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Using biological traits to explain ladybird distribution patterns

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ABSTRACT

Aim Determining to what extent differing distribution patterns are governed by species' life-history and resource-use traits may lead to an improved understanding of the impacts of environmental change on biodiversity. We investigated the extent to which traits can explain distribution patterns in the ladybird fauna (Coleoptera: Coccinellidae) of Great Britain.

Location The British mainland and inshore islands (Anglesey, the Isle of Wight and the Inner Hebrides).

Methods Distributions of 26 ladybirds resident in Britain were characterized in terms of their range size (from 2661 10-km grid-squares across Britain) and proportional range fill (at 10- and 50-km scales). These were assessed relative to five traits (body length, elytral colour pattern polymorphism, voltinism, habitat specificity and diet breadth). The role of phylogenetic autocorrelation was examined by comparing the results of phylogenetic and generalized least-squares regressions.

Results Diet breadth was the only trait correlated with range size: species with broad diets had larger range sizes than dietary specialists. Range fill was sensitive to the average recording intensity of a species across inhabited squares; models including both recording intensity and range size provided more explanatory power than models incorporating ecological traits alone.

Main conclusions Habitat specificity is often invoked to explain the distribution patterns of species, but here we found diet breadth to be the only ecological correlate of both range fill and range size. This highlights the importance of understanding predator–prey interactions when attempting to explain the distribution patterns of predatory species.

Our results suggest that the diet breadth of predatory species is a better correlate of range size and fill than other measures such as habitat specificity.

Keywords

Coccinellidae, diet breadth, distribution, Great Britain, insects, niche breadth, range fill, range size, traits.

INTRODUCTION

The striking differences in the spatial distribution of taxonomically related species are intriguing, and understanding the processes governing these spatial distribution patterns is one of the central themes of ecology (e.g. Andrewartha & Birch, 1954; MacArthur, 1972). In recent years species distributions have been shifting in response to climate change (Hickling *et al.*, 2006; Poyry *et al.*, 2009) and so biogeographical studies have assumed an added significance. By exploring the relationships between species' distribution patterns and their life-history and resource-use characteristics, we may

gain a better understanding of the biological mechanisms underpinning range size and fill (Ockinger *et al.*, 2010), which can inform conservation management.

Species' distribution patterns can be characterized either in terms of extent of occurrence (EOO, defined as the area encompassed by the outermost geographic limits of a species' occurrence) or area of occupancy (AOO, the area within those limits where the species actually occurs) (Gaston & Fuller, 2009). The AOO is usually measured in terms of the number of grid cells occupied (typically 1-, 10- and 100-km square grid cells), and can also be characterized by the proportion of the potential range that is actually occupied ('range fill' or 'aggregation') (Gregory & Gaston, 2000; Wilson *et al.*, 2004).

Life-history and resource-use characteristics (hereafter referred to as 'traits') are distinct, heritable characteristics of the species' phenotype. Traits of vertebrate and plant taxa have been widely studied and used in systematic biogeographical investigations to explain patterns of distribution (Pocock *et al.*, 2006; Van der Veken *et al.*, 2007; Bradshaw *et al.*, 2008; Blackburn *et al.*, 2009; Wang *et al.*, 2009; Astegiano *et al.*, 2010; Navarro *et al.*, 2010). Less consideration, however, has been given to assessing the relationship between multiple traits and the distribution patterns of invertebrates (e.g. Brändle *et al.*, 2002).

Body size is often invoked as a species trait correlated with the distribution patterns of species (e.g. Juliano, 1983; Tingley *et al.*, 2010; Verberk *et al.*, 2010). However, body size is strongly correlated with other traits such as dispersal ability (Rundle *et al.*, 2007a) and trophic level (Romanuk *et al.*, 2011). Species that are generalists in terms of both dietary and habitat requirements occupy larger ranges and exhibit a greater proportion of range fill in many taxa, such as tropical sphingid moths (Beck & Kitching, 2007), and British bumblebees (Goulson *et al.*, 2005). The ability to survive in a wide range of habitats is strongly associated with commonness among native species (Cadotte & Lovett-Doust, 2002), and with an alien species' likelihood of becoming invasive (Blackburn *et al.*, 2009). The underlying factors determining the distribution of habitats (geology, land-use history, rainfall, etc.) are spatially structured, leading to patterns in the distribution of plant species (Pocock *et al.*, 2006), and thus also the distribution of species which feed on the different plant species. Therefore species which can utilize more of the available resources (food or habitat types) have a larger niche breadth (Gaston & Blackburn, 2000) and are likely to be able to survive and reproduce across a wider geographical range.

Variation in other life-history traits, e.g. polymorphism and voltinism (the number of generations per year), may also allow species to achieve larger range sizes and a greater degree of range fill. For example, species with high voltinism have, by definition, a shorter generation time than similar species with lower voltinism. This means they often achieve a higher reproductive rate, and so have more opportunities for dispersal per year, potentially resulting in greater colonization of marginal habitats, and therefore both larger range sizes and a greater degree of range fill (Altermatt, 2010). Polymorphic species, with the extended phenotypic range of several distinct forms, could potentially fill a wider niche, so colonizing larger areas. In the grasshoppers *Chorthippus parallelus* (Zetterstedt) and *Tetrix undulata* (Sowerby), for example, different colour morphs have been found to preferentially inhabit differing habitat types, and to vary in fecundity (Ahnesjö & Forsman, 2003, 2006; Unsicker *et al.*, 2008).

In this paper we investigate distribution patterns in relation to ecological traits (body size, habitat and dietary specialization, voltinism and phenotypic polymorphisms) for 26 species of ladybird (Coleoptera: Coccinellidae) resident in Great Britain. Ladybirds provide key ecological services as predators of crop pest insects (Day *et al.*, 2006; Costamagna & Landis, 2007; Obrycki *et al.*, 2009) and provide a novel contrast to previous studies of range characteristics which have focused on herbivores (Goulson *et al.*, 2005; Beck & Kitching, 2007; Unsicker *et al.*, 2008). Britain has an unparalleled history of biological recording schemes, with excellent spatial, temporal and taxonomic

coverage, which presents the opportunity to carry out a detailed study on distribution patterns across a large geographical region.

By combining detailed trait data and biological records within the same model framework, we examine the relative importance of resource use (diet breadth, habitat specialisation) and life-history traits (body size, voltinism, and elytral colour pattern polymorphism) in explaining the distribution patterns (range size and fill) of ladybirds in Britain. European subfamilies and guilds of ladybirds are well represented in Britain and there is evidence to suggest that, as for other insect groups, responses to environmental change have been shown to be broadly equivalent between Britain and continental Europe (Parmesan *et al.*, 1999; Hill *et al.*, 2003).

MATERIALS AND METHODS

Distribution data

The distribution data for the 26 ladybird species were taken from the UK Ladybird Survey (UKLS; www.harlequin-survey.org and www.ladybird-survey.org). The recording scheme contains over 140,000 ladybird records from 1832 to the present day, both casual sightings and the results of systematic surveys (e.g. from county atlases). Data are much less extensive for the 21 smaller inconspicuous coccinellids and these are excluded from the current analysis. All records used in this analysis have been identified to species by experts, either in the field or from a specimen or good photo submitted to the recording scheme.

The 30-year period from 1980 to 2009 (inclusive) was chosen as the study period because it encompasses the two main periods of intense recording activity. The first of these was during the 1980s and early 1990s, when widely publicized through the Cambridge Ladybird Survey (Majerus, 1994), and the second from 2004 to date when the arrival of the invasive alien ladybird *Harmonia axyridis* (Pallas) again raised the public profile of the recording scheme (Brown *et al.*, 2010; Roy *et al.*, 2011).

The range size of ladybirds was characterized as presence/absence at a 10-km grid square resolution over the 30-year period. The study area used was mainland England, Scotland and Wales, plus the inshore islands of Anglesey, the Isle of Wight and the Inner Hebrides, but excluding Northern Ireland and the offshore islands of Scilly, Man, Lundy, Shetland, Orkney, the Outer Hebrides and the Channel Islands, to avoid species' distribution patterns being influenced by the mosaic of land and sea common in archipelagos. This yielded a total of 86,259 records across the 26 ladybird species (ranging from eight records for *Hippodamia tredecimpunctata* L. to 21,761 for *Coccinella septempunctata* L.).

For each species, the proportion of squares occupied (counted from a nationwide total of 2662) was calculated. This was then logit-transformed to produce the variable 'range size'. This transformation has been shown to be a valid means of achieving normality in range size datasets which are bounded at the right and left of the distribution (Williamson & Gaston, 1999). Range fill was calculated from the 10-km grid square distribution pattern following a method developed by Condit *et al.* (2000), and used by Wilson *et al.* (2004, outlined in their supplementary material), modified here to account for the configuration of land and sea in coastal squares. For each grid square, the number of occupied squares whose central point lies within circular radii of 10- or 50-km from the central point of the tested square was counted. This was divided by the total number of squares possible given a circle of this size (four or 80, respectively, minus any squares that were purely marine). This gives a value of between zero and one for each square-species combination (zero – no other squares occupied, one – all possible squares occupied). These square values were averaged for each species across the study area at each spatial scale to produce a range fill score, D_x (where x is the spatial scale).

Explanatory traits

Ecological traits

Ecological traits with the potential to influence distribution characteristics were selected a priori on the basis of evidence from the literature. Overall, 352 sources were used (3–151 sources per species. An EndNote (Thompson Reuters, New York, USA) library of these references is available on request). Ecological traits were subdivided into life-history traits and resource-use traits as follows.

1. Life-history traits:

- (i) Voltinism, defined as the number of generations per year for each species within Britain (ranging from one to three). There is variation within species between localities and years, so the modal value was used.
- (ii) Elytral colour pattern polymorphism, characterized as a binomial presence/absence of melanic forms, following Roy *et al.* (2011). Individual-level variation within colour forms is not captured by this measure, but it avoids the problem of the different levels of study for different species.
- (iii) Body size, defined as the length in mm from head to abdomen tip, calculated as the mid-point of the upper and lower body lengths quoted in Roy *et al.* (2011) (range from 3 to 7.8 mm). These are from Pope (1953) and Hawkins (2000), based on measurements from populations across Britain, except for *H. axyridis* which was taken from Kuznetsov (1997) and checked against specimens submitted to the recording scheme from across Britain. Although the full extent of within-species variation is not captured by this measure, we believe it provides a reasonable reflection of body size differences among species.

2. Resource-use traits:

- (i) Habitat use, measured as the number of EUNIS level 2 habitat categories (ranging from 1 to 11) which the species has been recorded from in Britain. The EUNIS (European Nature Information System) habitat classification is a pan-European classification of terrestrial, freshwater and marine habitats that has been developed for the European Environment Agency by the European Topic Centre on Biological Diversity (ETC/BD). The latest version can be accessed at <http://eunis2.eea.eu.int/>.
- (ii) Diet breadth, measured as the number of prey families (ranging from 1 to 12) consumed by either adults or larvae of each species. Only natural diets were considered and laboratory diets such as drone powder, *Ephestia* eggs and agar-based diets were excluded.

We also included a measure of the recording intensity for each species. A potential problem with data from this kind of survey, with a high proportion of citizen science involvement, is that recording intensity may vary amongst species and across geographical regions. Some species are under-recorded, and the extent of this is likely also to depend on other traits such as habitat use, with, for example, strictly tree-dwelling species under-recorded. Although it is difficult to eliminate all such biases from the data, a range size-independent measure of recording intensity per species was included as a covariate in the pool of potential explanatory variables. This was the mean number of records across the 10-km squares occupied by a species.

Data analysis

The relationships between species traits and range characteristics were examined using generalized linear models (GLM; (McCullagh & Nelder, 1989) implemented in the statistical software program R, version 2.10.1 (R Development Core Team, 2009, Vienna, Austria). Three global GLMs were constructed with all five traits (and recording intensity) as explanatory variables and the range size, D_{10} or D_{50} in turn as the dependent variable. For the measures of range fill, D_{10} and D_{50} , the best traits models were compared to models using range size and recording intensity as the only explanatory variables. This comparison was performed because although range size has been found to be a strong correlate of range fill in other taxa (Wilson *et al.*, 2004; Pocock *et al.*, 2006), the importance of primary biological traits that govern both range size and range fill was the focus of our study.

Collinearity between trait variables was tested for by calculating variance inflation factors (VIFs) for each trait in each model using the 'car' package (Fox & Weisberg, 2011). A common rule of thumb is that VIFs exceeding five indicate high levels of multiple collinearity. All the VIFs in the global GLMs were below five, hence severe collinearity was not observed and all traits were retained in the global models. A correlation analysis was also carried out on the traits, and found no significant correlation between them (Kendall's $T < 0.7$ in all cases) (Table 1).

Table 1 Table of Kendall's tau for correlations between the explanatory trait variables habitat use, diet breadth, body size, voltinism and elytral colour pattern polymorphism for British ladybirds. Significance of the tau values is indicated as * $P = 0.05$, ** $P = 0.01$, *** $P = 0.001$ for these univariate comparisons.

Traits	Habitat use	Diet breadth	Size	Voltinism
Diet breadth	0.39 *			
Size	-0.09	0.02		
Voltinism	0.29	0.30	0.26	
Polymorphism	0.11	0.46 **	0.16	0.29

The final GLM for each dependent variable was selected using a stepwise optimal model selection procedure based on corrected Akaike's information criterion (AIC_c) values, appropriate for small sample sizes (Akaike, 1974; McQuarrie & Tsai, 1998; Burnham & Anderson, 2002). To verify the robustness of the final model, a bootstrap procedure with 10,000 replicates was implemented in the 'boot.StepAIC' package within R (Austin & Tu, 2004). This approach uses random bootstrap samples drawn from the original dataset to investigate the variability of model selection under the step AIC stepwise algorithm (Austin & Tu, 2004). Within each bootstrap sample, forwards and backwards stepwise selection was used to determine the most parsimonious model, based on AIC_c (ΔAIC_c of 2 required to incorporate an additional term). AIC_c values were also calculated for the global and null (intercept-only model without any explanatory variables) models for each range characteristic to assess the importance of the final model. Goodness-of-fit was also calculated as deviance for each model.

To avoid the problem of phylogenetic autocorrelation, phylogeny was controlled for using a phylogenetic least squares approach (Freckleton *et al.*, 2002), and the performance of the phylogenetic and non-phylogenetic regression approaches compared using information criteria. Expected covariance between species was calculated on the basis of a phylogeny based on the taxonomy of Duff (2008), assuming equal branch lengths (computed after Grafen, (1989). The tree was created using the program TREEMAKER 1.3 (Crozier *et al.*, 2005) and the R package 'ape' (Paradis *et al.*, 2004). The R package 'CAIC' (Agapow & Isaac, 2002) was used to fit a phylogenetic generalized linear model (PGLM) (Freckleton *et al.*, 2002) equivalent to each of the three best GLMs, and selection between the PGLM and equivalent GLM for range characteristics was made on the basis of AIC_c . In the event that the PGLM performed better than the original GLM, Pagel's λ (Pagel, 1999) was used to estimate the degree of phylogenetic autocorrelation in the model, where 0 indicates no phylogenetic signal in the data and 1 indicates perfect phylogenetic correlation. The `pglmEstLambda` function of the 'CAIC' package was used to identify the maximum likelihood value of the lambda parameter and to test whether this value was significantly different from 0 or 1 using a log-likelihood test (Agapow & Isaac, 2002; Freckleton *et al.*, 2002). Residuals from all models were checked for normality using normal probability graphs, and for heteroscedasticity by plotting residuals against fitted values.

Selection between PGLMs and GLMs was made on the basis of AIC_c and goodness of fit (deviance, D^2 , adjusted for small sample sizes), which allows for comparison between models with different numbers of parameters. Univariate models were also constructed for each of the traits as a comparison for the best traits models.

RESULTS

Table 2 Comparative performance of models at predicting range characteristics of British ladybirds (range size and range fill at the 10-km and 50-km scale): global models (all traits: body size, voltinism, elytral colour pattern polymorphism, diet breadth, habitat use), null models (no explanatory traits: the null hypothesis), range size and recording intensity-only models, and the best ecological traits-only models. GLM = generalized linear model fitted by ordinary least squares regression. PGLM = GLM fitted using phylogenetic generalized least squares regression. Deviance is the model residual deviance. ΔAIC_c (corrected Akaike's information criterion) was calculated from the model with the lowest AIC (marked by '–' in the ΔAIC_c column). Models selected as 'best models' in the text are marked with *.

(a) Range size					
Model	Traits	Deviance (Adj. deviance)	AIC _c	ΔAIC_c	λ (PGLMs only)
Best trait PGLM	Diet breadth	41.94 (43.64)	91.82	–	5.099×10^{-5}
Best trait GLM*	Diet breadth	41.94 (43.64)	93.31	1.49	–
Null GLM		63.92 (63.92)	101.70	9.88	–
Global GLM		34.57 (34.57)	105.66	13.84	–
(b) D_{10} – Range fill at 10-km grid square resolution					
Model	Traits	Deviance (Adj. deviance)	AIC _c	ΔAIC_c	λ (PGLMs only)
Range size & recording intensity PGLM*	Range size, recording intensity	0.19 (0.12)	–50.26	–	0.627
Range size & recording intensity GLM	Range size, recording intensity	0.18 (0.11)	–46.05	4.21	–
Best trait PGLM	Recording intensity	0.50 (0.48)	–23.27	26.99	6.662×10^{-5}
Best trait GLM	Recording intensity	0.50 (0.48)	–21.78	28.48	–
Global GLM		0.36 (0.36)	–13.13	37.13	–
Null GLM		1.15 (1.15)	–2.76	47.5	–
(c) D_{50} – Range fill at 50-km grid square resolution					
Model	Traits	Deviance (Adj. deviance)	AIC _c	ΔAIC_c	λ (PGLMs only)
Range size & recording intensity PGLM	Range size, recording intensity	0.11 (0.03)	–60.29	–	6.611×10^{-5}
Range size & recording intensity GLM*	Range size, recording intensity	0.10 (0.03)	–59.66	0.63	–
Best trait GLM	Diet breadth, size, recording intensity	0.36 (0.26)	–25.17	35.12	–
Best trait PGLM	Diet breadth, size, recording intensity	0.35 (0.26)	–24.9	35.39	6.004×10^{-5}
Global GLM		0.33 (0.33)	–15.46	44.83	–
Null GLM		1.20 (1.20)	–1.77	58.52	–

Table 3 Univariate models showing the individual contribution of traits selected in the range fill models (recording intensity, diet breadth, body size) and range size, used as an explanatory trait. ΔAIC_c (corrected Akaike's information criterion) was calculated as the difference between the AIC_c of the univariate models compared to that of the best model (at that grid square resolution), presented in Table 1.

D_{10} – Range fill at 10-km grid square resolution, component models							
Trait	Coefficients (\pm SE)	Intercept (\pm SE)	t-value	R^2 (adj. R^2)	P-value	AIC _c	ΔAIC_c
Range size & recording	RS: 0.08 (0.01) RI: 0.02 (0.003)	0.54 (0.05)	RS: 8.16 RI: 6.07	0.891 (0.881)	<0.001	–50.26	–

intensity PGLM							
Range size	0.11 (0.02)	0.70 (0.04)	7.20	0.683 (0.670)	<0.001	-30.10	20.17
Recording intensity	0.03 (0.01)	0.24 (0.04)	5.57	0.564 (0.546)	<0.001	-21.78	28.48

D_{50} – Range fill at 50-km grid square resolution, component models

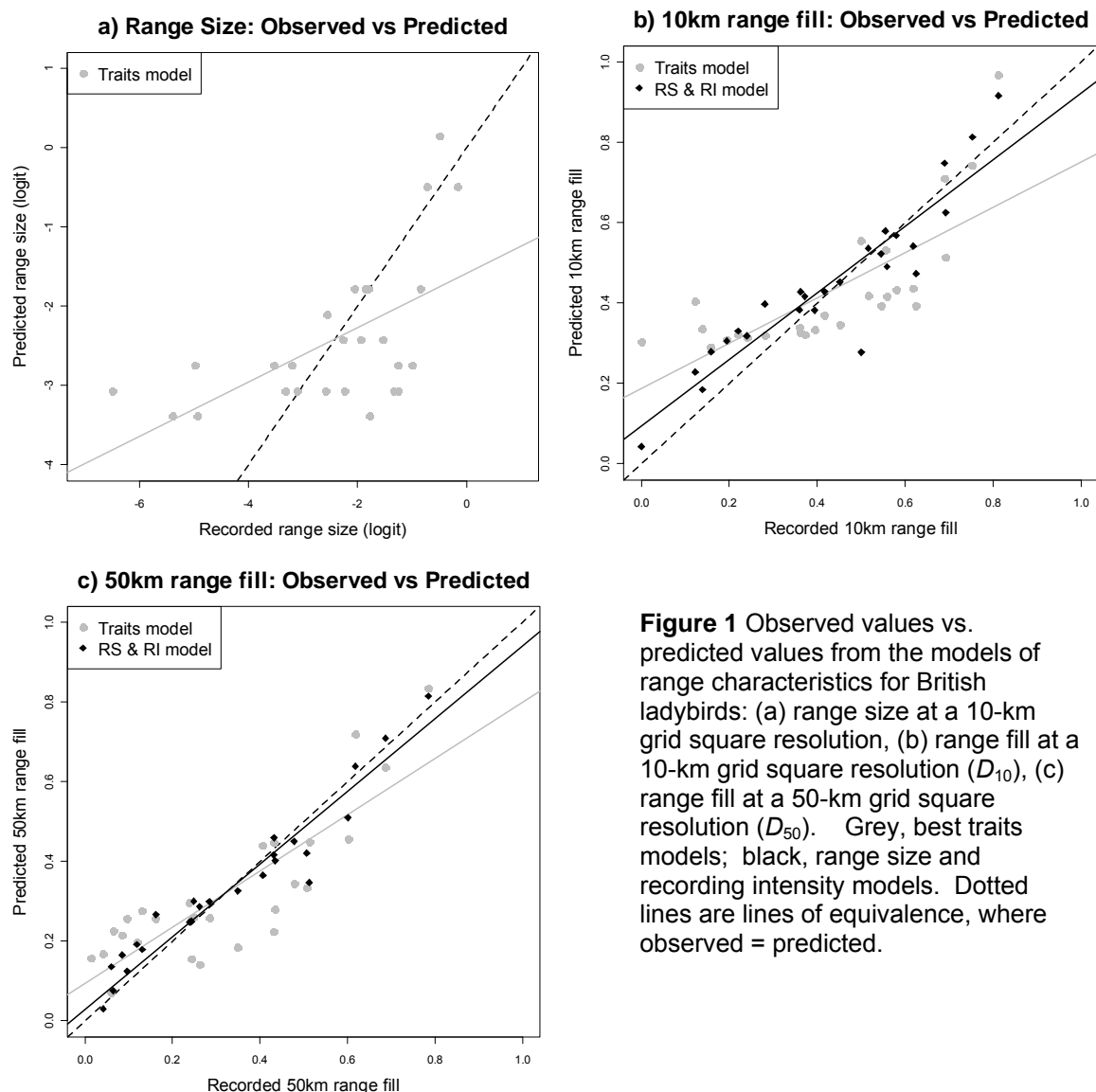
Trait	Coefficients (\pm SE)	Intercept (\pm SE)	t -value	R^2 (adj. R^2)	P -value	AIC _c	Δ AIC _c
Range size & recording intensity GLM	RS: 0.09 (0.01) RI: 0.02 (0.003)	0.42 (0.04)	RS: 9.41 RI: 6.25	0.912 (0.905)	<0.001	-59.66	–
Range size	0.12 (0.01)	0.61 (0.04)	8.79	0.763 (0.753)	<0.001	-36.67	23.66
Recording intensity	0.04 (0.01)	0.12 (0.05)	5.70	0.575 (0.557)	<0.001	-21.45	38.84
Diet breadth	0.05 (0.01)	0.10 (0.05)	5.15	0.525 (0.505)	<0.001	-18.54	41.75
Body size	-0.01 (0.04)	0.34 (0.18)	-0.15	<0.001 (-0.041)	0.88	0.78	61.07

The degree of phylogenetic autocorrelation in relationships between range characteristics and ecological traits was found to be negligible in all three traits models and in the model for D_{50} containing range size and recorder intensity only (Pagel's λ not significantly different to 0), so GLMs were preferred for these. There was significant phylogenetic autocorrelation in the residuals of the model for D_{10} containing range size and recorder intensity (Pagel's $\lambda = 0.627$, $P < 0.001$), so the PGLM was retained (Table 2).

Diet breadth was the only trait variable retained in the final model for range size, explaining 31.7% of the variation in range size between species ($F_{1,24} = 12.58$, $P = 0.0016$, slope = 0.32 ± 0.09 , intercept = -3.71 ± 0.45) (Fig. 1a). A lack-of-fit sum of squares test was performed, which rejected the nonlinear model ($F_{6,18} = 0.2254$, $P = 0.9632$).

Range fill at a 10-km grid square resolution, D_{10} , was not significantly related to any ecological traits, but was significantly related to recording intensity (slope = 0.034 ± 0.006 , intercept = 0.24 ± 0.04), which explained 54.6% of the variation in range fill at this scale ($F_{1,24} = 31.05$, $P < 0.001$) (Fig. 1b). The D_{10} range size and recording intensity model, by contrast, explained 83.3% of the between-species variation ($F_{2,23} = 63.27$, $P < 0.001$) (Fig. 1b).

Three variables were significantly related to range fill at a 50-km grid square resolution, the traits model explaining 66.7% of the total variation between species in D_{50} ($F_{3,22} = 17.65$, $P < 0.001$) (Fig. 1c). The significant variables were diet breadth, recorder intensity (both positively related to range fill), and body size (negatively related). The alternative model (containing just range size and recorder intensity as explanatory variables) explained 90.5% of the variation in D_{50} ($F_{2,23} = 119.6$, $P < 0.001$) (Fig. 1c). The most important univariate variable in both the D_{10} and D_{50} models was range size (Table 3).



DISCUSSION

Diet breadth of ladybirds is positively correlated with range size. This is consistent with the literature for other groups, particularly Lepidoptera (Quinn *et al.*, 1997; Beck & Kitching, 2007; Garcia-Barros & Benito, 2010). The fact that this relationship is found across taxa, and is so strong for ladybirds, suggests that diet breadth should be considered a key niche-breadth determinant, particularly for predatory groups.

Many historical and geographical events can affect the realized distribution of species, so very precise predictions of range characteristics cannot be expected from species-specific traits alone (Beck & Kitching, 2007). Indeed, for range fill at both the 10- and 50-km grid-square level, models including range size and recorder intensity predicted observed distribution patterns far better than traits-only models. At the 10-km level, no resource-use or life-history traits were included in the minimum adequate models, although the relationship between range size and diet breadth suggests the latter may play a role in structuring the pattern of range fill and it is explicitly selected at the 50-km level.

The diet breadth achieved by a species is intuitively dependent, in part, on the distribution of the prey organisms encountered in its range. In general, species that consume a greater number of species are likely to have a wider distribution than species with more limited prey ranges (although it is possible that a species which consumes a few common species could have a wider distribution than a species which feeds on several rare species, all other factors being equal). For example, *Ichneumon eumerus* (Wesmael) is a specialist parasitoid of two endangered lycaenid butterfly species, *Phengaris rebeli* (Hirschke) and *P. alcon* (Denis & Schiffermüller) (Thomas & Elmes, 1993; Tartally, 2005), but is considerably rarer than another specialist parasitoid wasp, *Listrodromus nycthemerus* (Gravenhorst), which feeds only on the widespread lycaenid butterfly *Celastrina argiolus* (L.) (Heath & Emmet, 1989; Revels, 2006).

It should be noted that no distinction was made between essential and alternative food sources within this analysis. Essential food sources are those on which the ladybird can feed solely while retaining the ability to mature and reproduce, whereas alternative food sources are those on which the ladybird can survive, but without reproducing (Hodek & Honek, 1996). Essential and alternative food sources have only been categorized comprehensively for a few intensively studied species. Although individuals show decreased fecundity or increased mortality in the laboratory when fed solely on alternative prey (Hodek & Honek, 1996; Jalali *et al.*, 2009), an ability to prey on alternative species allows individuals to survive longer periods without essential prey (Hodek & Michaud, 2008). Across taxa, species with a wide diet breadth, including a wide range of alternative prey should therefore be able to persist for longer in less favourable areas than diet specialists, and exhibit a greater degree of range fill and a larger range size.

The phylogenetic signal visible in the range fill model residuals at the 10-km scale indicates that, at a local scale, closely related species share similar variance around the relationship between range fill and range size/recording intensity. This probably arises because species within the same families may be subject to a similar level of recording intensity, or may be sampled intensively within similar geographic areas. However, this phylogenetic signal was not present at the larger scales studied, reinforcing the view that different and potentially opposing factors may be important in determining species ranges at different spatial scales (Hamilton *et al.*, 2005; Cadotte *et al.*, 2009).

For range size, there is an apparent group of four species which are particularly restricted in Britain, compared to their distributions as predicted from their traits: these are *Hippodamia tredecimpunctata*, *Coccinella magnifica* Redtenbacher, *Henosepilachna argus* (Geoffroy), and *Coccinella quinquepunctata* L. *Hippodamia tredecimpunctata* has recently (2011) re-established itself as a breeding species on the south coast after being declared extinct in Britain in 1952, and is otherwise only recorded as an occasional immigrant (Comont & Willerton, 2012), while *H. argus* is a recent establishment in Britain (1997) and is only spreading slowly (Menzie & Spooner, 2000). Neither species is therefore likely to have a distribution in equilibrium with its environment in Britain. Neither *C. quinquepunctata* nor *C. magnifica* is currently restricted by historical factors, but each has specific habitat requirements (river shingle banks and an association with species of *Formica* ants, respectively). Both these species have restricted distributions in Britain when compared to the availability of their specific habitats, and all four species are likely to be limited in Britain by a combination of thermal and dispersal factors that are not captured by a coarse habitat categorisation system such as EUNIS. However, only *H. tredecimpunctata* is identified statistically as an outlier (Grubbs' test).

The other recent addition to the ladybird fauna of Britain, *H. axyridis*, is still found in fewer grid squares than is predicted by the models, but to a far smaller degree than the previous four species: *H. axyridis* is recorded from 1009 10-km grid squares (predicted 1428 grid squares, 70.66% colonization); *C. magnifica* 18/161, 11.18%; *C. quinquepunctata* 19/87, 21.84%; *H. argus* 12/87, 13.79%; *H. tredecimpunctata* 4/118, 3.39%. This is likely to result from the combination of extremely rapid colonization (Brown *et al.*, 2008) and a thorough recording through well-publicized citizen-science recording scheme targeted particularly at this species (<http://www.harlequin-survey.org>).

A species' spatial distribution pattern is the result of the interplay between its life-history traits coupled with the biotic and abiotic components of the environment (Lambdon, 2008). Our analyses cannot determine the causal mechanisms of the resulting correlations, but may allow predictions that help in the identification of conservation priorities and extinction risks as part of the wider process of identification of correlates of rarity. Whilst the direction of causality can be disputed, the large changes in AIC when traits are dropped from the best models strongly suggest that the selected traits all make independent contributions.

Our results demonstrate that, for ladybirds, species' resource-use traits better explain range size and fill than do life-history traits. Species that can utilize a greater range of prey species have larger range sizes and a greater degree of range fill (at the 50-km grid square level). A life-history trait, body size, was important at the 50-km grid square level of range fill, however, with smaller species exhibiting a greater degree of range fill than larger species, which is likely to result from the correlation between body size and other traits, particularly dispersal ability.

Dispersal ability is likely to be important for ladybirds and other predatory beetle species, as it is for freshwater invertebrates such as the Odonata (and, to a lesser extent, Plecoptera and Ephemeroptera), where it has been suggested that dispersal ability, and in particular wing size, is the trait which links size and distribution patterns (Malmqvist, 2000; Rundle *et al.*, 2007a; Rundle *et al.*, 2007b). Species with more limited dispersal abilities, such as the smaller ladybirds, tend to spread in smaller increments, creating a more clumped distribution pattern, with high levels of range fill when compared to more dispersive species.

Unfortunately, it did not prove possible to include a direct measure of dispersal ability as an explanatory variable, as this information is lacking for most ladybird species. Some ladybird species also possess wing-length polymorphisms (fully-winged, brachypterous, apterous forms), which will clearly have an effect on a species' dispersal ability, and thus also on distribution patterns, but this is rare and only one species in Britain is known to exhibit brachyptery: *Subcoccinella vigintiquatuorpunktata* (L.) (Pope, 1977). This would be an important parameter to include for taxa which exhibit this variation, e.g. the Orthoptera or Heteroptera.

A potential problem with data from this kind of survey, with a high proportion of citizen science involvement, is that recording intensity may vary among species. Widespread, common species are frequently better-studied and better-recorded than are rare species, and recorder intensity was an important contributor to range fill, with more intensively recorded species having a higher proportion of range fill than less intensively recorded species. It is interesting to note, however, that recording intensity was not a significant variable in the range size model, possibly because ladybirds are charismatic species that are all quite well recorded.

CONCLUSIONS

Our results suggest that a species' ability to feed on a wide range of prey taxa can be a better correlate of both range fill and range size than more usual measures, such as habitat specificity. This may be particularly true of predatory taxa, where the presence of prey species is a major factor in determining habitat suitability (Kruess & Tschardt, 1994; Verberk *et al.*, 2010) (22 of the 26 ladybird species resident in Britain are primarily carnivorous, and only one species has not been recorded as a facultative predator). While species such as *H. argus* are likely to remain comparatively geographically restricted through reliance on a single plant species, other species may be threatened in the short to medium term not only by their narrow diet breadth but also by their niche overlap with dominant competitors such as *H. axyridis*.

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