LETTER

Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms

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Abstract

Relationships between traits of organisms and the structure of their metacommunities have so far mainly been explored with meta-analyses. We compared metacommunities of a wide variety of aquatic organism groups (12 groups, ranging from bacteria to fish) in the same set of 99 ponds to minimise biases inherent to meta-analyses. In the category of passive dispersers, large-bodied groups showed stronger spatial patterning than small-bodied groups suggesting an increasing impact of dispersal limitation with increasing body size. Metacommunities of organisms with the ability to fly (i.e. insect groups) showed a weaker imprint of dispersal limitation than passive dispersers with similar body size. In contrast, dispersal movements of vertebrate groups (fish and amphibians) seemed to be mainly confined to local connectivity patterns. Our results reveal that body size and dispersal mode are important drivers of metacommunity structure and these traits should therefore be considered when developing a predictive framework for metacommunity dynamics.

Keywords

Active dispersal, dispersal limitation, MEM analysis, passive dispersal, pond, propagule size, spatial context, spatial scale, species sorting, variation partitioning.

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INTRODUCTION

Metacommunity ecology studies local communities as interacting species assemblages connected by dispersal and thus integrates both regional and local dynamics (Leibold *et al.* 2004; Holyoak *et al.* 2005). Understanding how and to what extent organism traits drive the structure of metacommunities is one of the major challenges of this relatively new but rapidly expanding discipline (Cottenie 2005; Logue *et al.* 2011). Body size demonstrates universal scaling relationships with a suite of other organism traits (Brown *et al.* 2004; Woodward *et al.* 2005) that may strongly affect metacommunity dynamics. Through its negative association with key demographical traits, such as population size, development time and population growth rate (i.e. maximum rate of exponential increase) (Brown *et al.* 2004; Jonsson *et al.* 2005), body size has strong potential to determine the relative impact of spatial vs. environmental factors on local community composition (e.g. Hillebrand *et al.* 2001; Finlay 2002; Shurin *et al.* 2009; Ptacnik *et al.* 2010). Compared with macroscopic organisms, for example, the large size of microbial populations renders them less sensitive to drift effects and local extinctions (Blackburn & Gaston 1999) and enables the production of higher numbers of propagules, which increases the potential for dispersal events (Fenchel & Finlay 2004; Martiny *et al.* 2006). Because of the relatively short generation times and high population growth rates of small species, the composition of their communities can quickly track changes in the local environment (Korhonen *et al.* 2010). Their populations can also grow very rapidly after the initial

colonisation of vacant but suitable habitat patches and as such quickly erase the 'ghost' of past extinctions. Compared with larger organisms, demographical characteristics of small organisms should thus enable efficient species sorting and weaken the potential of dispersal limitation to generate spatial patterns in metacommunities (Van der Gucht *et al.* 2007).

In addition to body-size related demographical factors, the dispersal ability of organisms is another key trait with strong potential to determine metacommunity structure (Damschen *et al.* 2008). Dispersal strategies are evolutionary versatile and involve trait complexes that integrate morphological, behavioural, physiological and biochemical aspects (Bowler & Benton 2005). Yet, while acknowledging this complexity, a number of general predictions can be made (Bilton *et al.* 2001). Body size is expected to interact with mode of dispersal in determining dispersal ability. In passive dispersers, propagules are dispersed by vectors, such as wind, water or animals (Vanschoenwinkel *et al.* 2008), and the efficiency of dispersal decreases with increasing propagule size (Vagvolgyi 1975; Bruun & Poschold 2006; Soons *et al.* 2008). In contrast, dispersal capacity of active dispersers is believed to be positively correlated with body size (Jenkins *et al.* 2007; Shurin *et al.* 2009). Active dispersers are potentially more efficient dispersers than passive ones because they are independent from vectors and may actively select for suitable habitat (Resetarits 2001). However, their dispersal will also be highly dependent on the specific mode of active dispersal (flight, swimming, mobile on ground), of which the efficiency can depend strongly on the quality and configuration of connections between habitat patches (Fahrig & Merriam 1994).

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A number of studies have investigated the association between traits of organism groups and diverse parameters of community turnover through the meta-analysis of datasets encompassing broad ranges of organism size, dispersal mode and spatial scale in a variety of biomes (terrestrial, marine and freshwater). They found variable evidence for a general relationship between body size and spatial patterns of community similarity that are considered indicative for dispersal limitation. Hillebrand *et al.* (2001; aquatic) observed a slower decay of community similarity with geographical distance for small vs. larger aquatic organisms. This is in agreement with Finlay *et al.* (1998; aquatic) and Drakare *et al.* (2006; terrestrial and aquatic) who reported a positive association between body size and the slope of the species–area relationships across organism groups. Cottenie (2005; terrestrial and aquatic) found no strong associations with body size but suggested an important effect of dispersal mode. Soininen *et al.* (2007b; terrestrial and aquatic) not only reported a positive association between body size and hierarchical community turnover but also found higher beta diversity among communities of active than of passive dispersers. Shurin *et al.* (2009; aquatic) reported differences in distance decay between fish and invertebrates, but no relationships with body size or dispersal mode within invertebrates. These studies have contributed in important ways to the development of metacommunity theory, yet an intrinsic risk to the meta-analysis approach is that variability in sampling design, spatial scale, patch configuration and methodological quality may bias, obscure or confound important patterns (Astorga *et al.* 2012).

Only few studies have compared metacommunity structure across multiple organism groups in one and the same set of locations. Those that did (e.g. Beisner *et al.* 2006; Mazaris *et al.* 2010; Hájek *et al.* 2011; Astorga *et al.* 2012; all aquatic) were never based on data of more than four organism groups and were therefore limited to qualitative comparisons. With this study, we set out to formally test predictions on relationships between body size, dispersal mode and metacommunity structure for a large number of widely different organism groups sampled in one set of locations. More specifically, we studied community variation of 12 organism groups, ranging from bacteria to fish, in 99 small farmland ponds distributed over most of the Belgian territory (30.500 km²). For metacommunities of passive dispersers, we predicted that a larger body size would be associated with a stronger dispersal limitation and a reduced efficiency of species sorting. Large-bodied passive dispersers would therefore be expected to show more pronounced spatial patterns and a reduced match with environmental gradients than small-bodied passive dispersers. We also predicted that organisms with an active dispersal mode would deviate from these general relationships and that these deviations would depend on the mode of active dispersal. More specifically, we predicted that flying insects should show less dispersal limitation than passive dispersers of the same body size whereas organisms that mainly disperse through hydrological connections should show strong effects of dispersal limitation.

MATERIALS AND METHODS

Study area, sample collection and sample analysis

During the summer of 2003 (end of July until beginning of September), we simultaneously surveyed 12 aquatic organism groups in a total of 99 small but permanent farmland ponds distributed over almost the entire Belgian territory (*c.* 30 500 km²) (see Declerck

et al. 2006). We sampled seven groups of passive dispersers (bacteria, phytoplankton, phytobenthos, cladocerans, rotifers, macrophytes and molluscs), three flying insects (chironomids, heteropterans and coleopterans) and two vertebrate (amphibians and fish) groups. The surface area of the ponds ranged between 12 and 3674 m² and 90% of the ponds were smaller than 400 m².

Physical, chemical and morphometric pond variables were determined as in Declerck *et al.* (2006). We refer to Appendix S1 for a detailed description of the sample collection protocol. We analysed water samples for the concentration of chlorophyll a, nutrients (total phosphorus and nitrates), alkalinity and some major ions (calcium, chloride and sulphate ions, water hardness). Community composition in bacterioplankton was studied using denaturing gradient gel electrophoresis (DGGE). All other groups were studied through the taxonomic analysis of samples, except for fish and amphibians that were counted and identified in the field. All these groups were identified to the species level, except rotifers and phytoplankton, which were identified to the genus level. We refer to Appendix S1 and S2 for a detailed account on the sample analysis methodology for each of the groups.

Statistical analysis

Variation partitioning of community data in relation to spatial and environmental factors

We analysed the metacommunity structure of each of the twelve organism groups with variation partitioning (Peres-Neto *et al.* 2006). Using redundancy analysis (RDA), we constructed two explanatory models: an environmental RDA model, based on a parsimonious combination of environmental variables, and a spatial RDA model, describing spatial patterns in the community data.

We constructed environmental models for the different organism groups by applying the forward selection procedure of Blanchet *et al.* (2008) to environmental variables (see Appendix S3 for a complete list). To avoid overfitting, this analysis was limited to an *a priori* defined subset of environmental variables (see Appendix S4) for which an effect on the respective communities could be reasonably expected based on prior ecological knowledge of the organism groups (Burnham & Anderson 2002). We also omitted those variables that were intrinsically linked with the focal organism group (e.g. vegetation cover for macrophytes). We constructed spatial RDA models using spatial variables extracted by MEM analysis (Moran's Eigenvector Maps, see Dray *et al.* 2006). The MEM analysis produces a set of orthogonal spatial variables that are derived from geographical coordinates of the study sites and that can be used as explanatory variables to model spatial relationships in community data. The type of MEM variables computed in the present study was formerly called principal coordinates of neighbour matrices (PCNM: Borcard *et al.* 2004). This procedure yielded a total of 50 MEM variables, each of which corresponds to a specific spatial structure and scale (see Appendix S5): the first MEM variables can model coarse patterns in the community data, whereas the subsequent variables progressively represent finer-scale patterns (Borcard *et al.* 2004). For each of the organism groups, we constructed a parsimonious spatial model by running a forward selection on the MEM variables. Because MEM analysis is inefficient in covering linear trends, we tested for linear trends in the community data prior to MEM analysis. This was done using X and Y geographical coordinates as explanatory variables in an RDA model. When linear

trends were detected, we performed forward selection on MEM variables using the detrended residuals of the response variables from the RDA model. In these cases, the final spatial model incorporated both the linear variables and the MEM variables (Borcard *et al.* 2004).

With variation partitioning, we decomposed total community variation into a purely spatial component (S|E), a purely environmental component (E|S), a component representing spatially structured environmental variation (E ∩ S) and the remaining unexplained variation. The magnitude of a significant environmental component (E|S) can be used as a conservative indicator for the degree to which community variation is uniquely structured by the environment (species sorting, Cottenie 2005). The magnitude of a significant spatial component (S|E) is indicative for the amount of spatial variation caused by dispersal limitation or mass effects (Legendre & Legendre 1998). We tested the significance of both components with Monte Carlo permutations (1000 new values under the reduced model). We corrected estimates of explained variation for the number of predictor variables and sampling sites (R² adjusted) following the procedure proposed by Peres-Neto *et al.* (2006).

To further explore the spatial architecture of the metacommunities, we divided the MEM variables of the spatial models into three categories of spatial scale, following the approach of Bellier *et al.* (2007): broad-scale (linear trends and MEM 1–16), intermediate-scale (MEM 17–33) and fine-scale spatial patterns (MEM 33–50) with wavelengths of c. 30–200, 8–30 and 1–8 km respectively. Next, with variation partitioning analysis, we calculated the relative contribution of each of these three categories to the S|E-component of explained community variation. These contributions reflect the scales at which spatial metacommunity patterns are most pronounced. A dominant contribution of the broad-scale MEM category, for example, signifies that spatial patterns in the metacommunity pertain mainly to the largest spatial scales. A strong contribution of the fine-scale MEM category indicates important patterning at the scale of neighbouring ponds. We repeated the analysis using five instead of three MEM categories but our results proved robust (results not shown).

Spatial patterns and environmental control in relation to dispersal type and propagule size
To test our expectation that the effects of dispersal limitation on metacommunity structure should increase with body size in passive dispersers, we used nonparametric Spearman-rank correlation analysis to investigate the relationships between the S|E- and E|S-components of these organism groups with the size of their propagules. We then compared the S|E- and E|S-components of flying insects with passive dispersers using analysis of covariance (ANCOVA), taking into account propagule size as covariable. With propagule we refer herein to the life stage during which the organisms are known to disperse; this can be the adult individual (flying insects, amphibians, fish, molluscs), but also seeds (macrophytes), dormant eggs (zooplankton) or spores (bacteria, benthic diatoms, phytoplankton) (Martiny *et al.* 2006; Jenkins *et al.* 2007). For each organism group propagule size was calculated as the average size (i.e. the greatest axial length of the relevant stage) of all taxa occurring in at least 5% of the sampled locations (see Appendix S2). To test the idea that the spatial signature of increasing dispersal limitation is associated with a poorer match between community variation and important environmental gradients, we also calculated the Spearman-rank

correlation between the S|E- and E|S-components over all organism groups. In this analysis we corrected for the intrinsic interdependence of both fractions by dividing S|E by [100 − (E|S)], and E|S by [100 − (S|E)].

We performed the analyses on both presence-absence and abundance data, but focus mainly on the results obtained from the presence-absence data. The latter type of data should be better in reflecting distributional patterns that are generated by dispersal limitation as they are less confounded by the relative ecological success of species in local habitat patches (Declerck *et al.* 2011). Furthermore, macrophytes and amphibians were sampled qualitatively and for these groups we only have presence-absence data available. Both presence-absence and abundance data were Hellinger-transformed prior to analysis (Legendre & Gallagher 2001). Environmental variables (except pH) were transformed logarithmically. For bacteria, phytoplankton and benthic diatoms, the total number of samples was limited to 51, 71 and 90 respectively. All statistical analyses were performed in R (v2.13.1; R Development Core Team 2011). The R-script is included in Appendix S6.

We aggregated the data of all groups to the genus level and repeated all statistical analyses (Appendix S7). In addition, we performed all analyses on the level of individual taxa (species, genera or OTU's) that occurred in at least 5% of the sample locations. We performed these analyses to demonstrate that our results are robust against variation in taxonomic resolution or analysis approach (i.e. univariate vs. multivariate).

RESULTS

Variation partitioning

In most organism groups, variation among communities (see Appendix S8) could be not only significantly explained by variation in the environment but also exhibited purely spatial patterns indicative for dispersal limitation (cf. the E|S- and S|E-components, respectively, see Appendix S8). Groups with relatively pronounced spatial patterns were less controlled by the environment whereas groups that were more strongly determined by the environment showed weaker spatial patterns (Fig. 1; $r_{SP} = -0.58$; $P = 0.04$). Communities of the smallest organisms, the bacteria, showed no significant spatial patterns and most of the explained community variation could be attributed to the environment (Appendix S8). Conversely, variation in fish community composition could not be explained by any of the studied environmental variables, but exhibited relatively strong and significant spatial patterns (Appendix S8).

Spatial metacommunity structure, propagule size and dispersal mode

For the passively dispersing groups, we found a positive association between propagule size and purely spatial variation in presence-absence data ($r_{SP} = 0.85$; $P = 0.013$; Fig. 2a). This correlation was considerably weakened upon incorporation of groups with other dispersal modes in the analysis ($r_{SP} = 0.46$; $P = 0.12$; Fig. 2a). This was because spatial patterns in flying insect groups were less pronounced than in passive dispersers of similar propagule size (ANCOVA; MS = 50.6; $F_{1,7} = 29.8$; $P = 0.001$). Conversely, spatial structure in the metacommunities of amphibians and fish tended to
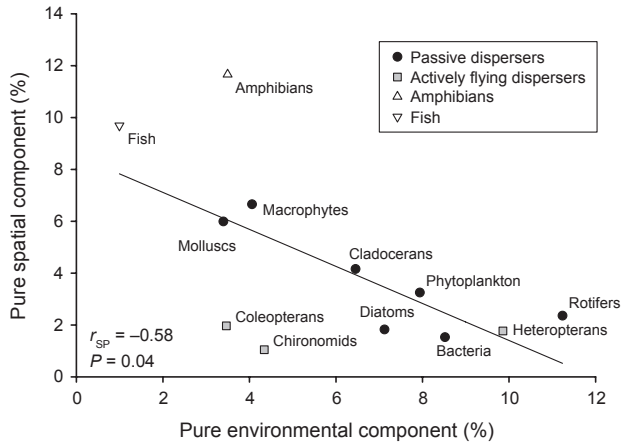
Figure 1 Relation between the purely spatial and purely environmental components of community variation, after correction for mutual interdependence: the spatial component represents $(S|E)/[100\% - (E|S)]$ and the environmental component represents $(E|S)/[100\% - (S|E)]$.
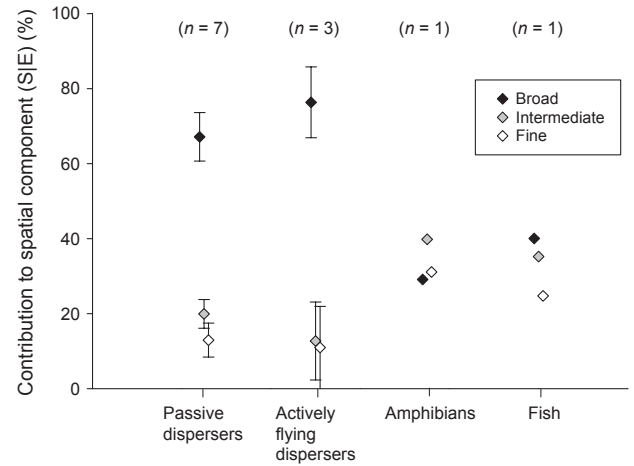

Figure 3 Mean contribution of fine, intermediate and broad scale MEM variable categories to the variation that is uniquely explained by the spatial model, based on presence-absence data. The number of organism groups representing each category is also indicated. Error bars indicate the standard error of the mean.

be stronger than what would be expected based on propagule size (Fig. 2a). Variation partitioning analyses performed for each taxon separately supported these conclusions (Fig. 2b).

Metacommunities of the passively dispersing groups and flying insects (Fig. 3) mainly exhibited broad-scale spatial patterns of community variation. In these groups, the contribution of the category

of broad-scale MEM variables to purely spatial variation ranged between 52% and 100%, although in the group of passive disperses there was a tendency for a declining importance of this scale category with increasing propagule size ($r_{SP} = -0.67$; $P = 0.09$; Appendix S9). The spatial architecture of the amphibian and fish metacommunities differed considerably from the passive dispersers
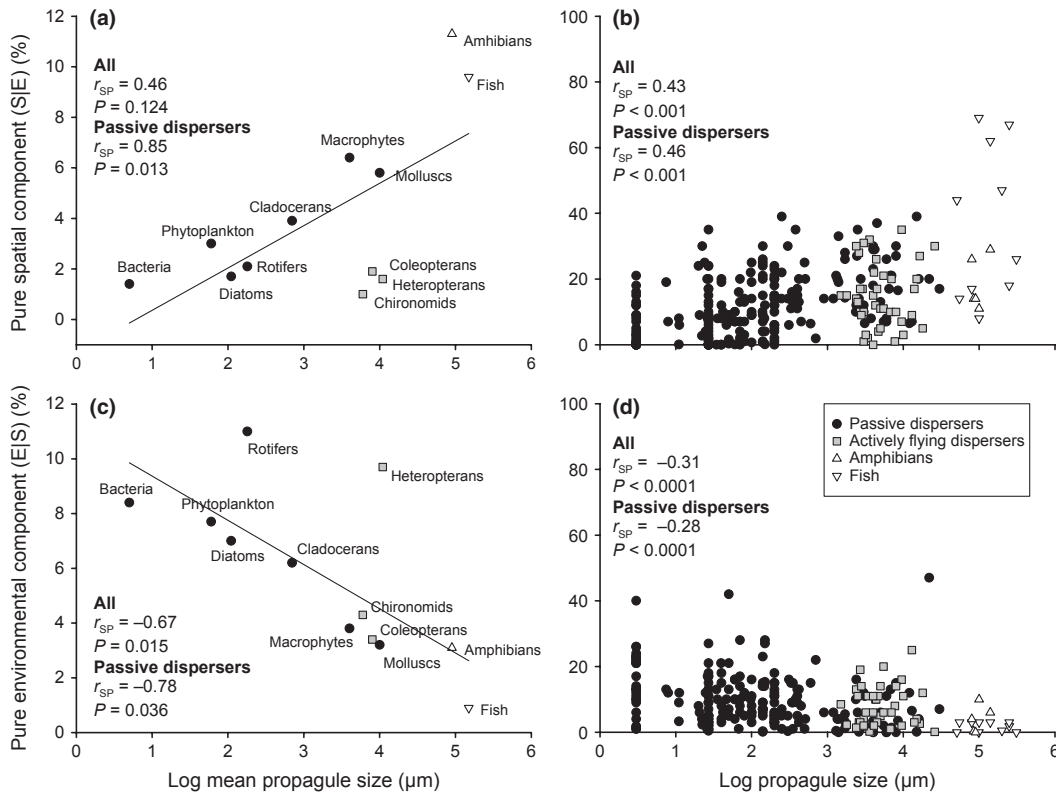
Figure 2 Variation uniquely explained by space (a, b) and by the environment (c, d) in relation to propagule size. (a) and (c) represent partial RDA results for data organised by organism group. (b) and (d) represent analysis results for individual taxa that occurred in at least 5% of the sample locations. All analyses were based on presence-absence data.

and flying insects in that the relative contribution of the small- and intermediate-scale MEM variables was larger at the expense of the contribution of the large-scale MEM category (Fig. 3).

Environmental control, propagule size and dispersal mode

We detected a negative association between the propagule size of the organism groups and the amount of variation in presence-absence data that could be explained by the environment ($r_{SP} = -0.78$; $P = 0.036$; Fig. 2c). Community composition of small-sized passive dispersers was relatively well-explained by environmental variables but this was less so in groups with larger propagule size. Environmental variables were relatively poor in explaining community variation of amphibians and fish. These results were also confirmed by analyses performed on the level of individual taxa (Fig. 2d).

Analyses on abundance data

Abundance data yielded similar results as those obtained for presence-absence data, such as a positive association across organism groups between propagule size and the amount of purely spatial variation and a negative association between propagule size and the strength of environmental control (Appendix S10). The major difference was found in the purely spatial variation in flying insect communities, which tended to be larger for abundance than for presence-absence data (see Appendix S10 A). Furthermore, abundance data of flying insects also revealed more small-scale community variation than presence-absence data, reflected by the larger contribution of the small-scale MEM variable category (see Appendix S11).

DISCUSSION

Body size has long been recognised as a key trait that is related to a host of other organism traits (Peters 1983). Scaling relationships between body size and organism traits have been used to predict patterns in population demography, food webs, species richness and ecosystem functions (e.g. Brown *et al.* 2004; Woodward *et al.* 2005). Using data covering a wide range of passively dispersing organisms, we herein demonstrate a strong relationship between body size and the strength and extent of spatial patterns in metacommunities, suggesting that dispersal limitation is more important for large than for small organisms. However, dispersal mode causes strong deviations from such relationship. Organisms with a flying stage (flying insects) showed a weak signature of dispersal limitation compared with passive dispersers of comparable body size. Conversely, active dispersers that are typically confined by hydrological connections (fish) or can only travel short distances over land (amphibians) showed relatively strong dispersal limitation at small spatial scales.

Due to their small bodies and large population sizes, free-living microscopic organisms have been regarded as being qualitatively different from larger organisms because they are assumed to be ubiquitous dispersers of which the spatial distribution is determined by environmental sorting and not by dispersal limitation ('everything is everywhere but the environment selects'). Finlay (2002), for example, predicted that organisms should become dispersal-limited only when they exceed a critical size threshold of 1 mm. More recently, however, this view has increasingly been contested due to

accumulating evidence that micro-organisms do show biogeographical patterning (Martiny *et al.* 2006; Vyverman *et al.* 2007; Heino *et al.* 2010). We detected no significant spatial patterns in the metacommunities of bacteria although our results do not preclude the existence of dispersal limitation at the larger continental or intercontinental scales (but see e.g. Van der Gucht *et al.* 2007). Despite the limited geographical range of our study area, however, we did find evidence for dispersal limitation in metacommunities of other microscopic organisms, such as phytoplankton, benthic diatoms and zooplankton (e.g. cladocerans and rotifers), although the spatial signal remained rather weak. This is largely in agreement with the findings of Hillebrand *et al.* (2001), Soininen *et al.* (2007b,c) and Shurin *et al.* (2009). Our results also do not support the existence of a discrete boundary between microbes and macro-organisms (Astorga *et al.* 2012), but rather suggest a gradual increase in dispersal limitation with body size in passive dispersers. Furthermore, we found indications for a relationship between body size and the spatial scales at which dispersal limitation is manifested. Metacommunities of protists (benthic diatoms, phytoplankton) and small metazoans (rotifers) showed only weak spatial patterns that mainly pertained to spatial scales corresponding to the entire study area (ranging between 30 and 200 km). Conversely, metacommunities of passive dispersers with larger propagules, such as molluscs and macrophytes, also showed spatial pattern at intermediate (8–30 km) and small (1–8 km) spatial scales.

Several meta-analysis studies encompassing a wide variety of organisms, spatial scales and biomes have suggested the existence of relationships between body size and the strength of dispersal limitation (Hillebrand *et al.* 2001; Drakare *et al.* 2006; Soininen *et al.* 2007a). The existence of a general scaling relationship between body size and dispersal has, however, been questioned (Jenkins *et al.* 2007; Shurin *et al.* 2009; Hájek *et al.* 2011; Astorga *et al.* 2012). The fact that we did find a robust association between body size and patterns of dispersal limitation for the category of passive dispersers may be due to a number of unique features of our study design: (1) Our study differs from meta-analysis based studies (Hillebrand *et al.* 2001; Cottenie 2005; Drakare *et al.* 2006; Soininen *et al.* 2007c; Shurin *et al.* 2009) in that we have analysed metacommunity structure of organism groups in a same set of locations according to a standardised protocol, which allowed us to avoid confounding effects of variation in spatial scale, patch configuration, habitat type and sampling methodology; (2) Unlike most other field-based studies (Beisner *et al.* 2006; Soininen *et al.* 2007a; Mazaris *et al.* 2010; Hájek *et al.* 2011; Astorga *et al.* 2012), our study encompasses a much larger number of organism groups covering a wider range of body sizes; (3) In contrast to most studies that use distance decay analysis (e.g. Soininen *et al.* 2007c; Shurin *et al.* 2009), variation partitioning on redundancy models allows to distinguish between purely spatial patterns generated by dispersal-related dynamics and patterns that are confounded by the environment (Beisner *et al.* 2006; Hájek *et al.* 2011).

Inclusion of active dispersers in our analyses caused strong deviations from the body scaling relationship observed for passive dispersers. Astorga *et al.* (2012) also found variation among patterns of similarity decay between groups of river macroinvertebrates with different dispersal ability. In his meta-analysis, Cottenie (2005) found stronger associations of spatial metacommunity patterning with dispersal mode than with body size. In contrast to passive dispersers, patterns of metacommunity structure in actively dispersing

organisms were more complex, as the relative importance of environmental and spatial processes appeared to additionally depend on habitat type and spatial scale (Cottenie 2005). The relative performance of different types of active dispersal in a landscape can thus be highly variable, context dependent and difficult to predict. In our study, organisms with the ability to fly (i.e. flying insects), showed much weaker spatial patterns than passive dispersers with similar-sized propagules (cf. macrophytes and molluscs). The degree of dispersal limitation in these groups rather approximated that of small passive dispersers (e.g. phytoplankton, diatoms and rotifers), at least at the spatial scales covered by our analysis. Spatial patterns in actively flying insects were also most pronounced at the largest spatial scales, indicating that dispersal limitation in flying insects mainly plays at a scale approximating the entire study area (c. 30 000 km^2). For the landscape context and spatial scale under study, our results thus suggest that some of the limitations related to a relatively large body size (e.g. small population sizes and relatively low population growth rates) and the absence of the ability to form dormant propagule banks can be compensated by advantages of active flight, such as independence of vectors and hydrological connections, and the ability to actively select for appropriate habitats.

In contrast to flying insects, fish and amphibians showed strong spatial patterns at small, intermediate and large spatial scales. Beisner *et al.* (2006) and Shurin *et al.* (2009) also found more pronounced spatial patterns in fish than in invertebrates and microorganisms. Amphibians are very limited in covering distance through overland dispersal and the small scale patterns of community variation detected for this group indicate strong dependency of dispersal movements on local connectivity patterns (e.g., regional stream, river and ditch networks, flooding events, or fragmentation of amphibian migration through barriers such as roads and urban development). Fish are known to have strong dispersal potential within well-connected river and wetland systems, but dispersal of this group among isolated ponds such as the ones in our study may depend on rare flooding events and human translocations. The strong patterns of dispersal limitation observed for this group indeed suggest that fish rather behave as passive than active dispersers in our study system and illustrate how the performance of dispersal modes can strongly depend on the specific landscape context.

Dispersal limitation can impede the ability of species to reach suitable habitat patches and thereby weaken the strength of environmental control (Leibold *et al.* 2004). Metacommunities of microscopic organisms were found to be strongly environmentally controlled, suggesting efficient species sorting at relatively large spatial scales, concordant with the observations of Beisner *et al.* (2006), Van der Gucht *et al.* (2007) and Astorga *et al.* (2012). This is not necessarily only the result of high dispersal rates but probably also mediated by other, body size related traits, such as fast population growth that allows rapid population responses to spatio-temporal gradients of local environmental conditions (Van der Gucht *et al.* 2007; Korhonen *et al.* 2010). With increasing body size, environmental variables gradually became less powerful in explaining community variation. In addition to the effect of higher extinction frequencies and lower dispersal rates, the re-establishment of populations of large organisms after colonisation of vacant habitat patches may be slower due to Allee effects. Compositional community responses of large organisms to changed environmental conditions will also be slower, due to low intrinsic population growth rates.

Spatial patterns in metacommunities can also be caused by mass effects (Cottenie 2005), when high dispersal rates of individuals among patches overwhelm local population dynamics (Mouquet & Loreau 2003). Given the isolated nature of the ponds, (cf. absence of direct hydrological connections) it is unlikely that such mass effects have generated the spatial patterns observed in our study. Spatial patterns generated by mass effects should also be more pronounced at local than at large spatial scales and therefore be better represented by small than large-scale MEM variables (Declerck *et al.* 2011). For most organism groups, we observed the opposite, suggestive of dispersal limitation being the key driving force of spatial structure. However, flying insects could represent a special case. Using presence-absence data, we found a consistent weak spatial signal for these organism groups compared to other organism groups. Conversely, no such systematic deviation from the S|E-body size relationship was found using abundance data. After correction for the environment, presence-absence data are relatively straightforward in reflecting distributional patterns that are generated by dispersal limitation. Abundance data on the other hand are expected to be quantitatively affected by mass effects. The very weak spatial patterns in the presence-absence data of the flying insects reflect a high mobility of these organism groups at the local scale compared with other organism groups, and this high mobility may have generated spatial patterns in the abundance data as a result of mass effects.

The R^2-values in our study overall tend to be rather low. High residual variation is typical for studies based on survey data and results from the accumulation of errors related to sampling (e.g. spatial and temporal patchiness within habitats), patch history (pond age, management history, priority effects) and intrinsic variability (stochasticity, alternative stable states). We also took a conservative approach by correcting R^2-values by the number of explanatory variables, using the procedure proposed by Peres-Neto *et al.* (2006). Studies that have applied this procedure obtained proportions of explained variation similar to ours (Beisner *et al.* 2006; Hájek *et al.* 2011). Importantly, however, the main conclusions of our study are based on the formal analysis of patterns of R^2-values across organism groups rather than on the actual values of these estimates themselves.

IMPLICATIONS

A trait-based approach has strong potential to contribute to the development of a more predictive framework of metacommunity ecology if it is able to demonstrate systematic relationships between metacommunity structure and organism traits that are known to be mechanistically linked with metapopulation demography and dispersal biology. Focusing on body size and dispersal mode, our study is the first to demonstrate such consistent relationships using a dataset encompassing a broad range of organism groups sampled in one and the same set of locations. With increasing spatial scale, metacommunities tend to shift from being environmentally controlled to being dispersal controlled (e.g. Declerck *et al.* 2011). Our study illustrates that the spatial scale at which this shift occurs differs strongly among organism groups and is associated with body size and dispersal mode. A better understanding of how and why patterns of community variation differ among organism groups and across spatial scales is important for conservation biology and landscape planning, as it may reveal the mechanisms that generate and

maintain beta and gamma diversity (Hendrickx *et al.* 2009). In our study systems, small passive dispersers and flying insects were found to be primarily determined by the environment, suggesting that conservation of the biodiversity of these groups should target local habitat quality and environmental landscape heterogeneity. For the large passive dispersers and vertebrates that strongly rely on hydrological connections (amphibians and fish), dispersal limitation is an additional point of major conservation concern.

AUTHORSHIP

S.A.J.D., T.D.B. and L.D.M. conceived the idea for this study. T.D.B. and S.A.J.D. designed and performed the statistical analyses and did most of the writing; L.D.M, K.M., K.V.d.G., L.B. and W.V. contributed with ideas for analysis and interpretation; K.M. played a pivotal role as co-ordinator of the project. T.D.B. and D.E. co-ordinated the sampling; B.G., D.E., J.V.W., H.H., L.V., K.V.d.G., L.D. and T.D.B. were involved in field work and sample analysis. All co-authors contributed with important suggestions for manuscript improvement.

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