NATURAL HISTORY

Geographic variation in the habitat preference of a scarce predatory insect: evolutionary and conservation perspectives

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Abstract. 1. While there has been considerable focus on prey occurrence as a factor determining the habitat preference of predators, the roles of other factors related to the habitat are less well characterised.

2. In aphidophagous ladybird beetles (Coleoptera: Coccinellidae), a number of species are more restricted in the habitats in which they live than are their prey. A number of such ladybirds appear to show geographic variation in habitat preference.

3. To better understand these phenomena, this study considered geographic variation in habitat preference in one such species, the 5-spot ladybird, Coccinella quinquepunctata. Because of this ladybird’s scarcity, a combination of over 20 years’ observations, habitat surveys and online data was used to reach the study’s conclusions.

4. The data collected indicate that the ladybird is specialised in pioneer habitats close to water, but broadens its range to non-riverine pioneer habitats in north-west continental Europe, where it is likely that a damper (micro)climate allows it to do so. Thus, microclimatic factors appear to be important in determining the habitat of this and probably other predators that are not constrained by prey occurrence.

5. Although threatened by river management elsewhere, in north-western Europe, this species clearly benefits from human activity, which creates many of the disturbed habitats it colonises there. This finding provides further support for the contention that many ladybirds are net beneficiaries of human influence, although they are often characterised as threatened.

Key words. anthropogenic habitats, climate, Coccinella quinquepunctata, Coccinellidae, latitudinal variation, pioneer species.

Introduction

Understanding the reasons why organisms live where they do is a significant challenge for ecologists and evolutionary biologists. Even a description of the habitat preference is challenging because habitat selection occurs on a diversity of scales and habitats are not homogeneous; furthermore, there may be subjectivity or bias in the choice of habitat characteristics (Baguette & Mennechez, 2004; Beyer et al., 2010). Nonetheless, the characteristics of an organism’s habitat relevant to its preference are important, not only to better understand its evolution but also to facilitate conservation measures for threatened organisms (e.g. Massaro et al., 2017; Rada et al., 2017) and to understand how they may respond to anthropogenic threats, such as climate change (e.g. Sampaio et al., 2016a, 2016b; Stuhlbrecher & Fartmann, 2018).

In animals, while it is true that habitat and feeding preferences are closely associated, the two things are not synonymous, even in phytophagous taxa (e.g. Ohsaki & Sato, 1999; Friberg et al., 2008) and the relationship is likely to be weaker still for predators, which often have broader feeding niches than herbivores. Thus predators are particularly interesting and challenging to study, and potentially provide different insights into habitat preference evolution than those provided by phytophages. In aphid-eating ladybird beetles (Coleoptera: Coccinellidae), some species show habitat specificity directly

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associated with the aphid species that they eat (Sloggett & Majerus, 2000a; Sloggett, 2008a); however, a number of taxa apparently consume a broad variety of aphid species, but are still limited to certain environments, which are not the exclusive provenance of their prey (Sloggett & Majerus, 2000a; Sloggett, 2008a). In some cases, such habitats may provide an especially abundant, reliable or durable aphid source facilitating specialisation (Sloggett & Majerus, 2000b). However, this is unlikely to be universal; nor is it clear what the costs of such specialisation are or how habitat-related factors may interact with food-related ones (Sloggett, 2008a).

The situation is further complicated, as several such Palaeartic ladybirds have been suggested to exhibit geographic variation in habitat preference, being more specialised in the north and west of their range and increasingly less habitat-specific towards southern and central Europe (Sloggett & Majerus, 2000a). It has been suggested that longer potential breeding seasons across a diversity of habitats in southern and eastern Europe reduce the benefits of specialising in a single habitat (Sloggett, 2008a). However, detailed knowledge of such variation in habitat preference is often lacking, with a clearer geographic comparison needed before generalisations can really be made. A complicating factor for such studies is that the species involved are often relatively scarce as a consequence of their habitat specialisation.

A better understanding of such species can potentially enhance our understanding of how ladybird habitat preferences evolve. In this paper we examine the habitat preferences of the 5-spot ladybird, _Coccinella quinquepunctata_ L., to gain such insights. This species, which is generally accepted to be an aphidophagous generalist (Majerus, 1994; Honěk & Hodek, 1996; Klausnitzer & Klausnitzer, 1997), was the first such case of geographic habitat variation proposed (Majerus & Fowles, 1989). _Coccinella quinquepunctata_ has a very broad range, extending across Europe, north Africa and Asia (Iablokoff-Khnzorian, 1982), but though widespread, in Europe at least, it is often locally of limited occurrence (e.g. Classen et al., 2016; Deflorenne et al., 2017). In Britain the species was rediscovered in the 1980s living in river shingle habitats, after being thought to be extinct (Majerus & Fowles, 1989). At the time this was thought to be an edge-of-range habitat phenomenon: on the basis of observations in continental Europe, Majerus argued this species is a broad habitat generalist elsewhere and only specialised on shingle in Britain (Majerus & Fowles, 1989; Majerus, 1994, 2016). Sloggett and Majerus (2000a) reported this as a species exhibiting a north-west European habitat specialisation; by this time it appeared that this specialisation might extend into northern France and it has been treated as a more widespread phenomenon since then (Sloggett, 2008a). In continental Europe there are conflicting reports of its habitat preference. It was reported as a herbaceous layer generalist in the Netherlands and Germany (Klausnitzer & Klausnitzer, 1997; Cuppen et al., 2017). In the Czech Republic, it was recorded specifically in crop fields, albeit in sparse stands (Honěk, 1982, 1983); subsequent work found that it occurred in trees early in the year and on herbs later on, in sunny areas (Honěk, 1985). In Belgium, Baugnée and Branquart (2000) reported it as preferring hot, dry habitats, the opposite of those suggested by Majerus in Britain, while Deflorenne et al. (2017) carried out a detailed study of _C. quinquepunctata_ on two spoil heaps at a site in northern France. They concluded that this species preferred open pioneer habitats.

In this paper we examine how the habitat preferences of this species vary latitudinally in western Europe, to resolve these conflicting reports, and because we believe that a better knowledge of this species facilitates a greater understanding of the habitat preferences of ladybirds and other predators. The scarcity of _C. quinquepunctata_ poses a challenge for data collection and we have used data from a wide diversity of sources, including our own observations over 20 years, a one-season geographic study and online data, to provide an overall synthesis of the habitat biology of this species. On the basis of our results we propose a model for how trade-offs related to specialisation mediate geographic variation in the habitat preferences of this species and, intriguingly, how this species benefits from anthropogenic habitat change in parts of its range, but suffers a cost elsewhere.

**Materials and methods**

**Initial observations of Coccinella quinquepunctata**

Initial, and often incidental, observations on the presence or absence of _C. quinquepunctata_ in habitats were made from 1990 at sites in England, France, Germany and The Netherlands. They were used as a starting point for further work detailed in the following. Additional details are provided in Methods and Results S1.

**Western European habitat survey**

From May to July 2012 we carried out a habitat survey for _C. quinquepunctata_ along a geographic transect from Groningen, in the north of the Netherlands, to Madrid in Spain (Fig. S1). The survey focused on six types of habitats: river shingle habitats, non-riverine pioneer habitats (also comprising areas of stony substrate with limited herbaceous plant cover), vegetated stable non-shingle riverbanks, grassland, broadleaf trees, and coniferous trees (Table S1). Sites were classified with respect to _C. quinquepunctata_ as: (i) _C. quinquepunctata_ absent; (ii) occurrence of an isolated individual (only a single specimen present); (iii) extant population (a number of individuals or immature life-history stages).

Further methodological details are provided in Methods and Results S2. Other species of aphidophagous Coccinellinae and Chilicorinae (Nedvěd & Kovář, 2012) were also recorded in our survey.

**Online data on the habitat of Coccinella quinquepunctata in the southern part of its range**

The western European habitat survey suggested that _C. quinquepunctata_ was not found in non-river shingle pioneer habitats in southern Europe, while it could still persist in river shingle. We therefore hypothesised that _C. quinquepunctata_ was
exclusively or largely restricted to humid habitats in the drier southern part of its range. Internet records of *C. quinquepunctata* from south-western Europe south of latitude 48.25°N were used to further investigate this.

Two parallel approaches were carried out. The first focused on the immediate area in which ladybirds were found. The search engine Google (https://www.google.nl) was used (details of search methodology in Methods and Results S3) and habitat was identified on the basis of a description, or if the location coordinates were sufficiently accurate by reference to an aerial photographic map [Google Maps (https://www.google.nl/maps) and/or Google Earth Pro 7.3.2.5491], or from a combination of the two. Records were classified into six categories: river shingle habitat; near (<1 km) to river shingle; other water body; near (<1 km) to other water body; no water body; and, insufficient information (further details in Methods and Results S3). Records were also classified on the basis of whether they were for single or multiple ladybirds.

The second approach used a substantial number of records found for southern France, in which the spatial resolution of locations was limited to 10 km × 10 km squares. These records were obtained from the GBIF online database (https://www.gbif.org/). The 10 × 10-km squares for each record were examined using Google Maps and Google Earth Pro 7.3.2.5491 and classified according to whether they contained river shingle, other open or sparsely vegetated habitats near water, or neither. These data were compared with 20 randomly selected 10 × 10-km squares in southern France, which were examined for the same habitats in the same way. Further methodological details are provided in Methods and Results S3.

**Location of Coccinella quinquepunctata pupae in pioneer habitats in the field**

During the course of the western European habitat survey in 2012 we recorded numbers of *C. quinquepunctata* pupae at two non-riverine pioneer sites, Verdun (France), the southern-most (49.15°N) on 8 July and Marche-en-Famenne (Belgium, 50.22°N) on 15 July. After the end of the survey on 13 August 2012 we further recorded pupae at a more northerly pioneer site in Eindhoven (The Netherlands, 51.4543°N, 5.4666°E). At each of these sites we carried out an exhaustive visual survey of plants above ground and under stones, turning over all stones at the surface of open ground sized over about 2.5 × 2.5 cm. We recorded all living pupae observed in the two different categories of microhabitat, under stones and on plants. Frequencies of pupae on plants and under stones were compared across the three sites using a Fisher–Freeman–Halton test in spss 24.

**Seasonal habitat surveys in the Netherlands**

Over two years, surveys were carried out for *C. quinquepunctata* in the southern Netherlands in different habitats over the course of an entire season. In 2013 this was carried out in Eindhoven, North Brabant (51.45°N, 5.48°E), and in 2014 in Sittard, Limburg (51.00°N, 5.85°E). Surveys were conducted between late April or early May and October in both years.

During the 2013 Eindhoven survey, the habitats corresponded to one of each of the habitats given in the western European habitat survey. Further details are given in Methods and Results S4. Habitats were surveyed at approximately 3-week intervals. The 2014 (Sittard) survey was carried out every c. 4 weeks. The range of habitats was different from those used previously, comprising: a piece of pioneer waste ground near a building site; the edge of a wheat field; a broad grassy verge with wildflowers; a mixed hedgerow; and broadleaf lime trees (*Tilia sp.*) bordering a road (for more details see Methods and Results S4).

**Persistence of Coccinella quinquepunctata populations**

In order to assess the persistence of this species at individual sites, the sites of three *C. quinquepunctata* populations used in other parts of this study were visited between 3 months and 1 year after populations were initially observed. At this time all three sites were visibly more overgrown than they had been when the original observations had been made. The populations were: a river shingle population site at Diekirch, Luxembourg first observed in the western European habitat survey (Table S3; Figs. 1c and S1); a breeding pioneer habitat population in Eindhoven, The Netherlands also used in the pupal study (see Results, Fig. 3) and seasonal habitat survey (Fig. S2a); and, a breeding pioneer habitat population found in Sittard, The Netherlands also used in the seasonal habitat survey (Fig. S2b). Monitoring of sites used in seasonal surveys followed that method. On other occasions a thorough visual inspection of the site was carried out.

**Overwintering of Coccinella quinquepunctata on pine trees in the Netherlands**

Because in initial observations we had quite frequently found *C. quinquepunctata* overwintering on pine trees in the Netherlands, we made more systematic observations on this phenomenon in the winters of 2015/16 and 2017/18. Observations in 2015/16 were made at De Plateaux nature area on the southern border of the Netherlands (51.271°N, 5.404°E), while in both years observations were made at Cadettenkamp, near Breda (51.601°N, 4.833°E). Both sites have areas of open sandy heathland with scattered Scots pine (*Pinus sylvestris L.*) trees and saplings. These plants were searched for the ladybirds, and searches were carried out by eye.

**Results**

**Initial observations of Coccinella quinquepunctata**

Three significantly sized populations were found in central Germany (Bayreuth). In two cases the habitats were relatively sparsely vegetated gravel car parks. The third site was on railway track ballast, also sparsely vegetated. None were near water. Isolated adults of the species were occasionally also found in diverse habitats on a variety of plants. A similar situation
Fig. 1. Maps showing the occurrence of *Coccinella quinquepunctata* in different habitats in western Europe in 2012. (a) Non-pioneer habitats (i.e. non-river shingle or other pioneer habitats) including non-shingle riverbank (R), grassland (G), broadleaf trees (B), conifers (C), and other (O) (details given in Table S3); (b) river shingle habitats; (c) non-riverine pioneer habitats. Open circles, no *C. quinquepunctata*; shaded circles, single occurrence; black circles, multiple occurrences. Basic map from Eurostat (https://ec.europa.eu/eurostat/) © European Union, 1995-2020 © EuroGeographics for the administrative boundaries.

occurred in The Netherlands, where isolated individuals were also found in diverse habitats; the only population comprised multiple individuals on sparsely vegetated waste ground, away from water. Some *C. quinquepunctata* were also found overwintering on conifers.

No *C. quinquepunctata* were located in Britain or France. The former is noteworthy as searches in south-east England were very frequent (weekly or monthly) over a period of 9 years and supports the given restricted northern and western British range for this species (Roy et al., 2011).

More detailed information on initial observations may be found in Methods and Results S1.

**Western European habitat survey**

We recorded 112 adult or immature *C. quinquepunctata*, including 79 adults (5.0% of all ladybird adults) and seven larvae (1.0% of all ladybird larvae) at nine sites, emphasizing the overall scarcity of this species. Of the nine sites, only one was neither a river shingle nor a non-riverine pioneer habitat. In this case, an isolated adult was found on a broadleaf (oak) tree in a park in Arnhem, the Netherlands, at the start of the survey (7 May; Fig. 1a; Table S3). We thus conclude that *C. quinquepunctata* does not regularly occur in other habitats, suggesting it is not a generalist in western Europe,
but is restricted to sparsely vegetated riverine and non-riverine habitats.

Of the other eight incidences, two isolated individuals were at separate non-riverine pioneer sites in Arnhem. Of the cases involving multiple individuals and in some cases immatures, which can all certainly be considered viable populations, three were at river shingle sites (Fig. 1b; Table S3) and three were non-riverine pioneer sites (Fig. 1c; Table S3). Although the total number of sites from which we recorded _C. quinquepunctata_ was small, they appeared to be a geographic pattern in habitat use. Non-riverine pioneer sites appeared to be inhabited by the ladybird only in the north. A comparison of sites with _C. quinquepunctata_ (including the two Arnhem ones) and uninhabited sites north and south of 48.25°N (100 km south of Verdun, this being the most southerly non-riverine pioneer record) was significant (north, five of 18 sites with _C. quinquepunctata_; south, none of 16 sites with _C. quinquepunctata_; one-tailed Fisher’s exact test, _P_ = 0.03), although it should be noted that this test is not based on _a priori_ reasoning. For river shingle sites, there was no significance (using the same division north and south of 48.25°N; north, two of five sites with _C. quinquepunctata_; south, one of nine sites with _C. quinquepunctata_; one-tailed Fisher’s exact test, _P_ = 0.27).

It is worth noting that in the extreme south, no _C. quinquepunctata_ were found at all in Spain (Fig. 1; Table S3), although this species has been recorded there (e.g. Bertolaccini et al., 2011; see Table S4).

*Online data on the habitat of Coccinella quinquepunctata in the southern part of its range*

The internet yielded 22 southern records, which were a mixture of online records and published data (Table S4). The paucity of southern records stood in marked contrast to the much more abundant records to the north (e.g. see map in GBIF Secretariat, 2020). Although this might be due to differences in searching intensity, references for southern France indicated that this species was rare (e.g. Bal, 2012; Classen et al., 2016), and the species was undetected in several regional surveys (e.g. Nicolas, 2014, 2016).

Of the 22 records, four (Table S4, nos. 1, 2, 6 and 7) from two papers (Wyss, 1996; Eschen et al., 2007) were excluded as one or two _C. quinquepunctata_ were detected in surveys in which in excess of 1000 ladybirds were collected. These are most likely to be vagrants and not indicative of a habitat association. Of the remaining 18 records, 10 (55.6%) directly involved river shingle or were close to river shingle, while another four records (22.2%) were at or close to other water bodies. Notable amongst these was the southernmost record, from Sicily (Table S4, no. 19), of multiple _C. quinquepunctata_ from a sandy river. In only two cases (11.1%) was no association with water found (Table S4, nos 4 and 5). These involved multiple individuals of _C. quinquepunctata_ in potato fields in northern Switzerland (Fenjves, 1945). As these were recorded at a relatively high latitude and altitude, it seems likely that these cases group with the habitat preferences of more northerly populations of _C. quinquepunctata_. The species has occasionally been recorded in similar agricultural habitats further north (Jansen & Warnier, 2004; Vandereycken et al., 2015).

The southern French (10 × 10-km squares) dataset (GBIF.org, 2018) contained 29 unique records covering 15 different squares, all in southern France (Table S5a). Multiple records from the same square might potentially constitute different sites or return visits to the same site. Data was thus analysed per record (n = 29) and also per square (n = 15), the latter being compared with the random sample of squares (Table S5b; n = 20). The data are summarised in Fig. 2. All squares contained either river shingle or open wetland, with wetland being present in all squares without shingle; when grouped together there was a significantly higher proportion of these squares than in the random sample (one-tailed Fisher’s exact test, _P_ = 0.01). Only wetland squares gave multiple records, meaning that shingle squares outnumbered wetland squares but that wetland records outnumbered shingle ones. All wetland records were from a small area of southern France centred on the Camargue, and thus in a broader context in a river (Rhône) delta or floodplain environment (Arnaud-Fassetta & Provansal, 2014).

*Location of Coccinella quinquepunctata pupae in pioneer habitats in the field*

The frequencies of pupae on plants versus under stones (Fig. 3) varied significantly across the three sites (Fisher–Freeman–Halton test, _P_ < 0.001), from being exclusively on plants at the northernmost site to being exclusively under stones at the southernmost site. Thus, we conclude that as the climate becomes drier to the south, non-riverine pioneer habitat populations of _C. quinquepunctata_ progressively pupate more at ground level where the microclimate is likely to be damper; this is not the case in damper more northerly climates.

*Seasonal habitat surveys in the Netherlands*

In 2013 in Eindhoven, a total of three _C. quinquepunctata_ adults were found in the pioneer habitat in May and July, while
five individuals were spread across three other habitats. The latter were found either at the start (28 April) or at the end of monitoring (11 August to 14 October; Fig. S2a). Three of these were in conifers, possibly initiating or ending overwintering diapause (cf. final section of results). In Sittard in 2014, the highest numbers of adult *C. quinquepunctata* were found in the pioneer habitat at the start of monitoring, declining to none by 25 July (Fig. S2b). Immature stages were also observed on 31 May, indicating a breeding population. Across the five other habitats only two adults were found, one on 1 May and one on 21 August, again towards the beginning and end of the season (Fig. S2b).

We therefore conclude that in habitats other than their regular pioneer habitats (including river shingle, though not surveyed here), *C. quinquepunctata* are likely to be dispersing adults searching for suitable pioneer habitats to colonise, or inactive at overwintering sites. They are probably more abundant in other habitats at the start and end of the year as they move between overwintering sites (see final section of results) and breeding sites. It is worth noting that in the Czech Republic, Honěk (1985) also records *C. quinquepunctata* on trees early on but not later in the year.

**Persistence of Coccinella quinquepunctata populations**

At Diekirch, a collection of 25 adult *C. quinquepunctata* from the river shingle population was made on 10 and 11 May 2012 at a shingle site on the Sauer (partial data in Table S3), but at a subsequent visit on 18 August 2012 none of this species could be found. Because collecting had been carried out earlier, it is not possible to say with certainty whether the collecting or habitat changes at the site could explain the later absence of the ladybird.

At the Eindhoven site after 5 August 2012, a collection of 95 adults and 19 pupae was made, when the population was first observed. By 2013 only three adults were observed between April and October (Fig. S2a). In this case it seems less likely that collecting was responsible as *C. quinquepunctata* were found nearby in 2013 and could have easily colonised the site.

At Sittard in 2014, a breeding population from May, of minimally 21 adults as well as larvae and pupae, had disappeared completely by 25 July (Fig. S2b). In subsequent visits to the site in 2014, at which time it was already becoming visibly more overgrown, no *C. quinquepunctata* were found (Fig. S2b). No *C. quinquepunctata* were found at the site in 2015, by which time plant coverage was much higher. No *C. quinquepunctata* were ever removed from this site, and thus the disappearance of *C. quinquepunctata* was most likely a consequence of habitat change due to plants overgrowing the site.

We conclude that *C. quinquepunctata* typically persists and breeds at sites for a very short period of weeks or maximally months. This seems likely to be because of specific habitat requirements (most likely bare sparsely vegetated ground) which only occur for a short period during plant succession at a site.

**Overwintering of Coccinella quinquepunctata on pine trees in the Netherlands**

At De Plateaux we recorded 13 *C. quinquepunctata* on pine trees and saplings over an area of c. 50 000 m² on 14 November 2015. Most were found in a smaller area (c. 30 000 m²) where the saplings were less dense with open ground and heather between them. These were often in aggregations with *Coccinella septempunctata* L., which was over 10-fold more abundant, and occasional other species.

At Cadettenkamp, we recorded 56 *C. quinquepunctata* on pine saplings over an area of c. 100 000 m² on 30 and 31 January 2016. Much of the area was open and sandy with pine trees and saplings concentrated in clumps of varying density. In 2018, we collected 11 adults on pine saplings in a much smaller (c. 12 000 m²) area sparsely populated by these trees (estimated at one sapling per 100 m²) on 1 January, and another five individuals at the same area on 25 March, at the end of overwintering. In both years, these were accompanied by much greater numbers of *C. septempunctata*, and also *Coccinella undecimpunctata* L. All three species were found in aggregations together. In 2016 ladybirds of all species were apparently much more abundant than in 2018.

**Discussion**

Our observations re-emphasise that *C. quinquepunctata* is scarce in the west of Europe. Even over the extended time frame of this study, evidence has accumulated slowly and it has been necessary to integrate diverse data sources to build an overall picture. More recently, access to internet observations has been useful, although interpretation of these data can be difficult due to limited habitat or geographic information. In future it seems very likely that database mining will make studies of such species more achievable, but our study serves to illustrate some of the challenges currently associated with this approach.

Nonetheless, the accumulated total evidence has provided a clearer insight into the habitat preference of *C. quinquepunctata*, and a number of lines for further research. At least in the region studied here, nowhere does *C. quinquepunctata* truly

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Fig. 3. Occurrence of *Coccinella quinquepunctata* pupae on plants and under stones at three non-riverine pioneer sites in western Europe at different latitudes.
appear to be a habitat generalist. Except during overwintering, only isolated individuals were ever found in habitats that were not either river shingle or other non-riverine pioneer habitats, characterised by limited plant coverage on a typically stony substrate. However, there is variation in the habitat preference of the species, albeit not that which was previously proposed. In fact, this variation in large part appears to be the opposite of these earlier interpretations. The species appears to colonise river shingle and other sparsely vegetated habitats associated with water throughout its range. We found evidence for this habit at southern latitudes and as far north as Belgium. The absence of this habit from the Netherlands can be explained by the absence of such habitats in a country that is largely flat and thus devoid of the topography required to produce river shingle banks or other disturbed habitats in the vicinity of water.

However, in the 2012 field survey, in northern France, Belgium and The Netherlands, as well as earlier in Germany, this species was found in a broader range of habitats than elsewhere. These habitats share some characteristics with river shingle, i.e. they exhibit limited plant coverage and a stony substrate, but they are not near water. The ladybird was never found in these habitats in southern Europe in our survey. Furthermore, a search of records from the south also failed to find good evidence of colonisation of such habitats. Southern records were often associated specifically with river shingle, or minimally with habitats near water which probably also exhibited sparse vegetation on bare sandy or muddy ground. This was even observable with geographically coarse-grained information on C. quinquepunctata, with the ladybird recorded only in 10 x 10-km squares with shingle rivers or large areas of wetland in them.

We consider that this broader habitat preference in the north is most likely to be facilitated by climatic factors, notably microclimatic humidity, which plays a significant role in the habitat preferences of many taxa (e.g. Cox & Cox, 2015; Fernández et al., 2017; Teofilova, 2018). Ladybird species are known to vary in their tendency to water loss associated with their habitat preferences; unlike many other ladybirds inhabiting drier environments, ladybirds living close to water appear to use evaporative cooling (Pekin, 1996), which presumably limits their ability to live elsewhere. It seems reasonable given its relationship with river shingle that its water relations would be similar, although C. quinquepunctata has not yet been studied in this respect. Hot, dry environments, such as those in southern Europe, would limit C. quinquepunctata to humid river shingle habitats. In more northerly regions, the higher precipitation coupled to lower temperatures would mean that this species could colonise shingle habitats away from rivers. Geographic variation in the pupation site of pioneer populations supports this view, with southern pupae occurring under stones, where the microclimate would be more humid.

The fact that C. quinquepunctata is apparently restricted to river shingle in Britain is particularly interesting given our findings. It is noteworthy that British C. quinquepunctata are restricted to Scotland and Wales (Roy et al., 2011), the wettest parts of the country. South-east Britain, which has little river shingle, also exhibits generally lower soil humidity than the adjacent continent (Willmott & Kenji, 2001; European Soil Data Centre, 2016). This is consistent with the absence of C. quinquepunctata from England, while it occurs on the nearby continent in non-riverine pioneer habitats. Soil humidity, rather than climatic variables, probably provides a reasonably reliable guide to microclimatic humidity. Our observations disagree with Baugnée and Bransquant (2000), who argue that this species prefers hot, dry sites in Belgium, but it is questionable whether any site in this country could truly be described as hot and dry in comparison with similar types of sites in southern Europe. Interestingly, as one moves south, the species appears to become rarer, as might be expected as its habitat requirements become more stringent.

Although detailed prey lists do not exist, previous authors, as well as our own observations, indicate that this is an aphidophagous generalist (e.g. Klausnitzer & Klausnitzer, 1997; Roy et al., 2011). There is therefore no reason to think that C. quinquepunctata is limited in its habitat due to a specialised aphid diet. This does not necessarily mean that food availability or durability, rather than aphid species, has not led to the habitat association; feeding in humid areas might provide C. quinquepunctata with access to populations of long-lasting aphids that would die off earlier in drier habitats elsewhere (Sloggett & Majerus, 2000a; Majerus, 2016). However, it seems that habitat-related characteristics rather than dietary ones act to ‘trap’ the ladybird in the habitat as a specialist. Because the habitat is humid, the ladybird cannot persist for long periods at lower humidities. Non-riverine populations in northern Europe probably exist away from water bodies because in these regions such pioneer habitats have a humid microclimate, facilitating expansion from rivers into these habitats. The habitat preference is the same but manifested differently. On this basis, C. quinquepunctata is a single entity, not divided into genetically differentiated non-riverine and riverine populations with different habitat preferences. Indeed, in places where C. quinquepunctata inhabits riverine and non-riverine areas, it probably moves between the two equally suitable humid habitats. Although diet as a cause of habitat change and diversification has been emphasised in a variety of predators (e.g. Sadeghi & Gilbert, 1999, 2000; Pekár et al., 2012; Scharrweber et al., 2016), including aphidophagous ladybirds (e.g. Rana et al., 2002; Fukunaga & Akimoto, 2007; Sloggett, 2008b), this study serves to emphasise that other environmental factors can play a significant role for predators in determining suitable habitat (Honěk, 1985; Tschá & Pie, 2019).

Specialist ladybirds often persist in one patch or area for long period of time, within and across seasons (e.g. Majerus, 1989; Sloggett et al., 2008). However, associated with its preference for pioneer habitats, which rapidly become overgrown, C. quinquepunctata population turnover appears to be high and it typically persists at individual sites for a short period of time. It is worth noting that with human intervention, some populations, such as the railway sidings in Bayreuth, seemed to be of longer duration, probably because vegetation management/removal meant they were permanently maintained with the optimal limited vegetation cover. The overwintering biology of C. quinquepunctata also warrants further investigation. Majerus (1994, 2016) states that riverine populations of C. quinquepunctata in the U.K. overwinter on or near to the shingle banks and this may be true for other shingle populations of C. quinquepunctata. Some non-riverine pioneer populations also
occur in their summer habitat, as in Bayreuth; however, evidence from The Netherlands, suggests that many *C. quinquepunctata* disperse to other areas, notably conifer stands, to overwinter. This again might be associated with microclimate: overwintering among living pine needles might constitute a more humid environment with a lower risk of freezing than exposed terrestrial pioneer sites. Dispersal to and from overwintering habitats and between both types of pioneer sites can explain records of isolated *C. quinquepunctata* in other habitats, as indicated by seasonal surveys, and probably the claims that it is a habitat generalist in continental Europe.

In recent years ladybirds have been emphasised as a group containing species under threat and requiring conservation (e.g. Losey et al., 2007; Adriaens et al., 2015). Many of the causes of species decline are attributed to competition with invasive ladybirds, but other factors, such as habitat destruction, are also thought to play a role (Roy & Majerus, 2010). In this context *C. quinquepunctata* is interesting because of its scarcity and the geographic variation it shows in the habitat it occupies. In areas where the species is restricted to river shingle, it has probably lost habitat due to river straightening and flood control, which can lead to the loss of natural river dynamics and shingle banks (Brooker, 1985; Majerus, 1994). However, by contrast, in non-riverine pioneer habitats, *C. quinquepunctata* is certainly a beneficiary of human activity, as many disturbed habitats are created by humans. In this study, they comprised railway sidings, car parks, building sites, and waste ground. Thus in northern Europe this species appears to be a commensal of humans. This latter beneficial effect of human activities mirrors that already proposed for the generalist 2-spot ladybird, *Adalia bipunctata* (L.), which is often suggested to be under threat (Sloggett, 2017). It makes it clear that beneficial anthropogenic effects may hold more broadly for ladybirds, for specialists as well as generalists. It is notable that assessments of the threat to *C. quinquepunctata* vary depending on location (e.g. Roy et al., 2011; Adriaens et al., 2015), along with habitat preference. Assuming that *C. quinquepunctata* is a single species, as we suggest here, arguably the greatest ultimate threat it faces is climate change. This could reduce the cooler, wetter regions where this species can successfully live away from rivers as a beneficiary of human activity.

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### Author contributions

JJS originally formulated the idea. JJS and IZ developed the methodology, conducted the fieldwork and developed further ideas based on earlier findings. JJS conducted non-fieldwork aspects of the research and wrote the manuscript with editorial advice from IZ.

### Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

### Methods and Results S1. Additional information for the main paper sections *Initial observations of Coccinella quinquepunctata.*

### Methods and Results S2. Additional information for the main paper sections *Western European habitat survey.*

### Methods and Results S3. Additional information for the main paper sections *Online data on the habitat of Coccinella quinquepunctata in the southern part of its range.*

### Methods and Results S4. Additional information for the main paper sections *Seasonal habitat surveys in the Netherlands.*

Table S1. Types of habitats surveyed during the western European habitat survey in 2012.

Table S2. Aphidophagous ladybird species recorded during the western European habitat survey in 2012.

Table S3. Summary of results of the western European habitat survey in 2012.

Table S4. Details of online records of south-west European *C. quinquepunctata* and the habitat assessments made from them.

Table S5a. Occurrence and habitat data from southern French 10km x 10km squares.

Table S5b. Randomly selected 10km x 10km squares in southern France and habitat type.

Fig. S1. Map of all site locations visited during the course of the western European habitat survey in 2012.

Fig. S2. Numbers of *C. quinquepunctata* adults recorded in the seasonal habitat surveys in the Netherlands in (a) Eindhoven in 2013 (b) Sittard in 2014.

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