

WHAT DRIVES NON-NATIVE AMPHIPOD DISTRIBUTIONS IN THE RIVER THAMES?  
THE ROLE OF HABITAT AND HUMAN ACTIVITY ON SPECIES ABUNDANCE

BY

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ABSTRACT

Increasing colonization of non-native amphipod species in the River Thames, United Kingdom, has altered aquatic ecology and called existing management practices into question. We studied the distribution patterns of recent non-native (*Dikerogammarus haemobaphes* (Eichwald, 1841)), established non-native (*Crangonyx pseudogracilis* (Bousfield, 1958)), and native amphipod (*Gammarus pulex* (Linnaeus, 1758)) species, as well as habitat and human influences across 84 sites in the upper Thames catchment. Our findings showed widespread distribution and density of *G. pulex* relative to *D. haemobaphes*, suggesting that the full impact

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of the current spread has yet to be felt since its 2012 introduction. Different habitat utilization patterns are explained through habitat partitioning: both *D. haemobaphes* and *C. pseudogracilis* occupied vegetative habitats, not pebble/gravel habitats where the native *G. pulex* was most often found. The association between *D. haemobaphes* and boating presence implies that effective biosecurity would be best focused on boat traffic in the Thames and Cherwell.

## INTRODUCTION

Globally, freshwater ecosystems are experiencing significant ecological change and deterioration in function due to environmental pressures, and in particular, from biological invasions or an increase in range of non-native species (Sala et al., 2000; sensu Coullatti et al., 2004; JNCC, 2013; UN Convention on Biological Diversity). More so than terrestrial ecosystems, freshwater ecosystems are vulnerable to the spread of non-native species due to a high degree of natural isolation and endemism (Richter et al., 1997, Ricciardi & Rasmussen, 1998). The introduction and occurrence of non-native aquatic species, particularly from the Ponto-Caspian region into Western Europe (Gallardo & Aldridge, 2015), highlights the susceptibility of UK navigable waters to generalist invaders. Moreover, invertebrates worldwide (including freshwater) have largely been ignored in conservation policies and studies (Zamin et al., 2010; Cardoso et al., 2011), despite their remarkable diversity and vital role in ecosystem function (Wilson, 1987). Thus, the protection of freshwaters will depend on identifying those risks and pathways that facilitate the spread of non-native species. For rivers such as the Thames where the full impact of non-native species on ecosystem function is poorly understood, it may be prudent to incorporate knowledge of risks and pathways into Statutory Agency policy, advice and best practice in order to minimize the dispersal of non-native species.

The River Thames is currently one of the world's most highly invaded freshwater ecosystems (Jackson & Grey, 2013). Invasion rates in the Thames have accelerated since the mid-20<sup>th</sup> century because favourable climate, habitat overlap, and efficiencies in global trade have facilitated colonization (Jackson & Grey, 2013). Species introductions in major estuaries provide a consistent source of propagules leading to the potential establishment of non-native populations throughout a catchment (Jackson & Grey, 2013) where dispersal is facilitated by waterways linking aquatic habitats (Rahel & Olden, 2008). Common vectors that transport aquatic non-native species into the UK include ballast water, ornamental plants and animals, and aquatic equipment such as boats and fishing gear.

Over the last two centuries, Ponto-Caspian aquatic species, native to the Black, Azov and Caspian Seas, have increased their range across continental Western Europe via the Rhine estuary and Dutch ports, and into the River Thames (and other locations in the UK) (Ketelaars, 2004; Gallardo & Aldridge, 2015). Compared to other non-natives, Ponto-Caspian species are highly suited to colonize south eastern UK (Gallardo & Aldridge, 2015) due to climatic and habitat similarities between the two regions (Gallardo & Aldridge, 2013), and they pose a documented deleterious effect on UK ecology and economy (Oreska & Aldridge, 2011). Despite that, little is known about the interaction effects between Ponto-Caspian non-native species, other invading species, and native species both generally and in UK freshwater.

The River Thames now contains a total of 96 non-native freshwater species and of these non-natives, 23 originate from the Ponto-Caspian region and 12 belong to the Subphylum Crustacea, Order Amphipoda (Gallardo & Aldridge, 2015). Non-native amphipod species are of high ecological concern because they can dramatically change community structure (Slothouber Galbreath et al., 2010; MacNeil et al., 2014) and functional groups (Constable & Birkby, 2016).

They can also cause native species extinction (Krisp & Maier, 2005), reduce species richness and diversity (Dick & Platvoet, 2000), and can result in losses to fish productivity (Kelly & Dick, 2005). For instance, the Ponto-Caspian amphipod species *Dikerogammarus villosus* (Sowinsky, 1894) has been shown to eliminate populations of native *Gammarus duebeni* (Lilljeborg, 1851) in the Netherlands (Dick & Platvoet, 2000).

Recent identifications of Ponto-Caspian amphipod species in UK freshwater have raised concern about an unprecedented ‘invasion’ of Ponto-Caspian species that poses a unique threat to national biosecurity (Gallardo & Aldridge, 2015). For example, *D. villosus* was reported in 2010 at Grafham Water Reservoir, Cambridgeshire (MacNeil et al., 2010), and then in May 2012 *Dikerogammarus haemobaphes* (Eichwald, 1841) was recorded in the River Severn in Gloucestershire (Aldridge, 2013); both were likely transported via recreational boating or aquatic equipment (Larson et al., 2010, MacNeil & Dick, 2014). Previous research has focused on literature-based analyses, meta-analyses, or horizon scanning to provide risk-based approaches to the management of the spread of non-natives (Jackson & Grey, 2013; Roy et al., 2014; Gallardo & Aldridge, 2015), e.g. distribution maps of high-risk areas with regard to Ponto-Caspian species in the UK and Europe (Gallardo & Aldridge, 2015). Gallardo and Aldridge (2013) claim that aggressive behavior and opportunistic feeding habits of Ponto-Caspian species allows for a dominance in the food web and subsequent displacement of native and other non-native species. In our study in the Thames catchment, our assumption is that proliferation of non-native species is potentially detrimental to aquatic ecosystem function, and that non-natives may have a negative interaction with native species. A lack of field-based surveys has limited our understanding of species interaction patterns at the site-scale, despite the potential importance of

habitat indicators in the assessment of invasive species impacts within UK freshwater (Gaertner et al., 2009).

Field studies of invertebrate distribution patterns are needed to characterize population ranges in situ between native, established non-native, and invasive amphipod species. Biotic factors, such as competition and predation, and interacting abiotic factors, such as water quality drive freshwater distribution patterns and are likely to shape competitive dynamics among resident and non-native species (Lodge & Hill, 1994; Petren & Case, 1996; Strayer, 2009, MacNeil & Dick, 2014; Ashelby et al., 2016). In order to explore the distribution patterns of key amphipod species, we used the River Thames and selected tributaries in Oxfordshire as a model of an invaded system. The River Thames contains a wide diversity of habitats and uses, which allows for hypothesis testing related to ecological and anthropogenic controls on non-native colonization. We aimed to evaluate the distribution patterns of non-native, established non-native, and native amphipod species, as well as habitat and human influences. We used field surveys to answer two key questions: 1) What are the distribution patterns of native and non-native amphipod species and is the relative abundance of species positive, neutral (co-existence) or negative? 2) How do habitat and human activities affect these distribution patterns?

## MATERIAL AND METHODS

### Site description and survey design

Our study area focused on the benthic communities of the River Thames and its upper tributaries in the county of Oxfordshire. A total of 84 sites were sampled, 67 of which contained amphipod species, across 24 rivers and their tributaries in June 2015 (tables I, II). Sites were sampled to represent a range of substrate types, exposures to human activity, and river sizes.

Each river sampled was grouped according to its 'order' which was defined by convention using first order streams as the smallest at the 1:250,000 scale (Gordon et al., 2004). Using this approach, and for the purposes of this study, the River Thames in Oxfordshire was classified as a fourth order river. The 84 sites were chosen in consultation with the Environment Agency, who conduct routine monitoring on many of these watercourses, but had not carried out any recent surveys, specifically for invasive shrimps, at any of these locations.

At each site, a semi-quantitative adapted kick sampling method was employed. To standardise the catch effort, a standard of 20 kicks (Wheater et al., 2011) were taken using a standard kick net (150 mm frame, 1mm polyester mesh, supplied by EBE & GB NETS; Environment Agency, 2003). Field parameters recorded were: human activity at time of sampling (boats, fishing, farming, none) and dominant observable broad substrate types (pebbles/gravel, vegetation or silt) after MacNeil & Dick (2014); additional parameters were site location and river order. Substrate parameters were restricted to the substrate sampled, rather than the overall river bed substrate. The vegetation parameter was limited to submerged aquatic species at the sampling site, not larger riparian habitats. Amphipod species were preserved on the same day of sampling in 70% ethanol and were later identified to species level and for gender (based on Dobson, 2013 and Gledhill et al., 1993) using a Leica MZ10F stereomicroscope equipped with a Moticam 580 camera. Specimen photos were taken for reference with the built-in software, Motic Images Plus 2.0. A count of shrimp per sample was used as a measure of abundance (Magurran, 2009).

## Data analysis

ArcGIS software (ESRI ArcMap 9.3.1) was used to create geo-referenced maps of the spatial distribution data. Statistical analyses on the presence/absence data for the 67 sites were carried out using R Studio Version 3.1.1 (R Development Core Team, 2015). Generalized linear models (GLM) were built in a stepwise fashion with consideration to AIC values and variables were added to models only when the significance level threshold of 0.01 or below was achieved. GLMs were used to examine associations among species and between species and the covariates river order, substrate type and human activity. Wald's odds ratio tests were performed on relevant coefficients to determine the overall significance of effects.

## RESULTS

### Patterns of amphipod species distribution in the field

We recorded widespread distributions of three amphipod species across the upper reaches of the River Thames (fig. 1, table I). Native *Gammarus pulex* (Linnaeus, 1758) was the most widespread throughout the sampled catchment and was recorded at 47 out of a total of 67 sites. The two non-native species were less widespread: *Crangonyx pseudogracilis* (Bousfield, 1958) was found at 21 out of a total of 67 sites, and *D. haemobaphes* was recorded at 16 sites. Species density is defined as the number of species per specified collection area or unit (Magurran, 2009), in this case one kick sample, while frequency is the number of sampling units in which a species occurs (Magurran, 2009). Compared to the non-natives, *G. pulex* populations were more frequent and abundant overall as well as consistently dense along the surveyed length of the tributaries (e.g. on the River Windrush there was an average of 59 *G. pulex* and a range of 3 to 125 specimens,  $n = 9$ ). Relatively small populations of *C. pseudogracilis* were recorded in tributaries of the Thames as far north as the Sor Brook. In contrast, *D. haemobaphes* appeared

confined to the River Thames, downstream of the highest lock at Lechlade, and the River Cherwell downstream of its interaction with the Oxford canal. No amphipod species were found at 17 sample sites, including sites along all river orders.

#### River order

River order was not a statistically significant factor contributing to population density distributions of *C. pseudogracilis*, *G. pulex*, or *D. haemobaphes*, the latter of which was restricted to fourth order rivers (including the Seacourt Stream which is an anabranch of the Thames).

#### Species co-occurrence and presence/absence

Native *G. pulex* was found more frequently and in consistently greater abundance across the sample sites than the other two species. Of the 67 sites containing amphipod species, 37 sites contained only *G. pulex*, 9 contained only *D. haemobaphes*, 5 contained only *C. pseudogracilis*, and 0 contained all three species. *G. pulex* was largely absent at sites with *D. haemobaphes* but both co-occurred with *C. pseudogracilis* (table II).

Based on density measurements, we observed that *G. pulex* was dominant in habitats where it co-occurred with *C. pseudogracilis* but data were inconclusive regarding *D. haemobaphes*. *G. pulex* occurred with only *C. pseudogracilis* at 10 sites, and there was an average of 12 *G. pulex* compared to an average of 4 *C. pseudogracilis*. *G. pulex* and *D. haemobaphes* were found together only once, where *D. haemobaphes* dominated 10 to 1. From the 16 sites where *D. haemobaphes* was found, 6 sites contained *D. haemobaphes* and *C.*



*pseudogracilis*, where the average abundance of *D. haemobaphes* was 7 compared to 2 for *C. pseudogracilis*.

From the presence/absence data, the relationship between *G. pulex* and the presence of *D. haemobaphes* was significant with *G. pulex* being strongly negatively associated with *D. haemobaphes* (GLM estimate = -4.93, P = 0.000014) (table III). Similarly, the relationship between *G. pulex* and the presence of *C. pseudogracilis* was significant and *C. pseudogracilis* was strongly negatively associated with *G. pulex* (GLM estimate = -1.51, P = 0.0085). *D. haemobaphes* and *C. pseudogracilis* were not significantly related.

#### River habitat characteristics

Variation in substrate type, measured as pebble/gravel, silt or submerged vegetation, had a significant association on the population sizes of all shrimps (table III). The relationship between the presence of *D. haemobaphes* and the substrate classed as vegetation was significant, and positively associated (GLM estimate = 1.41, P = 0.0335), whereas the presence of *D. haemobaphes* was negatively associated with pebbles/gravel (GLM estimate = -1.76, P = 0.000066). Likewise, *C. pseudogracilis* was positively associated with vegetation (GLM estimate = 1.53, P = 0.014) and negatively associated with pebbles/gravel (GLM estimate = -1.42, P = 0.00032). *G. pulex*, in contrast, was negatively associated with vegetation (GLM estimate = -1.30, P = 0.038) and positively with pebbles/gravel (GLM estimate = 1.42, P = 0.00032).

Wald's odds ratio test was consistent with findings from the generalized linear regression models. The test indicated that for the presence of *D. haemobaphes* and *C. pseudogracilis*, the chance of finding either shrimp was approximately 4 times more likely in vegetation compared

to pebbles/gravel, and nearly 3 times more likely in silt than pebbles. For *G. pulex*, the Wald test indicated the reverse: *G. pulex* was more likely found in pebbles/gravel than vegetation.

### Human activities

Boats were present at 11 sample sites (all on River Thames) and 3 sites contained fishing areas, while 6 sites were directly adjacent to or on farms. Linear models showed that human activity (boats, fishing, farming) was not significantly associated with presence measurements. Yet, boats may be a major vector for upstream transport of invasive species (Leung et al. 2006; Jackson & Grey 2013). As a proof of concept, attached algae growing on 2 boats along Port Meadow in Oxford were randomly sampled below the water line by scraping a net through the algae and 6 *C. pseudogracilis* specimens were found within the bio-film.

## DISCUSSION

### Ecological implications for the River Thames case study

Our study is the first to document the distribution patterns of a native, established non-native, and recently arrived non-native amphipod species in the River Thames catchment. The results presented here illustrate an early snapshot of a recently-arrived non-native amphipod species in a catchment containing high numbers of non-native aquatic species, and we predict that, in time, *D. haemobaphes* will replace *G. pulex* across the catchment. Furthermore, data collected by the UK Environment Agency (Biosys database) for the River Thames from 2005 to 2016 (table IV) illustrates the changing abundance of *G. pulex* and *D. haemobaphes*; *G. pulex* has not been recorded at some sites recently, which corroborates our 2015 data of relatively reduced *G. pulex* counts compared to the other two species (table IV). Our findings are based on

semi-quantitatively sampled data for the presence/absence and abundance of three amphipod species in the upper Thames catchment. Count data revealed higher densities of *D. haemobaphes* when it occurred with *C. pseudogracilis*, but nearly equal density of both when they occurred separately. Habitat partitioning may explain our findings: e.g. both invasive species occurred in diverse habitats such as solid substrates and in macrophytes, but showed a preference for habitats with vegetation cover. By contrast, pebble/gravel rich sites were more likely to provide habitats with greater feeding opportunities for *G. pulex* and these areas were located in the upper reaches of the River Thames where the species occurred. Furthermore, Aldridge et al. (2004) provide evidence for direct habitat facilitation with other non-native Ponto-Caspian species such as *Dreissena polymorpha* (Pallas, 1771; zebra mussel) which can provide habitat for gammarid shrimps in the form of mussel shells and byssus threads.

The recorded abundance of *C. pseudogracilis*, where it occurred with either *G. pulex* or *D. haemobaphes*, was lower relative to the other two amphipod species. *G. pulex* was only recorded with *D. haemobaphes* at one site, with the latter's abundance being greater. Our regression models predicted fewer *G. pulex* when *D. haemobaphes* was present, and fewer *C. pseudogracilis* when *G. pulex* was present. We expected higher proportions of *D. haemobaphes* where they co-existed with other amphipod species because they are known to outcompete other similar species elsewhere e.g. the Ponto-Caspian amphipod species *Pontogammarus robustoides* (Sars, 1894) and *Echinogammarus ischnus* (Stebbing, 1899) (Jazdzewski et al. 2004), and our finding with *C. pseudogracilis* supported this hypothesis. *D. haemobaphes* was introduced to the UK relatively recently, and our data still only reflect an early snapshot of non-native distributions. Jackson (2015) speculates that the duration of many individual studies are too short to detect negative interspecific effects, thus global meta-analyses find a predominance of neutral

interactions and additive impacts. Although focused on a different species, the study by Truhlar & Aldridge (2015) on behavioural traits and interactions between invasive *D. villosus* and native *G. pulex* provides a helpful approach to the interpretation of our data. They explored boldness, aggression, activity, exploration and sociability as a means of explaining invasion success and displacement of native Gammarid species. They found that *D. villosus* is not an active disperser (low activity and exploration, high sociability) but driven by passive invasive means (drifting and transportation on boats).

The widespread distribution and density of *G. pulex* across the catchment relative to *D. haemobaphes* suggests several interpretations: First, this work was conducted during the first three years of the arrival of *D. haemobaphes* in the River Thames and the full impact of the current spread of species has yet to be felt. Second, the native species is exerting biotic resistance to the incoming non-native, although this seems unlikely given the reported spread of *D. haemobaphes* in Central Europe (Bacela-Spychalska & van der Velde, 2013; Bacela-Spychalska 2016) and the observed absence of *G. pulex* on much of the main River Thames (table IV), where it has previously been recorded by the Environment Agency. Third, that the sampling technique we employed in our study may have biased the collection of *G. pulex*.

*D. haemobaphes* has been recorded by the EA in other UK catchments and tributaries, suggesting that colonization may have not yet reached some areas of the upper River Thames catchment. This may be due to the presence of locks or weirs preventing their progress, or because of low propagule pressure, and not because *D. haemobaphes* is unsuited to these habitats or *G. pulex* is actually dominating. Like our study, EA abundance data show that *D. haemobaphes* tends to outnumber and then effectively replace *G. pulex* in English rivers when they initially co-occur; the EA uses a standard 3-minute kick sample for surveying

macroinvertebrates (Murray-Bligh, 1999), which differs from our study where a 20 kick sample (Wheater et al., 2011) was used. Thus, comparisons of EA abundance and presence/absence data from our study and that collected by the EA are not directly comparable. Furthermore, sampling higher order rivers, such as the main channel of the River Thames, can be problematic using a kick sampling method. Suction sampling of large and deep rivers may yield a more representative sample of species abundance and diversity.

In addition, predation of *C. pseudogracilis* by *G. pulex* might explain the discrepancy in population where both species co-occur in the field, or differences in habitat preference. Originally from the North American Great Lakes, *C. pseudogracilis* may prefer lentic and littoral habitats in Oxfordshire, as demonstrated by the results of MacNeil et al. (2014) who found that the species has adapted to slow flowing environments on the Isle of Man. Laboratory studies on the interaction between *Gammarus spp.* and *C. pseudogracilis* support our findings and indicate that the latter is subject to intense predation from the former if they encounter one another in the same microhabitat (MacNeil & Dick, 2014). A laboratory study (Mantzorou, 2013, unpublished thesis) focusing on *C. pseudogracilis*, *G. pulex*, and *D. haemobaphes* found that *C. pseudogracilis* shifted its diet to a higher trophic level, using diet partitioning as a means to avoid interspecific competition, though no predatory superiority of *D. haemobaphes* over *G. pulex* was found. Our findings indicate otherwise: *G. pulex* and *D. haemobaphes* were collected together only once and at all other locations on the River Thames where *D. haemobaphes* was recorded, *G. pulex* had previously been present prior to the arrival of *D. haemobaphes*. Bovy et al. (2015) conducted further laboratory experiments and confirmed that *D. haemobaphes* did not exhibit the same predatory ability as *D. villosus* but was able to exploit alternative foods which benefitted population growth. *D. haemobaphes* was able to prey successfully on the invasive

tube-building amphipod species *Chelicorophium curvispinum* (Sars, 1895), leading them to hypothesize that an established non-native facilitated the establishment of *D. haemobaphes*.

Although other studies and our data do not show competition between non-natives in the field or laboratory, a study conducted over time could provide evidence for another hypothesis, which suggests that different non-native species come to dominate a community by out-competing others (Lohrer & Whitlatch, 2002). For instance, *D. villosus* is expected to eventually colonize in the UK and outcompete *D. haemobaphes*, as it did in the Danube following an initial *D. haemobaphes* invasion (Grabowski et al., 2007). The underlying assumption of this hypothesis is that species are ‘ecologically equivalent’ and competitive; as Dick (1996) shows, it is necessary for ecological equivalents to occupy the same habitat range before species replacements via interspecific interactions occur. Interspecific interactions, abiotic conditions and the combined effects of the two influence the structure and species assemblages of non-native and native species (MacNeil & Dick, 2014). For instance, Ashelby et al. (2016) investigated seasonal competitive dietary interactions between a native and non-native shrimp species of *Palaemon* in the tidal River Thames and found a higher degree of dietary overlap, and therefore competition, in winter compared to summer. Whether similar seasonal interactions occur between shrimp species in the freshwater River Thames may provide insight to the degree of competition between native and non-native shrimp species across the catchment.

In this study, we have shown that three amphipod species have different habitat utilization patterns. We found that both *D. haemobaphes* and *C. pseudogracilis* occupied vegetative habitats and were far less likely to be found in pebble/gravel habitats, where the native *G. pulex* was most often found. Of the habitat types measured, native *G. pulex* preferred predominantly pebbled/graveled areas compared to silty areas or submerged vegetation. Elliott

(2005) found that stony substratum with varied interstice sizes provided refuge from currents and predators, which may help explain the association we found for *G. pulex* and this habitat. Conversely, we found that both non-native species were associated with vegetation and silt habitat types. Our findings concerning *D. haemobaphes* corroborated the work of Pöckl (1988) who found that the amphipod species exists in diverse habitats including solid substrates, macrophytes and algae at the local scale, as well as MacNeil & Dick (2014) who suggested that macrophyte cover provided the best habitat for *C. pseudogracilis* in the Isle of Man.

### Management implications

Though ballast water is one possible vector for non-native amphipod species into the Thames Estuary (Jackson & Grey, 2013), boat traffic and contaminated equipment are the most likely cause of species introductions higher into the Thames catchment. In this study, the association between *D. haemobaphes*, fourth order rivers and boating presence, implies that effective biosecurity and management strategies would be best focused on managing boat traffic in rivers such as the Thames and Cherwell.

It is possible that *D. haemobaphes* has not been found above the Thames at Lechlade or in small tributaries because of barriers such as locks and weirs, but transportation via fishing or aquatic sports equipment may bring them into new habitats, a passive invasion process substantiated by the experimental work of Truhlar and Aldridge (2015). A recent study by Anderson et al. (2015) demonstrating that hot water (45°C for 15 mins) kills 99% of all organisms found in water sports equipment, could be advertised as a national recommendation to boating and fishing clubs alike. Updating the recreational guides published by local boat clubs

and cruising clubs to emphasize the significance of cleaning practices in non-native abatement (e.g. Clean Check Dry) could limit non-native species spread in the Thames River.

Experimental research by Bacela-Spychalska (2016) reinforces the types of management strategies needed by demonstrating the tenacity of two species of invasive shrimp, *D. haemobaphes* and *P. robustoides* to removal: these amphipod species stayed attached to sailing and angling rope despite repeated shaking. In the UK, *D. villosus* was first discovered in a reservoir, suggesting transmission not by ballast water but by boat or fishing equipment. Although populations are presently restricted to a few locations in Cambridgeshire, Norfolk and South Wales, *D. villosus* has been shown to eliminate populations of native *G. duebeni* in the Netherlands (Dick & Platvoet, 2000) and is thus of great concern to British amphipod species diversity, particularly in locations where other non-natives, such as *D. haemobaphes* are already established.

#### ACKNOWLEDGMENTS

We thank Dr. Sammy De Grave for advice on specimen identification at the Museum of Natural History. We thank Mona Edwards at the School of Geography and the Environment, University of Oxford for use of the microscope and field equipment; and Michael Chipps at Thames Water for help with this project and discussion of the data. The research was supported by a Sir Peter Elworthy grant, School of Geography and the Environment, University of Oxford, and a Rhodes Scholarship.

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Fig. 1. Maps of presence/absence data for three amphipod species at all sites in June 2015, Oxfordshire, UK. Colored circles reflect species presence and black circles represent species absence.