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ORIGINAL PAPER

Ecological correlates of local extinction and colonisation in the British ladybird beetles (Coleoptera: Coccinellidae)

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Abstract Five main drivers of population declines have been identified: climate change, habitat degradation, invasive alien species (IAS), overexploitation and pollution. Each of these drivers interacts with the others, and also with the intrinsic traits of individual species, to determine species' distribution and range dynamics. We explored the relative importance of life-history and resource-use traits, climate, habitat, and the IAS *Harmonia axyridis* in driving local extinction and colonisation dynamics across 25 ladybird species (Coleoptera: Coccinellidae).Species were classified as continually present, continually absent, extinct, or colonising in each of 4,642 1-km^2 grid squares. The spatial distribution of local extinction and colonisation events (in the grid squares) across all species' ranges were related to ecological traits, overlap with *H. axyridis*, climate, and habitat factors within generalised linear models (GLMs). GLMs were also used to relate species' traits, range characteristics, and niche overlap with *H. axyridis* to extinction and colonisation rates summarised at the species level. Bayesian model averaging was used to account for model uncertainty, and produce reduced sets of models which were well-supported by data. Species with a high degree of niche overlap with *H. axyridis* suffered higher extinction rates in both analyses, while at the spatial scale extinctions were more likely and colonisations less likely in areas with a high proportion of urban land cover. In the spatial analysis, polymorphic species with large range sizes were more likely to colonise and less likely to go extinct, and sunny grid squares were more likely to be colonised. Large, multivoltine species and rainy grid squares were less likely to colonise or be colonised. In conclusion for ladybirds, extinction and colonisation dynamics are influenced by several factors. The only factor that both increased the local extinction likelihood and reduced colonisation likelihood was urban land cover, while ecological overlap with *H. axyridis* greatly increased extinction rates. Continued spread of *H. axyridis* is likely to adversely affect native species and urban areas may be particularly vulnerable.

Keywords Climate · Coccinellidae · Colonisation · Extinction · Niche overlap · Traits

Introduction

Increased population-level, regional, and global extinctions of species is a major concern (Thomas

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et al. 2004). Long-term declines have been reported for well-studied insect taxa such as Lepidoptera (Fox et al. 2011; Fox 2012), Hymenoptera (Goulson et al. 2005; Connop et al. 2009) and Coleoptera (Roy et al. 2012). Five main drivers of population declines have been identified: climate change, habitat degradation, invasive alien species (IAS), overexploitation and pollution (Millennium Ecosystem Assessment 2005; UK National Ecosystem Assessment 2011). Each of these drivers interacts with the others, and also with the intrinsic traits of individual species, to determine species' distribution and range dynamics (Brook et al. 2008). As short-lived ectotherms, many of which are reliant on a single host or prey species, insects are likely to respond particularly quickly to changes in these drivers (McIntyre et al. 2001; Musolin 2007).

Controversy has arisen over whether biological invasion is a leading cause of species extinction (e.g. Gurevitch and Padilla 2004; Ricciardi 2004) since evidence cited in favour of this hypothesis was based on simple spatial or temporal correlations between dominance of IAS and native species decline in degraded ecosystems (Didham et al. 2005). Recent work, largely in marine systems, has highlighted the necessity of considering invasion impacts alongside competing causes of extinction within the same analytical framework (e.g. Light and Marchetti 2007) and of examining extinction at the population level rather than species level (Ricciardi 2004).

Relating population changes to ecological characteristics (traits) across taxa (Tremlova and Munzbergova 2007; Barbaro and van Halder 2009; Poyry et al. 2009; Bell and Sotka 2012; Salido et al. 2012) has shed some light on the traits that make species more vulnerable to environmental change and permitted the design of indicator species for monitoring change (e.g. the habitat-based wild bird indicators used in the UK (Newson et al. 2006). However, few studies have investigated how traits and environmental factors interact to govern species' range dynamics. These interactions have implications for predicting where, and under which conditions, species loss is likely to occur and for understanding how community composition and ecosystem function may alter under environmental change (Webb et al. 2010). Long-term and large-scale presence–absence distribution datasets, such as those compiled through the Biological Records Centre (www.brc.ac.uk) within the Centre for Ecology and Hydrology, offer opportunities to understand how traits and environmental factors influence distribution changes through their impacts on the probability of local extinction and colonisation events (Doxford and Freckleton 2011).

The breadth of trait characteristics amongst British ladybirds (Coleoptera: Coccinellidae) makes them an ideal group to investigate trait–environment relationships, particularly as range characteristics have already been shown to be dependent on ecological traits, such as diet breadth (Comont et al. 2012). As well as being subject to land use and environmental changes of varying intensity across Britain, native ladybird communities are also currently being disrupted by the invasion of *Harmonia axyridis* (Pallas), a large ladybird species native to temperate Asia. This species has been widely used as a biocontrol agent against pest aphids and is now an IAS in more than 30 countries worldwide (van Lenteren et al. 2008; Brown et al. 2011a). It became established in Britain in 2004, and has been implicated in the declines of native ladybirds (Ware and Majerus 2008; Brown et al. 2011b; Roy et al. 2012). The diversity of habitat and dietary preferences amongst native ladybird species provides a spectrum of overlap with the ecological niche of the invasive alien ladybird species, *H. axyridis*. This provides an ideal system for understanding the importance of invasion versus abiotic drivers and trait–environment interactions in underpinning species declines. We investigated the influence of habitat, climate and an IAS on local extinctions and colonisations of ladybirds within Britain with the following specific objectives:

1. to understand whether species-level rates of local extinction/colonisation and proportional range change, summarised across their ranges, are predictable from biological traits;
2. to understand the relative importance of biological traits, environmental factors and trait–environment interactions in determining where particular species are vulnerable to local extinction or able to colonise.

Methods

Distribution data

The distribution data for all ladybird species were taken from the UK Ladybird Survey (UKLS; www.harlequin-survey.org and www.ladybird-survey.org).

Table 1 Summary of ladybird distribution in Britain

Category	Count
Total number of records (all years, all species)	106,952
Total number of surveyed 1-km^2 1991–2010	18,546
Total number of 1-km^2 used for analysis	4,642
Number of 1-km^2 used for local extinction analysis	2,704
Number of 1-km^2 used for colonisation analysis	4,642
Number of 1-km^2 with *Harmonia axyridis* recorded present	1,978

Data were collected by volunteers and collated through a national recording scheme, the UK Ladybird Survey: each record corresponds to an observation of a ladybird species within a 1-km^2 grid square in a year. Our analyses were based on a filtered data set which excluded *H. axyridis* (Pallas), and consisted of records from 1-km^2 grid squares which were 'well-sampled' i.e. contained at least three species records in both of the study periods (1991–2003 and 2004–2010)

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 verified to species either in the field or from a specimen or photograph submitted to UKLS.

Ladybird distribution was characterised as presence/absence at a 1-km^2 grid square resolution across mainland England, Scotland and Wales (i.e. excluding Northern Ireland and the offshore islands of Scilly, Man, Lundy, Shetland, Orkney, the Outer Hebrides and the Channel Islands). These were then aggregated into two periods: 1991–2003 (before the establishment of *H. axyridis*), and 2004–2010 (post-establishment), such that each database row represented a unique species-1-km^2-period combination.

For analysis, we included only 1-km^2 grid squares which were 'well-sampled' in both periods, such that if at least three species were recorded in a particular grid square-period combination, we inferred that all other species were absent (after Biesmeijer et al. 2006; Roy et al. 2012). These criteria restricted our dataset to a subset of high-quality data (Roy et al. 2012), 4,642 1-km^2 grid squares in total (Table 1). *H. axyridis* was removed from the dataset as a species because, as a recent colonist, its distribution was not at equilibrium during the study period.

Environmental and trait data

Climate and habitat predictors were obtained for each 1-km^2 grid square within the subset, along with the year that *H. axyridis* was first recorded in each grid square (if at all). Habitat predictors were taken from the 1990, 2000, and 2007 editions of the Land Cover Map (LCM) of Great Britain (Barr et al. 1993; Fuller et al. 2002; Smith et al. 2007). Although the maps were created using different methods and classification groupings, the data were extracted at the aggregate class level, where such differences were minimal. Four habitats were chosen (broadleaf woodland, coniferous woodland, natural grassland and urban areas), as these cover the major habitats for the majority of the ladybirds in Britain. Aggregate classes rejected were either of extremely limited value for ladybirds (e.g. freshwater, saltwater, and coastal), or of value only to a few rare species (e.g. the 'mountain, heath and bog' category, which is of value mainly to the scarce *Coccinella hieroglyphica* L.). A mean percentage cover value was taken for each habitat in each grid square, averaged across each of the three LCM editions (Table 2). We predict that a high proportion of the four specified habitats (broadleaf woodland, coniferous woodland, natural grassland and urban) within a grid square will promote colonisation and limit extinction across ladybirds (Hodek et al. 2012).

Climate data were taken from the Met Office's UK Climate Projections (UKCP09) dataset (downloadable from http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/). Three predictors were chosen for the analysis: rainfall, sunshine and growing degree-days (GDD) (Table 2). We predict that decreasing rainfall, increasing sunshine and growing degree-days will be positively associated with colonisation of a grid square, and conversely negatively associated with extinction in a grid square.

The invasion and *H. axyridis* overlap traits include measures of the dietary and habitat niche overlap between *H. axyridis* and each other ladybird species. The number of years that *H. axyridis* has been present in each grid square was calculated as a geographic measure of impact. We hypothesise that the effect of *H. axyridis* is likely to scale with duration of temporal overlap (i.e., worse impact the longer the species have co-occurred within the grid square), and with the intimacy of ecological overlap

Table 2 The traits and environmental predictors used to model local-scale extinction and colonisation in the British ladybirds

Predictor type	Predictor	Description
Environmental		
Climate	Growing degree-days	20-Year mean (1987–2006) of annual degree-days over 5.5 °C, per 1-km^2 grid square
	Sunshine	20-Year mean (1987–2006) of annual hours of sunshine, per 1-km^2 grid square
	Rainfall	20-Year mean (1987–2006) of annual millimetres of rainfall, per 1-km^2 grid square
Habitat	Broadleaf woodland	% Cover of broadleaf woodland per 1-km^2 grid square
	Coniferous woodland	% Cover of coniferous woodland per 1-km^2 grid square
	Natural grassland	% Cover of unimproved grassland per 1-km^2 grid square.
	Urban	% Cover of urban and suburban habitats per 1-km^2 grid square
Invasion	Years with *H. axyridis*	Number of years between the arrival of *H. axyridis* in a grid square and the end of the study period (0 if never present in a grid square)
Recording	Square recording intensity	Total number of ladybird records in a grid square over study period
Traits		
Ecological overlap with *Harmonia axyridis*	Dietary niche overlap	Calculated as an inverse Bray–Curtis dissimilarity index, such that 1 indicates the same diet composition and 0 indicates no shared dietary items between *H. axyridis* and native species. See Electronic Supplementary Material for the Supporting Information S1
	Habitat niche overlap	Calculated as an inverse Bray–Curtis dissimilarity index, such that 1 indicates the same habitat use and 0 indicates no shared habitats between *H. axyridis* and native species. See Electronic Supplementary Material for the Supporting Information S2
Resource use	Diet breadth	Number of prey families (ranging from 1 to 12) recorded as 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
Life-history	Polymorphism	Elytral colour pattern polymorphism, characterised as a binomial presence/absence of melanic forms, following Roy et al. (2011)
	Body size	Length (mm) from head to abdomen tip, calculated as the mid-point of the upper and lower body lengths quoted in Roy et al. (2011) (3–7.8 mm). Data 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
	Maximum voltinism	The maximum number of generations per year recorded in the field in Britain for each species
Range characteristics	Species recording intensity	Mean number of records per 1-km^2 grid square for each species (2004–2010)
	Range size	Number of grid squares that each species was recorded from (2004–2010)

Climate data were extracted from the Met Office's UK Climate Projections (UKCP09) dataset, and habitat data from the 1990, 2000, and 2007 editions of the Land Cover Map of Great Britain at the aggregate class level. Resource use and life-history predictors were taken from the literature (352 sources examined, see Comont et al. (2012) for details), and ecological overlap predictors were calculated from data in the literature. Range characteristics and invasion predictors were calculated from the distribution data of the UK Ladybird Survey (1991–2010)

(i.e., species with a greater niche overlap will be affected to a greater extent than those with lower niche overlap).

The Bray–Curtis similarity index (Somerfield 2008) was used to measure habitat use and diet overlap of each species with *H. axyridis* (cf. Adriaens et al. 2008). This is the inverse of the Bray–Curtis index of dissimilarity, and is calculated as $1/BCD_{i,j}$, where $BCD_{i,j}$ is the Bray–Curtis dissimilarity score between species i and j, k is the resource use measure (number of species eaten in family y or presence/absence in habitat y), and n is the total number of species. This index ranges between 0 (no similarity, i.e. no resource overlap between species) and 1 (identical resource use). See Electronic Supplementary Material for the Supporting Informations S1 and S2.

Ecological traits with the potential to influence population and distribution characteristics were selected a priori from the literature (Table 2). We predict that large, polymorphic, multivoltine species with a wide diet breadth but with limited overlap with *H. axyridis* are more likely to colonise and resist local extinction in comparison to species not exhibiting these traits.

To account for variation in recording intensity amongst species and geographic regions, range size and recording intensity (measured at both the species and grid-square levels) were included as covariates (Doxford and Freckleton 2011) (Table 2).

Modelling approach

Spatial models

We performed a spatially-explicit, local scale (1-km^2 grid squares) analysis to consider the relative importance of environmental factors (climate and habitat, recording intensity), species traits, range characteristics, and measures of niche overlap with *H. axyridis* in determining where ladybirds are vulnerable to local extinction or able to colonise (hereafter referred to as spatial models). From species' presence or absence in the two periods, we determined whether each species had colonised, persisted, gone locally extinct, or never occupied each 1-km^2 grid square. Extinction/persistence and colonisation/continued absence were then extracted and used as binary response variables in separate analyses of local extinction and colonisation. For these, we used generalised linear models (GLMs) with Bernouilli errors (special case of binomial where there is a single observation of an event per sample unit) fitted using R version 2.15 (R Development Core Team 2011). Interactions included were between 'years with *H. axyridis*' and the habitat use and dietary niche overlap predictors, as overlap with *H. axyridis* would only be relevant if *H. axyridis* was present in the grid square. Model residuals were assessed for spatial and phylogenetic autocorrelation using the package 'ape' version 3.0-6 within R (Paradis et al. 2004). Though both species and grid square effects are incorporated in these models, for convenience we hereafter refer to these as local extinction and colonisation models.

To reduce the uncertainty implicit in model predictor selection, Bayesian model averaging (BMA) was applied throughout, as implemented in the R package 'BMA', version 3.15.1 (Raftery et al. 2012). Rather than try to identify a single best model, BMA averages over a set of competing well-fitting alternatives, weighted by their posterior probabilities (the likelihood of each model being the best fit to the data) (Raftery 1995). This package uses the 'leaps and bounds' algorithm to identify up to 1,000 good models per number of predictors, which were fitted and then further reduced to a set of well-fitting models by the Occam's window method, whereby models 20 times less likely than the best-supported model were discarded (Madigan and Raftery 1994). All models in the well-fitting set have Bayesian Information Criteria (BIC) values within 6 BIC units of the model with the highest posterior probability. As a measure of the overall conformity of the top models to the data, the area under the curve (AUC) (Fielding and Bell 1997) statistic is calculated. AUC ranges between 0.5 and 1.0, with 0.5 indicating no discrimination ability; values below 0.7 are low, values between 0.7 and 0.9 are useful in some cases, and values >0.9 indicate high discrimination (Swets 1988).

Species models

We used binomial GLMs to examine which species-level traits were best correlated with local extinction and colonisation rates, calculated for each species at a national scale by summarising the 1-km^2-scale data. Local extinction rate was calculated as the total number of extinction events out of the number of grid squares reported occupied in the first period (formatted as a two column binomial dependent variable—number of extinctions, number of sustained presences), whilst colonisation rate was the total number of colonisation events out of the number of grid squares unoccupied in the first period (formatted as a two column binomial dependent variable—number of colonisations, number of sustained absences).

Results

Ladybirds were more likely to go extinct than colonise over the study period. The mean local extinction rate across the 25 ladybird species was 0.84 (SD ± 0.20) (where 1 is complete local extinction and 0 is complete local persistence) and the mean colonisation rate was 0.098 (±0.15). Each species colonised 161.4 (±194.0) grid squares on average, but went locally extinct in a mean of 210.44 (±242.9) squares.

The BMA set (all the models with a BIC within six units of the best model) for species-level local extinction rates contained eight models, with a cumulative posterior probability (the likelihood of each model being the best fit to the data) across the best five models of 0.891 (see Supplementary Table S3). Within this model set four predictors had a significant impact on species extinction rates, i.e. had a greater than 90 % probability that the coefficient was not equal to 0 ($p \neq 0$) (Table 3). This showed that species with a higher dietary niche overlap with *H. axyridis*, a lower maximum voltinism, a lower range size or a lower recording intensity were more likely to go extinct.

The species-level colonisation rate BMA set contains seven models, the best five of which have a cumulative posterior probability of 0.921 (see Supplementary Table S3). Within this model set five predictors had a significant impact on species colonisation rates (Table 3). Species a higher habitat overlap with *H. Axyridis* and which had larger range sizes or were small bodied were more likely to colonise new grid squares, (Table 3). Species that were recorded less intensively and had a lower maximum voltinism were more likely to colonise new grid squares, as well as being more likely to go extinct across their distributions than those recorded more intensively with a high maximum voltinism (see above).

The BMA set for spatial models of local extinction contained 16 models and had a cumulative posterior probability for the best five models of 0.612. The equivalent set for spatial models of colonisation contained 11 models (best five models cumulative posterior probability 0.811) (Table 4). Both analyses had a good discriminatory ability (high area under curve (AUC) score), and were well calibrated (Table 4).

Table 3 Model-averaged coefficients for trait effects on species-level extinction and colonisation rates (in 1-km^2 grid squares) for British ladybirds

Trait group	Predictors	Extinction rate				Colonisation rate			
		$p \neq 0$	% Included	EV	SD	$p \neq 0$	% Included	EV	SD
Ecological overlap with *Harmonia axyridis*	(Intercept)	**100.0**	**100**	**3.264**	**0.136**	**100.0**	**100**	**−2.112**	**0.059**
	Dietary niche overlap	**100.0**	**100**	**2.180**	**0.079**	23.0	57	−0.041	0.254
	Habitat niche overlap	14.2	25	−0.184	0.022	**100.0**	**100**	**0.680**	**0.077**
Resource use	Diet breadth	11.0	25	0.000	0.005	87.8	86	−0.031	0.008
Life history	Body size	24.9	50	0.061	0.002	**100.0**	**100**	**−0.263**	**0.020**
	Polymorphism	12.5	25	0.028	0.003	18.4	43	0.071	0.099
	Maximum voltinism	**100.0**	**100**	**−0.598**	**0.052**	**92.5**	**86**	**−0.167**	**0.050**
Range characteristics	Range size	**100.0**	**100**	**−0.001**	**0.000**	**100.0**	**100**	**0.002**	**0.000**
	Species recording intensity	**100.0**	**100**	**−0.261**	**0.010**	**97.4**	**86**	**−0.211**	**0.007**

Values presented are means across each Bayesian model averaging (BMA) model set. For each predictor, EV is the coefficient, averaged across models, SD is the standard deviation of the coefficient, $p \neq 0$ is the probability that the coefficient is not equal to zero (i.e., the probability that that predictor should be included in the model), and % included is the percentage of models within the BMA set which include that predictor. Terms in bold are those which have a greater than 90 % probability that the coefficient (EV) is not equal to 0, terms in italics are where this probability is between 80 and 90 %

Table 4 Results of colonisation and local extinction of British ladybirds obtained by Bayesian model averaging (BMA) of spatial generalised linear models (GLMs)

Model diagnostics	Spatial scale	
	Extinction	Colonisation
No. data points	6,276	51,734
No. species	25	25
No. 1-km^2	2,699	4,642
No. models in BMA dataset	16	11
Posterior probability of best model	0.163	0.260
Cumulative posterior probability of BMA dataset best five models	0.612	0.811
AUC	0.854	0.900
AIC best model (AIC null model)	4,201 (4,542)	19,808 (22,974)
BIC (null model)	4,282 (4,562)	19,941 (23,001)
LogLik (null model)	−2,089 (−2,268)	−9,889 (−11,484)
Deviance (null model)	4,177 (4,536)	19,778 (22,968)

Model diagnostics include the area under the receiver operating characteristics curve (AUC) and the posterior probabilities that the model terms are equal to zero, compared to the null model

The BMA model set for spatial models of local extinction contains six predictors with a >90 % probability that the coefficient is not equal to zero. Local extinctions were more likely in grid squares with a higher proportion of urban area. Species were also more prone to local extinction if they had smaller range sizes, were not facultatively multivoltine, or had a greater dietary niche overlap with *H. axyridis* and in squares that were recorded less intensively. Local extinctions were negatively correlated with the interaction between habitat niche overlap with *H. axyridis* and the number of years that the invader was present in the grid square, suggesting that species which share habitat preferences with *H. axyridis* were less likely to be lost from a grid square when the invader has been present for a longer period (Table 5).

The BMA set for spatial models of colonisation contains ten predictors with a >90 % probability that the coefficient is not equal to zero. Colonisations were more likely in grid squares which received more sunshine and less rainfall, and which contained a lower proportion of urban areas. Species were more likely to colonise new grid squares if they had a smaller body size, had larger range sizes, were not facultatively multivoltine, had a smaller diet breadth, or were polymorphic and in squares that were recorded more often. Colonisation was also positively correlated with an interaction between habitat niche overlap and years with *H. axyridis* (0.26 ± 0.026), suggesting species which share habitat preferences with *H. axyridis* were more likely to colonise grid squares where the invader has been present for longer (Table 5).

The observed and predicted extinction and colonisation rates were highly correlated (Fig. 1) showing that the models explained substantial proportions of spatial and species variability in these rates although this correlation was lower for spatial models, particularly for local extinction.

Discussion

Most studies exploring the interactions between ecological traits of species and environmental factors do not consider population or distribution changes. A few recent studies have examined the role of ecological traits in explaining distribution patterns of animals. For example, habitat use and diet breadth are important traits in explaining distribution patterns of isopods (Purse et al. 2012) and coccinellids (Comont et al. 2012) respectively. However, the dual effects of both ecological traits and environmental drivers in determining distribution trends (colonisation and local extinction) of species have largely been ignored, making it difficult to understand where species with particular ecological characteristics (and performing particular ecosystem functions) will decline, and, why. Here we investigated determinants of local extinction and colonisation events at both the species and population level (as recommended by Ricciardi 2004), and detected significant impacts of both ecological traits and environmental factors on the dynamics of ladybirds. Additionally we revealed that an IAS, *H. axyridis*, constitutes a key biotic environmental pressure on native ladybirds, and has species-specific impacts, depending on overlap of resource use of individual species with the invader. Here we discuss the potential biological mechanisms underpinning the significant trait and abiotic environmental affects before considering the wider implications of the impacts of *H. axyridis* on native ladybirds.

Local extinction and colonisation rates were predicted more accurately at the species-level rather than the spatial scale (Fig. 1), but taking a spatially-explicit, population approach (so-called spatial models above) revealed the environmental conditions that

Table 5 Model-averaged coefficients for environmental and trait effects on the 1-km^2-scale probabilities of local extinction and colonisation in British ladybirds (spatial models)

Trait group	Predictor	1-km^2 Extinction				1-km^2 Colonisation			
		$p \neq 0$	% Included	EV	SD	$p \neq 0$	% Included	EV	SD
Climate	(Intercept)	**100.0**	**100.0**	**4.98**	**1.02**	**100.0**	**100.0**	**−2.25**	**0.34**
	Growing degree-days	52.5	37.50	−0.00	0.00	3.8	9.1	0.00	0.00
	Sunshine	39.2	37.50	−0.02	0.02	**96.2**	**90.9**	**0.03**	**0.01**
	Rainfall	*86.7*	*87.50*	*0.00*	*0.00*	**100.0**	**100.0**	**−0.00**	**0.00**
Habitat	Broadleaf woodland	38.6	50.0	−0.00	0.01	46.0	54.6	−0.00	0.00
	Coniferous woodland	48.2	50.0	−0.01	0.01	70.5	72.7	0.01	0.00
	Natural grassland	0.0	0.0	0.00	0.00	*86.5*	*81.8*	*−0.00*	*0.00*
	Urban	**97.0**	**87.50**	**0.01**	**0.00**	**100.0**	**100.0**	**−0.01**	**0.00**
Invasion	Years with *H. axyridis*	0.0	0.0	0.00	0.00	1.5	9.1	0.00	0.01
Recording	Square recording intensity	**100.0**	**100.0**	**−0.05**	**0.00**	**100.0**	**100.0**	**0.01**	**0.00**
Ecological overlap with *Harmonia axyridis*	Dietary niche overlap	**100.0**	**100.0**	**2.45**	**0.51**	9.5	27.3	0.04	0.14
	Habitat niche overlap	0.0	0.0	0.00	0.00	0.0	0.0	0.00	0.00
	Dietary niche overlap × years with *H. axyridis*	0.0	0.0	0.00	0.00	0.0	0.0	0.00	0.00
	Habitat niche overlap × years with *H. axyridis*	**100.0**	**100.0**	**−0.40**	**0.05**	**100.0**	**100.0**	**0.26**	**0.03**
Resource use	Diet breadth	0.0	0.0	0.00	0.00	**100.0**	**100.0**	**−0.07**	**0.01**
Life-history	Body size	0.0	0.0	0.00	0.00	**100.0**	**100.0**	**−0.36**	**0.02**
	Polymorphism	0.0	0.0	0.00	0.00	**100.0**	**100.0**	**0.21**	**0.05**
	Maximum voltinism	**100.0**	**100.0**	**−0.68**	**0.19**	**100.0**	**100.0**	**−0.26**	**0.06**
Range characteristics	Range size	**100.0**	**100.0**	**−0.00**	**0.00**	**100.0**	**100.0**	**0.00**	**0.00**

Values presented are means across each Bayesian model averaging (BMA) model set. For each predictor, EV is the coefficient, SD is the standard deviation of the coefficient, $p \neq 0$ is the probability that the coefficient is not equal to zero, and % included is the percentage of models within the BMA set which include that predictor. Terms in bold are those which have a greater than 90 % probability that the coefficient (EV) is not equal to 0, terms in italics are where this probability is between 80 and 90 %

made species vulnerable to local extinction (e.g. areas with a high degree of urban cover) and indicated a wider range of traits to be involved in buffering species against environmental change. Key impacts of intrinsic traits that were consistent between species-level and spatial models included those of range size, voltinism and habitat overlap with *H. axyridis* on colonisation rates, and those of range size, voltinism and diet overlap with *H. axyridis* on local extinction rates. The key environmental factor that both increased the likelihood of local extinction and reduced that of colonisation was urban land cover. More marginal effects included diet breadth, polymorphism, body size, recording intensity, sunshine and rainfall.

Urbanisation was shown to be an important driver of both local extinction and colonisation at the 1-km^2 scale. Although gardens and parks in urban areas often seem to be favourable for individual ladybird species (Roy et al. 2011), our results indicate that overall increases in urban land cover are not favourable for ladybirds as a group. In terms of habitat specificity, ladybirds in Britain span the range from generalist (e.g., *Coccinella septempunctata* L. and *H. axyridis*) to highly specialist (*Myrrha octodecimguttata* L., found in the canopies of mature pines, and *C. hieroglyphica*, found in heather on heath and moorland). Urban areas are probably good for the small subset of eurytopic (habitat-generalist) species but poor for specialist species, leading to decreasing colonisations and increasing local extinctions. This may be the result of destruction and fragmentation of the preferred habitats of specialist species, promoting biotic homogenisation (McKinney 2006), but may also be

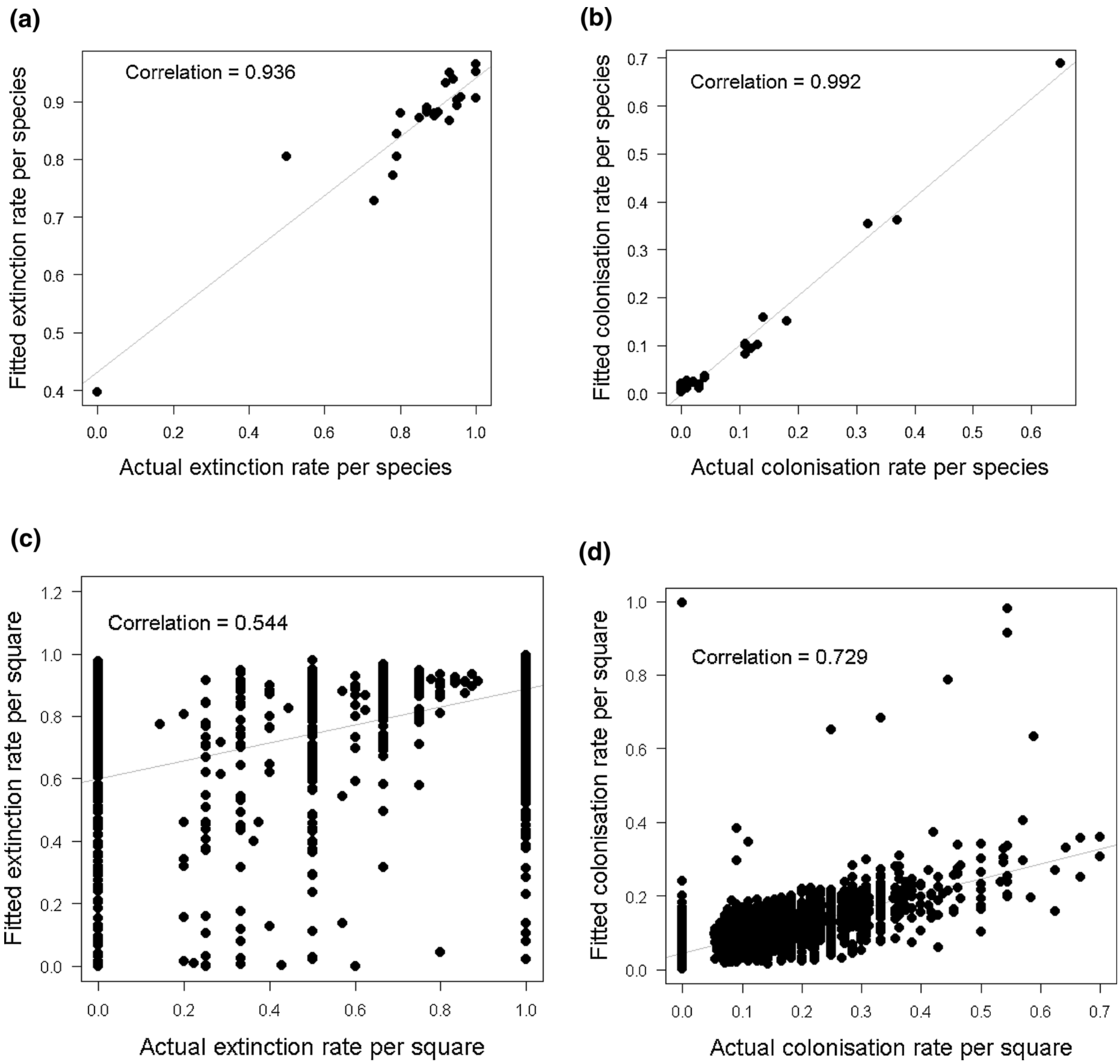

Fig. 1 Goodness-of-fit plots for the models of species and spatial variability in extinction and colonisation rates across British ladybirds. Actual values are plotted against fitted values extracted from the best models (**a** local extinction rate per species, **b** colonisation rate per species, **c** local extinction rate per 1-km^2 grid square, **d** colonisation rate per 1-km^2 grid square). Expected rates for individual species and grid squares were calculated from the means of the fitted probabilities of the best model (Cox 1970)

exacerbated by competition from increased prevalence of eurytopic species such as *H. axyridis* in urban areas.

Ladybird species with larger range sizes were more likely to colonise new grid squares and less likely to suffer local extinctions than those with smaller range sizes. Large range sizes (high occupancy) are often associated with high abundance (Quinn et al. 1997; Freckleton et al. 2005) and more abundant species are less likely to go locally extinct and more likely to colonise by virtue of their larger population size than less abundant species (Breininger et al. 1999; McCarthy and Thompson 2006). As expected, colonisation events were more likely and extinction events less likely in grid cells that were recorded more intensively. However, at the species-level, species recorded more intensively were less likely to colonise new grid squares across their distribution overall than less intensively recorded species. Species may be intensively recorded because they are common and abundant and encountered frequently or because they are rare and their records are much sought after (Roy et al. 2011). In fact the direction of the relationship between recording intensity and species colonisation rates was determined largely by *Coccinella quinquepunctata* that is absent from much of Britain and colonised only a single square of between the two periods but has been recorded very intensively in that square (Roy et al. 2011). This illustrates the potential superiority of geographical versus species measures of recording intensity for understanding drivers of colonisation and extinction—by averaging across common and rare species, geographical measures smooth out impacts of species attractiveness on recording intensity.

Species which are capable of having more than one generation were less likely to go extinct, and were also less likely to colonise new grid squares than univoltine species. This produces a more stable distribution pattern than is present in species which are declining or colonising. Species which are facultatively multivoltine may be more buffered against changes in the environment, as they can produce more offspring in favourable conditions (Pereira et al. 2012) and may also benefit from greater genetic exchange between generations (Watts and Thompson 2011).

The negative impacts of *H. axyridis* were greater in species with high dietary niche overlap with the invader, both at a species and spatial scale: native species which had a high dietary niche overlap with *H. axyridis* were more likely to go locally extinct than species with a low niche overlap. This supports recent studies which have implicated *H. axyridis* in the declines of native ladybird species. Ware and Majerus (2008) found that *H. axyridis* was a predator of native species in captivity, and declines have been found in native species after the arrival of *H. axyridis* at a local (Brown et al. 2011b) and European scale (Roy et al. 2012). Diet overlap was a more consistent predictor of local extinction or colonisation than habitat niche overlap, suggesting that competition for food is the most important mechanism by which *H. axyridis* causes declines in native ladybird species. This is despite the existence of species such as *Halyzia sedecimguttata* (L.) and *Exochomus quadripustulatus* (L.), which share habitat with *H. axyridis* but have very limited dietary niche overlap. However, it should be noted that predation may also play an important role: within a given habitat, species exploiting the same food resource as *H. axyridis* are likely to come into contact with the invader more frequently, and so be at a risk of predation, which correlates positively with encounter rate (Raak-van den Berg et al. 2012). Phenology may also play a role in regulating both competition and predation: larval *H. sedecimguttata* are thought to be at risk from predation by *H. axyridis* larvae as a consequence of developing late in the year, when aphids are scarce (Roy et al. 2012).

The interaction between habitat use and the number of years that *H. axyridis* has been present in a grid square was positively associated with continued presence in a grid square, and with local colonisation. This suggests that the negative effects of *H. axyridis* were reduced in eurytopic species, even where more of this niche was potentially shared with the invader. This may indicate that these species are able to utilise habitat patches which are less-favoured by *H. axyridis* as refugia, due to their low habitat specificity. This has been found in North America (Evans 2004), where native ladybird species were displaced from agricultural areas after the arrival of *C. septempunctata*, and in freshwater fish species in Lake Nabugabo, Uganda, after the establishment of the Nile perch, *Lates niloticus* L. (Chapman et al. 1996). Alternatively, it may indicate that eurytopic species are colonising the same grid squares as *H. axyridis*, at a higher rate than other species, potentially under the influence of an unmeasured environmental factor.

Species which are polymorphic are more likely to colonise new grid squares than monomorphic species, and grid squares which receive more hours of sunshine are more likely to be colonised than less sunny areas. It is probable that the effect of polymorphism results from species with an extended phenotypic range of several distinct forms being able to inhabit a wider range of habitats/microclimates, so colonising more grid squares. Differences in large-scale distribution patterns have been found to be related to changes in colour pattern in the ladybird *A. bipunctata* in the Netherlands (Brakefield 1985; de Jong et al. 1996; de Jong and Brakefield 1998), and the grasshopper *Chorthippus parallelus* (Zetterstedt) and the groundhopper *Tetrix undulata* (Sowerby) have been found to have different colour forms preferentially inhabiting different habitat types (Ahnesjo and Forsman 2003, 2006). As ectotherms, ladybirds are dependent on environmental heat sources, particularly temperature. Sunshine and temperature are usually positively correlated, and ladybirds can minimise their reliance on the external temperature by basking in sunshine to raise their body temperatures above ambient (de Jong et al. 1996; Clusella Trullas et al. 2007), which seems to be important in allowing dispersal to colonise new grid squares.

At a local (1-km^2) scale, increased rainfall decreases the probability of colonisation. This is probably because wet weather tends to be unsuitable for insect activity, so reducing both dispersal into a grid square and the chances of establishing there. For example, rainfall has been found to be strongly negatively correlated with apparent butterfly abundance on transects (Pollard 1988), and to be a strong driver of decreased adult survival in *Culex* mosquito species (Jones et al. 2012). Ladybirds with a large body size, and those which had a wide diet breadth were also less likely to colonise new grid squares than small ladybirds with narrow diet breadth. This may be because these small specialist species were already at their range limit during the first period, as range size and range fill in ladybirds is driven by diet breadth (Comont et al. 2012), and body size is often found to correlate strongly with the range size of insects (Bräendle et al. 2002; Chown and Gaston 2010).

Overall, it is clear that external environmental factors, species-level life-history and resource-use traits are having effects on ladybird local extinction and colonisation dynamics, both at a species level and 1-km^2 spatial scale. However, even with these effects taken into account, the invasive alien ladybird *H. axyridis* is having a significant deleterious impact on native species, greatly increasing extinction rate at both the 1-km^2 and large scale. These results, particularly when considered with those of Roy et al. (2012), who found that seven of eight common native ladybird species began to decline, or began to decline faster than before, after the arrival of *H. axyridis* at a local level across Britain and Belgium, suggest that the continued spread *of H. axyridis* will lead to the ecological extinction (Estes et al. 1989) of native species, particularly those with a high niche overlap with *H. axyridis*. Areas of Britain that are urban or undergoing urbanisation in which *H. axyridis* has invaded may be particularly vulnerable to loss of ladybird biodiversity.

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