

# Explaining abundance–occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters

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## Summary

1. A positive interspecific abundance–occupancy relationship is one of the most robust patterns in macroecology. Yet, the mechanisms driving this pattern are poorly understood. Here, we use biological traits of freshwater macroinvertebrates to gain a mechanistic understanding and disentangle the various explanations. We ask whether mechanisms underlying the abundance–occupancy relationship differ between species, and whether information on individual species can be used to explain their contribution to the interspecific relationship.

2. We test the hypothesis that the importance of metapopulation dynamics or niche differences in explaining the relationship differs between species, varying in relation to their habitat breadth. In addition, we analyse how a species' biological traits shape its habitat breadth and its abundance and occupancy.

3. The abundance and occupancy of the 234 different aquatic macroinvertebrate species were strongly and positively related. Marked differences were found between habitat specialists and habitat generalists in the goodness-of-fit of abundance–occupancy relationships. The occupancy–frequency distribution was bimodal for habitat generalists, allowing 'satellite species' to be distinguished from 'core species'.

4. Habitat generalists appeared to be more widespread but less abundant than habitat specialists, suggesting that the jack-of-all-trades may be master-of-none. Species traits (trophic position and other life-history traits) explained a significant part of the variation around the general relationship. Among habitat specialists, more species showed synchronized life cycles, a low dispersal capacity or clustered oviposition, being better adapted to predictable habitats. Among habitat generalists, more species had long-lived adults, spreading reproductive effort in time and space, and were strong dispersers, being better adapted to unpredictable habitats.

5. Interspecific abundance–occupancy relationships can be best understood by examining the contribution of individual species. For habitat specialists, the interplay between niche differences (diet and habitat use) and the underlying spatial distribution of environmental conditions result in competitive displacement and differences in species' success. For habitat generalists, differences in colonization and extinction rates between species are more important. Therefore, both metapopulation dynamics and niche differences can operate simultaneously but apply to different species, thus constituting different endpoints of the same continuum.

**Key-words:** aggregation, aquatic insects, biological traits, causal mechanisms, core–satellite hypothesis, density, dispersal, distribution, metapopulation dynamics, niche breadth

## Introduction

Widespread species are likely to occur in high densities whereas species restricted in their distribution tend to be scarce. This positive interspecific abundance–occupancy rela-

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relationship across different species is one of the most robust patterns in macroecology (Gaston *et al.* 2000; Blackburn, Cassey & Gaston 2006) and is observed on different scales (Brown 1984; Cowley *et al.* 2001a). This relationship is intimately linked to species–area relationships and species–abundance distributions (Leitner & Rosenzweig 1997; McGill & Collins 2003) and has significant implications for reserve selection and predicting extinction risk (Lawton 1993; Brown, Mehlman & Stevens 1995; Gaston 1999).

Explanations for interspecific abundance–occupancy relationships include possible artefacts related to sampling and phylogenetic non-independence, as well as more ecologically based explanations, which mainly focus on either niche differences between species or metapopulation dynamics (Gaston, Blackburn & Lawton 1997). Although the pattern under investigation is generated across many species, the position of each data point, the abundance and occupancy of a single species, is driven by causal mechanisms operating at the level of that species, something which is rarely explicitly considered.

According to metapopulation-based explanations of abundance–occupancy relationships, locally abundant species have higher chances of becoming widespread due to a lower extinction rate, a higher colonization rate or both (Gotelli 1991; Nee, Gregory & May 1991; Freckleton *et al.* 2005). In addition, widespread species have the best chances of filling up empty patches, thereby reducing the probability of local extinction (rescue effect) and becoming locally abundant (Hanski & Gyllenberg 1993; Hubbell 1997). The abundance and occupancy of a single species may therefore feedback into each other through (meta)population dynamics, i.e. reproduction, dispersal and establishment of individuals (Fig. 1). Different species may occupy different points along

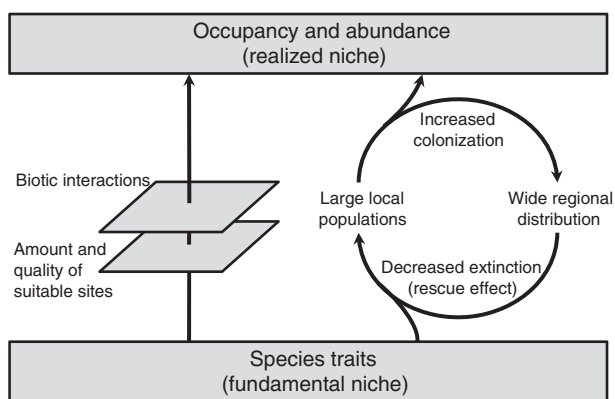
their trajectories (Brown *et al.* 1995), thus giving rise to a positive interspecific abundance–occupancy relationship.

Whereas metapopulation-based explanations frequently assume species and patches are equivalent (Hengeveld & Walter 1999), differences between species and patches are at the core of niche-based explanations. Niche differences between species may result in competitive displacement and habitat partitioning (Fig. 1). Here, the abundance and occupancy of a single species may be linked indirectly if the local amount of resources (or patch quality) and their regional distribution (or the proportion of habitable patches) are linked themselves (termed the resource availability hypothesis by Gaston *et al.* 1997). As a result, when locally abundant resources are also widely distributed and vice versa, the interspecific abundance–occupancy relationship of species utilizing these resources will also be positive. Axiomatically, when patch quality is normally distributed among patches and assuming a quality threshold above which a patch is habitable, this condition is fulfilled (Freckleton *et al.* 2005). Alternatively, a positive relationship can arise when species with a broad niche are able to tolerate a broad set of environmental conditions and use a wide range of resources, which enable them to become both locally abundant and widespread, i.e. the ‘jack-of-all-trades’ is master of all (Brown 1984; Brown *et al.* 1995; Gaston *et al.* 1997).

Both explanations similarly predict positive relationships and even random distributions may generate a positive relationship (Wright 1991). Thus, not all positive relationships are the same (Hartley 1998). Furthermore, the explanations are not mutually exclusive and could act in concert; each explanation may be valid, albeit on different scales or under different environmental conditions (Gaston *et al.* 1997, 2000; Bossuyt, Honnay & Hermy 2004; Heino 2005). In addition, each explanation may be hypothesized to be valid but apply to different sets of species within regional assemblages. To understand interspecific patterns, such as abundance–occupancy relationships, it may therefore be fruitful to deconstruct these patterns into their more basic components, i.e. by examining the contribution of individual species, rather than further analysing the relationship itself (Wright 1991; Cowley *et al.* 2001a; Gaston, Chown & Evans 2008).

Previous studies that focused on the contribution of individual species, have either looked at the influence of basic species attributes on the relationship, including body size, dispersal mode, diet (Murray *et al.* 2002; Tales, Keith & Oberdorff 2004; Foggo, Bilton & Rundle 2007) or analysed subsets of species categorized by some emergent attributes such as habitat preference, population status and trend (e.g. Holt & Gaston 2003; Webb, Noble & Freckleton 2007) or both (e.g. Cowley *et al.* 2001b; Bossuyt *et al.* 2004).

In the present study of lentic freshwater macroinvertebrates, we employ both a bottom-up approach, using basic biological species traits, and a top-down approach, using the emergent species attribute of habitat breadth to investigate the observed abundance–occupancy relationship. We ask whether mechanisms underlying this relationship differ



**Fig. 1.** Schematic representation of communities structured by either (left) niche differences with a large role for filters set by environmental conditions and biotic interactions or (right) population dynamics, where local and regional patterns are linked through colonization and extinction. For reasons of clarity, we have only shown the situation applying to core-populations, with positive feedbacks between local abundance and regional distribution. In both explanatory frameworks, differences in biological traits between species (e.g. reproduction, dispersal and trophic position) may influence their success at a local (abundance) and regional scale (occupancy).

between habitat generalists and habitat specialists, and whether information on individual species can be used to explain their contribution to the overall relationship. Biological species traits shape a species' fundamental niche and also its realized niche, through interactions with their environment including other species (Southwood 1977; Hengeveld & Walter 1999; Chase & Leibold 2003; McGill *et al.* 2006). Additionally, differences in the rate of colonization and extinction between species are themselves rooted in biological traits related to reproduction and dispersal. With species traits (fundamental niche) as the mechanistic drivers giving rise to patterns in the abundance and occupancy of species (i.e. realized niches) for both explanatory frameworks (Fig. 1), the bottom-up approach and the top-down approach provide complementary ways to study abundance–occupancy patterns.

We begin by outlining how niche-based explanations would predict different occupancy–frequency distributions and differences in the goodness-of-fit of the relationship compared to metapopulation-based explanations. We test the (top-down) prediction that niche-based mechanisms operate mainly for species discriminating strongly between different types of water bodies (habitat specialists), whereas metapopulation-based mechanisms will operate for species not discriminating in this way (habitat generalists). We outline expected differences in abundance and occupancy between species that differ in life-history strategy and trophic position, and explicitly test whether observed deviations from the abundance–occupancy pattern match these expected differences. We then relate both approaches, and test the expectation that habitat specialists and habitat generalists differ in life-history strategy and trophic position.

#### EXPECTED DIFFERENCES BETWEEN NICHE-BASED AND METAPOPOPULATION-BASED EXPLANATIONS

As metapopulation-based explanations assume species and patches are equivalent, they are more likely to hold for habitat generalists, as they discriminate less between different types of water body and effectively perceive the landscape as being more homogenous. In contrast, niche-based mechanisms are more likely to operate for habitat specialists, as they strongly respond to variation in environmental conditions (Collins & Glenn 1997; Bossuyt *et al.* 2004). Although for both explanatory frameworks a positive interspecific abundance–occupancy relationship is most likely, they are expected to differ in two aspects.

First, a better fit (less scatter) of the abundance–occupancy relationship is expected to result from metapopulation-based mechanisms, as abundance and occupancy would be closely and directly linked as they feedback into each (Fig. 1). Within the niche-based framework, a positive abundance–occupancy relationship arises indirectly if patch quality and the availability of habitable patches are themselves positively correlated (Gaston *et al.* 1997). However, what constitutes a suitable habitat differs between species. Even when quality and availability are positively related, each species will track

a different relationship providing a high degree of scatter. The niche-based framework also predicts a positive relationship if species with a broad niche are both abundant and widespread and vice versa (Brown 1984). This is almost identical to the previous rationale, but here the suitability of a habitat is defined from a species' attributes, rather than its resources (i.e. high-quality habitats are widespread and vice versa due to interspecific differences in the determinants of habitat suitability). However, within the niche-based framework it is not impossible, or even unlikely, for species to have a high density in particular highly suitable patches (Brönmark & Hansson 2005; Komonen, Päävinen & Kotiaho 2009), with the scarcity of suitable patches precluding a wider distribution. The resulting combination of a high density and a low occupancy weakens the abundance–occupancy relationship, but this effect does not operate within the metapopulation-based framework.

Secondly, the positive feedbacks between regional occupancy and local abundance in metapopulation-based explanations predict bimodal occupancy–frequency distributions, where most populations of species are either liable to extinction or relatively stable, termed satellite and core species respectively (Hanski 1982; Gotelli 1991). In contrast, niche-based mechanisms explain occupancy and abundance in relation to the fit of environmental conditions matching the niche requirements of species, which is predicted to result in a gradual decline of species distributions with most species being narrowly distributed and a few widespread, leading to a unimodal, right-skewed distribution (Brown 1984).

#### EXPECTED DEVIATIONS IN SPECIES DIFFERING IN LIFE-HISTORY STRATEGY AND TROPHIC POSITION

Few studies have examined abundance–occupancy relationships in lentic macroinvertebrates, but water bodies, like true islands, offer excellent opportunities to study fundamental ecological patterns and processes (Whittaker 1998). The clear boundaries between – potentially – suitable and unsuitable habitat in water bodies provide the advantage that many different species groups of aquatic macroinvertebrates could be included, providing strong contrasts between species in their biological traits and trophic position. Rather than focussing on separate traits we focus here on the combination of traits possessed by a species, as traits usually act in concert and are interrelated through trade-offs (Stearns 1976; Stutzner *et al.* 1997; Olden, Poff & Bestgen 2008). For example, species with short-lived adults usually undertake few migration events and oviposit their eggs in a single or a few large batches, whereas species with long-lived adults show directed migration and spread oviposition of single eggs or small batches over many locations. Based on combinations of traits, life-history strategies for aquatic macroinvertebrates have been previously defined (Verberk, Siepel & Esselink 2008a; Table 1). For each life-history strategy, we made qualitative predictions concerning their abundance and occupancy, based on differences in their traits (Fig. 2). All else being equal, traits expected to increase the abundance of a species

**Table 1.** Overview of the life-history strategies and their most defining species traits in relation to occupancy and abundance. Less defining species traits and species traits varying within a strategy are left blank. Strategies are ranked from highest to lowest relative abundance (see text). Abbreviations of life-history strategies follow Verberk *et al.* (2008 a,b)

Life-history strategy	Number of species	Active dispersal	Rate of juvenile development	Adult longevity	Synchronization of juvenile development	Synchronization of adult emergence	Type of oviposition	Clutch size	High voltinism	Hermaphroditism	Asexual reproduction	Rank order
R4	8	None	Rapid		No	No				x	x	1
T2	7	None	Slow	Months–years	No	No				x	x	1
R2	3	None	Slow	Months	Some					x		2
R3	3	None	Rapid	Months	Low			Small	x	x		2
D2	4	Strong	Slow			Yes	Clustered	Large				3
D3	11	Moderate	Rapid		No	No	Clustered		x		(x)	3
S1	19	Moderate	Slow	Weeks		Yes	Clustered				(x)	3
T1	49	Weak	Slow		Low							3
S4	13	None	Rapid	Months–years	Yes	Yes		Small		x		4
S2	24	Moderate	Rapid		Yes	Yes	Scattered					5
S3	21	Moderate	Rapid	Months–years	Yes	Yes	Scattered					5
D1	45	Strong	Rapid	Months–years		Some	Scattered					6
R1	27	Moderate	Rapid	Months–years			Scattered	Small				6

are related to a high reproductive output (Blackburn, Gaston & Gregory 1997; Holt *et al.* 1997), including body size, large clutch size, multiple generations or asexual reproduction. Likewise, distribution is expected to increase with traits related to dispersal, such as wing size, body size and dispersal mode (e.g. active or passive dispersal) (Hanski & Gyllenberg 1993; Gutiérrez & Menendez 1997; Foggo *et al.* 2007; Rundle *et al.* 2007). In addition, increased aggregation (e.g. by restricting dispersal, or clumped egg deposition) can shape abundance–occupancy relationships (Hartley 1998), elevating local abundance, while simultaneously decreasing occupancy. As many more factors interact to set a species' absolute abundance and occupancy (e.g. the environment, species interactions and colonization and extinction processes; Fig. 1), we focussed our expectations on the deviations around the relationship, rather than the relationship itself (Wright 1991; Cowley *et al.* 2001a). Therefore, we combined the qualitative predictions for abundance and occupancy to rank life-history strategies from being relatively abundant, for a given occupancy, to being relatively scarce (or alternatively from relatively restricted to widespread): R4, T2 (highest relative abundance) > R2, R3 > D2, D3, S1, T1 > S4 > S2, S3 > D1, R1 (lowest relative abundance).

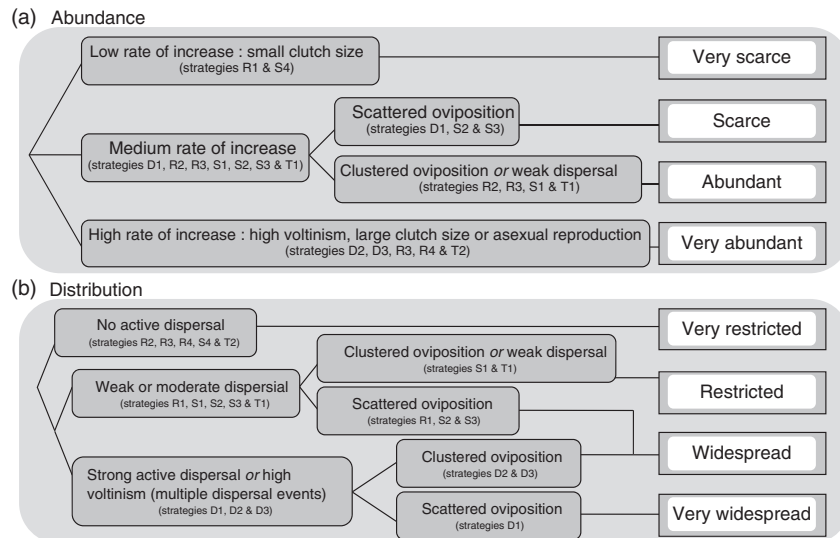
Furthermore, as less and less energy is transferred through each successive link in the food chain, predators are expected to be relatively less abundant (or alternatively more widespread) than prey of comparable body size and reproductive rate due to energetic limitations (Hutchinson 1959; Heino 2008).

## Materials and methods

### STUDY AREA AND SAMPLING

The study was conducted in the Korenburgerveen nature reserve in the Netherlands (N51°59'; E6°39'; 310 ha). In this heterogeneous wetland, 37 water bodies were sampled for aquatic macroinvertebrates using a standard 30 × 20 cm pond net with a mesh size of 0.5 mm. Samples consisted of a sweep starting from the substrate and from more or less open water into denser vegetation near the shore. To obtain a sample that is representative for the water body, separate subsamples were taken to include different distinguishable microhabitats, where appropriate. All subsamples from a site were pooled before further analyses. Samples were sorted in the laboratory. Tricladida, Hirudinea, Oligochaeta, Araneae, Crustacea, Odonata, Hemiptera (adults and nymphs), Ephemeroptera, Plecoptera, Megaloptera, Coleoptera (adults and larvae), Diptera (Cylindrotomidae, Chaoboridae, Dixidae, Culicidae and Chironomidae) and Trichoptera were identified to the lowest taxonomic level possible, which in most cases was to species.

All water bodies were sampled twice (spring and autumn). On each site (pooling seasons and microhabitats), the total area sampled was on average 0.78 m<sup>2</sup> and on average 1107 individuals were collected with a minimum of 137. Comparing the observed species richness with total species richness, estimated using the Abundance-based Coverage Estimator (ACE) of species richness (using Estimates, version 8.20, R.K. Colwell,



**Fig. 2.** Flow diagram visualizing how traits related to dispersal, reproduction and egg deposition are predicted to affect the abundance and occupancy of species. Life-history strategies (representing different combination of traits, see Table 1) are shown in brackets.

http://purl.oclc.org/estimates), yielded a sampling efficiency of about 75% for the pooled data. Preliminary analyses on either spring or autumn data generated strong and positive interspecific abundance–occupancy relationships. An even stronger relationship was found when data from both seasons were combined (in effect increasing the sample effort), demonstrating that the relationship did not artificially arise from low sampling effort (Gaston *et al.* 1997). A species’ abundance on a site is expressed as the number of individuals per m<sup>2</sup> bottom surface area.

LIFE-HISTORY STRATEGIES

All 234 taxa collected were assigned to a life-history strategy, based on information regarding the species traits they possessed, the inter-relationships between traits known from life-history theory and the functional implications of the different combinations of species traits (see Verberk *et al.* 2008a; Verberk, Siepel & Esselink 2008b; Appendix S1, Supporting Information for a list of species and their life-history strategies). Life-history strategies focus on a species’ capabilities

and constraints, connecting species and their environment and aggregating species with similar causal connections.

HABITAT BREADTH

Sampled water bodies were previously classified into three main types of water body and eight subtypes. These categories of water body provide a relevant framework for calculating a species’ habitat breadth as they reflect relevant differences in environmental conditions for aquatic macroinvertebrates (nutrient concentrations, acidity, alkalinity, soil type, dimensions, degree of shading and vegetation composition; Table 2). The derivation and description of this typology is reported in detail elsewhere (Verberk *et al.* 2006, 2008b).

Habitat breadth was calculated with the proportional similarity (PS) index (Feinsinger, Spears & Poole 1981), relating the proportion of a species’ population found in each category of water body to the proportion of sampling effort (area sampled) for that category:

**Table 2.** Subdivision of the 37 sampled water bodies in three main water types and eight water subtypes. Differences in physical and chemical conditions between the different water types are shown as averages ± standard error

Main type	Subtype (no. water bodies sampled)	pH	Alkalinity (meq L <sup>-1</sup> )	NO <sub>3</sub> <sup>-</sup> (µmol L <sup>-1</sup> )	Size (m <sup>2</sup> )	Depth (cm)	Shading (%)	Temporary <sup>a</sup>
Bog pools	Large bog pools ( <i>n</i> = 6)	3.7 ± 0	0 ± 0	4.3 ± 0.6	34 ± 15	0.5 ± 0.2	27 ± 9	0 ± 0
	Small bog pools ( <i>n</i> = 5)	3.8 ± 0.1	0 ± 0	5 ± 0.6	19 ± 10	0.5 ± 0.1	32 ± 7	0.1 ± 0.1
	Small, shaded bog puddles ( <i>n</i> = 4)	3.8 ± 0.1	0 ± 0	5.1 ± 0.9	5 ± 3	0.5 ± 0.3	51 ± 25	0.3 ± 0.3
Water bodies in wet forests	Water bodies in <i>Salix–Betula</i> forests ( <i>n</i> = 3)	5.1 ± 0.6	0.31 ± 0.25	3 ± 0.5	22 ± 4	0.4 ± 0	51 ± 27	0.4 ± 0.1
	Water bodies in <i>Salix–Alnus</i> forests ( <i>n</i> = 7)	6.2 ± 0.3	1.63 ± 0.43	41.4 ± 26.6	25 ± 7	0.3 ± 0.1	56 ± 17	0.4 ± 0.2
Mesotrophic waters	Shallow mesotrophic puddles ( <i>n</i> = 3)	5.3 ± 0.5	0.25 ± 0.1	4 ± 0.1	20 ± 4	0.4 ± 0.1	30 ± 13	0.3 ± 0.2
	Mesotrophic pools ( <i>n</i> = 5)	5.7 ± 0.2	0.36 ± 0.16	4.6 ± 0.8	408 ± 236	1.1 ± 0.2	13 ± 5	0 ± 0
	Buffered mesotrophic pools ( <i>n</i> = 4)	6.5 ± 0.2	1.13 ± 0.24	1.8 ± 0.2	128 ± 55	0.8 ± 0.1	25 ± 4	0.1 ± 0.1

<sup>a</sup>Propensity to desiccation of a water body, ranging from 0 (permanent) to 1 (temporary).

$$\text{PS index} = 1 - 0.5 \sum_i |p_i - q_i|, \quad \text{eqn 1}$$

where  $p_i$  is the proportion of individuals in water bodies of category  $i$  and  $q_i$  is proportion of area sampled relative to the total area sampled in all water bodies. Values for the PS index express variation in a species' habitat breadth, which is an important aspect of its realized niche, and range from 1.0 for the broadest possible niche to  $[\min q_i]$  for the narrowest possible niche (a population is restricted exclusively to the rarest category of water body and consequently bypasses all other water bodies). Species captured in only one water body were classified as rare species and excluded from most analyses as no reliable measure of niche breadth could be calculated. The PS index was calculated separately for each category of water body (the three main types and the eight subtypes), generating two scores (PS index<sub>subtype</sub> & PS index<sub>main type</sub>). Species which scored high for both categories, indicating a broad niche, were classified as habitat generalists when the product of both their rank-transformed PS indices fell in the upper third percentile. The remaining species were classified as habitat specialists and were subdivided into habitat specialists (rank-transformed PS index<sub>subtype</sub> > PS index<sub>main type</sub>) and strict habitat specialists (rank-transformed PS index<sub>subtype</sub> < PS index<sub>main type</sub>). Species and their habitat breadths are listed in Appendix S1.

Species were classified independent of their absolute abundance and occupancy, through the use of the PS index. This allows abundant and widespread species to be also classified as habitat specialists when high proportions of individuals are found in a single category of water body and vice versa. In addition to a categorical classification of habitat breadth, a continuous measure of habitat breadth was calculated by multiplying their rank-transformed PS indices for both categories of water body (cat. 1: the three main types and cat. 2: the eight subtypes).

#### TROPHIC POSITION

For each species, information on their diet (algae, detritus and animals) was taken from the literature. As most biomass is assimilated during the larval stage, the diet of larvae took precedence for species with feeding adults and larvae. Species which are documented to feed exclusively on detritus, algae or animals were classified as detritivores, algivores or carnivores, respectively. Species documented to feed on two or more food sources were classified as omnivores. The trophic position of species is listed in Appendix S1.

#### DATA ANALYSIS

To measure the goodness-of-fit for all species and subsets of species differing in habitat breadth, Pearson correlations between abundance and occupancy were calculated. Here, we take the most commonly used measure of mean local abundance (abundance averaged over occupied samples). Preliminary analyses yielded similar results for other measures of abundance, including maximum abundance (maximum abundance within the set of samples) and total mean abundance (abundance averaged over all samples), demonstrating that for our data, Wilson's assertion (2008) that abundance–occupancy relationships may be influenced by the type of abundance measure used does not apply.

Frequency distribution plots for the occupancy of species differing in habitat breadth (strict habitat specialists, habitat specialists and habitat generalists) were statistically analysed following the approach given by Tokeshi (1992). The occupancy–frequency distributions had

10 classes with even interval widths (i.e. 0.1). Tokeshi's test allows the calculation of significant deviations from a uniform distribution (no pattern) for the total distribution ( $P_c < 0.05$ ) as well as for different frequency classes separately. Although this latter analysis is usually restricted to the left-most and right-most classes ( $P_l$ ,  $P_r$ ), it can be used for each class ( $P_n$ ) to assist visual interpretation of modality. Significant deviations in one frequency class or several consecutive classes would indicate a unimodal distribution, whereas multiple non-consecutive deviations would indicate bimodal or multimodal distributions. To test if occupancy–frequency distributions were unimodal in strict specialists and specialists but bimodal in generalists, we calculated  $P$ -values for the total distributions ( $P_c$ ) and  $P$ -values for each class ( $P_{n1} \dots P_{n10}$ ). We used an interval width of 0.2 to calculate the  $P_c$  for generalists due to the low number of species in the left-most frequency class and an interval width of 0.1 in all other calculations.

To examine the contribution of individual species to the interspecific abundance–occupancy relationship, we analysed deviations from the relationship using an ANCOVA approach. We took abundance as a dependent variable and occupancy as a covariate. Both the bottom-up and top-down modelling approaches were employed. Differences between slopes and intercepts were tested using ANCOVA with trophic position and the rank order of life-history strategies as fixed factors in the bottom-up model and habitat breadth as fixed factor in the top-down model. For the bottom-up model, we fitted the full model (trophic position + rank order + trophic position  $\times$  rank order) and three simplified models (trophic position; rank order; trophic position + rank order) and calculated the Akaike's information criterion (AIC) of each to select the best-supported model, using the formulae given in Johnson & Omland (2004). For all analyses, occupancy was calculated as the proportion of all sites at which a species occurred (ranging from 0 to 1), and abundance as mean density per m<sup>2</sup>. Abundance was log-transformed and occupancy was logit-transformed (base 10) to improve normality. All statistical analyses were performed using SPSS version 16.0. (SPSS Inc., Chicago, Illinois, USA)

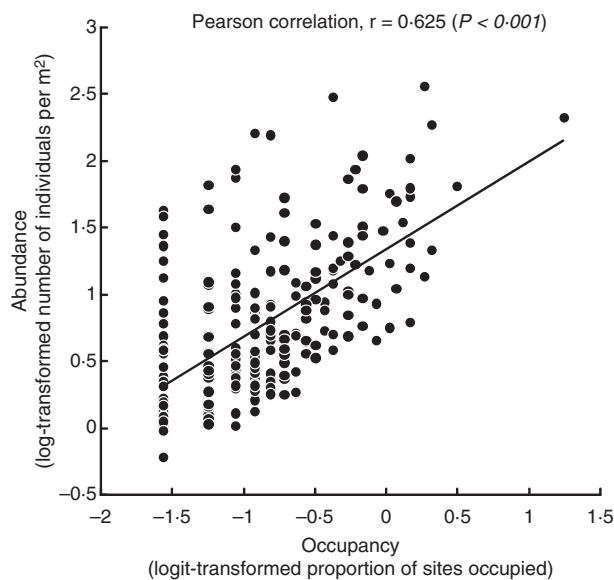
The choice of the dependent variable (abundance or occupancy) depends on which one is the driver and which one is the response. As causality can be argued to run from either abundance to occupancy or vice versa, both approaches can be justified and indeed have been used in the literature (Brown 1984; Blackburn *et al.* 1997; Quinn *et al.* 1997; Heino 2008). Here, we have chosen abundance as the dependent variable, as in both explanatory frameworks occupancy can set local abundance; either directly through the rescue effect, or indirectly by giving an approximation of the amount of suitable habitat, which in turn shapes species–abundance through its association with the degree of suitability. Furthermore, in our data occupancy has a lower variability compared to abundance (having been established through the larger sampling effort of all water bodies, rather than just the occupied ones) and therefore better meets the statistical requirements of linear regressions where the regressor is assumed to be free of error. Finally, most species were found at few sites, yet despite their low variation in occupancy, they varied widely in abundance. Regression lines taking abundance as the dependent variable better capture this variation and intersect with the abundance axis, giving an intercept that is biologically interpretable as an average threshold density below which species cannot persist (Freckleton *et al.* 2005). Better interpretation also applies to the investigation of habitat breadth and trophic position as possible causes for variation around the relationship as these are more likely to cause deviations primarily in abundance rather than occupancy (Gaston *et al.* 1997; Leibold *et al.* 2004).

## Results

### EXPECTED DIFFERENCES BETWEEN NICHE-BASED AND METAPOPULATION-BASED EXPLANATIONS

More than 44 000 individuals belonging to 234 species were captured and identified. The abundance and occupancy of these species were strongly and positively correlated (Fig. 3). The goodness-of-fit differed between habitat specialists and generalists and confirmed the prediction that for habitat generalists the abundance was more closely related to occupancy compared to habitat specialists (Table 3).

The occupancy-frequency distributions shown in Fig. 4 all significantly deviated from a uniform distribution (Tokeshi test,  $P_c < 0.0057$ ). The occupancy-frequency distribution for all species was strongly right-skewed and exhibited no bimodality (Fig. 4a). However, species differing in habitat breadth exhibited different distribution patterns, which matched our predictions. For strict habitat specialists and habitat specialists (Fig. 4b,c), the occupancy-frequency distributions were again strongly right-skewed but for habitat generalists (Fig. 4d), the distribution was found to be bimodal, with frequencies peaking around 10–30% (*c.* 7 sites



**Fig. 3.** Interspecific relationship between log abundance (number of individuals per  $m^2$  averaged across all occupied water bodies) and occupancy (proportion of occupied water bodies). Each data point represents a different species ( $n = 234$ ).

**Table 3.** Pearson correlations between the log abundance and logit occupancy of all species and different subsets of species. All correlations were highly significant ( $P < 0.001$ )

Species analysed ( $n$ )	Pearson correlation, $r$
All species (234)	0.625
Strict habitat specialists (49)	0.594
Habitat specialists (66)	0.541
Strict specialists and specialists (115)	0.579
Habitat generalists (57)	0.836

occupied) and 50–60% (*c.* 20 sites occupied) ( $P_n < 0.024$ ). Thus, it seems possible to distinguish ‘satellite species’ from ‘core species’ in habitat generalists but not in habitat specialists.

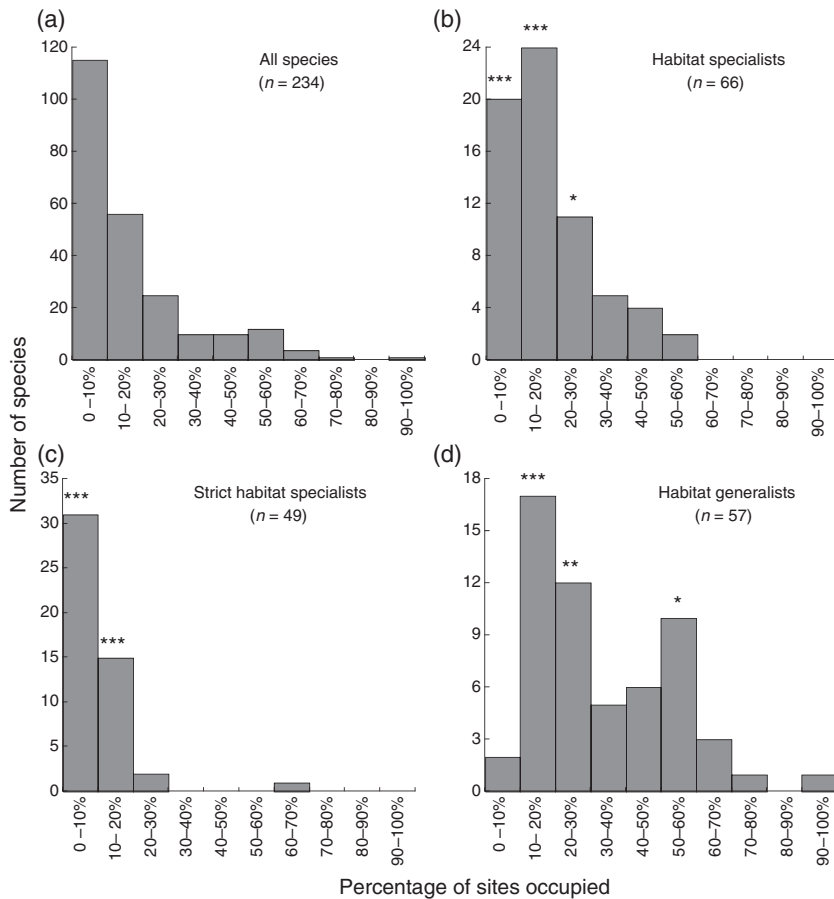
### VARIATION AROUND THE ABUNDANCE–OCCUPANCY RELATIONSHIP

ANCOVA indicated no significant differences between the slopes of the abundance–occupancy relationships of the various subsets of species differing in their habitat breadth, trophic position or rank order of life-history strategy. However, differences between the intercepts were evident for all subsets, indicating that the observed deviations from the abundance–occupancy relationship (Fig. 3) were at least partly related to interspecific differences in both habitat breadth (Table 4, top-down model) and a combination of trophic position and life-history strategy (Table 4, bottom-up model). Both models were highly significant and explained most of the variation (adjusted  $R^2 > 0.793$ ). Whittingham *et al.* (2006) advise to fit full models when the AIC of simplified models is only marginally lower. Therefore, we show the test results for the full, most comprehensive, bottom-up model as its AIC of  $-401.1$  fell in the lower range (from  $-387.1$  to  $-404.5$ ).

For a given occupancy, habitat specialists were more abundant than habitat generalists [Fig. 5a, multiple linear regression, standardized partial regression coefficient (beta) =  $-0.473$ ,  $t_{1,169} = -7.418$ ,  $P < 0.001$ ]. To visualize the differences in relative abundance for species differing in life-history strategy and trophic position, we plotted the intercepts from the abundance–occupancy relationships calculated from separate ANCOVAs (Fig. 5b,c). The predicted rank order based on a species’ life-history strategy matched the pattern in relative abundance (Fig. 5b). Species without active dispersal and a high intrinsic rate of increase (strategies R3, R4 and T2) showed high relative abundance, being more abundant than expected based on their occupancy (or vice versa, having a lower occupancy than expected based on their abundance). In contrast, species with widely scattered oviposition and moderate or strong active dispersal (strategies R1, S2, S3 and D1) showed low relative abundance. Relative abundances also covaried with a species’ trophic position, with non-carnivores being more abundant, especially detritivores (Fig. 5c). This observed trend corresponds with the expectations based on energetics and food web position.

### RELATING HABITAT BREADTH TO TROPHIC POSITION AND LIFE-HISTORY STRATEGY

The habitat breadth of a species was found to be associated with its life-history strategy, trophic position or a combination thereof (Fig. 6). For species with a synchronized life cycle (strategies S1, S2, S3 and S4), a higher percentage was assigned as habitat specialists or strict habitat specialists, whereas more species with long-lived adults spreading reproductive effort in time and space (strategies D1, R1, R2 and R3) were assigned as habitat generalists. For the remaining



**Fig. 4.** Frequency distributions of the occupancy for all species (a) and subsets of species differing in habitat breadth (b-d). Asterisks denote significant deviations from a uniform distribution: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

**Table 4.** Results of ANCOVA tests taking log-transformed mean local abundance as the dependent variable and logit-transformed occupancy as a covariate. Results are shown for both the bottom-up model (taking life-history strategy and trophic position as independent variables) and the top-down model (taking habitat breadth as independent variable). Significant  $P$ -values shown in bold

Source	SS (Type III)	d.f.	$F$ -ratio	$P$ -value
Top-down model (Adj. $R^2 = 0.793$ , AIC = -394.0)				
Model	163.90	5	180.31	< 0.0001
Occupancy	22.98	1	126.42	< 0.0001
Habitat breadth <sup>a</sup>	116.99	4	160.88	< 0.0001
Error	41.63	229		
Bottom-up model (Adj. $R^2 = 0.809$ , AIC = -401.1)				
Model	169.40	19	53.04	< 0.0001
Occupancy	20.52	1	122.08	< 0.0001
Life-history strategy <sup>b</sup>	2.69	5	3.20	0.00827
Trophic position	2.14	3	4.25	0.00609
Life-history strategy <sup>b</sup> × Trophic position	2.33	9	1.54	0.134
Error	36.14	215		

<sup>a</sup>Categorical measure with four categories (strict habitat specialists, habitat specialists, habitat generalists and rare species).

<sup>b</sup>Predicted rank order of life-history strategies (six categories, see text).

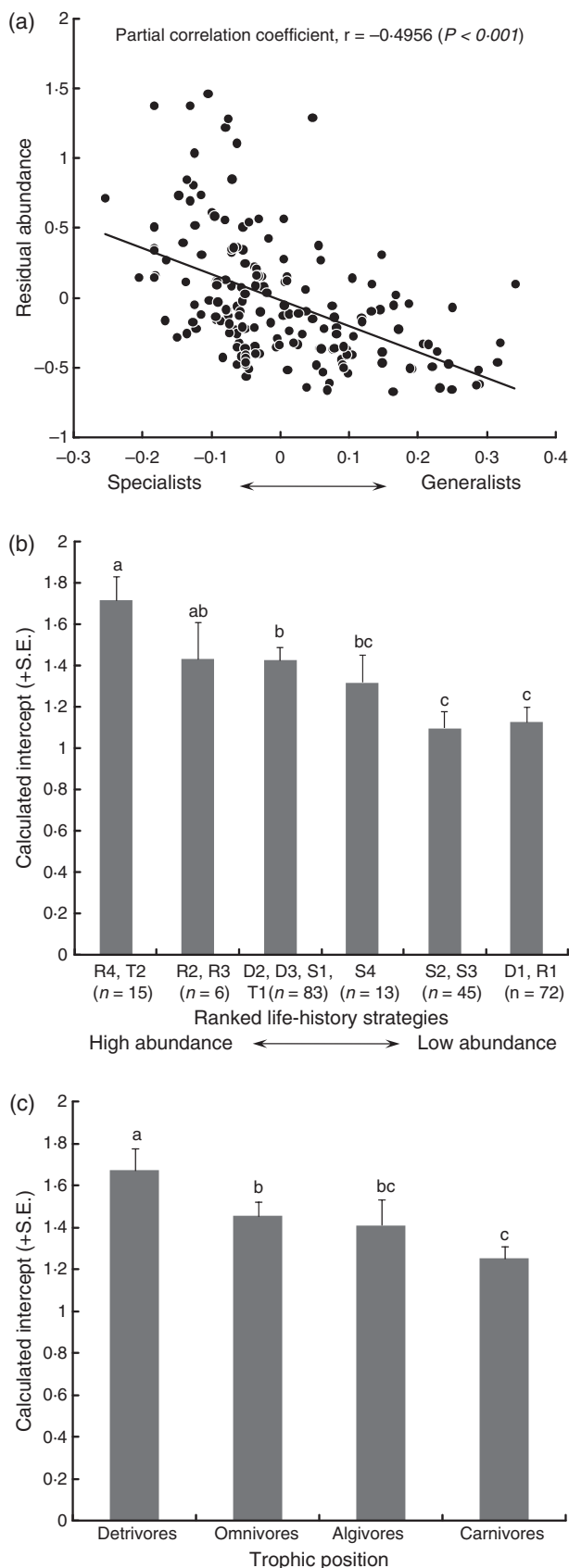
species that lacked active dispersal (strategies T2 and R4), more were assigned as habitat specialists or strict habitat specialists.

Habitat breadth also covaried with trophic position. Many habitat generalists fed on high-quality food sources (algivores and carnivores) whereas many habitat specialists and strict habitat specialists fed on low-quality food sources (detritivores and detri-algivores). This difference was more pronounced when only species with a slow juvenile development were included in the comparison (strategies D2, R2, S1, T1 and T2), indicating a combined effect of trophic position and life-history strategy in shaping a species' habitat breadth. Similarly, a connection between a species' trophic position and its life-history strategy is indicated by the striking result that all of the 15 algivorous species are capable of active dispersal.

## Discussion

Here, we report a positive relationship between a species' abundance and its occupancy across a diverse assemblage of species from various systematic groups occurring within standing water bodies (Fig. 3). Despite the generality of such positive relationships, the bulk of variance typically remains unexplained, with median values around 20–30% (Gaston 1996). Part of this unexplained variation may be related to



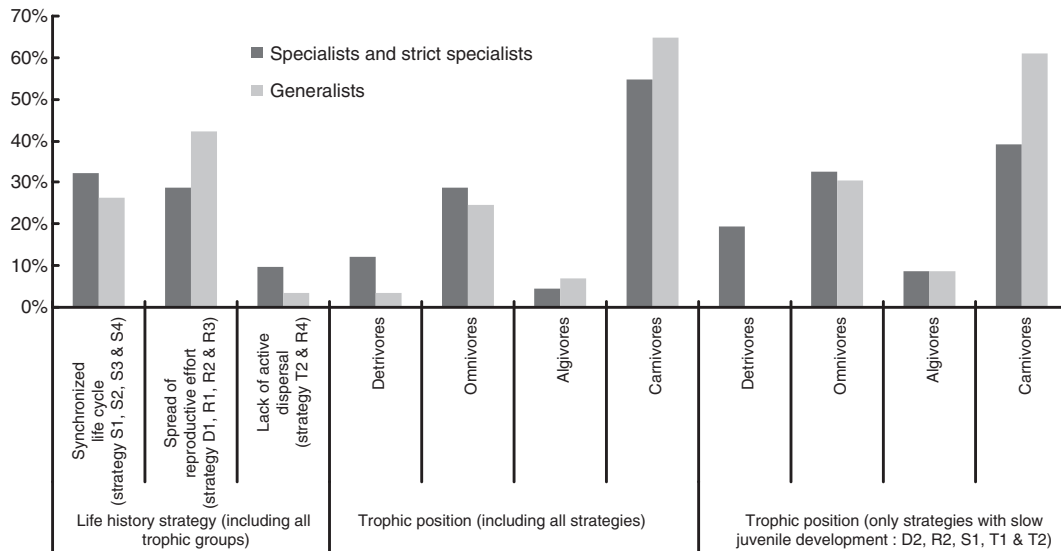


**Fig. 5.** Effect of habitat breadth (a), life-history strategy (b) and trophic position (c) on the abundance (accounting for occupancy). Effects of habitat breadth (expressed as a continuous variable) are shown in a partial correlation plot (both abundance and habitat breadth adjusted for occupancy). Each data point represents a different species ( $n = 172$ ). Effects of life-history strategy and trophic position show the calculated intercepts (slopes were homogeneous) from separate ANCOVAs. Different letters indicate non-overlapping 95% confidence intervals.

extinction processes. Indeed, habitat generalists showed a tighter relationship with less scatter compared to habitat specialists (69.9% vs. 33.5%; Table 3), suggesting generalists were less affected by the underlying spatial distribution of environmental conditions. Generalists also exhibited a bimodal frequency distribution of their occupancy (Fig. 4) indicating a large role for colonization and extinction processes in shaping interspecific differences in their occupancy and abundance. By incorporating species-specific information on habitat breadth, the bulk of variance could be explained (79.3%). Species traits essentially provide the mechanistic drivers of both niche-based and metapopulation-based explanations (Leibold *et al.* 2004; McGill *et al.* 2006), and thus constitute a complementary approach to study abundance–occupancy relationships. Incorporating species-specific information on reproduction, dispersal and trophic position yielded a percentage of explained variation similar to that observed for habitat breadth (80.9%). The small extent of our case study limits the possibilities to relate our results directly to the geographical distribution of species, but allowed accurate measures of abundance and occupancy to be obtained through extensive sampling. Furthermore, incorporating species-specific information on either habitat breadth or species traits successfully explained most of the variation around the relationship, demonstrating the value of such an approach in providing insight in the determinants of the observed abundance–occupancy relationship.

Brown's (1984) hypothesis states that species that have broad environmental tolerances and are able to use a wide range of resources will be both locally abundant and widespread; the 'jack-of-all-trades' is master of all. In contrast, we found habitat specialists to be more abundant compared to habitat generalists for a given occupancy. We observed this effect irrespective of whether niche breadth was expressed as a continuous value or a categorical value (Fig 5a; Table 4). Moreover, a different measure of niche breadth, such as Schoener's (1974) selectivity index, yielded similar results (data not shown). If habitat specialists are restricted in their distribution, their high abundances (relative to occupancy) may change the slope of abundance–occupancy relationships from a positive to a negative one (Komonen *et al.* 2009). Indeed, many studies report a positive relationship between niche breadth and *occupancy* (e.g. Cowley *et al.* 2001b; Gaston & Spicer 2001; Heino 2005), yet only a few report a positive relationship between niche breadth and *abundance* and some even report a negative relationship (Gaston *et al.* 1997; Thompson, Hodgson & Gaston 1998; Päävinen *et al.* 2005). Our study and those of others suggest that the jack-of-all-

the underlying spatial distribution of environmental conditions, time-lags (e.g. Conrad, Perry & Woiwod 2001; Webb *et al.* 2007), or the effect of stochastic colonization and



**Fig. 6.** Percentual distribution of species across life-history strategies, trophic positions and a combination of thereof. Habitat specialists ( $n = 115$ ) and habitat generalists ( $n = 49$ ) are shown separately.

trades (i.e. species with a broad niche) is in fact master-of-none. This may solve the difficulty of explaining the existence of habitat specialists, which are presumed to be restricted and scarce, and therefore prone to extinction (Lawton 1993). To compensate extinction, high speciation rates have been invoked in such taxa (Brown 1984). With the alternative presented here, species with a broad niche can persist by spreading risks of reproductive failure, being present in a variety of different habitat types. Conversely, species with a narrow niche can persist through numerical larger local populations, suggesting that specialization is an evolutionary stable strategy.

The implicit assumption in Brown's hypothesis is that species using a broad range of resources (diet generalists) also have wide environmental tolerances (habitat generalist) and this may partly explain the observed discrepancy. We believe that separating both aspects of a niche (diet and habitat use) as suggested by Gaston *et al.* (1997) is appropriate as a species' diet is more tightly connected to biological traits pertaining to feeding; e.g. morphological traits, such as piercing jaws or filtering mouth parts and physiological traits, such as digestive enzymes. In contrast, a species' habitat use constitutes a meta-attribute which results from the interplay between internal and external factors (Lambdon 2008), i.e. species traits and the spatiotemporal distribution of environmental conditions. With habitat use being the resultant of the relevant external and internal factors, grouping species by habitat use (habitat specialists–habitat generalists) may provide a useful starting point to search for underlying mechanisms, although in itself habitat breadth does not provide an explanation.

Species traits are key to linking pattern and process (Hengeveld & Walter 1999; McGill *et al.* 2006; Statzner, Bonada & Dolédec 2008). As traits are basic, measurable properties of a species that are not contingent on their

surroundings, they offer a more parsimonious explanation for a species' performance than a meta-attribute such as habitat breadth. Significant differences in the relative abundance of species with different combinations of species traits expressed in different life-history strategies were found and matched our *a priori* predictions. Previous studies have found it difficult to account for the variation around relationships as a product of variation in species traits (Blackburn *et al.* 1997; Quinn *et al.* 1997). The effects of separate traits may be distorted when interrelationships between traits are not taken into account (Mattila *et al.* 2008; Olden *et al.* 2008; Verberk *et al.* 2008b). For example, expectations for mobile and *semelparous* species (e.g. strategy S1) differ radically from mobile and *iteroparous* species (e.g. strategy R1). Our results demonstrate the value of using combinations of species' traits in explaining variation in the abundance of aquatic macroinvertebrates, as this approach allows an integral understanding of the underlying mechanisms. By taking water bodies as a study system, species with contrasting life-history strategies could be included, as water bodies harbour a taxonomically diverse assemblage of macroinvertebrates, yet provide clear boundaries between – potentially – suitable and unsuitable habitat. Other studies have predominantly focussed on to ecologically similar groups (e.g. birds, beetles, butterflies, dragonflies, fish), where differences in life-history traits may be less pronounced and relevant differences may be more evident in their physiological performance (Gaston & Spicer 2001; Calosi *et al.* 2009).

Taking the effects of physiology and life history into account will enable more accurate predictions of a species' abundance from its occupancy, which has much value for predicting extinction risks (Lawton 1993; Suding *et al.* 2005; Mattila *et al.* 2008; Olden *et al.* 2008). Importantly, the shape of the relationship may also be understood from the perspective of species traits. Negative relationships such as observed

for butterflies in Finland (Päivinen *et al.* 2005) for example can arise when a trait has strong but opposite effects on abundance and occupancy, as can be true for dispersal (Päivinen *et al.* 2005) or body size (Tales *et al.* 2004). This further emphasizes the need to take the effect of combinations of species traits into account, for instance by grouping them into life-history strategies (Verberk *et al.* 2008a).

Differences in habitat breadth were manifest in relation to both a species' diet and its life-history strategy. In general, habitat specialists were better adapted to stable, predictable habitats, as they were more sedentary, synchronized their life cycles and employed clustered oviposition. In contrast, habitat generalists were generally better adapted to unstable habitats, being dispersive and spreading their reproductive effort in time and space by having several generations, a protracted oviposition period, or both. Differences between habitat specialists and generalists in their trophic position had repercussions that could also be related along an environmental axis of predictability. Algal food sources are more variable in time and space, necessitating good dispersal capacity. Carnivores need to be mobile for similar reasons, as they can deplete a local food supply and need to move on (Nilsson & Söderström 1988; Lundkvist *et al.* 2003). Consequently, many algivores and carnivores were habitat generalists and there were no algivores with no or poor dispersal capacities. In contrast, habitat specialists opted for more stable food sources with many detritivores being habitat specialists, especially in species having a long larval development. With habitat generalists being better adapted to unpredictable conditions, it is interesting to note that others have emphasized a role of higher disturbance in generating bimodal patterns (Collins & Glenn 1991; Heino & Virtanen 2006), which corroborates theoretical considerations that metapopulation dynamics only apply when the degree of extinction and colonization are similar in magnitude (Freckleton *et al.* 2005).

In our study system, a heterogeneous bog remnant, elements of reproduction, dispersal and aggregation proved important in distinguishing habitat specialists from generalists. McAbendroth *et al.* (2005) suggested a similar co-occurrence of traits on dispersal and habitat breadth (termed ecological tolerance in their paper) for aquatic macroinvertebrates in heathland ponds, yet in streams other traits govern a species' specialization and abundance (Statzner *et al.* 2008). What traits characterize a habitat specialist or a habitat generalist is thus contingent on the type of ecosystem studied, blurring the line between generalists and specialists. Thus, our results support the notion that niche and population dynamics are operating simultaneously, constituting different endpoints of the same continuum (Gaston *et al.* 2000; Chase & Leibold 2003; Thompson & Townsend 2006). We can add to Tilman's (2004) statement of 'rather than thinking that either deterministic processes (niche) or stochastic processes (dispersal) are all explaining, they may act together simultaneously on different spatial and temporal scales' that they may also act simultaneously albeit for different species.

In conclusion, the interspecific abundance–occupancy relationship can be best understood by examining the contri-

bution of individual species. The abundance and occupancy of each species results from and varies through time as a result of both population dynamics and the interplay between environmental conditions and various biological traits. Niche and population dynamics therefore operate simultaneously, constituting different endpoints of the same continuum and their importance differs between species (habitat generalists and habitat specialists). As species traits provide the causal mechanisms to explain species specific variation, testable predictions can be generated by selecting species traits related to putative mechanisms. By grouping species based on species trait combinations, patterns aggregated across species can be analysed without losing sight of the underlying causal mechanisms (Verberk 2010). Such an integrative approach based on species trait combinations can bring about a synthesis of the various explanations and determine their relative importance under different circumstances, involving different species.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** List of species and their life-history strategy, trophic position, calculated niche breadth, occupancy (number of occupied water bodies) and abundance (number of individuals per m<sup>2</sup>).

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