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Diversity and Distributions – Biodiversity Research

Invasive alien predator causes rapid declines of native European ladybirds

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HER, TA and MK led data collection and collation. NJBI, TO and DM assembled the data and performed the analyses with assistance from HER, LH, RC and GSM. HER, TA, RP and PMJB collated the national distributional data. PMJB, RF, GSM, LH, J-CG, J-CB, RE, JVV, RZ and MK conducted the field surveys resulting in abundance data. HER wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Abstract

Invasive alien species (IAS) are recognised as major drivers of biodiversity loss but few causal relationships between IAS and species declines have been documented. We report rapid, dramatic and ongoing declines in the distribution of formerly common and widespread native ladybirds in Belgium and Britain following the arrival of *Harmonia axyridis*, a globally rapidly expanding IAS. Four (Belgium) and seven (Britain) of eight species studied show substantial declines attributable to the arrival of *H. axyridis*. Indeed, the 2-spot ladybird, *Adalia bipunctata*, declined by 30% (Belgium) and 44% (Britain) over five years after the arrival of *H. axyridis*. Trends in ladybird abundance revealed similar patterns of declines across three countries. Together, these analyses show *H. axyridis* to be displacing native ladybirds with high niche overlap, probably through predation and competition. Such rapid biotic homogenisation at the continental scale could impact on the resilience of ecosystems and severely diminish the services they deliver.

Keywords

Harmonia axyridis, invasive alien species, non-native species, Coccinellidae, biological control, biological invasion, population decline, citizen science, biotic homogenisation

Introduction

Rates of global extinction are orders of magnitude higher than historical estimates and show no sign of slowing (Millenium Ecosystem Assessment, 2005). The Convention on Biological Diversity and the 10th Conference of the Parties (Nagoya in 2010), identified invasive alien species (IAS) as one of five major pressures driving biodiversity loss, and ultimately extinction of species (Winter *et al.,* 2009, Hooper *et al.,* 2005, Thomas *et al.,* 2004). IAS have direct ecological effects on other species through a variety of mechanisms (Parker *et al.,* 1999). In particular, invertebrate predators may displace indigenous species by direct predation, exploitative competition for food or space, lower immunity to shared natural enemies, introduction of new pathogens or disrupted mating systems (Snyder & Evans, 2006, Kenis *et al.,* 2009).

IAS are unlike other drivers of change because the time at which an IAS arrives within an ecosystem is often known. Perhaps surprisingly then, there have been few clear demonstrations that IAS cause biodiversity loss. The majority of studies implicating IAS in species declines involve basic correlations in degraded ecosystems (Didham *et al.,* 2005, Gurevitch & Padilla, 2004) at small spatial-scales and over short time-scales. Such evidence has been criticised as circumstantial, leading to suggestions that IAS might be passengers, as opposed to drivers, of change (MacDougall & Turkington, 2005). The difficulty of distinguishing between correlates and causes of population decline has been widely debated by ecologists (Ricciardi, 2004, Clavero & Garcia-Berthou, 2005, Didham *et al.,* 2005). Likewise, it is equally difficult to determine the relative importance of different causal mechanisms acting on the same system (Didham *et al.,* 2005). The correlation between the presence of the invasive alien zebra mussel, *Dreissena polymorpha* (Pallas), and decline of unionid mussels in North America (Ricciardi & Rasmussen, 1999, Ricciardi *et al.,* 1998) is unquestionable (Ricciardi, 2004) but the arrival of this particular IAS appears to be only one link in the "chain of causality" (Didham *et al.,* 2005).

The arrival of the alien predator *Harmonia axyridis* (Pallas) in Europe provides an opportunity to investigate the distribution status of native species before and after establishment of an IAS. *Harmonia axyridis*, a native of central and eastern Asia, was released for the control of pest insects across North America from 1916 and Europe from the late 1980s (Brown *et al.,* 2008, Brown *et al.,* 2008). It is now considered an IAS in North America and many European countries, having undergone a period of rapid expansion, spreading in many countries without deliberate release (Brown *et al.,* 2008). *Harmonia axyridis* is a large and voracious predator that threatens biodiversity because it outcompetes and displaces native ladybirds and other aphidophagous insects (Majerus *et al.,* 2006, Roy *et al.,* 2011, Brown *et al.,* 2011). The potential loss of such beneficial and charismatic organisms is an important issue because of their important role in maintaining a properly functioning ecosystem and their intrinsic aesthetic value (Department for Environment, Food and Rural Affairs, 2011).

Here we document trends in the distribution and abundance of native ladybird species during the period of arrival and rapid expansion of *H. axyridis.* We take advantage of extensive citizen-driven field surveys in Belgium and Britain spanning decades, as well as intensive monitoring by scientists in three countries. The combination of fine-scale data collection, replicated in time (over decades and including detailed observations before and after the arrival of an IAS) and with extensive coverage in

three European countries, allied with powerful modern statistical techniques, thus provides a uniquely rigorous test of the impacts of an IAS on biodiversity.

Methods

Distribution data source: Large-scale ladybird surveys

The Belgian and British checklists contain 38 and 25 native ladybird species (Roy *et al.,* 2011, Baugnée *et al.,* 2011) respectively from the subfamilies *Chilocorinae*, *Coccinellinae* and *Epilachninae*. Distribution data have been collated largely through public participatory surveys. In Britain a Coccinellidae Recording Scheme has been run through the Biological Records Centre (NERC Centre for Ecology & Hydrology) since 1964 with an on-line survey launched in 2005 (Brown *et al.,* 2008). In Belgium the Coccinellidae Recording Scheme has been active since 1999 with an on-line survey (Baugnée *et al.,* 2011), however ad hoc earlier records exist and were included in analyses. All records used in these analyses have been verified by a recognised expert. The observations are georeferenced to 1-km^2 resolution using the Ordinance Survey British national grid reference system in Britain and the Universal Transverse Mercator (UTM) in Belgium. The Britain and Belgium databases contain 89 994 and 67 561 observations, respectively (Table 1).

Distribution data analysis

Analyses are based on separate datasets for each country from the respective survey databases, in which each row of data corresponds to a unique combination of year and 1-km^2. The columns refer to different ladybird species, and the data are 1 (Present, i.e. recorded) and 0 (Absence inferred) for each species 1-km^2-year combination. The survey database contains presence-only records and so the absence of ladybird species was inferred from the presence of others (Biesmeijer *et al.,* 2006). We guarded against the possibility that incorrectly inferring absence might lead to spurious results by restricting our analyses to a small number of 'focal' species in 'well-sampled' 1-km^2. Focal species are those for which there were >1000 observation per country since 1990 (9 species in each country, including *H. axyridis*). All ladybird species included were conspicuous, widespread and common (Roy *et al.,* 2011) and so we were confident in inferring absence of a species on the basis of presence of other species. We defined 'well-sampled' combinations as those in which at least two focal species were observed. Furthermore, we included only 1-km^2 that were 'well-sampled' in at least three years. These criteria restricted our dataset to the small proportion (7% in Britain, 14% in Belgium) of high-quality data (Table 1). We repeated our analyses with different thresholds for the definition of 'well-sampled', but the results were qualitatively unchanged (Supplementary Table 1).

To analyse the distribution data, we used generalised linear mixed-effects models (GLMMs) with binomial errors and logit link function. For each species and country, we modelled the probability of 1-km^2 occupancy (presence versus absence) as the sum of two linear trends, *Y* and *H.* Parameter *Y* is the linear occupancy trend in the absence of *H. axyridis*, estimated using a fixed effect of year centred on the time of *H. axyridis* arrival in the respective country (2001 in Belgium and 2004 in Britain). Parameter *H* estimates the net effect of *H. axyridis* in that 1-km^2 (years prior to arrival and 1-km^2 that were never colonized were coded as zero). Thus, our null hypothesis for each species is that parameter *H* is equal to zero. We included 1-km^2 as random intercept and year as random slope (to allow for different trends in each 1-km^2), as well as an observation-level random effect to account for overdispersion. All models were fitted in R 2.11.1 (Ihaka & Gentleman, 1996) with the lme4 package version 0.999375-37 (Bates & Maechler, 2010).

Systematic surveys of ladybird abundance

Ladybird abundance data were collected using systematic fortnightly surveys in Brussels (Belgium) during spring 2003, 2005 and 2008, in lime (*Tilia* x *vulgaris* Hayne) and sycamore (*Acer pseudoplatanus* L.) trees in 12 urban localities (parks, avenues and roadsides). Surveys at 4 sites in Cambridgeshire (Britain) and 15 sites in North-Western Switzerland span 2006 to 2010: each site was surveyed 7-9 times per year between April and October. Cambridgeshire sites consisted of deciduous and conifer trees and herbaceous vegetation; Swiss sites were 50m sections of mixed deciduous hedges. In all countries surveys were conducted using standard sampling methods including tree-beating and sweeping-netting (Eschen *et al.,* 2007, Adriaens & Maes, 2004, Brown *et al.,* 2011). Adults of all ladybirds were counted and identified before being released on-site.

Population data analysis

We modelled the abundance of each species in each country separately, using only deciduous tree species for which at least 50 individuals were captured. We also modelled the total abundance of all native species and the total number of species. We used GLMMs with Poisson errors and log link with the year centred on the year of the arrival of *H. axyridis* (2001 in Belgium, 2004 in Britain, 2006 in Switzerland) as a fixed effect. The random effects included site, visit and observation (to account for overdispersion).

Results

Distribution data: Large-scale ladybird surveys

The median year of arrival of *H. axyridis* in Belgium was 2004 and in Britain 2007 (Table 1). *Harmonia axyridis* colonised approximately 269 of the 365 1-km^2 (74%) analysed for Belgium and 249 of the 411 1-km^2 (61%) analysed for Britain (Table 1). In the absence of *H. axyridis*, similar numbers of species expanded and contracted their British ranges, whereas in Belgium there were more species expanding than contracting (Table 2; Fig. 2). *Harmonia axyridis* had a significant negative impact ($H < 0$) on the distribution of four species (*A. bipunctata*, *Adalia decempunctata* (L.), *Exochomus quadripustulatus* (L.) and *Propylea quattuordecimpunctata* (L.) in Belgium and all but one (*Coccinella septempunctata* L.) of the eight species in Britain (Table 2). The magnitude of these effects is large, i.e. $|H| > |Y|$, such that these species have shown substantial range retraction (Table 2; Fig. 2). This is exemplified by *A. bipunctata,* which declined by 30% in Belgium and 44% in Britain over the five years following the arrival of *H. axyridis* (Fig. 1). A few ladybirds were declining prior to the arrival of *H. axyridis* ($Y < 0$) but *H. axyridis* has significantly accelerated the rate of this decline. Conversely, the arrival of *H. axyridis* appears to have had a negligible effect on *C. septempunctata* and a positive effect on Belgium populations of *Calvia quatuordecimguttata* (L.) (Table 2).

Systematic surveys of ladybird abundance

Population trends, revealed by data from systematic surveys at specific sites in Belgium, Britain and Switzerland, strongly supported the distribution trends (Table 3). One species (*A. bipunctata*) showed significant declines in abundance in all three countries and another species (*E. quadripustulatus* showed significant declines in two countries (Britain and Switzerland). Three species showed significant declines in only one of the three countries (Table 3). All three countries showed a significant increase in the abundance of *H. axyridis* (Table 3), while at the same time the total ladybird abundance (excluding *H. axyridis*) declined significantly in all three countries.

Discussion

Here we have assessed the effects of the arrival of an IAS on the distribution and abundance of native species across European countries. Our results clearly indicate that native ladybirds have declined markedly in response to the arrival of *H. axyridis*. This finding represents the strongest example to date of a causal link between the arrival of an IAS and decline in native biodiversity.

The decline in the distribution and abundance of previously widespread and common native ladybirds after the arrival of *H. axyridis* is striking. The dramatic decline of *A. bipunctata* over the five years following the arrival of *H. axyridis* is of particular note. This species is now near the

threshold of detection, both in Europe (Brown *et al.,* 2011) and North America (Harmon *et al.,* 2007), in habitats in which it was previously common. *Harmonia axyridis* appears to be displacing those native ladybirds with which it shares a high niche overlap (Adriaens *et al.,* 2008), such as *A. bipunctata*. The likely mechanisms are both intra-guild competition and predation based on asymmetry of body size (*H. axyridis* is about 1.5 times larger than *A. bipunctata*) and superior physical and chemical defences in comparison to other species of ladybird (Pell *et al.,* 2008, Roy *et al.,* 2008). Laboratory studies have indicated the potential for *H. axyridis* to act as a unidirectional intra-guild predator of entomopathogenic fungi (Roy *et al.,* 2008), coccinellids (Ware & Majerus, 2008, Ware *et al.,* 2009) and other invertebrates (Koch & Galvan, 2008, Roy *et al.,* 2011). Additionally a recent field study, in which exogeneously sequestered alkaloids were used as a tool for detecting the consumption of other coccinellids, revealed a high prevalence of intra-guild predation (Hautier *et al.,* 2008, Hautier *et al.,* 2011) by *H. axyridis*. In some sites more than 30 % of *H. axyridis* larvae contained the alkaloids adaline, calvine or propyleine representing intra-guild predation of *Adalia* spp.*, Calvia* spp. and *P. quattuordecimpunctata* (Hautier *et al.,* 2011).

All the species included within our study are predatory with the exception of *Halyzia sedecimguttata* (L.) which is a mycophagous ladybird and is, therefore not in competition with *H. axyridis* for food. This ladybird has undergone a dramatic increase in abundance and distribution in Britain (Roy *et al.,* 2011) and Belgium which reflects a recent shift in habitat preference, previously associated with oak it is now also commonly found feeding on mildew of ash and sycamore trees (Roy *et al.,* 2011). It is possible that climate warming has increased the availability of mildew for this mycophagous species. However, this trend is reversed in Britain in the presence of *H. axyridis*. The feeding niches of *H. axyridis* and *H. sedecimguttata* do not overlap but their habitats do. *Halyzia sedecimguttata* is likely to be particularly vulnerable to intra-guild predation by *H. axyridis* in the autumn when, unlike most ladybird species, *H. sedecimguttata* and *H. axyridis* exist predominantly as larvae and pupae (immature stages) at this time. At this time the aphids, the main prey of *H. axyridis*, are in decline and so alternative prey including the immature stages of other insects such as *H. sedecimguttata* are consumed (Brown *et al., 2011*). It is likely that subtle differences in the phenology of ladybirds within Belgium and Britain alter the interactions between species.

One species, *C. septempunctata*, within our study provides a particularly interesting contrast in that its distribution and abundance of appears to be stable across Europe despite the arrival of *H. axyridis*. This common ladybird is mainly associated with herbaceous vegetation (Roy *et al.,* 2011) and so does not overlap with *H. axyridis* to the extent of the four tree specialists (*A. bipunctata*, *A.*

decempunctata and *C. quattuordecimguttata* and *E. quadripustulatus*). Additionally, *C. septempunctata* is a large ladybird, of similar size to *H. axyridis*. *Coccinella septempunctata* is itself a successful IAS in the USA and Canada, where it is thought to have contributed to declines in native species (Harmon *et al.,* 2007).

Historically, the decline of widespread and common species has gone largely unnoticed and there is a paucity of quantitative information on such declines (Van Dyck *et al.,* 2009, Gaston & Fuller, 2007), especially among invertebrates. The pronounced decline of species widely regarded as unthreatened (none of the declining species are categorised according to IUCN conservation designations) highlights the importance of continued large-scale monitoring of both rare and common species within the wider countryside. The decline in ladybird species across Europe and associated alterations to community composition could have far-reaching effects on ecosystem services (Hooper *et al.,* 2005). Predatory ladybirds are known to provide a major ecosystem service by regulating pest insects. Although *H. axyridis* is an effective biological control agent in crop systems (Tedders & Schaefer, 1994, Brown & Miller, 1998, Alyokhin & Sewell, 2004, Heimpel *et al.,* 2010), it is unclear whether it can fulfil all the functional roles of the species it is displacing. *Harmonia axyridis* is rapidly expanding its global range: our results imply this will cause ecological extinctions (Estes *et al.,* 1989) of native species, notably deciduous tree specialists, over large areas.

There is considerable debate over the relationship between species diversity and ecosystem processes. It is apparent that species diversity enhances productivity and stability in some ecosystems, but not in others (Johnson *et al.,* 1996). However, it is often difficult to predict which species are critical to functioning or provide resilience and resistance to environmental changes. Additionally the arrival of an IAS (or, indeed, other anthropogenic perturbation) is more likely to change the relative abundance of species rather than result in extinction of a species but the relationship between community composition (species richness) and ecosystem functioning has focussed on effects of species extinctions (Chapin *et al.,* 2000). We predict the dominance of *H. axyridis*, and associated reduction of diversity, will decrease the resilience of aphidophagous guilds and severely diminish the services they deliver (Biesmeijer *et al.,* 2006, Winter *et al.,* 2009).

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Table 1. Summary of ladybird distribution data in Belgium and Britain.

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Table 3. Trends in the abundance of European ladybirds after the arrival of the invasive alien predator *Harmonia axyridis*. Numbers are parameters extracted from mixed-effects models for each species. n = number of individual ladybirds. *** p<0.001, ** p<0.01, * p<0.05.

Figure 1. Invasion of Belgium and Britain by *Harmonia axyridis,* expressed as the percentage of colonised 1-km^2. The diffuse ribbons delimit the 95% confidence intervals.

Figure 2. Effects of *Harmonia axyridis* on the distribution of eight native ladybirds based on predictions for an average 1-km^2. Absent assumes the 1-km^2 is not colonised by *H. axyridis*, present assumes the 1-km^2 was colonised in 2001 (Belgium) or 2004 (Britain) by *H. axyridis*.

Supplementary Table 1. Distributional trends for eight native ladybird species, using different thresholds for including data in the analysis. nYr is the number of years in which a 1-km2 needed to be 'well-surveyed' in order to be considered in the analysis. nFocal is the threshold number of focal species (including *Harmonia axyridis*) to consider a 1-km2 'well-surveyed' in any one year. Setting both thresholds to zero includes all possible combinations, including those based on incidental records from poorly-sampled areas. Setting nYr= 3 and nFocal=2 (the penultimate model for each species) correspond to the results shown in the main document. Columns b(Y), z(Y) and p(Y) are the slope, effect size and p-value for the trend in the absence of *H. axyridis*; b(H), z(H) and p(H) are comparable values for the effect of *H. axyridis* on the distribution trend. n is the sample size (number of 1-km2-year combinations) generated by the thresholds applied; obs is the number of combinations in which the focal species was present.

Table 1. Summary of ladybird distribution data in Belgium and Britain.

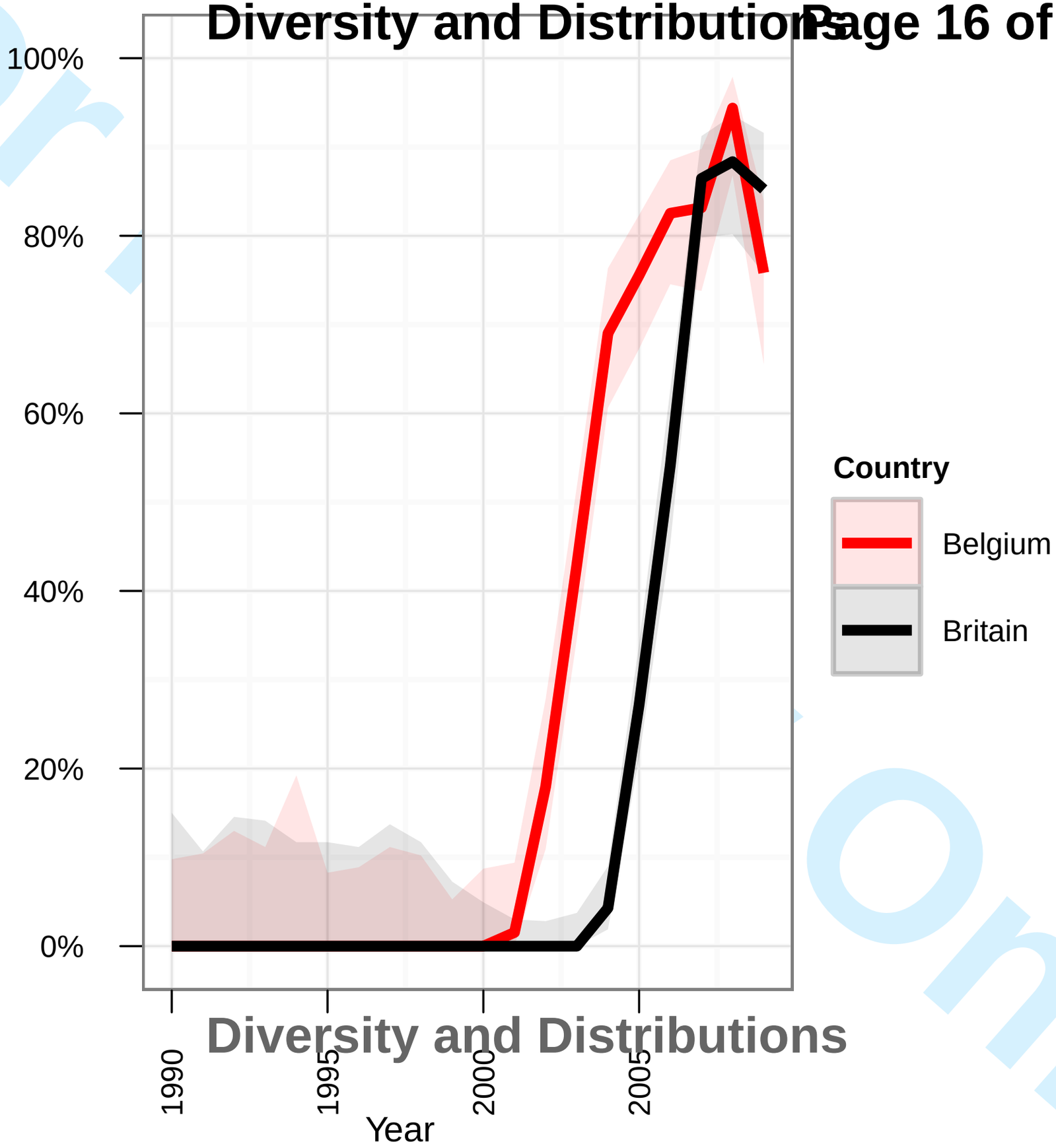
Species	Belgium	Britain
Total number of records (all years, all species)	67 560	89 994
Total number of surveyed 1-km^2 since 1990[a]	5 300	14 364
Number of 1-km^2-year combinations since 1990	9 889	23 929
Number of 1-km^2-year combinations used for analysis[b]	1 419	1 746
Number of 1-km^2 used for analysis[b]	365	411
Number of 1-km^2 with *Harmonia axyridis*	269	249
Median year of arrival	2004	2007

[a] focal species only

[b] only includes 1-km^2 with $\geq$2 focal species recorded in each of $\geq$3 years

Table 2. Trends in the distribution of European ladybirds before and after the arrival of the invasive alien predator *Harmonia axyridis*. Numbers are parameters extracted from mixed-effects models for each species based on 1419 and 1746 observations (1-km^2-year combinations) for Belgium and Britain respectively. % = percentage of observations where the species is present, a = intercept (logit probability at year of first introduction), Y = trend in the absence of *H. axyridis* and H = effect of *H. axyridis* presence on the trend. *** p<0.001, ** p<0.01, * p<0.05.

	Belgium				Britain			
Species	%	a	Y	H	%	a	Y	H
Harmonia axyridis	42	-2.160	0.826***		25	-18.191	9.540***	
Adalia bipunctata	52	0.521	-0.106***	-0.216***	68	1.294	0.059***	-0.535***
Adalia decempunctata	22	-1.251	0.051**	-0.187**	32	-0.888	-0.024	-0.330***
Calvia quatuordecimguttata	28	-0.975	0.013	0.139*	21	-1.775	-0.051*	-0.205*
Coccinella septempunctata	78	1.392	0.002	0.014	75	1.403	-0.016	-0.092
Exochomus quadripustulatus	24	-1.556	0.078**	-0.187**	33	-1.032	0.091***	-0.216**
Halyzia sedecimguttata	25	-1.458	0.125***	-0.085	22	-1.532	0.200***	-0.396***
Propylea quatuordecimpunctata	55	0.336	-0.018	-0.104*	41	-0.405	-0.045**	-0.307***
Psyllobora vigintiduopunctata	40	-0.504	-0.021	0.033	28	-1.312	-0.070***	-0.285***



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Proportion of 10-km^2 with *H. axyridis*

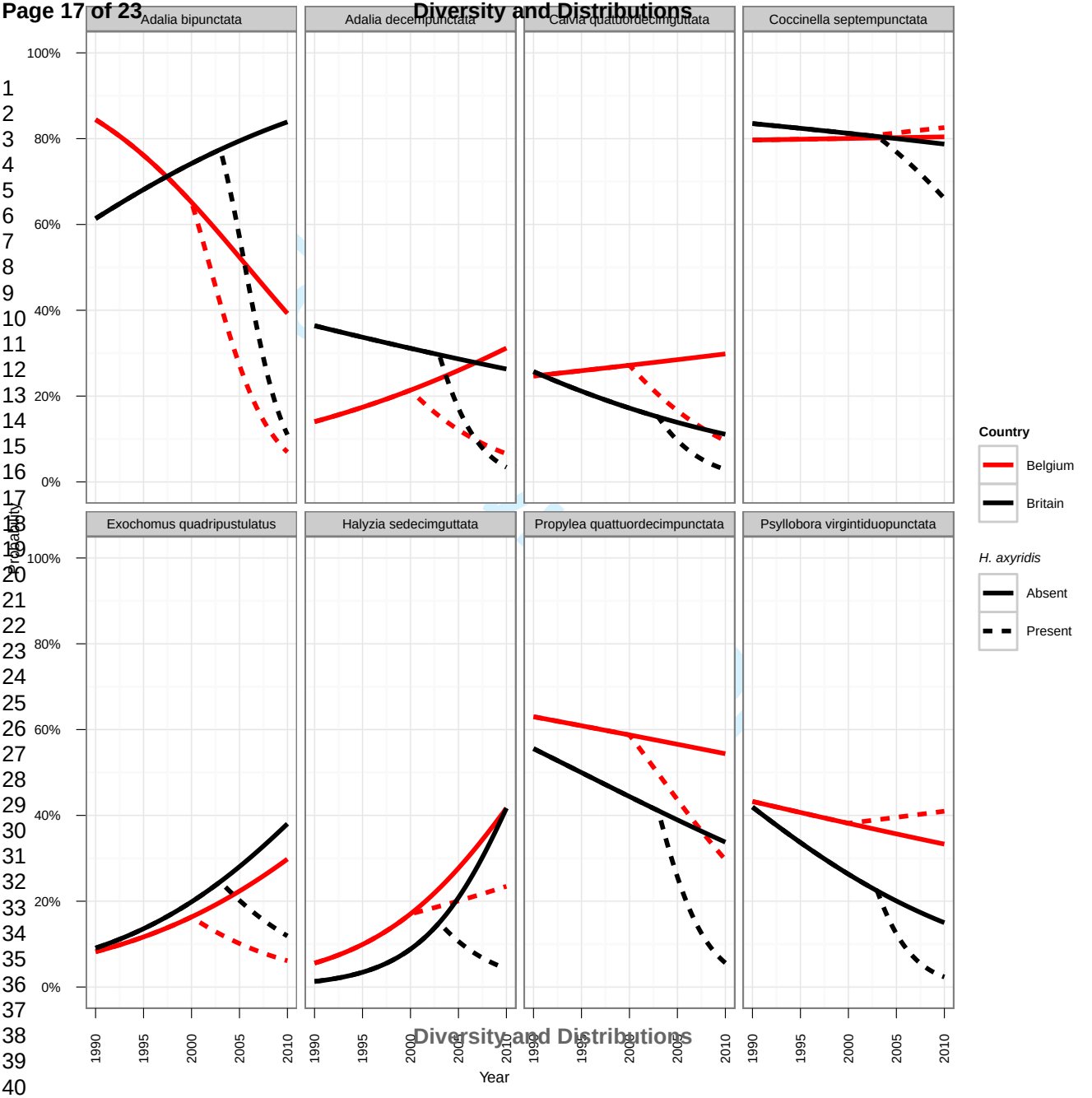
Adalia bipunctata
Adalia decempunctata
Calvia quattuordecimguttata
Coccinella septempunctata
Exochomus quadripustulatus
Halyzia sedecimguttata
Propylea quattuordecimpunctata
Psyllobora virgintiduopunctata
100%
80%
60%
40%
20%
0%
Probability
1990
1995
2000
2005
2010
Year
Country
Belgium
Britain
H. axyridis
Absent
Present

Table 3. Trends in the abundance of European ladybirds after the arrival of the invasive alien predator *Harmonia axyridis*. Numbers are parameters extracted from mixed-effects models for each species. n = number of individual ladybirds. *** p<0.001, ** p<0.01, * p<0.05.

	Britain		Belgium		Switzerland	
Species	n	Trend	n	Trend	n	Trend
Harmonia axyridis	1 824	1.278***	2 651	0.550***	1 344	0.894***
Adalia bipunctata	931	-0.472***	689	-0.877***	293	-0.571**
Adalia decempunctata	1 702	-0.169*	198	-0.125	356	-0.058
Calvia quatuordecimguttata	249	0.031	145	0.035	138	-0.272
Coccinella septempunctata	1 557	0.193	.	.	.	.
Exochomus quadripustulatus	753	-0.200*	160	-0.192	83	-0.957***
Halyzia sedecimguttata	.	.	126	0.397***	.	.
Propylea quattuordecimpunctata	428	-0.039	66	-0.142	251	-0.629***
Calvia decemguttata	.	.	179	-0.091	.	.
Oenopia conglobata	.	.	125	-0.623***	.	.
Total (all native species)	10 793	-0.091*	1 711	-0.220***	1 376	-0.465***
Number of native species	16	-0.028	12	-0.084**	18	-0.329***

Supplementary Table 1. Distributional trends for eight native ladybird species, using different thresholds for including data in the analysis. nYr is the number of years in which a 1-km^2 needed to be 'well-surveyed' in order to be considered in the analysis. nFocal is the threshold number of focal species (including *Harmonia axyridis*) to consider a 1-km^2 'well-surveyed' in any one year. Setting both thresholds to zero includes all possible combinations, including those based on incidental records from poorly-sampled areas. Setting nYr= 3 and nFocal=2 (the penultimate model for each species) correspond to the results shown in the main document. Columns b(Y), z(Y) and p(Y) are the slope, effect size and p-value for the trend in the absence of *H. axyridis*; b(H), z(H) and p(H) are comparable values for the effect of *H. axyridis* on the distribution trend. n is the sample size (number of 1-km^2-year combinations) generated by the thresholds applied; obs is the number of combinations in which the focal species was present.

Country	Species	nYr	nFocal	Intercept	b(Y)	z(Y)	p(Y)	b(H)	z(H)	p(H)	n	obs
Belgium	Adalia bipunctata	0	0	-0.929	-0.108	-19.477	0.0000	-0.023	-0.923	0.3561	9889	2589
Belgium	Adalia bipunctata	0	1	-0.740	-0.109	-18.686	0.0000	-0.059	-2.298	0.0216	8918	2589
Belgium	Adalia bipunctata	0	2	0.320	-0.182	-17.649	0.0000	-0.021	-0.703	0.4819	4813	2115
Belgium	Adalia bipunctata	0	3	1.722	-0.395	-17.524	0.0000	0.086	1.993	0.0462	2825	1544
Belgium	Adalia bipunctata	1	0	-0.929	-0.108	-19.477	0.0000	-0.023	-0.923	0.3561	9889	2589
Belgium	Adalia bipunctata	1	1	-0.740	-0.109	-18.686	0.0000	-0.059	-2.298	0.0216	8918	2589
Belgium	Adalia bipunctata	1	2	0.320	-0.182	-17.649	0.0000	-0.021	-0.703	0.4819	4813	2115
Belgium	Adalia bipunctata	1	3	1.722	-0.395	-17.524	0.0000	0.086	1.993	0.0462	2825	1544
Belgium	Adalia bipunctata	2	0	-0.761	-0.080	-11.873	0.0000	-0.120	-4.362	0.0000	6229	1852
Belgium	Adalia bipunctata	2	1	-0.580	-0.073	-10.179	0.0000	-0.171	-5.820	0.0000	5460	1790
Belgium	Adalia bipunctata	2	2	0.418	-0.123	-8.918	0.0000	-0.157	-4.087	0.0000	2519	1230
Belgium	Adalia bipunctata	2	3	1.698	-0.328	-9.410	0.0000	-0.014	-0.245	0.8067	1276	750
Belgium	Adalia bipunctata	3	0	-0.609	-0.053	-6.238	0.0000	-0.199	-6.077	0.0000	4013	1299
Belgium	Adalia bipunctata	3	1	-0.424	-0.044	-4.865	0.0000	-0.241	-6.908	0.0000	3474	1233
Belgium	Adalia bipunctata	3	2	0.627	-0.106	-5.078	0.0000	-0.216	-4.256	0.0000	1419	740
Belgium	Adalia bipunctata	3	3	2.519	-0.453	-7.452	0.0000	0.014	0.170	0.8650	696	437
Britain	Adalia bipunctata	0	0	-8.839	0.000	-0.008	0.9934	-1.379	-3.421	0.0006	23929	4866
Britain	Adalia bipunctata	0	1	-10.473	-0.008	-0.077	0.9389	-1.248	-1.701	0.0890	21885	4866
Britain	Adalia bipunctata	0	2	0.311	0.045	7.768	0.0000	-0.276	-7.032	0.0000	6483	3710
Britain	Adalia bipunctata	0	3	1.253	0.067	6.957	0.0000	-0.262	-3.857	0.0001	3343	2459
Britain	Adalia bipunctata	1	0	-8.839	0.000	-0.008	0.9934	-1.379	-3.421	0.0006	23929	4866
Britain	Adalia bipunctata	1	1	-10.473	-0.008	-0.077	0.9389	-1.248	-1.701	0.0890	21885	4866
Britain	Adalia bipunctata	1	2	0.311	0.045	7.768	0.0000	-0.276	-7.032	0.0000	6483	3710
Britain	Adalia bipunctata	1	3	1.253	0.067	6.957	0.0000	-0.262	-3.857	0.0001	3343	2459
Britain	Adalia bipunctata	2	0	-1.140	-0.008	-1.487	0.1370	-0.743	-19.406	0.0000	13175	3298
Britain	Adalia bipunctata	2	1	-0.865	-0.021	-3.599	0.0003	-0.791	-20.086	0.0000	11621	3209
Britain	Adalia bipunctata	2	2	0.695	0.042	3.924	0.0001	-0.402	-7.511	0.0000	3020	1903
Britain	Adalia bipunctata	2	3	1.833	0.082	3.975	0.0001	-0.519	-5.482	0.0000	1433	1128
Britain	Adalia bipunctata	3	0	-0.848	0.011	1.529	0.1263	-0.666	-16.402	0.0000	7923	2392
Britain	Adalia bipunctata	3	1	-0.555	-0.004	-0.512	0.6086	-0.699	-16.683	0.0000	6789	2276
Britain	Adalia bipunctata	3	2	1.057	0.059	3.615	0.0003	-0.535	-7.891	0.0000	1746	1179
Britain	Adalia bipunctata	3	3	2.211	0.099	2.962	0.0031	-0.539	-4.503	0.0000	803	664
Country	**Species**	**nYr**	**nFocal**	**Intercept**	**b(Y)**	**z(Y)**	**p(Y)**	**b(H)**	**z(H)**	**p(H)**	**n**	**obs**
Belgium	Adalia decempunctata	0	0	-12.759	0.000	0.001	0.9992	0.057	0.042	0.9665	9889	1049
Belgium	Adalia decempunctata	0	1	-7.828	-0.007	-0.091	0.9271	-0.126	-0.458	0.6469	8918	1049
Belgium	Adalia decempunctata	0	2	-4.323	-0.004	-0.136	0.8920	-0.252	-2.112	0.0347	4813	943
Belgium	Adalia decempunctata	0	3	-0.916	0.033	2.858	0.0043	-0.141	-3.384	0.0007	2825	829
Belgium	Adalia decempunctata	1	0	-12.759	0.000	0.001	0.9992	0.057	0.042	0.9665	9889	1049
Belgium	Adalia decempunctata	1	1	-7.828	-0.007	-0.091	0.9271	-0.126	-0.458	0.6469	8918	1049
Belgium	Adalia decempunctata	1	2	-4.323	-0.004	-0.136	0.8920	-0.252	-2.112	0.0347	4813	943
Belgium	Adalia decempunctata	1	3	-0.916	0.033	2.858	0.0043	-0.141	-3.384	0.0007	2825	829
Belgium	Adalia decempunctata	2	0	-7.877	0.043	0.485	0.6279	-0.339	-1.172	0.2412	6229	730
Belgium	Adalia decempunctata	2	1	-7.717	0.114	1.102	0.2704	-1.148	-3.382	0.0007	5460	701
Belgium	Adalia decempunctata	2	2	-1.475	0.031	2.236	0.0254	-0.121	-2.681	0.0073	2519	519
Belgium	Adalia decempunctata	2	3	-0.867	0.053	2.850	0.0044	-0.173	-3.173	0.0015	1276	381
Belgium	Adalia decempunctata	3	0	-12.423	0.035	0.061	0.9514	-0.043	-0.027	0.9788	4013	517
Belgium	Adalia decempunctata	3	1	-8.147	0.049	0.368	0.7125	-0.188	-0.474	0.6353	3474	486
Belgium	Adalia decempunctata	3	2	-1.302	0.051	2.688	0.0072	-0.187	-3.217	0.0013	1419	316
Belgium	Adalia decempunctata	3	3	-0.736	0.070	2.613	0.0090	-0.202	-2.848	0.0044	696	223
Britain	Adalia decempunctata	0	0	-10.583	0.031	0.246	0.8055	-3.938	-3.363	0.0008	23929	2242
Britain	Adalia decempunctata	0	1	-9.785	0.024	0.266	0.7901	-1.583	-1.885	0.0594	21885	2242
Britain	Adalia decempunctata	0	2	-0.990	-0.034	-5.364	0.0000	-0.243	-4.857	0.0000	6483	1821
Britain	Adalia decempunctata	0	3	-0.211	-0.018	-2.265	0.0235	-0.194	-3.649	0.0003	3343	1447
Britain	Adalia decempunctata	1	0	-10.583	0.031	0.246	0.8055	-3.938	-3.363	0.0008	23929	2242
Britain	Adalia decempunctata	1	1	-9.785	0.024	0.266	0.7901	-1.583	-1.885	0.0594	21885	2242
Britain	Adalia decempunctata	1	2	-0.990	-0.034	-5.364	0.0000	-0.243	-4.857	0.0000	6483	1821
Britain	Adalia decempunctata	1	3	-0.211	-0.018	-2.265	0.0235	-0.194	-3.649	0.0003	3343	1447
Britain	Adalia decempunctata	2	0	-9.211	0.005	0.056	0.9552	-0.842	-1.384	0.1662	13175	1502
Britain	Adalia decempunctata	2	1	-11.966	-0.049	-0.115	0.9083	-0.710	-0.481	0.6307	11621	1457
Britain	Adalia decempunctata	2	2	-0.818	-0.023	-2.097	0.0360	-0.254	-4.160	0.0000	3020	940
Britain	Adalia decempunctata	2	3	-0.100	-0.015	-0.964	0.3350	-0.230	-3.232	0.0012	1433	646
Britain	Adalia decempunctata	3	0	-10.715	0.172	1.196	0.2317	-1.395	-1.516	0.1295	7923	1066
Britain	Adalia decempunctata	3	1	-9.522	-0.113	-0.793	0.4279	-0.530	-0.568	0.5701	6789	998
Britain	Adalia decempunctata	3	2	-0.794	-0.024	-1.341	0.1800	-0.331	-4.232	0.0000	1746	554
Britain	Adalia decempunctata	3	3	-0.044	0.011	0.432	0.6660	-0.304	-3.359	0.0008	803	373

Country	Species	nYr	nFocal	Intercept	b(Y)	z(Y)	p(Y)	b(H)	z(H)	p(H)	n	obs
Belgium	Calvia quatuordecimguttata	0	0	-7.477	0.000	0.000	0.9998	0.024	0.119	0.9054	9889	1350
Belgium	Calvia quatuordecimguttata	0	1	-6.250	0.076	1.976	0.0481	-0.462	-2.835	0.0046	8918	1350
Belgium	Calvia quatuordecimguttata	0	2	-1.165	-0.037	-4.262	0.0000	-0.046	-1.265	0.2058	4813	1212
Belgium	Calvia quatuordecimguttata	0	3	-0.496	-0.010	-0.876	0.3811	-0.130	-3.141	0.0017	2825	1026
Belgium	Calvia quatuordecimguttata	1	0	-7.477	0.000	0.000	0.9998	0.024	0.119	0.9054	9889	1350
Belgium	Calvia quatuordecimguttata	1	1	-6.250	0.076	1.976	0.0481	-0.462	-2.835	0.0046	8918	1350
Belgium	Calvia quatuordecimguttata	1	2	-1.165	-0.037	-4.262	0.0000	-0.046	-1.265	0.2058	4813	1212
Belgium	Calvia quatuordecimguttata	1	3	-0.496	-0.010	-0.876	0.3811	-0.130	-3.141	0.0017	2825	1026
Belgium	Calvia quatuordecimguttata	2	0	-9.013	-0.095	-0.811	0.4175	-1.947	-4.217	0.0000	6229	957
Belgium	Calvia quatuordecimguttata	2	1	-4.202	0.086	2.975	0.0029	-0.970	-8.144	0.0000	5460	926
Belgium	Calvia quatuordecimguttata	2	2	-1.084	-0.027	-2.268	0.0233	-0.048	-1.110	0.2671	2519	681
Belgium	Calvia quatuordecimguttata	2	3	-0.519	0.007	0.381	0.7033	-0.116	-2.117	0.0343	1276	470
Belgium	Calvia quatuordecimguttata	3	0	-6.671	-0.068	-1.063	0.2879	-0.093	-0.415	0.6781	4013	677
Belgium	Calvia quatuordecimguttata	3	1	-8.483	0.457	2.768	0.0056	-1.827	-3.165	0.0016	3474	645
Belgium	Calvia quatuordecimguttata	3	2	-0.985	0.013	0.735	0.4621	-0.139	-2.447	0.0144	1419	402
Belgium	Calvia quatuordecimguttata	3	3	-0.436	0.025	0.945	0.3448	-0.154	-2.185	0.0289	696	264
Britain	Calvia quatuordecimguttata	0	0	-6.446	-0.069	-2.575	0.0100	-0.490	-1.945	0.0518	23929	1521
Britain	Calvia quatuordecimguttata	0	1	-12.380	-0.089	-0.522	0.6017	-0.305	-0.213	0.8315	21885	1521
Britain	Calvia quatuordecimguttata	0	2	-3.120	-0.134	-9.697	0.0000	-0.421	-3.302	0.0010	6483	1182
Britain	Calvia quatuordecimguttata	0	3	-1.044	-0.039	-4.231	0.0000	-0.172	-2.505	0.0122	3343	932
Britain	Calvia quatuordecimguttata	1	0	-6.446	-0.069	-2.575	0.0100	-0.490	-1.945	0.0518	23929	1521
Britain	Calvia quatuordecimguttata	1	1	-12.380	-0.089	-0.522	0.6017	-0.305	-0.213	0.8315	21885	1521
Britain	Calvia quatuordecimguttata	1	2	-3.120	-0.134	-9.697	0.0000	-0.421	-3.302	0.0010	6483	1182
Britain	Calvia quatuordecimguttata	1	3	-1.044	-0.039	-4.231	0.0000	-0.172	-2.505	0.0122	3343	932
Britain	Calvia quatuordecimguttata	2	0	-5.724	-0.039	-1.453	0.1462	-0.704	-3.467	0.0005	13175	1044
Britain	Calvia quatuordecimguttata	2	1	-8.629	-0.049	-0.656	0.5120	-0.712	-1.413	0.1576	11621	1006
Britain	Calvia quatuordecimguttata	2	2	-1.624	-0.049	-3.869	0.0001	-0.151	-1.983	0.0473	3020	616
Britain	Calvia quatuordecimguttata	2	3	-0.916	-0.070	-3.912	0.0001	-0.123	-1.346	0.1781	1433	423
Britain	Calvia quatuordecimguttata	3	0	-8.081	0.030	0.274	0.7842	-1.260	-1.652	0.0986	7923	711
Britain	Calvia quatuordecimguttata	3	1	-7.773	-0.082	-0.806	0.4201	-1.577	-2.831	0.0046	6789	670
Britain	Calvia quatuordecimguttata	3	2	-1.571	-0.051	-2.566	0.0103	-0.204	-2.174	0.0297	1746	365
Britain	Calvia quatuordecimguttata	3	3	-0.716	-0.084	-2.455	0.0141	-0.396	-2.838	0.0045	803	250
Country	Species	nYr	nFocal	Intercept	b(Y)	z(Y)	p(Y)	b(H)	z(H)	p(H)	n	obs
Belgium	Coccinella septempunctata	0	0	0.037	-0.007	-1.368	0.1713	0.014	0.757	0.4491	9889	5073
Belgium	Coccinella septempunctata	0	1	0.310	0.002	0.342	0.7327	-0.051	-2.522	0.0117	8918	5073
Belgium	Coccinella septempunctata	0	2	1.115	0.005	0.573	0.5664	0.034	1.027	0.3044	4813	3568
Belgium	Coccinella septempunctata	0	3	11.742	-0.013	-0.023	0.9814	0.054	0.033	0.9740	2825	2294
Belgium	Coccinella septempunctata	1	0	0.037	-0.007	-1.368	0.1713	0.014	0.757	0.4491	9889	5073
Belgium	Coccinella septempunctata	1	1	0.310	0.002	0.342	0.7327	-0.051	-2.522	0.0117	8918	5073
Belgium	Coccinella septempunctata	1	2	1.115	0.005	0.573	0.5664	0.034	1.027	0.3044	4813	3568
Belgium	Coccinella septempunctata	1	3	11.742	-0.013	-0.023	0.9814	0.054	0.033	0.9740	2825	2294
Belgium	Coccinella septempunctata	2	0	0.153	-0.009	-1.330	0.1836	0.001	0.041	0.9673	6229	3347
Belgium	Coccinella septempunctata	2	1	0.417	0.001	0.179	0.8576	-0.041	-1.746	0.0808	5460	3224
Belgium	Coccinella septempunctata	2	2	1.230	0.001	0.075	0.9404	0.048	1.135	0.2566	2519	1914
Belgium	Coccinella septempunctata	2	3	12.137	-0.016	-0.017	0.9867	-0.006	-0.003	0.9980	1276	1077
Belgium	Coccinella septempunctata	3	0	0.233	-0.017	-1.947	0.0515	0.012	0.432	0.6654	4013	2231
Belgium	Coccinella septempunctata	3	1	0.495	-0.010	-1.020	0.3079	-0.022	-0.759	0.4476	3474	2111
Belgium	Coccinella septempunctata	3	2	1.389	0.002	0.125	0.9008	0.014	0.262	0.7935	1419	1105
Belgium	Coccinella septempunctata	3	3	13.327	-0.117	-0.101	0.9195	-0.224	-0.087	0.9303	696	611
Britain	Coccinella septempunctata	0	0	-0.188	-0.083	-23.217	0.0000	-1.093	-29.705	0.0000	23929	8395
Britain	Coccinella septempunctata	0	1	0.471	-0.371	-38.873	0.0000	-1.728	-25.844	0.0000	21885	8395
Britain	Coccinella septempunctata	0	2	1.347	-0.026	-3.610	0.0003	-0.238	-5.878	0.0000	6483	4773
Britain	Coccinella septempunctata	0	3	4.427	0.117	3.908	0.0001	-0.127	-0.615	0.5388	3343	2811
Britain	Coccinella septempunctata	1	0	-0.188	-0.083	-23.217	0.0000	-1.093	-29.705	0.0000	23929	8395
Britain	Coccinella septempunctata	1	1	0.471	-0.371	-38.873	0.0000	-1.728	-25.844	0.0000	21885	8395
Britain	Coccinella septempunctata	1	2	1.347	-0.026	-3.610	0.0003	-0.238	-5.878	0.0000	6483	4773
Britain	Coccinella septempunctata	1	3	4.427	0.117	3.908	0.0001	-0.127	-0.615	0.5388	3343	2811
Britain	Coccinella septempunctata	2	0	-0.302	-0.070	-12.646	0.0000	-0.645	-18.217	0.0000	13175	4788
Britain	Coccinella septempunctata	2	1	0.055	-0.105	-16.370	0.0000	-0.683	-18.255	0.0000	11621	4599
Britain	Coccinella septempunctata	2	2	1.362	-0.017	-1.383	0.1665	-0.152	-2.772	0.0056	3020	2227
Britain	Coccinella septempunctata	2	3	9.478	-0.140	-0.392	0.6952	3.631	2.514	0.0119	1433	1198
Britain	Coccinella septempunctata	3	0	-0.243	-0.050	-6.378	0.0000	-0.511	-12.931	0.0000	7923	3159
Britain	Coccinella septempunctata	3	1	0.112	-0.088	-9.787	0.0000	-0.521	-12.443	0.0000	6789	2963
Britain	Coccinella septempunctata	3	2	1.466	-0.016	-0.839	0.4017	-0.092	-1.317	0.1879	1746	1314
Britain	Coccinella septempunctata	3	3	13.649	-0.134	-0.074	0.9410	0.161	0.031	0.9749	803	692

Country	Species	nYr	nFocal	Intercept	b(Y)	z(Y)	p(Y)	b(H)	z(H)	p(H)	n	obs
Belgium	Exochomus quadripustulatus	0	0	-5.869	-0.120	-4.022	0.0001	-0.200	-1.854	0.0637	9889	1043
Belgium	Exochomus quadripustulatus	0	1	-10.295	0.091	0.679	0.4972	-1.229	-2.686	0.0072	8918	1043
Belgium	Exochomus quadripustulatus	0	2	-3.832	-0.059	-2.370	0.0178	-0.201	-1.961	0.0498	4813	919
Belgium	Exochomus quadripustulatus	0	3	-1.303	0.021	1.453	0.1463	-0.050	-1.118	0.2637	2825	773
Belgium	Exochomus quadripustulatus	1	0	-5.869	-0.120	-4.022	0.0001	-0.200	-1.854	0.0637	9889	1043
Belgium	Exochomus quadripustulatus	1	1	-10.295	0.091	0.679	0.4972	-1.229	-2.686	0.0072	8918	1043
Belgium	Exochomus quadripustulatus	1	2	-3.832	-0.059	-2.370	0.0178	-0.201	-1.961	0.0498	4813	919
Belgium	Exochomus quadripustulatus	1	3	-1.303	0.021	1.453	0.1463	-0.050	-1.118	0.2637	2825	773
Belgium	Exochomus quadripustulatus	2	0	-8.004	0.037	0.356	0.7219	-0.486	-1.441	0.1496	6229	743
Belgium	Exochomus quadripustulatus	2	1	-7.312	-0.057	-0.671	0.5020	-0.250	-0.826	0.4089	5460	710
Belgium	Exochomus quadripustulatus	2	2	-1.758	0.050	2.966	0.0030	-0.126	-2.608	0.0091	2519	547
Belgium	Exochomus quadripustulatus	2	3	-1.065	0.043	1.826	0.0679	-0.079	-1.414	0.1574	1276	407
Belgium	Exochomus quadripustulatus	3	0	-5.510	0.062	1.342	0.1795	-0.266	-2.029	0.0425	4013	529
Belgium	Exochomus quadripustulatus	3	1	-5.102	0.056	1.256	0.2091	-0.232	-1.719	0.0856	3474	500
Belgium	Exochomus quadripustulatus	3	2	-1.634	0.078	3.203	0.0014	-0.187	-3.043	0.0023	1419	335
Belgium	Exochomus quadripustulatus	3	3	-0.819	0.061	1.848	0.0646	-0.160	-2.168	0.0302	696	243
Britain	Exochomus quadripustulatus	0	0	-5.513	-0.078	-3.713	0.0002	-0.997	-5.620	0.0000	23929	1835
Britain	Exochomus quadripustulatus	0	1	-4.036	-0.117	-10.625	0.0000	-1.822	-18.462	0.0000	21885	1835
Britain	Exochomus quadripustulatus	0	2	-3.409	-0.050	-3.021	0.0025	-0.325	-2.818	0.0048	6483	1365
Britain	Exochomus quadripustulatus	0	3	-1.465	0.084	7.079	0.0000	-0.071	-1.130	0.2587	3343	1048
Britain	Exochomus quadripustulatus	1	0	-5.513	-0.078	-3.713	0.0002	-0.997	-5.620	0.0000	23929	1835
Britain	Exochomus quadripustulatus	1	1	-4.036	-0.117	-10.625	0.0000	-1.822	-18.462	0.0000	21885	1835
Britain	Exochomus quadripustulatus	1	2	-3.409	-0.050	-3.021	0.0025	-0.325	-2.818	0.0048	6483	1365
Britain	Exochomus quadripustulatus	1	3	-1.465	0.084	7.079	0.0000	-0.071	-1.130	0.2587	3343	1048
Britain	Exochomus quadripustulatus	2	0	-4.400	-0.053	-3.216	0.0013	-0.983	-10.043	0.0000	13175	1371
Britain	Exochomus quadripustulatus	2	1	-4.083	-0.058	-3.431	0.0006	-0.751	-7.303	0.0000	11621	1339
Britain	Exochomus quadripustulatus	2	2	-1.745	0.073	4.584	0.0000	-0.204	-3.007	0.0026	3020	815
Britain	Exochomus quadripustulatus	2	3	-0.945	0.087	4.033	0.0001	-0.040	-0.470	0.6382	1433	578
Britain	Exochomus quadripustulatus	3	0	-5.263	-0.014	-0.452	0.6514	-0.830	-5.362	0.0000	7923	1002
Britain	Exochomus quadripustulatus	3	1	-4.765	0.094	2.912	0.0036	-0.891	-6.531	0.0000	6789	964
Britain	Exochomus quadripustulatus	3	2	-1.396	0.091	3.832	0.0001	-0.216	-2.655	0.0079	1746	570
Britain	Exochomus quadripustulatus	3	3	-0.799	0.183	4.205	0.0000	-0.242	-2.032	0.0421	803	374
Country	**Species**	**nYr**	**nFocal**	**Intercept**	**b(Y)**	**z(Y)**	**p(Y)**	**b(H)**	**z(H)**	**p(H)**	**n**	**obs**
Belgium	Halyzia sedecimguttata	0	0	-7.104	0.011	0.193	0.8469	-0.148	-0.828	0.4075	9889	1183
Belgium	Halyzia sedecimguttata	0	1	-11.252	0.291	1.215	0.2243	-0.592	-0.968	0.3330	8918	1183
Belgium	Halyzia sedecimguttata	0	2	-5.107	-0.044	-1.097	0.2728	0.271	2.134	0.0328	4813	1007
Belgium	Halyzia sedecimguttata	0	3	-1.281	0.122	8.874	0.0000	-0.057	-1.477	0.1397	2825	840
Belgium	Halyzia sedecimguttata	1	0	-7.104	0.011	0.193	0.8469	-0.148	-0.828	0.4075	9889	1183
Belgium	Halyzia sedecimguttata	1	1	-11.252	0.291	1.215	0.2243	-0.592	-0.968	0.3330	8918	1183
Belgium	Halyzia sedecimguttata	1	2	-5.107	-0.044	-1.097	0.2728	0.271	2.134	0.0328	4813	1007
Belgium	Halyzia sedecimguttata	1	3	-1.281	0.122	8.874	0.0000	-0.057	-1.477	0.1397	2825	840
Belgium	Halyzia sedecimguttata	2	0	-5.420	-0.167	-4.546	0.0000	-0.202	-1.603	0.1089	6229	813
Belgium	Halyzia sedecimguttata	2	1	-7.649	-0.123	-1.893	0.0583	0.488	2.991	0.0028	5460	788
Belgium	Halyzia sedecimguttata	2	2	-1.754	0.113	6.757	0.0000	-0.056	-1.330	0.1835	2519	571
Belgium	Halyzia sedecimguttata	2	3	-1.120	0.127	5.867	0.0000	-0.083	-1.628	0.1036	1276	407
Belgium	Halyzia sedecimguttata	3	0	-12.411	0.090	0.147	0.8833	-0.016	-0.013	0.9899	4013	597
Belgium	Halyzia sedecimguttata	3	1	-11.204	0.271	0.693	0.4882	-0.253	-0.310	0.7567	3474	567
Belgium	Halyzia sedecimguttata	3	2	-1.583	0.125	5.441	0.0000	-0.085	-1.593	0.1111	1419	348
Belgium	Halyzia sedecimguttata	3	3	-0.935	0.137	4.673	0.0000	-0.095	-1.443	0.1490	696	244
Britain	Halyzia sedecimguttata	0	0	-4.650	-0.044	-3.181	0.0015	-1.604	-12.812	0.0000	23929	1815
Britain	Halyzia sedecimguttata	0	1	-3.726	-0.003	-0.299	0.7647	-1.348	-15.401	0.0000	21885	1815
Britain	Halyzia sedecimguttata	0	2	-3.560	0.044	2.488	0.0129	-0.595	-5.394	0.0000	6483	1045
Britain	Halyzia sedecimguttata	0	3	-5.021	0.260	3.763	0.0002	-0.383	-1.341	0.1801	3343	739
Britain	Halyzia sedecimguttata	1	0	-4.650	-0.044	-3.181	0.0015	-1.604	-12.812	0.0000	23929	1815
Britain	Halyzia sedecimguttata	1	1	-3.726	-0.003	-0.299	0.7647	-1.348	-15.401	0.0000	21885	1815
Britain	Halyzia sedecimguttata	1	2	-3.560	0.044	2.488	0.0129	-0.595	-5.394	0.0000	6483	1045
Britain	Halyzia sedecimguttata	1	3	-5.021	0.260	3.763	0.0002	-0.383	-1.341	0.1801	3343	739
Britain	Halyzia sedecimguttata	2	0	-9.305	-0.018	-0.170	0.8653	-0.859	-1.801	0.0716	13175	1239
Britain	Halyzia sedecimguttata	2	1	-6.039	0.046	1.082	0.2793	-1.391	-6.395	0.0000	11621	1209
Britain	Halyzia sedecimguttata	2	2	-3.784	0.308	8.123	0.0000	-0.557	-5.040	0.0000	3020	603
Britain	Halyzia sedecimguttata	2	3	-2.073	0.238	7.066	0.0000	-0.385	-3.772	0.0002	1433	386
Britain	Halyzia sedecimguttata	3	0	-6.656	0.038	0.717	0.4731	-0.540	-2.416	0.0157	7923	887
Britain	Halyzia sedecimguttata	3	1	-4.289	0.091	2.937	0.0033	-1.144	-8.244	0.0000	6789	842
Britain	Halyzia sedecimguttata	3	2	-2.335	0.200	6.137	0.0000	-0.396	-4.280	0.0000	1746	389
Britain	Halyzia sedecimguttata	3	3	-1.608	0.193	5.012	0.0000	-0.356	-3.065	0.0022	803	236

Country	Species	nYr	nFocal	Intercept	b(Y)	z(Y)	p(Y)	b(H)	z(H)	p(H)	n	obs
Belgium	Propylea quattuordecimpunctata	0	0	-0.988	-0.042	-7.993	0.0000	0.006	0.274	0.7843	9889	2682
Belgium	Propylea quattuordecimpunctata	0	1	-0.813	-0.038	-7.072	0.0000	-0.033	-1.480	0.1388	8918	2682
Belgium	Propylea quattuordecimpunctata	0	2	0.153	-0.051	-6.578	0.0000	-0.072	-2.664	0.0077	4813	2354
Belgium	Propylea quattuordecimpunctata	0	3	0.922	-0.075	-5.924	0.0000	-0.041	-1.164	0.2444	2825	1827
Belgium	Propylea quattuordecimpunctata	1	0	-0.988	-0.042	-7.993	0.0000	0.006	0.274	0.7843	9889	2682
Belgium	Propylea quattuordecimpunctata	1	1	-0.813	-0.038	-7.072	0.0000	-0.033	-1.480	0.1388	8918	2682
Belgium	Propylea quattuordecimpunctata	1	2	0.153	-0.051	-6.578	0.0000	-0.072	-2.664	0.0077	4813	2354
Belgium	Propylea quattuordecimpunctata	1	3	0.922	-0.075	-5.924	0.0000	-0.041	-1.164	0.2444	2825	1827
Belgium	Propylea quattuordecimpunctata	2	0	-0.866	-0.022	-3.302	0.0010	-0.061	-2.546	0.0109	6229	1844
Belgium	Propylea quattuordecimpunctata	2	1	-0.696	-0.015	-2.233	0.0256	-0.096	-3.810	0.0001	5460	1778
Belgium	Propylea quattuordecimpunctata	2	2	0.233	-0.035	-3.064	0.0022	-0.076	-2.243	0.0249	2519	1299
Belgium	Propylea quattuordecimpunctata	2	3	1.009	-0.076	-3.642	0.0003	-0.014	-0.295	0.7680	1276	856
Belgium	Propylea quattuordecimpunctata	3	0	-0.736	-0.014	-1.608	0.1078	-0.084	-2.988	0.0028	4013	1284
Belgium	Propylea quattuordecimpunctata	3	1	-0.562	-0.005	-0.528	0.5973	-0.114	-3.819	0.0001	3474	1220
Belgium	Propylea quattuordecimpunctata	3	2	0.354	-0.018	-1.143	0.2530	-0.104	-2.370	0.0178	1419	775
Belgium	Propylea quattuordecimpunctata	3	3	1.087	-0.056	-1.865	0.0622	-0.100	-1.560	0.1187	696	465
Britain	Propylea quattuordecimpunctata	0	0	-7.599	-0.027	-0.677	0.4987	-2.340	-5.599	0.0000	23929	3554
Britain	Propylea quattuordecimpunctata	0	1	-8.407	-0.028	-0.629	0.5294	-3.308	-7.167	0.0000	21885	3554
Britain	Propylea quattuordecimpunctata	0	2	-0.007	-0.036	-6.261	0.0000	-0.538	-10.835	0.0000	6483	2921
Britain	Propylea quattuordecimpunctata	0	3	0.817	-0.031	-3.458	0.0005	-0.496	-8.543	0.0000	3343	2049
Britain	Propylea quattuordecimpunctata	1	0	-7.599	-0.027	-0.677	0.4987	-2.340	-5.599	0.0000	23929	3554
Britain	Propylea quattuordecimpunctata	1	1	-8.407	-0.028	-0.629	0.5294	-3.308	-7.167	0.0000	21885	3554
Britain	Propylea quattuordecimpunctata	1	2	-0.007	-0.036	-6.261	0.0000	-0.538	-10.835	0.0000	6483	2921
Britain	Propylea quattuordecimpunctata	1	3	0.817	-0.031	-3.458	0.0005	-0.496	-8.543	0.0000	3343	2049
Britain	Propylea quattuordecimpunctata	2	0	-9.758	-0.026	-0.223	0.8239	-1.190	-1.280	0.2006	13175	2149
Britain	Propylea quattuordecimpunctata	2	1	-5.649	-0.114	-2.950	0.0032	-1.034	-3.797	0.0001	11621	2064
Britain	Propylea quattuordecimpunctata	2	2	-0.091	-0.055	-5.218	0.0000	-0.311	-5.179	0.0000	3020	1306
Britain	Propylea quattuordecimpunctata	2	3	0.653	-0.077	-4.031	0.0001	-0.247	-3.260	0.0011	1433	800
Britain	Propylea quattuordecimpunctata	3	0	-1.531	-0.070	-8.717	0.0000	-0.576	-9.622	0.0000	7923	1454
Britain	Propylea quattuordecimpunctata	3	1	-1.359	-0.088	-10.092	0.0000	-0.582	-9.443	0.0000	6789	1337
Britain	Propylea quattuordecimpunctata	3	2	-0.225	-0.045	-2.882	0.0040	-0.307	-4.122	0.0000	1746	711
Britain	Propylea quattuordecimpunctata	3	3	0.474	-0.005	-0.177	0.8598	-0.343	-3.557	0.0004	803	433

Country	Species	nYr	nFocal	Intercept	b(Y)	z(Y)	p(Y)	b(H)	z(H)	p(H)	n	obs
Belgium	Psyllobora virgintiduopunctata	0	0	-4.749	-0.048	-2.212	0.0270	-0.039	-0.437	0.6618	9889	1888
Belgium	Psyllobora virgintiduopunctata	0	1	-1.540	-0.022	-3.539	0.0004	0.068	2.756	0.0058	8918	1888
Belgium	Psyllobora virgintiduopunctata	0	2	-0.744	-0.019	-2.430	0.0151	0.029	0.989	0.3226	4813	1639
Belgium	Psyllobora virgintiduopunctata	0	3	-0.128	-0.014	-1.326	0.1848	0.005	0.128	0.8978	2825	1319
Belgium	Psyllobora virgintiduopunctata	1	0	-4.749	-0.048	-2.212	0.0270	-0.039	-0.437	0.6618	9889	1888
Belgium	Psyllobora virgintiduopunctata	1	1	-1.540	-0.022	-3.539	0.0004	0.068	2.756	0.0058	8918	1888
Belgium	Psyllobora virgintiduopunctata	1	2	-0.744	-0.019	-2.430	0.0151	0.029	0.989	0.3226	4813	1639
Belgium	Psyllobora virgintiduopunctata	1	3	-0.128	-0.014	-1.326	0.1848	0.005	0.128	0.8978	2825	1319
Belgium	Psyllobora virgintiduopunctata	2	0	-1.528	-0.012	-1.598	0.1101	0.043	1.634	0.1023	6229	1325
Belgium	Psyllobora virgintiduopunctata	2	1	-1.385	-0.006	-0.742	0.4580	0.019	0.689	0.4907	5460	1278
Belgium	Psyllobora virgintiduopunctata	2	2	-0.616	-0.019	-1.694	0.0904	0.010	0.276	0.7823	2519	935
Belgium	Psyllobora virgintiduopunctata	2	3	0.037	-0.034	-1.918	0.0551	0.037	0.778	0.4364	1276	644
Belgium	Psyllobora virgintiduopunctata	3	0	-1.383	-0.010	-0.993	0.3205	0.016	0.513	0.6078	4013	935
Belgium	Psyllobora virgintiduopunctata	3	1	-1.236	-0.003	-0.257	0.7968	0.002	0.063	0.9500	3474	888
Belgium	Psyllobora virgintiduopunctata	3	2	-0.483	-0.021	-1.329	0.1837	0.033	0.724	0.4689	1419	571
Belgium	Psyllobora virgintiduopunctata	3	3	0.152	-0.021	-0.839	0.4014	0.006	0.090	0.9285	696	369
Britain	Psyllobora virgintiduopunctata	0	0	-10.054	-0.073	-0.928	0.3536	-0.818	-1.258	0.2082	23929	1898
Britain	Psyllobora virgintiduopunctata	0	1	-5.655	-0.114	-4.797	0.0000	-1.160	-4.624	0.0000	21885	1898
Britain	Psyllobora virgintiduopunctata	0	2	-1.462	-0.071	-9.889	0.0000	-0.309	-4.824	0.0000	6483	1523
Britain	Psyllobora virgintiduopunctata	0	3	-0.651	-0.050	-5.846	0.0000	-0.225	-3.465	0.0005	3343	1171
Britain	Psyllobora virgintiduopunctata	1	0	-10.054	-0.073	-0.928	0.3536	-0.818	-1.258	0.2082	23929	1898
Britain	Psyllobora virgintiduopunctata	1	1	-5.655	-0.114	-4.797	0.0000	-1.160	-4.624	0.0000	21885	1898
Britain	Psyllobora virgintiduopunctata	1	2	-1.462	-0.071	-9.889	0.0000	-0.309	-4.824	0.0000	6483	1523
Britain	Psyllobora virgintiduopunctata	1	3	-0.651	-0.050	-5.846	0.0000	-0.225	-3.465	0.0005	3343	1171
Britain	Psyllobora virgintiduopunctata	2	0	-8.907	-0.050	-0.592	0.5540	-0.661	-1.169	0.2425	13175	1242
Britain	Psyllobora virgintiduopunctata	2	1	-6.761	-0.109	-2.491	0.0127	-0.595	-2.051	0.0402	11621	1200
Britain	Psyllobora virgintiduopunctata	2	2	-1.191	-0.068	-5.939	0.0000	-0.211	-3.009	0.0026	3020	800
Britain	Psyllobora virgintiduopunctata	2	3	-0.489	-0.066	-3.736	0.0002	-0.222	-2.562	0.0104	1433	540
Britain	Psyllobora virgintiduopunctata	3	0	-8.176	-0.093	-1.133	0.2572	-0.792	-1.487	0.1370	7923	897
Britain	Psyllobora virgintiduopunctata	3	1	-9.832	-0.084	-0.597	0.5503	-1.282	-1.569	0.1166	6789	832
Britain	Psyllobora virgintiduopunctata	3	2	-1.030	-0.070	-4.269	0.0000	-0.285	-3.341	0.0008	1746	486
Britain	Psyllobora virgintiduopunctata	3	3	-0.388	-0.088	-2.921	0.0035	-0.219	-1.991	0.0465	803	306