied. Solid line (unity) denotes points at which insect species would occupy all qualifying squares of their food plant. Lines for 90th (dashed) and 10th (dotted) percentiles were estimated using quantile regression.

attempt to equate recording effort between groups being compared. The range metric for each plant species was then taken to be the number of squares in which the species was recorded, expressed as a percentage of all qualifying plant squares. The equivalent metric for insect species was further constrained by inclusion of only those squares in which the host plant was also recorded. The data are held by individual recording schemes and the Biological Records Centre; for some groups, the data can also be accessed through the National Biodiversity Network Gateway.

Host plant specificity in phytophagous insects can vary from monophagous (feeding exclusively on a single plant species) to polyphagous (feeding on several plant species recruited from one or more genera or higher taxa). In the case of polyphagous insect species, the resource base can be considered as the combined geographical distributions of all plant species exploited; this was taken to be the total number of qualifying squares in which at least one of the known host plant species occurred.

Relationships between insect ranges and those of their food plants were explored using quantile regres-

sion, a statistical method that characterizes the relationship between predictor and response variables more fully than conventional linear regression techniques (Cade & Noon, 2003). Here, we used the 10th and 90th percentiles to approximate the lower and upper boundaries respectively of the triangular relationship between insect range and food plant range. Quantile regressions were performed in the statistical environment R, version 3.0.2 (R Development Core Team, 2007) using the ‘quantreg’ package (Koenker, 2013). Because insect range sizes are bounded between 0% and 100% of host plant range sizes, they were logit-transformed for analysis.

For monophagous macro-moths, we reconfirmed the relationship demonstrated by Quinn *et al.* (1997), here based on a considerably more extensive dataset (Fig. 1). As found previously, moths do not exploit the full range of their food plants, and so their distributions must be limited by further constraints. The regression line of the 90th percentile indicated that even the largest moth ranges remain well below those of their hosts. For example, at the largest end of the scale, although a widespread host plant may come

close to occupying all of the 2885 10-km squares in Britain, the commonest moths feeding on it would be likely to occur in less than 2000 of these squares (Fig. 1). At the same time, monophagous moths with highly restricted ranges feed on plants of all range sizes from small to large; the 10th percentile has a very shallow slope that is not significantly different from zero, suggesting that insect minimum range size does not increase with food plant range size (Table 1).

Similar patterns were found for the six additional taxonomic groups analyzed (Fig. 2, Table 1), each showing a triangular relationship between range sizes of plants and their insect herbivores, albeit with generally smaller proportions of food plant ranges occupied that are mostly attributable to lower recording effort. Notwithstanding these differences, the results are in accordance with those previously published for macro-Lepidoptera (Quinn *et al.*, 1997, 1998): widespread plants support widespread phytophagous insects, as well as geographically restricted ones; some insects with restricted ranges are associated with narrowly distributed plants but others feed on widespread species. With the exception of the Heteroptera, there was no indication that the minimum range size of phytophagous insects increased with food plant range; the 10th percentile regression lines had very shallow slopes that were not significantly different from zero. Also, there was no

indication that the insect groups dependent on their food plants at all stages in their life cycle (beetles and hemipteran bugs) showed stronger associations between their range sizes and those of their food plants than was the case with the Lepidoptera groups.

In addition to monophagous species rarely occupying the full range of their food plant, those sharing the same food plant species often have divergent distributions (Quinn *et al.*, 1997). The latter pattern might result from competitive interactions between species, in which case ranges would be expected to be non-overlapping. By contrast, Quinn *et al.* (1997) found that eight macro-moth species feeding exclusively on common reed, *Phragmites australis*, had nested distributions with maximum species richness focused on areas of Britain where the food plant had the greatest density at a landscape scale. Indeed, where more than one species exploits a particular plant species, co-existence is often possible through subtle differentiation of niches within the physical structure of the plant (Stiling, 1980; Tscharnkte & Greiler, 1995; Kaplan & Denno, 2007). For comparison, the ten monophagous species of Auchenorrhyncha (nine species of planthopper and one species of leafhopper) on *P. australis* (Nickel, 2003) that occur in Britain show similarly overlapping distribution patterns (Fig. 3). In this case, however, the plant's range that covers the whole of Britain except the

Table 1. Quantile regression parameters for the relationship between the geographical range sizes of seven phytophagous insect groups (number of species in parentheses) and the range sizes of their food plants

		90th percentile			10th percentile		
		Coefficient	SE	P	coefficient	SE	P
Macro-moths (monophages) (88)	Intercept	-3.226	0.646	< 0.001	-6.409	0.623	< 0.001
	Slope	0.0014	0.000	< 0.001	0.0005	0.000	0.249
Homoptera (246)	Intercept	-4.050	0.497	< 0.001	-6.388	0.971	< 0.001
	Slope	0.029	0.006	< 0.001	0.020	0.011	0.062
Heteroptera (237)	Intercept	-4.739	0.856	< 0.001	-7.448	0.733	< 0.001
	Slope	0.037	0.010	< 0.001	0.024	0.009	0.007
Gelechiidae (100)	Intercept	-4.635	0.234	< 0.001	-6.906	0.593	< 0.001
	Slope	0.038	0.004	< 0.001	0.014	0.008	0.068
Pterophoridae (22)	Intercept	-3.229	—	—	-7.858	—	—
	Slope	0.040	—	—	0.052	—	—
Chrysomelidae (218)	Intercept	-2.966	0.455	< 0.001	-6.143	0.791	< 0.001
	Slope	0.020	0.005	< 0.001	0.017	0.010	0.078
Curculionidae (354)	Intercept	-3.870	0.275	< 0.001	-5.875	0.034	< 0.001
	Slope	0.021	0.003	< 0.001	0.000	0.002	1.000

Regressions were performed on logit-transformed proportions of squares occupied; for macromoths, this was the proportion of the total number of potential host plant squares (2808); for all other groups, the proportion of 'qualifying' squares with a minimum threshold of recording effort was used (for details, see text). Because of the small sample size, SEs and significance could not be determined for Pterophoridae.

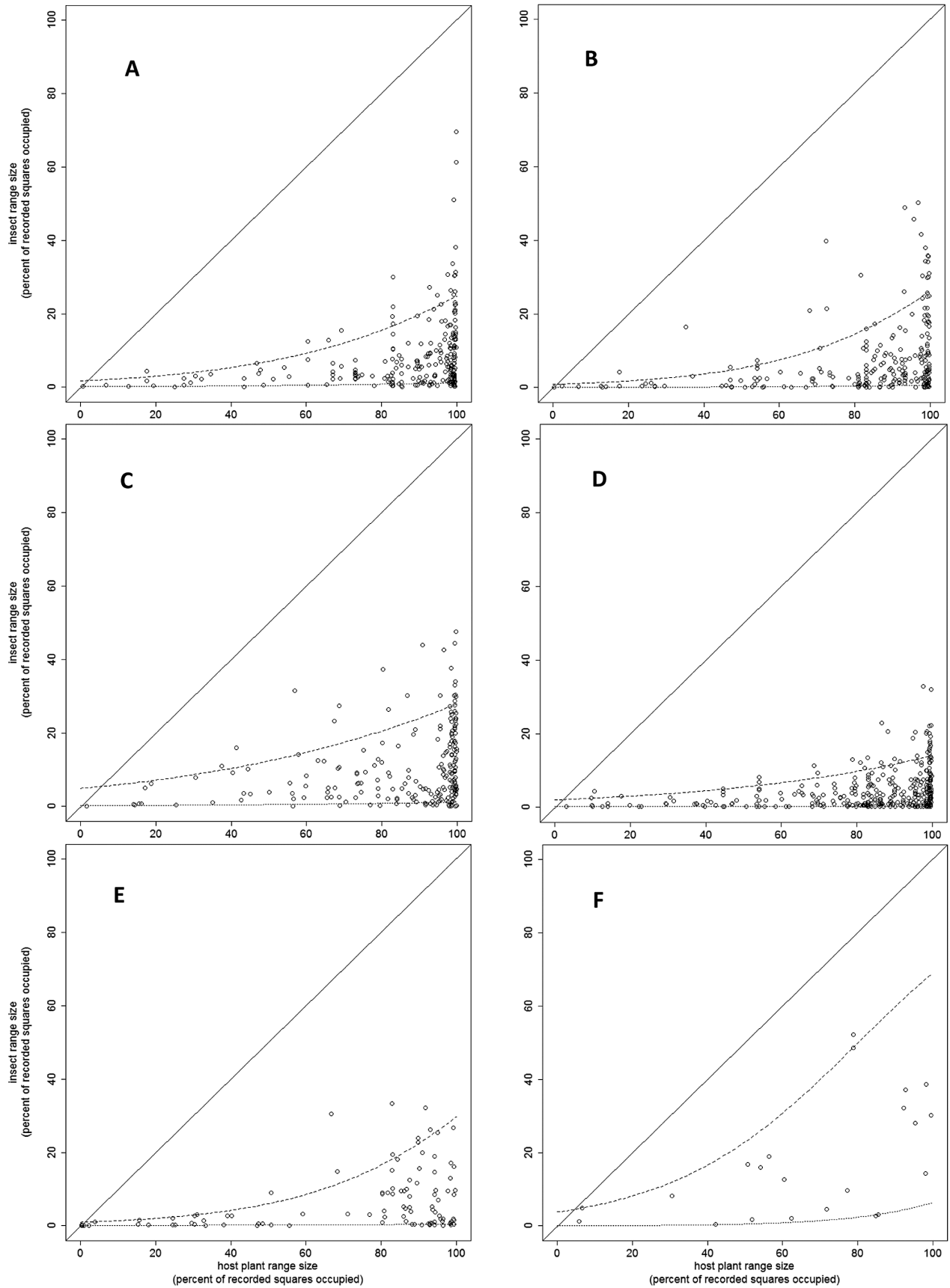


Figure 2. Relationship between the range size of a food plant and the percentage of that range occupied by a phytophagous insect species feeding on it. For an explanation of range size calculation, see text. Axes refer to the percentage of qualifying squares occupied by the species. Solid (unity) line signifies points at which insect species would occupy all qualifying squares of their food plant. Lines for 90th (dashed) and 10th (dotted) percentiles were estimated using quantile regression. Plant data are based on 2808 qualifying squares containing a minimum of 18 species. A, Auchenorrhyncha (based on 1205 qualifying squares containing a minimum of three species). B, Heteroptera (based on 1255 qualifying squares containing a minimum of three species). C, Chrysomelidae (based on 1828 qualifying squares containing a minimum of three species). D, Curculionidae (based on 363 qualifying squares containing a minimum of seven species). E, Gelechiidae (based on 1886 qualifying squares containing a minimum of one species). F, Pterophoridae (based on 1471 qualifying squares containing a minimum of one species). For the number of species in each group, see Table 1.

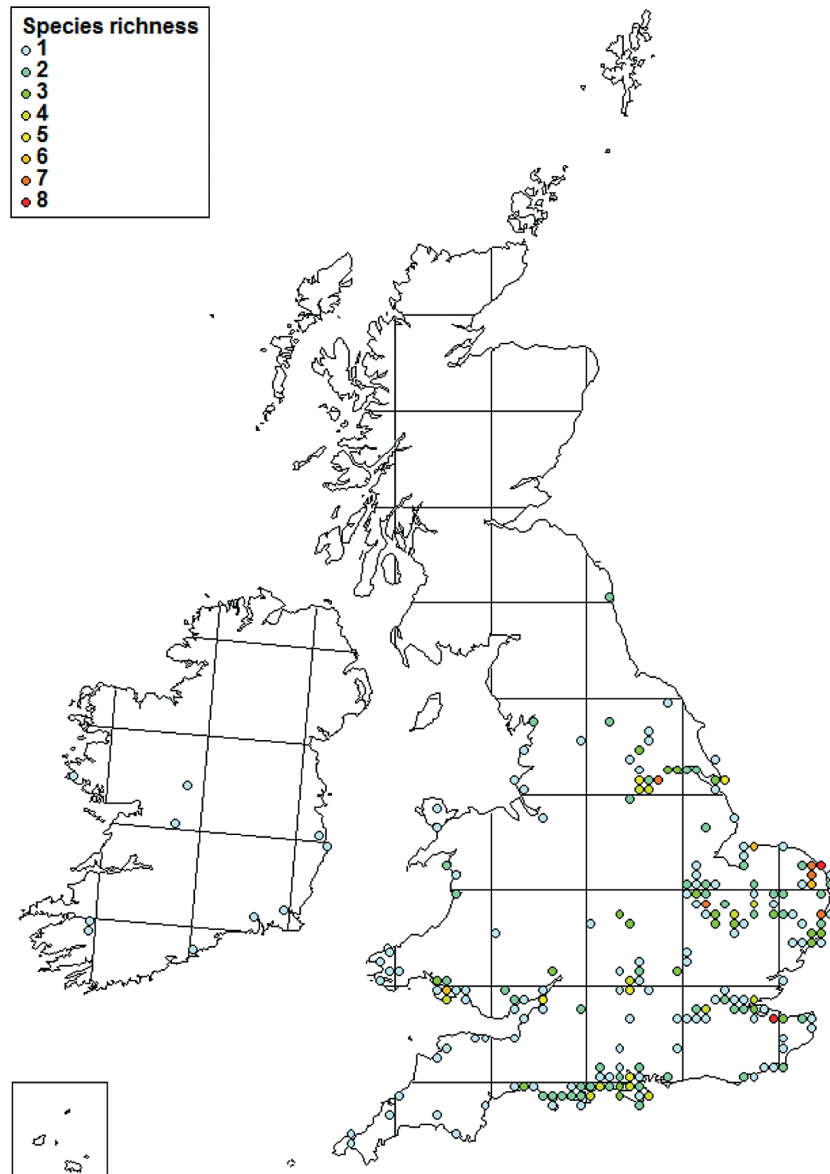


Figure 3. Species richness of ten Auchenorrhyncha species in Britain that feed monophagously on common reed, *Phragmites australis*. None of the squares supported more than eight of the species. The species are: *Pentastiridius leporinus*, *Delphax pulchellus*, *Delphax crassicornis*, *Euides speciosa*, *Chloriona dorsata*, *Chloriona glaucescens*, *Chloriona smaragdula*, *Chloriona unicolor*, *Chloriona vasconica*, *Paralimnus phragmitis*.

uplands, remains unexploited in its northern half, suggesting an additional climatic constraint.

RANGE CHANGES

A wide spectrum of taxa, including various phytophagous insect groups, have been shown to have expanded or shifted their ranges in a poleward direction over the last half century, apparently in response to climatic warming (Parmesan & Yohe, 2003; Hickling *et al.*, 2006). Habitat generalists with good dispersal ability have the best chance of tracking their climate envelope successfully. By contrast, species with limited dispersal ability, specialist habitat requirements or close associations with habitats that are highly fragmented may be unable to do so (Warren *et al.*, 2001). This may explain why there are few consistent patterns in rates of range shift when comparing different taxonomic groups (Chen *et al.*, 2011).

A change in the geographical range of a species may be prompted by human activities directly (e.g. persecution or deliberate introduction) or indirectly (e.g. through creation or destruction of habitat), by natural dispersal, changes in the availability and distribution of some critical resource (e.g. nest sites) or changing interactions with other species (competitors, prey/food or natural enemies). Externally-driven range shifts (e.g. resulting from changes in the climate) may in turn alter interactions between species, by severing certain links and enabling the formation of others. It is important to distinguish between range changes that comprise expansion or contraction of an existing range compared to wholesale shifts in distribution; the latter will involve shifts of both the expanding and retreating margins.

Trophically interacting species rarely have identical ranges. This means that areas of non-overlap provide opportunities for novel trophic interactions (e.g. exploitation of new food plant species) or escape from negative ones (e.g. competition or exploiters/enemies). The range of a specialist insect herbivore cannot exceed that of its food plant, except during a particular life stage that is not dependent on that resource. Some highly mobile butterfly species, for example, are recorded as dispersing adults well beyond the range of their larval food plant (Brimstone butterfly, *Gonepteryx rhamni*; Gutiérrez & Thomas, 2000) but cannot utilize such areas to breed.

As noted by Gröbner & Lewis (2008), the decline in species richness towards the poles that is shown by most taxonomic groups means that species shifting in that direction will generally encounter communities that are progressively species-poorer. The result will be reduced assemblages of resource, competitor or

natural enemy species with which to interact, in turn affecting the rate at which expanding species can spread. For example, the poleward spread of a phytophagous insect in response to climatic warming may be curtailed when it reaches the range margin of its food plant or be enhanced by escape from its parasitoids if their rate of spread lags behind. Additionally, insect ranges are known to have shifted both earlier and further in response to climatic warming compared to plant ranges (Parmesan, 2001).

Range expansion may be triggered by an externally-driven enhanced ability to disperse. Phenotypic plasticity in dispersal capability can facilitate rapid range expansion when suitable conditions arise. Thus, populations of wing-polymorphic insects can switch from dominance by short-winged (brachypterous) forms, which either cannot fly at all or only for trivial distances, to long-winged (macropterous) forms, which are fully capable of long-distance dispersal. Such changes are normally triggered by intraspecific overcrowding and/or deteriorating condition of the food plant and have been extensively researched in several insect groups, especially Hemiptera and Orthoptera (Zera & Denno, 1997). The well-documented expansion in range over recent decades within southern Britain of two bush cricket species, Roesel's bush-cricket, *Metrioptera roeselii*, and long-winged conehead, *Conocephalus discolor*, was facilitated by a very rapid increase in the proportion of macropterous forms in species that were previously almost entirely brachypterous (Thomas *et al.*, 2001).

DISRUPTION OF TROPHIC INTERACTIONS DRIVEN BY CLIMATE CHANGE

The 'climate envelope' concept has been widely adopted to model how the fundamental niche of an individual species will respond to climatic warming. This approach, however, suffers from the limitation that it does not allow for interactions, whether positive or negative, with other species or resources (Pearson & Dawson, 2003; Wisz *et al.*, 2013). For example, spatial mismatching of the responses of interacting species to climatic warming may result in the exclusion of consumer species from areas to which they are otherwise climatically suited. Thus, it is clear that a phytophagous insect cannot spread into new areas in response to climatic warming if its food plant cannot survive there, perhaps because the edaphic conditions are unsuitable for the plant, or because the plant's slow rate of dispersal means that it has not yet arrived. Imposition of different climate warming scenarios on the interaction between the specialist bog fritillary butterfly, *Boloria titania*, and its sole food plant common bistort, *Polygonum*

bistorta, shows that the butterfly will be unable to colonize large areas that become climatically suitable in eastern Europe and Iberia because conditions will have simultaneously become unsuitable for the plant (Schweiger *et al.*, 2008). Similar disruptions may occur as the altitudinal ranges of interacting species diverge in response to climatic warming. The black-veined white butterfly, *Aporia crataegi*, has retreated from lower elevations in the mountains of central Spain because these environments have become too warm, although it has been unable to colonize higher elevations where its food plants are too rare (Merrill *et al.*, 2008). An analysis of modelled altitudinal ranges for 92 butterfly and 136 food plant species in the Swiss Alps found that more than half the butterfly species were constrained at their upper elevational boundaries by food plant availability rather than climate (Hanspach *et al.*, 2014).

At a macro-ecological scale, climate has often been regarded as the most important abiotic determinant of the distribution of species, with biotic interactions and dispersal limitations considered to be factors that are both secondary and operating at smaller scales. Furthermore, the conventional view has been that the position of 'cold' range margins (set by either latitude or altitude) are primarily governed by abiotic factors, mainly climate, whereas 'warm' margins are controlled by biotic interactions (Brown, Stevens & Kaufman, 1996). A variant of this, the 'stress gradient hypothesis', suggests that abiotic factors limit distributions in highly stressed environments, whereas biotic interactions predominate in more benign environments. More recent studies suggest, however, that the balance between the constraints on phytophagous insects imposed by climate and food plant varies considerably between species but is strongly influenced by the range size of the food plant (e.g. spatial mismatching between butterfly and food plant is predicted to be most severe in species that are dependent on plants with restricted ranges) (Schweiger *et al.*, 2012).

Spatial mismatches resulting from differential responses to climate change may also arise between plants and their pollinators. Such disruptions in pollination services could seriously jeopardize the future viability of growing certain pollinator-dependent crops, especially fruits, in currently favoured areas (Polce *et al.*, 2014). Shifting distributions may also bring plant and pollinator species together in novel combinations. Non-native pollinators, for example, may fill niches previously occupied by native pollinators that have been displaced by climatic changes, thereby maintaining essential pollination services. Alternatively, non-native pollinators could exacerbate the problem of pollination deficits (e.g. through the introduction and spread of disease) (Schweiger *et al.*,

2010). Most insect pollinators are fairly generalized in the plant species that they pollinate (Waser *et al.*, 1996), so that changes in the species identity of flowering plants are likely to have less effect on pollinators than is the case with herbivorous species. The more specialized pollination relationships, however, may be especially vulnerable. Similarly, declines in pollinating insects may have serious implications for the pollination services provided to native plants, especially obligate outcrossing species (Biesmeijer *et al.*, 2006).

There is a growing literature on climate change-induced phenological changes that disrupt the links between interacting species (Thackeray *et al.*, 2010; Walther, 2010). A particular concern is where links between plants and their pollinators are disrupted because the phenologies of the two partners in the relationship diverge. Memmott *et al.* (2007) used a 19th Century dataset on the phenology of 15 000 interactions between 429 plant species and 1420 pollinator species in North America, coupled with experimental data on physiological responses to warming, to predict that up to a half of these interactions would be threatened under future climate change scenarios. This prediction was subsequently supported when Burkle, Marlin & Knight (2013) revisited the study sites 120 years after the original study and found that only 24% of the original interactions between a subset of 26 forb species and 109 bee species had survived.

Disruptions between plants and their pollinators may have quite subtle causes. The sexually deceptive early spider orchid, *Ophrys sphegodes* is pollinated by a single bee species, *Andrena nigroaenea* during pseudocopulation. Field and herbarium specimen data collected over many populations and years show that the plant's flowering season is advanced in warmer springs (Robbirt *et al.*, 2011). Similarly, field and museum specimen data on the occurrence of the bee pollinator, whose range is much wider than that of the orchid, also show advancement of the season in response to warmer springs. In this context, however, the significant feature of the bee's phenology is that females respond more strongly to warmer temperatures than males, potentially producing a reduced male : female sex ratio at a stage in the season when the orchid needs to attract male bees to pseudocopulate with the flowers. Robbirt *et al.* (2014) suggest that this may divert male bees away from the orchid flowers. The resultant disruption in pollination service may exert further constraining pressure on recovery of this orchid species whose range in Britain has declined substantially in recent years (Kull & Hutchings, 2006). Apart from its intrinsic interest and the implications for conservation of the orchid species, the study illustrates the

novel insights to be gained from linking data between interacting taxonomic groups and between field data and historical collections in museums and herbaria.

INVASION AND RANGE EXPANSION FACILITATED BY ESCAPE FROM NATURAL ENEMIES

Consumer species (whether herbivores or primary parasitoids) that have been artificially introduced into a novel region, perhaps across considerable distances and barriers to normal dispersal, may temporarily experience 'enemy-free space' (Jeffries & Lawton, 1984) and thus spread faster at their expanding margins until such time as their enemies catch up with them or new enemy species switch onto them from taxonomically similar hosts. The 'enemy-release-hypothesis' (ERH) (Keane & Crawley, 2002) seeks to explain the ability of non-native species to invade and spread into new geographical areas, facilitated by relative or complete freedom from natural enemy control in the introduced part of the range. This is the theory that underpins the introduction of non-indigenous species to control pests in classical biological control programmes (Huffaker & Messenger, 1976) and often largely explains the success of introduced species that become invasive, although the latter explanation is controversial (Colautti *et al.*, 2004). Species that are introduced over long distances into communities with which they share no co-evolutionary history may encounter few species that are pre-adapted to curtail their spread. This might explain why exotic species that are unrelated to species in recipient communities tend to be more invasive than native ones (Strauss, Webb & Salamin, 2006).

By contrast, where species ranges expand naturally and gradually, native and invading populations are more likely to remain in contact as a set of interacting species (Schönrogge *et al.*, 2012). Such species are more likely to encounter similar communities to those they leave behind, containing antagonistic species that check their rate of spread. Indeed, many non-native phytophagous insects invading Britain from the near continent have recruited full assemblages of generalist parasitoids from the native species pool rather quickly. The non-native leaf-mining moth, *Phyllonorycter leucographella*, experienced equivalent levels of parasitism and recruited a parasitoid community that was comparable in size to native leaf miners within 12 years of arriving in Britain (Godfray *et al.*, 1995). Similarly, the parasitoid community in Britain associated with the gall wasp *Andricus quercuscalicis*, a species that invaded in the 1950s, now closely resembles the community in its native

continental European range (Schönrogge, Stone & Crawley, 1996). A brief enemy-free window may be critical in the early stages of establishment and initial spread by invading species. The invasion zone in *P. leucographella*, for example, was characterized by fewer parasitoid species and lower parasitism rates compared to populations in the centre of its range (Gröbler & Lewis, 2008). Similarly, the size of the parasitoid assemblage attacking the Horse chestnut leaf miner, *Cameraria ohridella*, as it spreads across Europe appears to be a function of the time since host arrival (Grabenweger *et al.*, 2010).

The ERH may also apply to native species expanding their ranges. Thus, it has been shown that the expansion front of the brown argus butterfly, *Aricia agestis*, a native species expanding its range northwards within Britain, is characterized by reduced parasitism rates (Menéndez *et al.*, 2008). Another extension of the ERH is that phytophagous insect species could benefit from the enemy-free space created by switching onto a novel food plant. This has been shown experimentally (Gratton & Welter, 1999), although evidence from un-manipulated field populations is equivocal (Gröbler & Lewis, 2008).

RANGE EXPANSION FACILITATED BY EXPLOITATION OF NOVEL FOOD PLANTS

Some phytophagous insects have been able to extend their geographical ranges by changing their diet preferences, often from monophagy on plants with limited distributions to exploiting more common or widespread species. In some species, pre-existing plasticity in food plant preference has enabled a change in the frequency with which different plant species are used. The northward range extension since the 1940s of the comma butterfly, *Polygonia c-album*, for example, has been facilitated by a broadening of its larval food plant preferences from hops, *Humulus lupulus*, to members of closely-related plant families, particularly stinging nettle, *Urtica dioica*, and wych elm, *Ulmus glabra*. The range of this species has shown one of the most rapid responses to climatic warming of any butterfly species in Britain. Its larval performance on the new host species was shown under experimental conditions to be better than on the ancestral one (Braschler & Hill, 2007). The close relationship between the plant families involved is probably reflected in similarities in plant chemistry, especially of secondary defences. Host shifts by insect herbivores are often restricted to plants with similar chemistry, which in turn will govern opportunities for range expansion. Conversely, it has been suggested that chemical similarities between plant species have enabled the expansion of diet breadth in certain phytophagous pest insects, which have then

facilitated considerable expansion of their geographical range (Erbilgin *et al.*, 2014).

Historically, the primary larval food plant of the Brown Argus butterfly, *Aricia agestis*, was Rockrose, *Helianthemum nummularium*, itself mainly confined to calcareous grasslands. A shift in food plant preference in favour of the more common and widespread dove's-foot crane's-bill, *Geranium molle*, has enabled the butterfly to exploit a wider range of habitats and thereby substantially expand its range over 20 years by a process of both 80 km northwards extension and infilling (Pateman *et al.*, 2012; Bridle *et al.*, 2014). Rapid evolution of this novel interaction has apparently proceeded to the extent that populations in *Geranium*-dominated habitats now have reduced fitness when experimentally transferred to their ancestral food plant (Buckley & Bridle, 2014). Thus, populations at expanding range margins may be more specialized (Oliver *et al.*, 2009) and exhibit reduced adaptive variation compared to central ones. This finding also raises the intriguing possibility of disruptive selection and incipient speciation enabled by a novel interaction created as a species shifts its range.

By contrast, certain other herbivorous insects have evolved completely new food plant associations in response to changing environmental conditions and the novel availability of suitable hosts. For example, some populations of Edith's checkerspot butterfly, *Euphydryas editha*, in the western USA have switched to human-introduced alien plant species in preference to native hosts. This has enabled certain endangered subspecies of this butterfly to persist in the face of rapid environmental change, although limited dispersal ability has precluded any geographical spread. Ironically, conservationists are now concerned that some populations may have become dependent upon the continued creation and maintenance of the disturbed habitats that their newly adopted food plant requires (Singer, Thomas & Parmesan, 1993; Singer *et al.*, 2008).

Adoption of alternative food plants may explain the relatively sudden range expansions of individual species in other less well-studied groups of phytophagous insects (Stewart & Kirby, 2010). The juniper shieldbug, *Cyphostethus tristriatus*, for example, was a relatively uncommon insect on Juniper, *Juniperus communis*, in woodland and scrub until the 1980s. Subsequently, a shift to cypress trees in the genera *Cupressus* and *Chamaecyparis* (Carter & Young, 1974; Askew, 1983), widely cultivated as ornamental trees in gardens, has coincided with and probably been responsible for a rapid geographical spread across England and Wales (Fig 4). The rhopalid bug *Corizus hyoscyami* previously had a strongly western and coastal distribution within Britain with a narrow range of food plants (e.g.

species of *Erodium* and *Ononis*). Since 1990, it has adopted a wider range of hosts, including members of the Compositae, and habitats, including a variety of grasslands, waste ground, and gardens. This has enabled considerable inland and eastward (but interestingly not northward) expansion of its range (Fig 4). Perhaps the most spectacular example of a host shift facilitating range expansion, however, is the box bug, *Gonocerus acuteangulatus*. This coreid bug was traditionally known from only a limited number of box, *Buxus sempervirens*, bushes on Box Hill in Surrey, England. Since 1990, the bug has been recorded exploiting woody plant species across several genera, including *Crataegus*, *Rhamnus*, *Malus*, *Cupressus*, and *Taxus*, with a concurrent spectacular expansion in its geographical range (Fig 4).

If the spatial distribution of a food plant limits that of any monophagous insect herbivore that it supports, it follows that any changes in the large-scale range, local abundance or spatial continuity of the plant species, or its close relatives, will have knock-on effects on its specialist consumers. This appears to explain the considerable infilling (but not significant overall expansion in the extent of occurrence) of the ranges within Britain of two flea beetles (Chrysomelidae), flax flea beetle, *Longitarsus parvulus*, and large flax flea beetle, *Aphthona euphorbiae*, whose native food plants include various *Linum* species (Fig 5). Both beetle species have taken advantage of the increasingly widespread cultivation of flax, *Linum usitatissimum*, as a crop plant grown for linseed oil (Cox & Campbell, 1998). These particular cases may be atypical, however; the apparent success of these species in colonizing a substantial part of the range of their food plant is probably the result of the unnaturally high densities and geographical coverage of the crop under commercial cultivation.

CONCLUSIONS

The determinants of range size in phytophagous insects are clearly multifactorial. Ultimately, the range boundary of a species cannot exceed that of one of its critical resources: food plants in the case of phytophagous insects. Other factors, however, may further constrain distributions to relatively small subsets of what is dictated by the distribution of the food plant, including biotic interactions (both positive and negative) with other species, as well as responses to the abiotic environment. In general, the distributions of phytophagous insects are much more geographically restricted than their food plants. Certainly, in the context of modern intensively managed landscapes, larger scale factors such as climate and land use change are likely to be more significant

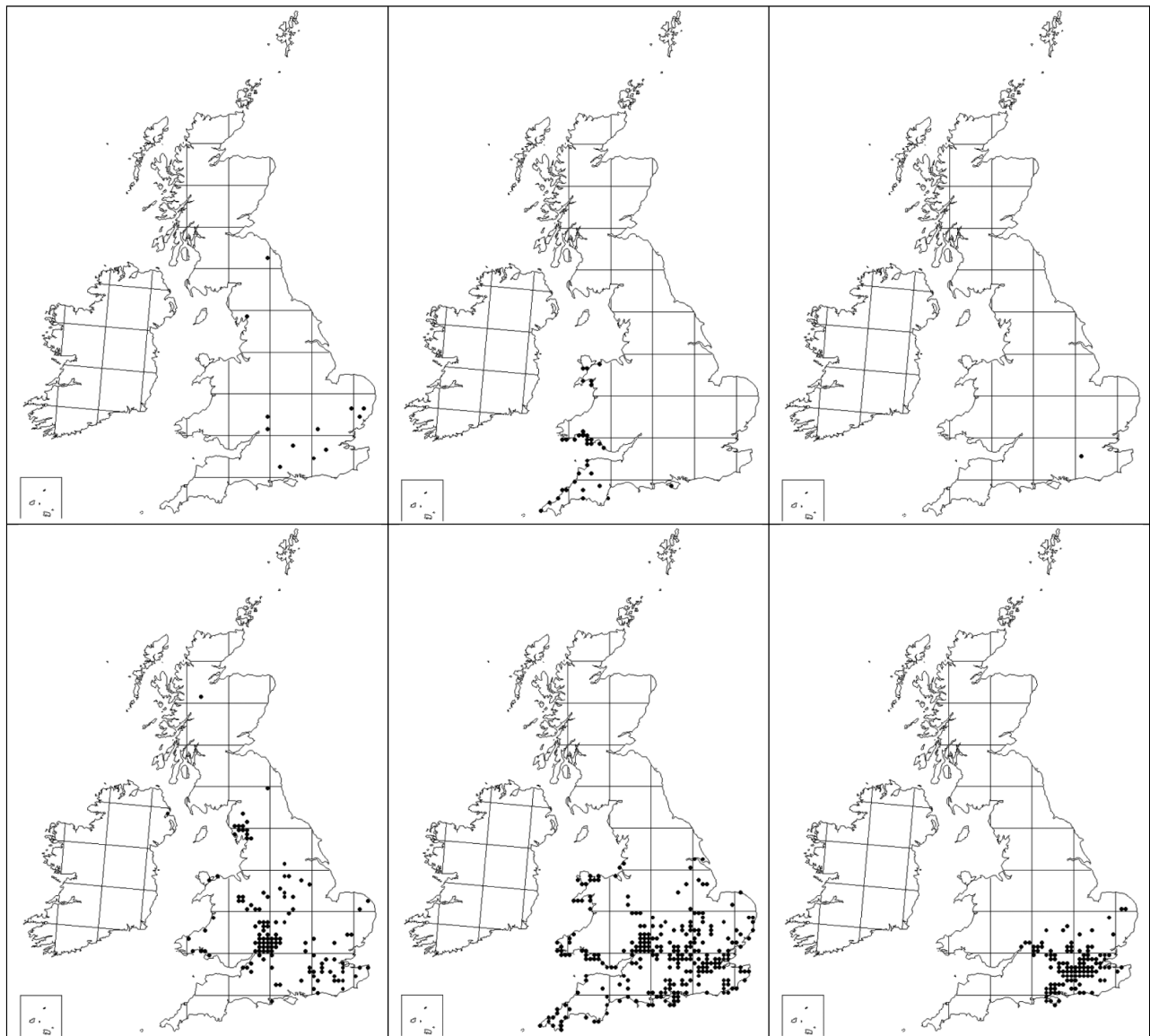


Figure 4. Range expansion in phytophagous Heteroptera species facilitated by shifts to novel food plants: *Cyphostethus tristriatus* (Acanthosomatidae) (left); *Corizus hyoscyami* (Rhopalidae) (middle); *Gonocerus acuteangulatus* (Coreidae) (right). Top: pre-1990; bottom: 1990 to present.

drivers of species distributions, and range changes, in phytophagous insects than the distribution of food plants *per se* (Fox *et al.*, 2014).

Nevertheless, a number of interesting questions remain to be explored, particularly in relation to predicting future range changes. To what extent do food plant traits determine how much of their range is exploited by the insects that feed on them? Are polyphagous insects expanding faster than their monophagous counterparts? Are insects that occupy only a small fraction of their food plant range expanding their own range faster than species that have colonized greater proportions? To what extent do indi-

vidual species occupy the full latitudinal range of their hosts, thus determining how much further north they can extend their range within the current range of their food plants? Is there a phylogenetic signal in the patterns of range size and range change? Are the patterns of exploitation different for native compared to newly arrived colonists? To what extent will the further range expansion of non-indigenous invasive species be curtailed by the distribution of their food plants?

There are also a number of methodological and technological issues to consider (August *et al.*, 2015; Powney & Isaac, 2015). Data from most of the smaller

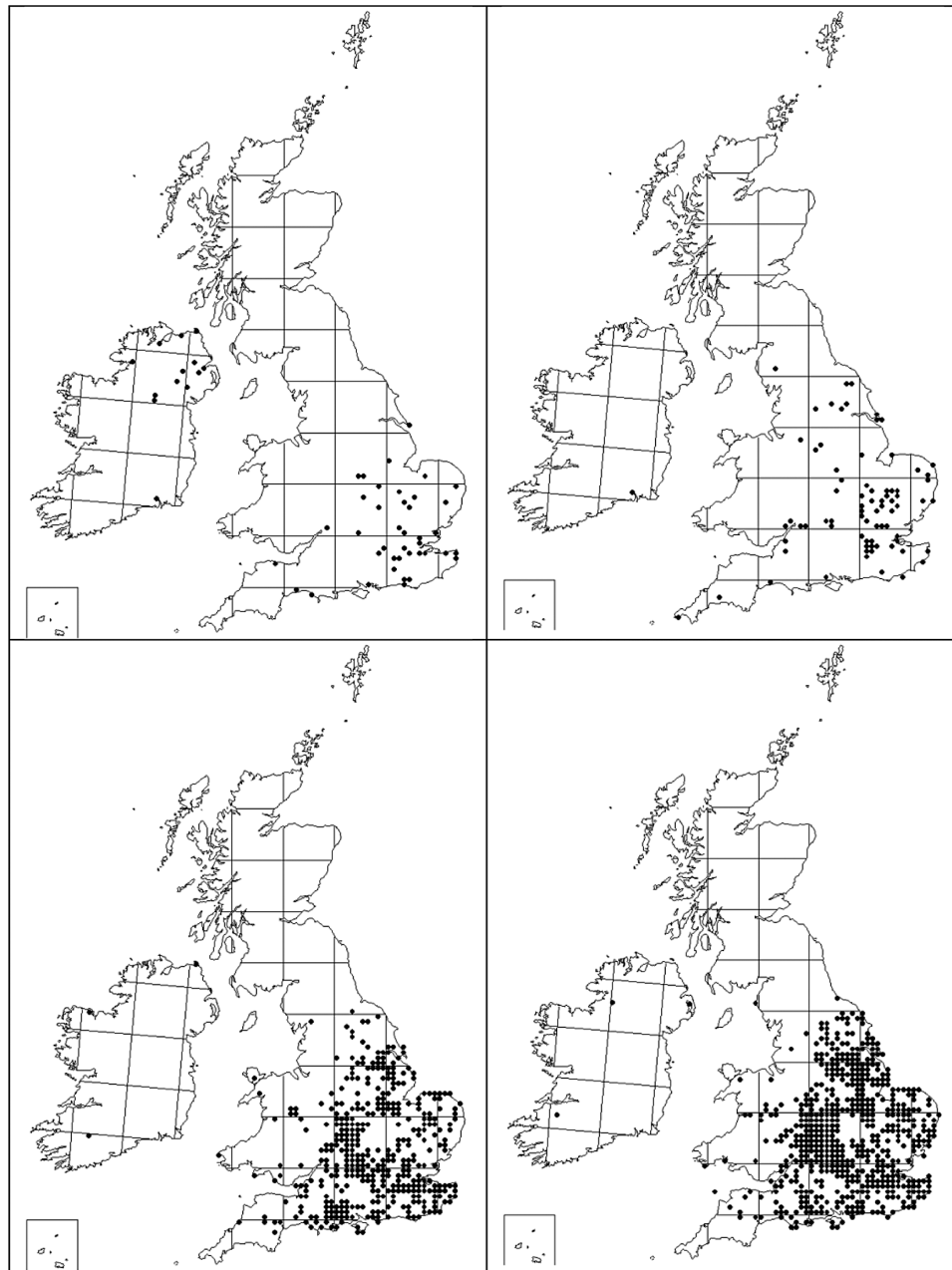


Figure 5. Range expansion in phytophagous leaf beetle species facilitated by range expansion of their food plants: *Longitarsus parvulus* (Chrysomelidae) (left); *Aphthona euphorbiae* (Chrysomelidae) (right). Top: pre-1980; bottom: 1980 to present.

recording schemes will suffer from under-recording or incomplete geographical coverage. The extent to which this might undermine the clarity of the emergent patterns is uncertain. Most analyses have been done at the 10-kilometre square level. Whether the general patterns remain when the data are analyzed at different levels of resolution is not known. Range size, measured as total area of occupancy, is likely to be a rather crude metric for comparisons between

insect herbivore species and their food plants. It does not account for the geographical spread of the range or the positions of the range centroid or boundaries in relation to those of the food plant. Thus, it does not indicate whether the northern or southern extremes of the range extend to the range margins of the food plant or fall short of them. Similarly, range size alone does not indicate whether the distribution is continuous or fragmented. The effects of such subtleties on

these interactions are not known but would be worth investigating.

It is clear that ecological communities will not necessarily respond to climate change as coherent entities with all internal interactions remaining intact as they shift geographically. Instead, the differential responses of individual species will result in some existing communities breaking up and new ones forming with novel combinations of species that have no current analogues. An understanding of these ecological interactions between species will be critical for predicting the composition of the communities that will emerge in future (Svenning *et al.*, 2014).

Finally, the increasing popularity of 'citizen science' (Pocock *et al.*, 2015) provides the field of biological recording with unique opportunities to collect more complex information than simple occurrence data. Species interactions should become an important part of the wider biological recording endeavour (Sutherland, Roy & Amano, 2015). Some taxonomic groups (e.g. leaf-miners, plant galls) lend themselves more readily than others to being recorded as part of an interaction between species. Nevertheless, it is apparent that more account will need to be taken of ecological interactions when predicting how species distributions will respond to current and future environmental change. Greater biological recording effort should therefore be encouraged towards recording these types of interactions.

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