

Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales

Duarte S. Viana, J. Figuerola, K. Schwenk, M. Manca, A. Hobæk, M. Mjelde, C. D. Preston, R. J. Gornall, J. M. Croft, R. A. King, A. J. Green and L. Santamaría

D. S. Viana (dviana@ebd.csic.es), J. Figuerola, A. J. Green and L. Santamaría, Estación Biológica de Doñana (EBD-CSIC), C/Américo Vespucio, Sevilla, s/n, ES-41092, Spain. – K. Schwenk, Inst. for Environmental Sciences, Univ. of Koblenz-Landau, DE-76829 Landau/Pfalz, Germany, and Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, DE-60325 Frankfurt am Main, Germany. LS and KS also at: Netherlands Inst. of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, NL-6708 PB Wageningen, the Netherlands. – M. Manca, CNR – Istituto per lo Studio degli Ecosistemi, Largo Tonolli 50, IT-28922 Verbania, Italy. – A. Hobæk, Norwegian Inst. for Water Research (NIVA), Branch Office Bergen, Bergen, Norway, and Dept of Biology, Univ. of Bergen, Bergen, Norway. – M. Mjelde, Norwegian Inst. for Water Research (NIVA), Gaustadalléen 21, NO-0349 Oslo, Norway. – C. D. Preston, Centre for Ecology and Hydrology, Wallingford, OX10 8BB, UK. – R. J. Gornall, Dept of Biology, Univ. of Leicester, Leicester, LE1 7RH, UK. – J. M. Croft, 12 Spaldwick Rd, Stow Longa, Huntingdon, Cambs, PE28 0TL, UK. – R. A. King, College of Life and Environmental Sciences, Univ. of Exeter, Stocker Road, Exeter, EX4 4QD, UK.

Niche and neutral processes drive community assembly and metacommunity dynamics, but their relative importance might vary with the spatial scale. The contribution of niche processes is generally expected to increase with increasing spatial extent at a higher rate than that of neutral processes. However, the extent to what community composition is limited by dispersal (usually considered a neutral process) over increasing spatial scales might depend on the dispersal capacity of composing species. To investigate the mechanisms underlying the distribution and diversity of species known to have great powers of dispersal (hundreds of kilometres), we analysed the relative importance of niche processes and dispersal limitation in determining beta-diversity patterns of aquatic plants and cladocerans over regional (up to 300 km) and continental (up to 3300 km) scales. Both taxonomic groups were surveyed in five different European regions and presented extremely high levels of beta-diversity, both within and among regions. High beta-diversity was primarily explained by species replacement (turnover) rather than differences in species richness (i.e. nestedness). Abiotic and biotic variables were the main drivers of community composition. Within some regions, small-scale connectivity and the spatial configuration of sampled communities explained a significant, though smaller, fraction of compositional variation, particularly for aquatic plants. At continental scale (among regions), a significant fraction of compositional variation was explained by a combination of spatial effects (exclusive contribution of regions) and regionally-structured environmental variables. Our results suggest that, although dispersal limitation might affect species composition in some regions, aquatic plant and cladoceran communities are not generally limited by dispersal at the regional scale (up to 300 km). Species sorting mediated by environmental variation might explain the high species turnover of aquatic plants and cladocerans at regional scale, while biogeographic processes enhanced by dispersal limitation among regions might determine the composition of regional biotas.

According to the metacommunity theory (Leibold et al. 2004), the spatial distribution of biodiversity in a landscape is determined by the rate of dispersal of organisms, the environmental heterogeneity of habitat patches, and the degree of functional equivalence among species (in terms of niche and fitness; Logue et al. 2011). Upon dispersal, the successful colonization of a habitat patch is determined by niche processes, acting through environmental filtering (Ricklefs 1987). If species arriving from distant sites are less well adapted to local environmental conditions than resident species, they will be at competitive disadvantage. Since environmental conditions vary in space, their spatial pattern might affect the spatial distribution of species (Cottenie 2005). For example, differences in beta-diversity along latitudinal

gradients are most often attributed to environmental variation (Qian and Ricklefs 2007).

Overall, regional (dispersal and species pool) and local (abiotic and biotic) factors determine community composition (Ricklefs 1987). Their relative importance is the key to understand the mechanisms of community assembly, and has been the object of intense debate. Until recently, some authors argued that stochastic (or 'neutral') processes are sufficient to explain the observed patterns of beta-diversity, even under the simplifying assumption of no ecological differentiation among species (Hubbell 2001). Others suggested that different species have different niches, and therefore deterministic processes (environmental filtering) are important to stabilize species diversity towards a deterministic compositional state (Levine and HilleRisLambers

2009). These views differ in the emphasis given to stochastic versus deterministic processes (see Vellend et al. 2014 for a review of concepts), but they are not mutually exclusive. For example, Gravel et al. (2006) suggest that niche and neutrality form a continuum established by the balance of competitive and stochastic exclusion.

Moreover, the importance of niche processes and dispersal limitation in explaining community composition might vary with the spatial scale. While the contribution of both niche and neutral processes tend to increase with increasing spatial extent (as both environmental variation and dispersal limitation increase), the former can be expected to increase at a higher rate than the latter (Chase 2014). Hence, niche processes should dominate over neutral processes at large spatial scales. However, the extent to what community composition is limited by dispersal over increasing spatial scales might depend on the dispersal capacity of composing species (Cadotte and Fukami 2005) and on landscape configuration, especially the distance between habitat patches and the presence of dispersal barriers (Shurin et al. 2009). Therefore, knowledge of the dispersal potential of species is needed to establish the spatial extent at which variation in community composition (beta-diversity) is determined by niche vs neutral processes.

Inland aquatic ecosystems consist of isolated habitats and yet many aquatic taxa show high dispersal abilities and colonisation rates (Santamaría 2002, Louette and De Meester 2005). Passive dispersers, such as aquatic plants and zooplankton, can be dispersed over long distances by different vectors (e.g. by wind and waterbirds; Cáceres and Soluk 2002, Figuerola and Green 2002, Van Leeuwen et al. 2012, Viana et al. 2013a, b). Indeed, experimental work in lentic systems suggests that niche processes, rather than dispersal limitation, primarily determine the species and genetic composition of aquatic plants and zooplankton communities (Shurin 2000, De Meester et al. 2002, Cottenie et al. 2003, O'Hare et al. 2012; but see De Bie et al. 2012).

Here we aimed at addressing the role of dispersal limitation and niche processes in structuring aquatic communities composed by species with high potential for long distance dispersal. For this purpose, we disentangled the relative contribution of niche processes and dispersal limitation to the composition of aquatic plant (angiosperms) and cladoceran communities surveyed over regional and continental scales (< 300 and < 3300 km, respectively). First, we investigated whether beta-diversity varied across the two spatial scales and determined the relative proportion of beta-diversity explained by spatial turnover (i.e. species replacement) and nestedness (i.e. differences in species richness). Second, we estimated the relative contribution of niche processes and dispersal limitation to explain variation in community composition at the regional and continental scale, i.e. to explain the beta-diversity patterns estimated in the first objective, by performing variation partitioning analyses.

Material and methods

Sampling design and data collection

During the summers of 1998 and 1999, we surveyed the angiosperm and cladoceran communities of 139 lakes located

at five different regions in Europe: the low Guadalquivir watershed (SW Spain), the upper and medium Po watershed (NE Italy), the low Rhine and Maas watersheds (the Netherlands), the Fife area (E Scotland) and several small, adjacent watersheds in central Norway (see map with the sampling locations in Supplementary material Appendix 1, Fig. A1). These surveys were performed according to a standardized protocol. At each region, we defined a circular area of 150 km radius and, based on available cartographic information, selected a random subset of 30 waterbodies found within that area (lakes, ponds and reservoirs – hereafter referred to as 'lakes'). In Spain and Italy, we were only able to survey 20 and 29 of these lakes respectively, due to accessibility and logistic constraints (see Supplementary material, Appendix 1 for a complete list of sites).

Floating and submerged angiosperms were sampled during the peak of the growth season (which varies largely from northern to southern Europe). The survey consisted of four transects departing approximately from the intersection of the lake shore with each of the four cardinal points and ending at the lake's centre. We sampled every 10 m along these transects, using visual surveys (walking or diving) in shallow lakes and rakes thrown from a boat in turbid/deeper ones. This approach was chosen to adjust the sampling effort to the lake's size, thus avoiding larger probabilities of missing rare species in larger lakes. To increase the probability of detecting rare species, we sampled the rest of the lake by surveying in zigzag the vegetated centre-to-shore band along the complete lake perimeter – for all but the largest lakes, where only haphazardly-chosen parts of the perimeter could be surveyed. Hybrid species were considered as different taxonomic units (see the list of species in Supplementary material Appendix 1).

Cladocerans were sampled with plankton nets and preserved in ethanol. To obtain a representative sample of both littoral and pelagic cladocerans covering the recent history of the lake, we also took samples of sediments at the deepest part of each lake (see the detailed methods in Supplementary material Appendix 2). Contrary to macrophytes, which can be reliably sampled during the peak of the growth season, zooplankton is highly dynamic over time; hence, sediment samples were required to obtain seasonally-integrated, representative assessments of extant communities (particularly in qualitative terms: presence-absence of species; Brendonck and De Meester 2003, Catalan et al. 2009). When species identification was not possible, the individual was ascribed to the lowest identifiable taxonomic level. Hybrid species were also considered as different taxonomic units (see the list of species in Supplementary material Appendix 1).

At each lake, we measured several physico-chemical variables *in situ*: altitude, maximum depth, water transparency (Secchi depth), conductivity, pH, calcium, and total phosphorous (TP). In the Scottish lakes, however, lake depth and Secchi depth could not be measured, albeit these variables were included in the analyses by imputing missing values (see below). Lake area was estimated based on the available cartography. Climatic variables (mean annual precipitation, mean annual temperature, mean temperature of the coldest month, and mean temperature of the warmest month) were obtained from the WorldClim dataset (Hijmans et al. 2005). The number and area of all neighbouring lakes within

a radius of 10 and 20 km of each surveyed lake were used as proxy of small-scale connectivity.

Data analysis

We first calculated the multiple-site Sorensen's index of beta-diversity, as well as its turnover and nestedness components (Baselga 2010, 2012), at two different scales: among lakes within regions (regional scale) and among all lakes (continental scale). Because in the variation partitioning analysis (see below) we used the subset of lakes for which both plants and cladocerans were sampled ($n = 103$), we calculated the beta-diversity indices using a subsample of 103 lakes and accounted for the variation spanned by the complete set of sampled lakes (114 lakes for plants and 123 lakes for cladocerans) by resampling 999 times a random subsample of 103 lakes. We also calculated the proportion of total beta diversity explained by nestedness (b_{ratio} ; Dobrovolski et al. 2012), as an indicator of the relative importance of turnover and nestedness. Spatial turnover is usually associated to niche processes mediated by local environmental factors, while nestedness is usually associated to historical processes and dispersal limitation (Baselga 2010). Note, nevertheless, that the association between patterns and processes is not unequivocal, as a given pattern can be accounted for by multiple processes. For example, other mechanisms such as nested habitats or the selective occupancy of sites according to tolerance to environmental stress can also lead to nested patterns (Ulrich et al. 2009). The interpretation of observed patterns must therefore be complemented with the variation partitioning analysis presented below.

To quantify the relative contribution of niche processes and dispersal limitation to explain community compositional variation, we used distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999) followed by variation partitioning analyses (Borcard et al. 1992, Peres-Neto et al. 2006). We aimed at capturing niche processes using a set of abiotic variables (physico-chemical and climatic variables) and a set of biotic variables (biotic interactions between plant and cladoceran species). Biotic variables were derived from a co-correspondence analysis (CoCA; ter Braak and Schaffers 2004) in which the community structure of one group (either plants or cladocerans) is used to predict the community structure of the other group, based on composition covariance between the two assemblages (see below). We aimed at capturing dispersal limitation using a set of variables describing small-scale connectivity (up to 20 km), the spatial configuration of surveyed lakes (up to 300 km) and region identity (up to 3300 km). After statistically accounting for the spatial structure, a significant effect of the environment is generally accepted to represent niche processes; while, after accounting for the effect of the environment, a significant effect of the spatial structure is usually taken to indicate dispersal limitation (though interpretation must be cautious; see a discussion in Gilbert and Bennett 2010, Smith and Lundholm 2010). Variation partitioning was used to estimate the relative contribution of the abiotic, biotic, connectivity, spatial and region variables (entered as separate matrices of predictor variables; hereafter called components) to explain observed levels of beta-diversity. Each

component entering the variation partitioning analysis was defined according to the following statistical procedures.

The abiotic component (A) was composed by forward-selected abiotic variables. The forward selection was performed according to Blanchet et al. (2008) on a response matrix consisting of the set of positive eigenvectors resulting from a principal coordinate analysis on dissimilarities of either plants or cladocerans. Only the selected abiotic variables were subsequently used in the variation partitioning analyses, for the sake of parsimony.

Biotic interactions (B component) were investigated because direct and indirect interactions between plant and cladoceran species have been reported (Whiteside 1970, Davidson et al. 2011). A Procrustes test supported the existence of significant concordance between the two communities across the surveyed lakes (sum of squares: $SS = 0.78$; correlation $(\sqrt{1 - SS}) = 0.47$; $p = 0.001$). The biotic component was defined using co-correspondence analysis (CoCA; ter Braak and Schaffers 2004). When a given taxonomic group was included as the response matrix, the other was included as the explanatory matrix. To test the accuracy of predictions, cross-validated fits ('leave-one-out' cross validation) were then calculated as $100 \times (1 - ssp_a / ssp_0)$, where ssp_a is the sum of squared prediction errors of the model and ssp_0 is the sum of squared prediction errors under the null model of no relationship (site-species independence; ter Braak and Schaffers 2004). Values above zero indicate that the prediction is better than that obtained by chance, therefore this procedure is also a validity test for the model. We chose the ordination axes containing the site scores that produced the best fits (maximum prediction accuracy) to enter the variation partitioning analysis. The CoCA results showed that the composition of plant and cladoceran communities were significantly correlated – a fact usually interpreted to indicate that these communities influenced each other's composition, though it could also reflect common responses to environmental gradients or shared biogeographical patterns (see Discussion). The cross-validated fits indicated that three axes were sufficient to represent the relationships between plants and cladocerans (Supplementary material Appendix 3, Fig. C1). Hence, the biotic component consisted of a matrix with three variables (CoCA site scores) for both the cladoceran analysis (in which plants were used as the explanatory matrix) and plant analysis (in which cladocerans were used as the explanatory matrix).

The connectivity component (C) was composed by the number and cumulative area of lakes within 10 and 20 km (as in Dodson 1992). These radii represent small-scale measures of connectivity, corresponding to approximately 5% of the maximum distance between lakes within regions (median distance = 25 km). A significant, positive effect of connectivity was interpreted to indicate dispersal limitation, i.e. a more likely arrival of species in lakes with more or larger nearby lakes that can potentially lead to higher compositional homogenisation among more connected lakes.

Because this study comprised two different spatial scales, which can be interpreted as hierarchical, we built one component representing the region (R) and another component representing the spatial relationships among lakes within each of these regions (S), using a procedure described in Declerck et al. (2011). The R component consisted of a matrix with

four dummy variables representing the identity of the region. The S component consisted of a staggered matrix of variables defined by Moran's eigenvector maps (MEM, Dray et al. 2006) calculated separately for each region and arranged in blocks, with each block corresponding to a different region. MEM, formerly called principal coordinates of neighbour matrices (PCNM, Borcard and Legendre 2002, Borcard et al. 2004), model spatial dependence in a set of locations as an orthogonal combination of MEM variables derived from a principal coordinate analysis on the distance matrix (euclidean distances among surveyed lakes). In addition, spatial relationships within regions were also tested using spatial correlation tests (on compositional dissimilarities) based on the Mantel statistic and visualised by means of correlograms (plots of spatial correlation values against distance classes; Supplementary material Appendix 3, Fig. C2).

We estimated the proportion of variation explained by the global, shared and exclusive fractions of the different components (abiotic, biotic, connectivity, spatial and region components) based on their adjusted coefficients of determination (R^2), according to the following procedures. Global fractions of explained variation, i.e. the proportion of variation explained by a given component without taking into account its covariance with other components, were calculated by means of dBRDA. Exclusive and shared fractions of explained variation (which, together, add up to the global fraction) were calculated using a subtractive procedure on hierarchically calculated coefficients of determination (Peres-Neto et al. 2006). The significance of global and exclusive fractions was assessed by permutation tests (maximum number of permutations = 9999; shared fractions can not be tested).

Although the region identity was taken into account (by including the R component), compositional variation potentially explained by regional drivers might be captured more efficiently by removing continental gradients. To control for differences arising from potential biogeographic effects, we repeated the same set of analyses for each region separately, thus checking whether specific environmental drivers could affect community composition within regions.

All data analyses were performed using incidence matrices derived from the subset of lakes for which both aquatic plants and cladocerans were sampled ($n = 103$). Because several abiotic variables had missing values (amounting to 4.6% of the complete dataset), we used an iterative method

based on random forest to impute missing values (miss Forest; Stekhoven and Bühlmann 2012). The performance of imputation was assessed using the normalized root mean squared error (NRMSE = 0.46; NRMSE ranges from 0 to 1, and approaches 0 for accurate estimations). All statistical analyses were performed in R (R Development Core Team), using the packages 'betapart' (Baselga et al. 2013), 'vegan' (Oksanen et al. 2013), 'packfor' (Dray and Blanchet 2013), 'cocorresp' (Simpson 2009) and 'PCNM' (Legendre et al. 2013).

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.p07r1>> (Viana et al. 2015).

Results

Beta-diversity

Aquatic plant and cladoceran communities showed high levels of beta diversity at the continental scale (0.98 and 0.97 for plants and cladocerans, respectively; Table 1). At the regional scale (within regions) beta-diversity was almost as high, ranging from 0.85 to 0.92 for both plants and cladocerans (Table 1). Community compositional variation was explained almost entirely by species turnover, rather than nestedness, at both spatial scales (Table 1).

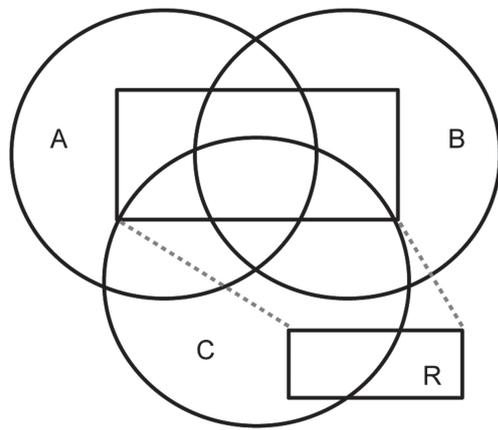
Variation partitioning

All components except the spatial component S significantly explained variation in community composition. The significant full model, which includes A, B, C and R, accounted for 54 and 50% of the variation in community composition of aquatic plants and cladocerans, respectively (Fig. 1). S was excluded from the variation partitioning analysis ($p > 0.999$ for the global fraction); hence, it is not represented in Fig. 1. Mantel correlograms also supported the lack of spatial correlation within regions (Supplementary material Appendix 3, Fig. C2).

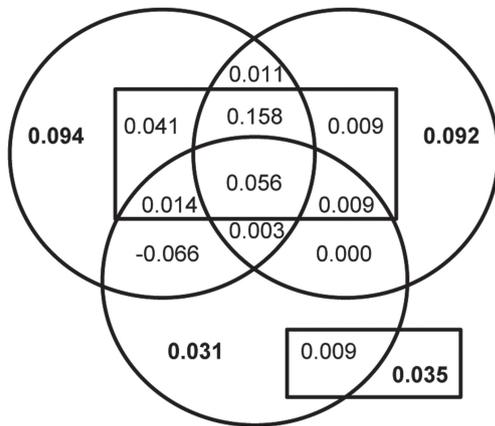
The abiotic (A), biotic (B) and regional (R) components accounted for similar proportions of explained compositional variation (global fractions of 37, 34 and 33% for plants; 34, 31 and 32% for cladocerans, respectively; Fig. 1; see the statistical results in Supplementary mate-

Table 1. Sorensen index of beta-diversity (SOR) and its decomposition into a turnover component (SIM) and nestedness component (NES). b_{ratio} is the ratio between NES and SOR. The global values include all possible pairs among communities (i.e. across all regions).

Taxon	Region	SOR	SIM	NES	b_{ratio}
Plants	Spain	0.855 ± 0.022	0.785 ± 0.039	0.070 ± 0.018	0.082
	Italy	0.869 ± 0.000	0.786 ± 0.000	0.083 ± 0.000	0.095
	Netherlands	0.908 ± 0.004	0.838 ± 0.008	0.071 ± 0.005	0.078
	Scotland	0.922 ± 0.002	0.862 ± 0.007	0.060 ± 0.006	0.066
	Norway	0.904 ± 0.000	0.850 ± 0.000	0.054 ± 0.000	0.059
	Global	0.980 ± 0.000	0.965 ± 0.000	0.014 ± 0.000	0.014
Cladocerans	Spain	0.857 ± 0.009	0.790 ± 0.011	0.067 ± 0.008	0.079
	Italy	0.853 ± 0.006	0.786 ± 0.009	0.067 ± 0.008	0.078
	Netherlands	0.885 ± 0.007	0.789 ± 0.016	0.095 ± 0.013	0.108
	Scotland	0.922 ± 0.000	0.860 ± 0.000	0.061 ± 0.000	0.067
	Norway	0.859 ± 0.000	0.806 ± 0.000	0.052 ± 0.000	0.061
	Global	0.974 ± 0.000	0.958 ± 0.001	0.016 ± 0.001	0.016



Plants



Cladocerans

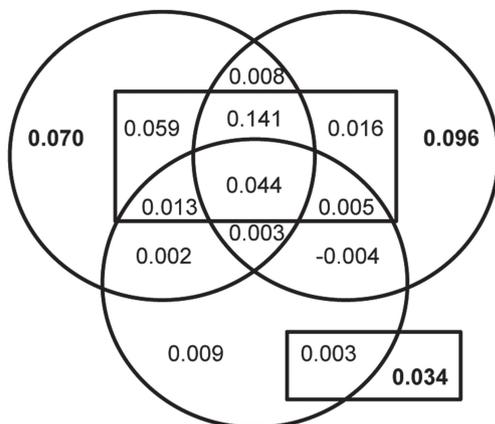


Figure 1. Variation partitioning results for plants and cladocerans. Values indicate the fraction of explained variation (adjusted coefficients of determination, R^2), of which statistically significant fractions are represented in bold face type. A, abiotic component; B, biotic component; C, connectivity component; R, regional component (region identity). The spatial component S was not significant and therefore not included in this figure.

rial Appendix 3, Table C1). The shared fraction among the region, abiotic and biotic components explained 16 and 14% of the total variance for plants and cladocerans respectively (Fig. 1), suggesting that a large proportion of the variation caused by the abiotic and biotic environment was region-

ally structured. Exclusive environmental fractions amounted to less than one third of the global fractions (7–9 and 10% for A and B, respectively). Connectivity (C) accounted for a much smaller, though still significant proportion of community compositional variation (global fractions of 12 and 8% for plants and cladocerans, respectively). Its exclusive contribution was small for plants (3%, $p = 0.009$) and not significant for cladocerans (0.9%, $p = 0.83$).

Repeating the variation partitioning analysis using a dataset with incomplete cases removed yielded similar results. The only noteworthy difference was that, for cladocerans, the exclusive contribution of region (R) was not significant, as a result of losing an entire region (Scotland) from the analysis (Supplementary material Appendix 3, Table C2).

When we ran the variation partitioning analysis separately for each region, we obtained similar results for aquatic plants and cladocerans (Supplementary material Appendix 3, Table C3). The environmental components, most notably A, contributed more to explaining compositional variation than the connectivity and spatial components (C and S). While the biotic component was important to explain compositional variation of plant communities in the two northernmost regions (Scotland and Norway), it explained a negligible fraction of such variation in the cladoceran communities of all five regions. Furthermore, C and S explained a significant fraction of variation for plant communities in three regions (Spain, Scotland and Norway), but their exclusive fractions were either smaller than those of the environment or not significant.

Discussion

The high beta-diversity in both aquatic plant and cladoceran communities across Europe was primarily explained by high species turnover, instead of nestedness. Hence, beta-diversity was mainly caused by variation in species composition, rather than differences in species richness, among lakes. The high species turnover and the greater contribution of the environmental components to explaining variation in community composition suggests an important role of niche processes in determining the assembly and dynamics of aquatic plant and cladoceran communities. Dispersal limitation might be an important factor in some regions, particularly for plant communities, but our results suggest that niche processes tends to dominate – i.e. immigrants often fail to establish owing to unsuitable abiotic conditions, competitive exclusion or a combination of both.

The relatively small effect of connectivity (C) and the lack of spatial correlation within most regions might be explained by the high dispersal potential of aquatic plants and cladocerans, at least at the regional scale (up to 300 km). For example, available estimates suggest that the propagules of aquatic plants and zooplankton are regularly dispersed by animal vectors (notably waterbirds; Figuerola et al. 2003, Charalambidou and Santamaría 2005) over distances that frequently reach tens of kilometres and, occasionally, hundreds to thousands of kilometres (Viana et al. 2013a, b). It should be noted, nevertheless, that significant spatial correlation within one out of the five regions for aquatic plants indicate that dispersal rates between habitat patches

may vary across different regions. In fact, other studies also reported significant spatial correlations for aquatic plants, cladocerans and other aquatic passive dispersers at scales smaller than our within-region surveys (Gray and Arnott 2011, De Bie et al. 2012). Furthermore, variation in dispersal pathways generated by different dispersal vectors and not captured by our analysis might contribute to the low explanatory power of connectivity and spatial variables (Gray and Arnott 2011, 2012).

At continental scale, however, we found significant spatial patterns reflected by the among-region variation. Compositional differences related to the exclusive fraction of region, which might be explained by limited dispersal at continental scale and/or environmental variation not captured by our analysis (e.g. environmental variables not included in models), were relatively small. These were instead largely explained by regionally-structured environmental variation (i.e. by the shared effect of R, A and B). In particular, the variables showing the largest effects were the climatic variables (Supplementary material Appendix 3, Table C4), i.e. those most likely to vary among regions to a greater extent. All in all, this suggests that regional differences in aquatic plant and cladoceran communities are primarily explained by large-scale environmental variation, though other biogeographical factors (including dispersal limitation at continental scale) may also play a significant role.

Independently of the spatial scale, high species turnover was explained to a large extent by significant environmental effects on community composition. While abiotic factors were found to determine beta-diversity patterns of both taxa in other studies (Cottenie et al. 2003, Declerck et al. 2007, O'Hare et al. 2012), biotic effects resulting from relationships between taxa at different trophic levels (such as plants and cladocerans) received less attention to date. Direct interactions between aquatic plants and zooplankton include the use of macrophytes as refuges against fish predation by large cladocerans (Declerck et al. 2007, Van Donk and Van de Bund 2002) and the repellency of certain cladoceran species, particularly specialized planktonic taxa, by allelopathic substances produced by macrophytes (Van Donk and Van de Bund 2002). Alternatively, the biotic relationships found in this study may be explained by indirect interactions, including shared responses to other environmental factors and multiple biotic factors associated to trophic cascades (Padiál et al. 2012). For example, the presence of zooplanktivorous fish might impact zooplankton community structure, which in turn influence phytoplankton and macrophyte communities (Jeppesen et al. 2000, Hobæk et al. 2002). Moreover, biotic interactions were not significant in most regions, suggesting that the overall contribution of the biotic component was probably driven by differences in regional biotas. At any rate, and independently of the specific causal path, our results suggest that abiotic and biotic environmental heterogeneity, which increases with spatial scale (mostly among regions), leads to high levels of beta-diversity.

In the light of the metacommunity framework (Leibold et al. 2004, Logue et al. 2011), our results suggest that species sorting operating through niche processes may explain the high beta-diversity among lakes separated by tens to a few hundred kilometres (regional scale). This mechanism was supported by 1) the large contribution of the environmental component to explain community compositional variation,

and 2) the remarkably high species turnover (78–86%), particularly when considering that most species occur over more than one region. Dispersal limitation might still be important in structuring communities within some regions, but its effects seem to be weaker than those of environmental filters (see also Viana et al. 2014, who report a significant, positive relationship between connectivity and species richness in the same set of lakes used here). It is, however, important to note that alternative mechanisms of community assembly might also account for the high levels of species turnover detected here. For example, small stochastic differences in the order of arrival in vacant habitat patches (which may occur in species with high dispersal abilities), followed by dominance by early arriving species through a combination of demographic effects and local adaptation (i.e. priority effects), may suffice to limit the establishment of subsequent immigrants (Shurin 2000, Chase 2003, Urban and De Meester 2009). Priority effects, which can to some extent explain residual variation in our model, may promote alternative stable states of species assemblages (Jiang et al. 2011) and, in conjunction with species sorting, lead to the observed high beta-diversity.

In conclusion, this study shows that high levels of beta-diversity might be achieved through niche processes mediated by environmental variation over regional and continental scales, while effects of dispersal limitation are only consistently detectable at continental scales. We suggest that species sorting primarily determines the structure of local aquatic communities, and that biogeographic processes, acting through large-scale environmental variation and dispersal limitation, determine the composition of regional biotas.

Acknowledgements – We wish to thank Steven Declerck, and the Subject Editor Luis Mauricio Bini, whose comments helped to improve the manuscript. This research was funded by the European Union project 'LAKES – Long distance dispersal of Aquatic Key Species', contract no. env4-ct-97-0585, and ESF-EURODIVERSITY project BIOPOOL, through the Spanish Ministry of Science project CGL2006-02247/BOS. DSV was supported by Fundação para a Ciência e Tecnologia SFRH/BD/48091/2008, co-financed by the European Social Fund (ESF).

References

- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. – *Global Ecol. Biogeogr.* 19: 134–143.
- Baselga, A. 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. – *Global Ecol. Biogeogr.* 21: 1223–1232.
- Baselga, A. et al. 2013. betapart: partitioning beta diversity into turnover and nestedness components. – R package ver. 1.2, < <http://CRAN.R-project.org/package=betapart> >.
- Blanchet, F. G. et al. 2008. Forward selection of explanatory variables. – *Ecology* 89: 2623–2632.
- Borcard, D. and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. – *Ecol. Model.* 153: 51–68.
- Borcard, D. et al. 1992. Partialling out the spatial component of ecological variation. – *Ecology* 73: 1045–1055.
- Borcard, D. et al. 2004. Dissecting the spatial structure of ecological data at multiple scales. – *Ecology* 85: 1826–1832.
- Brendonck, L. and De Meester, L. 2003. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. – *Hydrobiologia* 491: 65–84.

- Cáceres, C. E. and Soluk, D. A. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. – *Oecologia* 131: 402–408.
- Cadotte, M. W. and Fukami, T. 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. – *Ecol. Lett.* 8: 548–557.
- Catalan, J. et al. 2009. Ecological thresholds in European alpine lakes. – *Freshw. Biol.* 54: 2494–2517.
- Charalambidou, I. and Santamaría, L. 2005. Field evidence for the potential of waterbirds as dispersers of aquatic organisms. – *Wetlands* 25: 252–258.
- Chase, J. M. 2003. Community assembly: when should history matter? – *Oecologia* 136: 489–498.
- Chase, J. M. 2014. Spatial scale resolves the niche versus neutral theory debate. – *J. Veg. Sci.* 25: 319–322.
- Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. – *Ecol. Lett.* 8: 1175–1182.
- Cottenie, K. et al. 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. – *Ecology* 84: 991–1000.
- Davidson, T. A. et al. 2011. The role of cladocerans in tracking long-term change in shallow lake trophic status. – *Hydrobiologia* 676: 299–315.
- De Bie, T. et al. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. – *Ecol. Lett.* 15: 740–747.
- De Meester, L. et al. 2002. The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. – *Acta Oecol.* 23: 121–135.
- Declerck, S. et al. 2007. Plankton biodiversity along a gradient of productivity and its mediation by macrophytes. – *Ecology* 88: 2199–2210.
- Declerck, S. A. J. et al. 2011. Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. – *Ecography* 34: 296–305.
- Dobrovolski, R. et al. 2012. Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. – *Global Ecol. Biogeogr.* 21: 191–197.
- Dodson, S. 1992. Predicting crustacean zooplankton species richness. – *Limnol. Oceanogr.* 37: 848–856.
- Dray, S. and Blanchet, W. C. O. P. L. A. G. 2013. packfor: forward selection with permutation (Canoco p. 46). – R package ver. 0.0-8/r109, <<http://R-Forge.R-project.org/projects/sedar/>>.
- Dray, S. et al. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). – *Ecol. Model.* 196: 483–493.
- Figuerola, J. and Green, A. J. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. – *Freshw. Biol.* 47: 483–494.
- Figuerola, J. et al. 2003. Passive internal transport of aquatic organisms by waterfowl in Doñana, south-west Spain. – *Global Ecol. Biogeogr.* 12: 427–436.
- Gilbert, B. and Bennett, J. R. 2010. Partitioning variation in ecological communities: do the numbers add up? – *J. Appl. Ecol.* 47: 1071–1082.
- Gravel, D. et al. 2006. Reconciling niche and neutrality: the continuum hypothesis. – *Ecol. Lett.* 9: 399–409.
- Gray, D. K. and Arnott, S. E. 2011. Does dispersal limitation impact the recovery of zooplankton communities damaged by a regional stressor? – *Ecol. Appl.* 21: 1241–1256.
- Gray, D. K. and Arnott, S. E. 2012. The role of dispersal levels, Allee effects and community resistance as zooplankton communities respond to environmental change. – *J. Appl. Ecol.* 49: 1216–1224.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- Hobæk, A. et al. 2002. Factors influencing species richness in lacustrine zooplankton. – *Acta Oecol.* 23: 155–163.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.
- Jeppesen, E. et al. 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. – *Freshw. Biol.* 45: 201–218.
- Jiang, L. et al. 2011. Alternative community compositional and dynamical states: the dual consequences of assembly history. – *J. Anim. Ecol.* 80: 577–585.
- Legendre, P. and Anderson, M. J. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. – *Ecol. Monogr.* 69: 1–24.
- Legendre, P. et al. 2013. PCNM: MEM spatial eigenfunction and principal coordinate analyses. – R package ver. 2.1-2/r109, <<http://R-Forge.R-project.org/projects/sedar/>>.
- Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Levine, J. M. and HilleRisLambers, J. 2009. The importance of niches for the maintenance of species diversity. – *Nature* 461: 254–257.
- Logue, J. R. B. et al. 2011. Empirical approaches to metacommunities: a review and comparison with theory. – *Trends Ecol. Evol.* 26: 482–491.
- Louette, G. and De Meester, L. 2005. High dispersal capacity of cladoceran zooplankton in newly founded communities. – *Ecology* 86: 353–359.
- O’Hare, M. T. et al. 2012. Impacts of space, local environment and habitat connectivity on macrophyte communities in conservation lakes. – *Divers. Distrib.* 18: 603–614.
- Oksanen, J. et al. 2013. vegan: community ecology package. – R package ver. 2.0-9, <<http://CRAN.R-project.org/package=vegan>>.
- Padial, A. A. et al. 2012. Evidence against the use of surrogates for biomonitoring of Neotropical floodplains. – *Freshw. Biol.* 57: 2411–2423.
- Peres-Neto, P. R. et al. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. – *Ecology* 87: 2614–2625.
- Qian, H. and Ricklefs, R. E. 2007. A latitudinal gradient in large-scale beta diversity for vascular plants in North America. – *Ecol. Lett.* 10: 737–744.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. – *Science* 235: 167–171.
- Santamaría, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. – *Acta Oecol.* 23: 137–154.
- Shurin, J. 2000. Dispersal limitation, invasion resistance and the structure of pond zooplankton communities. – *Ecology* 81: 3074–3086.
- Shurin, J. et al. 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. – *Oecologia* 159: 151–159.
- Simpson, G. L. 2009. Co-correspondence analysis ordination methods. – R package ver. 0.2-0, <<http://cran.r-project.org/package=analogue>>.
- Smith, T. W. and Lundholm, J. T. 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. – *Ecography* 33: 648–655.
- Stekhoven, D. J. and Bühlmann, P. 2012. MissForest – non-parametric missing value imputation for mixed-type data. – *Bioinformatics* 28: 112–118.
- ter Braak, C. J. F. and Schaffers, A. P. 2004. Co-correspondence analysis: a new ordination method to relate two community compositions. – *Ecology* 85: 834–846.
- Ulrich, W. et al. 2009. A consumer’s guide to nestedness analysis. – *Oikos* 118: 3–17.

- Urban, M. C. and De Meester, L. 2009. Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. – *Proc. R. Soc. B* 276: 4129–4138.
- Van Donk, E. and Van de Bund, W. J. 2002. Impact of submerged macrophytes including charophytes on phyto- and zooplankton communities: allelopathy versus other mechanisms. – *Aquat. Bot.* 72: 261–274.
- Van Leeuwen, C. H. A. et al. 2012. Gut travellers: internal dispersal of aquatic organisms by waterfowl. – *J. Biogeogr.* 39: 2031–2040.
- Vellend, M. et al. 2014. Assessing the relative importance of neutral stochasticity in ecological communities. – *Oikos* 123: 1420–1430.
- Viana, D. S. et al. 2013a. Allometric scaling of long-distance seed dispersal by migratory birds. – *Am. Nat.* 181: 649–662.
- Viana, D. S. et al. 2013b. Migratory strategies of waterbirds shape the continental-scale dispersal of aquatic organisms. – *Ecography* 36: 430–438.
- Viana, D. S. et al. 2014. Environment and biogeography drive aquatic plant and cladoceran species richness across Europe. – *Freshw. Biol.* 59: 2096–2106.
- Viana, D. S. et al. 2015. Data from: Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.p07r1>>.
- Whiteside, M. C. 1970. Danish chydorid cladocera: modern ecology and core studies. – *Ecol. Monogr.* 40: 79–118.

Supplementary material (Appendix ECOG-01231 at <www.ecography.org/appendix/ecog-01231>). Appendix 1–3.