

# Effects of wind-driven spatial structure and environmental heterogeneity on high-altitude wetland macroinvertebrate assemblages with contrasting dispersal modes

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## SUMMARY

1. Dispersal is a major determinant of connectivity between communities that may modulate the importance of environmental and spatial processes on taxonomic composition. While wind is likely to influence transport distance, rate and direction for numerous species, its effects on community composition remain poorly understood.
2. Using eigenvector-based spatial analyses, we investigated the influence of wind flows, estimated by mesoscale models, on the spatial structure of benthic macroinvertebrate assemblages with contrasting flying abilities in high Andean wetlands (26–32°S). We further quantified the relative importance of local and regional processes through a variation partitioning approach.
3. The influence of environmental heterogeneity was prevalent and of relatively similar amplitude in both flying and non-flying assemblages. Significant spatial structure more strongly driven by wind flows than by Euclidean schemes was detected for both assemblages. As expected, the highest levels of spatial structure were observed for the flying macroinvertebrate assemblage and they occurred at a much larger spatial scale in this group, suggesting a greater dispersal aptitude of the flying taxa.
4. Our results show that environmental effects are predominant in shaping the spatial structure of macroinvertebrate communities in high Andean wetlands, as generally found in other systems. They also demonstrate the significance of wind flows in regulating high-altitude wetland macroinvertebrate communities and illustrate the importance of considering adequate spatial models and biological characteristics of species to advance our understanding of community patterns.

*Keywords:* benthic macroinvertebrates, dispersal, eigenvector maps, wetlands, wind

## Introduction

Dispersal can be defined as the movement of organisms or their propagules with potential consequences for gene flow across space (Ronce, 2007). It is a critical process in ecology, influencing a variety of patterns and processes such as species distribution, long-term persistence of populations and predator–prey interactions (Fahrig &

Merriam, 1994; Holyoak & Lawler, 1996; Cadotte, 2006b; Eklof, Kaneryd & Munger, 2012). Its role in biodiversity patterns has long been recognised (MacArthur & Wilson, 1967) and has been the subject of increasing scientific interest (Clobert *et al.*, 2012). Dispersal is considered as a prominent regional mechanism of community assembly and diversity, due to its effects on the geographical range and habitat connectivity of species (Mouquet & Loreau,

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2002; Loreau, Mouquet & Holt, 2003). It may also modulate the importance of processes operating at local scales (e.g. local filtering) by influencing the ability of species to track environmental changes and to reach potentially suitable habitats (Flinn *et al.*, 2010; Heino, 2013).

Dispersal is strongly dependent on the biological characteristics of species and on landscape structure and scale (Fahrig, 2007). Landscape connectivity refers to the ease with which organisms can move about within the landscape (Kindlmann & Burel, 2008). A popular way to estimate connectivity uses simple structural metrics (Dale & Fortin, 2010), for example Euclidean shortest distances between habitat patches. However, because these measures only describe physical relationships between habitats without considering how landscape characteristics actually facilitate or impede the movement of organisms between patches, they may not account well for functional connectivity (Taylor, Fahrig & With, 2006). Moreover, Euclidean networks usually assume that spatial processes are symmetric, whereas directional physical processes may result in asymmetric connectivity between patches (Blanchet, Legendre & Borcard, 2008b). For instance, water flows are expected to play a critical role on community and populations structures in river networks, and this expectation is supported by empirical studies demonstrating that spatial modelling of species distribution based on hydrological connections and water directionality outperforms models based on overland distances only (Blanchet *et al.*, 2011a; Liu *et al.*, 2013).

Wind is another element likely to influence the dispersal trajectory of numerous organisms. It is actually recognised as one of the main long-distance dispersal mechanisms (Van der Pijl, 1982), and its importance to transport distance and rate has been demonstrated for numerous animal and plant species (Horn, Nathan & Kaplan, 2001; Schooley & Wiens, 2003; Chapman *et al.*, 2011). This suggests that wind dynamics may influence critically the movement ecology of a number of organisms and that prevailing winds may generate asymmetric functional connectivity between patches (see Chapman *et al.*, 2011 for a review of dispersal patterns in relation to wind direction). Despite the recognised importance of wind on spatial patterns of movement, community responses to wind dynamics are poorly understood. The importance of wind as a natural dispersal vector for aquatic invertebrate taxa has long been acknowledged (Maguire, 1963) and has received growing empirical support (Cáceres & Soluk, 2002; Cohen & Shurin, 2003; Vanschoenwinkel *et al.*, 2008; Reynolds *et al.*, 2010). However, the transport distance resulting from wind-mediated dispersal may depend strongly on the ability of the aquatic macroinvertebrate

taxa to fly in the adult stage. Winged taxa may utilise active downwind migration to increase their dispersal range (Chapman *et al.*, 2011) and undertake windborne migration over hundreds of kilometres (Drake & Gatehouse, 1995). In contrast, wind-mediated dispersal of wingless taxa, occurring through the passive dispersal of their propagules, may only be effective over short distances not exceeding hundreds of metres (Cáceres & Soluk, 2002; Cohen & Shurin, 2003; Vanschoenwinkel *et al.*, 2008) as reported for wind-dispersed pollen and spores in many plant and fungus species with exceptional records of dispersal up to few kilometres (Ashley, 2010; Rieux *et al.*, 2014). The connectivity patterns generated by wind flows are thus likely to differ between macroinvertebrate taxa according to their dispersal mode and are expected to be scale dependent.

We therefore investigated the effects of wind flows on the assemblage composition of benthic macroinvertebrates from high Andean wetlands in north-central Chile (26–32°S), which resemble island ecosystems embedded in a semi-arid/arid matrix (Cepeda *et al.*, 2009). We utilised a variation partitioning approach (Legendre & Legendre, 1998) to examine whether wind flows, estimated by mesoscale models, influence the structure of high Andean wetland macroinvertebrate assemblages depending on their dispersal characteristics (flying versus non-flying). We hypothesised that wind could play a key role in maintaining connectivity among these habitat patches, as has been shown for other wetland systems (Amezaga, Santamaria & Green, 2002). To assess the relative importance of spatial and local processes in the composition of each assemblage type, we analysed their spatial structure considering either Euclidean symmetric spatial processes or asymmetric spatial patterns following the direction of prevailing winds. We hypothesised that dispersal characteristics will influence the spatial structure of the assemblages. Because most neighbouring habitats were at least several kilometres apart, we expected that wind flows would facilitate functional connectivity among wetland habitats mostly for those aquatic macroinvertebrate taxa capable of flight in the adult stage. Furthermore, we postulated that dispersal mode may influence the importance of local scale processes by affecting dispersal ability and rates.

## Methods

### *High-altitude wetlands of the central Andes*

High-altitude wetlands of the central Andes are commonly referred to as peatlands or 'bofedales' (Coronel

*et al.*, 2004; Squeo *et al.*, 2006). They are found in the central Andes of Bolivia, Peru, Argentina and Chile and occur in the low Alpine and sub-Alpine belts at elevations between 2800 and 5000 m.a.s.l. (Squeo *et al.*, 2006). They differ notably from peatlands of the Northern Hemisphere as they are dominated by low cushion-forming plants of the Juncacea family and not by *Sphagnum* mosses (Coronel *et al.*, 2004; Squeo *et al.*, 2006). The high Andean wetlands experience particularly harsh climatic conditions such as aridity, intense solar radiations, hypoxia, daily frost and high-velocity winds (Squeo *et al.*, 2006). They are sustained by precipitations, ground water and small glacier streams (Squeo *et al.*, 2006).

### Study area

We collected data on macroinvertebrate communities, water and habitat characteristics from 21 high Andean wetlands located along c. 600 km latitudinal range (between 26 °S and 32 °S) in north-central Chile. This region includes five main river basins (Fig. 1) with no hydrological connections between them. All these river basins have their outlet in the ocean, their aquifers are narrow and confined to the valley bottoms, and steep slopes of crystalline bedrock form impermeable barriers between each catchment (Favier *et al.*, 2009). The climate in this region varies from hyperarid in the north to Mediterranean in the south, with mean annual precipitation reaching 35 mm for the northernmost valley and 200 mm for the southernmost valley and a strong altitudinal gradient in the east–west direction. All the sampled wetlands belong to the subalpine range and are dominated by the Cyperaceae, *Carex gayana*, a relatively common wetland plant species. Their average area  $\pm$  SD is  $5.6 \text{ km}^2 \pm 4.4$ , and the distance between neighbouring wetlands ranges from 7 to 94 km.

### Data acquisition

**Macroinvertebrate data.** Benthic macroinvertebrates were sampled in March–April 2011 by collecting 10 Surber samples (0.07 m<sup>2</sup> area, 500  $\mu$ m mesh size) from each study site. The length of the wetland was first divided into five sectors, and two samples were taken in each sector from the principal water course or, when present, from the pools of water. As much as possible, samples were collected from different substrata (aquatic vegetation, stone, gravel, sand, plant debris accumulation, roots). The samples were immediately preserved in 95% ethanol and taken to the laboratory for further processing and identification. Due to the poor taxonomic

knowledge of Chile's benthic fauna, the macroinvertebrates were identified to the family level. While species level identification would be ideal, shortages of stream macroinvertebrate taxonomy and practical issues have forced many studies to use supra-specific resolution (Grenouillet *et al.*, 2008; Jacobsen & Marin, 2008; Jacobsen *et al.*, 2012; Heino, 2013). The family-level approach is expected to generate conservative estimates of environmental and spatial effects on community structure. Nevertheless, its adequacy is supported by observations that overall macroinvertebrate community patterns are invariant from species to family (Melo, 2005; Heino & Soininen, 2007), with evidence indicating that the levels of variation explained by environmental and spatial variables are relatively stable across taxonomic scales (Heino & Soininen, 2007). Family-level data are expected to perform particularly well in regions where species diversity within families is low and varies little and when a few common species are abundant (Mueller, Pander & Geist, 2013). Several lines of evidence suggest that this is the case in the studied area. Indeed, previous works identified very few morphospecies per benthic macroinvertebrate family in the region (average number of morphospecies per family varying from 1.35 to 1.92 in Figueroa *et al.*, 2009 and Carvacho Aránguiz, 2012, respectively) with more than 75% of the benthic macroinvertebrate families of the region being represented by only one morphospecies. Low species to family ratios are also suggested by mitochondrial cytochrome oxidase I DNA sequencing of three macroinvertebrate families from our samples with contrasting dispersal abilities (Elmidae, Hyallellidae and Baetidae), which also indicate that the species to family ratios ranged from one to three for the most and less vagile taxa, respectively, and in all three families, one species was largely dominant and common (Gouin *et al.* unpubl. data).

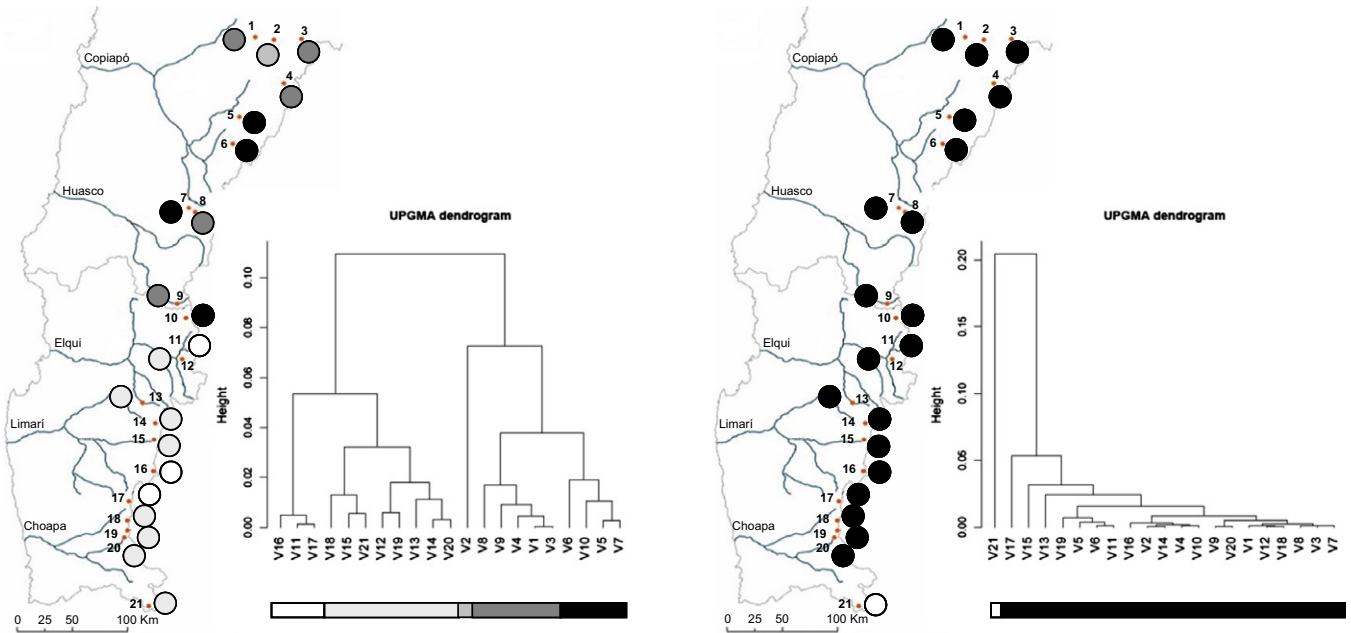
To evaluate whether dispersal mode influences the spatial structure of macroinvertebrate assemblages as well as the relative importance of spatial processes and environmental factors on assemblage composition, the benthic macroinvertebrate community was subdivided into assemblages by sorting taxa according to their ability to fly at the adult stage following Bilton, Freeland & Okamura (2001) and Verberk, Siepel & Esselink (2008) (See Table S1). The flying assemblage thus included all taxa capable of flight regardless of their actual dispersal ability and regardless of whether active aerial dispersal was their most dominant dispersal mode.

**Environmental data.** Environmental variables and habitat characteristics were sampled concurrently with the

Isotropic spatial structure – Euclidean schemes

(a) Flying assemblage

(b) Non-flying assemblage



Anisotropic spatial structure – Wind direction

(c) Flying assemblage

(d) Non-flying assemblage

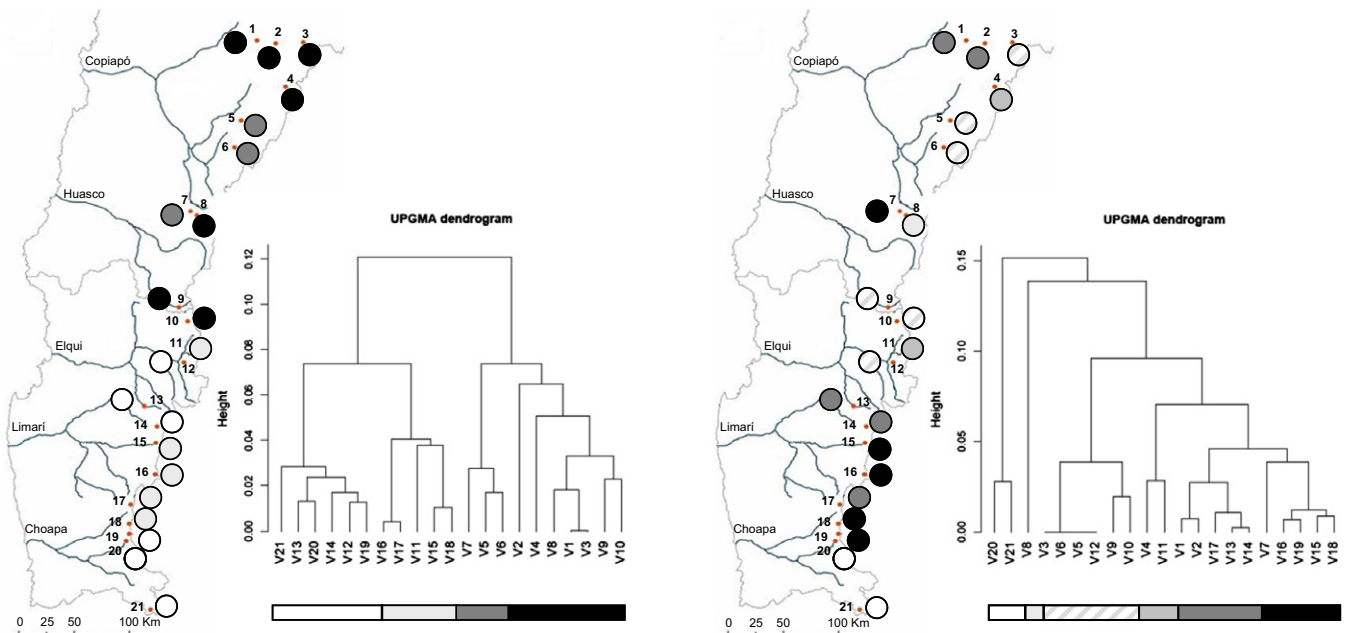


Fig. 1 Map of the clusters obtained from the fitted site scores of the significant redundancy analysis axes of the Moran eigenvector map analysis (a and b) and asymmetric eigenvector map analysis (c and d) of the flying and non-flying macroinvertebrate assemblages.

macroinvertebrates. Specifically, we recorded altitude, width and depth of the water course and current velocity and made visual estimates of the percentage substrata present (stones, aquatic vegetation and organic elements). A total of 25 physical–chemical water parameters were also measured. Temperature, pH, conductivity, dissolved oxygen and turbidity were recorded in the field using a portable pH-meter (Schott model Handylab CG-836/2046) and an oxygen meter (Hanna model 3180). Water samples of 1L, collected simultaneously with biological samples, were analysed in a certified laboratory (Geoquímica, Coquimbo ISO 9001:2000 certification) to quantify the concentrations of various nutrients and potentially toxic elements (aluminium, arsenic, cadmium, calcium, copper, iron, potassium, lead, sodium, magnesium, mercury, molybdenum, zinc, carbonates, chlorides, phosphates, phosphorus, nitrogen, dissolved solids and sulphates). For each wetland, average yearly precipitation was calculated from monthly precipitation data over a 32-year period (1975–2006), from a 1-km resolution gridded precipitation data set of the study region (Bourgin *et al.*, 2012). This data set was generated by interpolation of the precipitation gauges network operated by the Chilean water agency and validated in the high-altitude areas using snow depth measurements and catchment-scale water balance.

*Wind flow maps.* Because the spatial distribution of wind flow is strongly influenced by topography, wind speed and direction can experience large variations over small horizontal distances, especially in areas with complex topography such as the high Andes. Mesoscale modelling is a useful tool to evaluate the spatial distribution of wind flows. It allows evaluation of wind flows and other meteorological variables in large areas based on surface characteristics and synoptic conditions (Bischoff-Gauss, Kalthoff & Fiebig-Wittmaack, 2006).

Wind flow (direction and speed) maps were generated at 1-km resolution across north-central Chile (see Fig. S1) using the non-hydrostatic Karlsruhe Atmospheric Mesoscale Model KAMM (Adrian & Fiedler, 1991). An average wind flow map was produced for both spring and summer considering daily conditions over the season and over a 16-year period. Complete information about the KAMM model can be found in Bischoff-Gauss *et al.* (2006) and Montecinos *et al.* (2008). The model uses a large-scale synoptic weather situation (vertical profiles of temperature, humidity and wind) as well as topography, soil type and land-use data as input information. For each season, the daily mean meteorological condi-

tions were evaluated over 1990–2006. The land-use map was constructed based on the catalogue produced by CONAF, CONAMA (1999).

The methodology used a cluster analysis, grouping days from a given season into distinct clusters based on their similarity in zonal and meridional winds at 500 hPa, in a potential temperature gradient between 850 hPa and 500 hPa. For the clustering procedure, we used a pairwise Euclidean distance matrix as input and Ward's method as the grouping algorithm. A representative simulation with the KAMM model was carried out for each cluster. The initial atmospheric vertical profiles required by the model were gathered from the National Center for Environmental Prediction/NCAR Reanalysis (Kalnay *et al.*, 1996), and for each cluster, we used the mean values of all the members. The atmospheric profiles are used by the KAMM to construct the initial state of the atmosphere as starting data for the simulations. The simulations of the clusters were averaged, taking into account the statistical weight of the clusters. Mean diurnal cycles of the meteorological variables were estimated and checked for accuracy by comparing simulated data with observations taken from 30 ground meteorological stations distributed in the region.

#### *Statistical analyses*

All statistical analyses were performed with R.2.13.0 (R Development Core Team, 2011), often using scripts developed by Borcard, Gillet & Legendre (2010).

#### *Data transformation*

Rare taxa occurring at fewer than 5% of the sites were deleted from the macroinvertebrate matrix. A Hellinger transformation was then applied to the assemblage matrices. This transformation standardises the matrix elements by the sampling unit totals followed by a square root transformation of the resulting values and allows preservation of an adequate distance among sites (the Hellinger distance) for linear multivariate analyses (Legendre & Gallagher, 2001). Environmental variables with zero or negligible variance were eliminated.

#### *Modelling asymmetric spatial structure driven by wind flows*

An asymmetric eigenvector map analysis (AEM) was carried out to model spatial structure according to prevailing wind directions, because this method is

especially designed to model directional spatial structures (Blanchet *et al.*, 2008b). A complete description of the AEM method can be found in Blanchet, Legendre & Borcard (2008b). In short, it first involves the construction of a sites-by-edges matrix from a connection diagram. The spatial variables (the AEM variables) are the eigenvectors obtained by the principal coordinate decomposition of this matrix. Sorted in descending order of their eigenvalues, the spatial eigenvectors allow modelling of broad to fine geographical structure. In the present case, the presence of edges (i.e. connectivity) between sites was established from the wind flow maps produced for 10 m above ground level. Two connection diagrams were constructed this way, one for summer and one for spring (see Fig. S2). Direction was set according to wind direction by including connections to a hypothetical site located upwind of any sampled site (Blanchet *et al.*, 2008b). Weights were assigned to each connection in order to account for the ease of dispersal between sites. Specifically, we considered the between-site distance along the wind current (WD), the mean wind speed between two linked sites (WS) and the potential time needed to travel from one site to another ( $WT = WD/WS$ ). While high WS is expected to facilitate connectivity between sites, high WD and WT are predicted to make it more difficult. Thus, we applied similar functions for WD and WT:  $1 - (d_{ij}/d_{\max}(d_{ij}))^\alpha$  and  $1/d_{ij}^\alpha$ , respectively (Dray, Legendre & Peres-Neto, 2006) where  $d_{ij}$  represents either WD or WT between site  $i$  and  $j$ ; for each function, both  $\alpha = 1$  and  $\alpha = 2$  were considered (Blanchet *et al.*, 2011a). In contrast, we applied a different weighting function  $(d_{ij}/d_{\max}(d_{ij}))^\alpha$  for WS and considered  $\alpha = 0.5$  (concave-up),  $\alpha = 1$  (linear) and  $\alpha = 2$  (concave-down) (Blanchet *et al.*, 2011a).

The influence of the AEM variables on the assemblage composition was evaluated with redundancy analysis (RDA). For these analyses, only those spatial descriptors representing positive spatial autocorrelation were considered. They were selected by calculating Moran's autocorrelation coefficients. A forward selection was conducted on this set of variables using the double-stopping criterion of Blanchet, Legendre & Borcard (2008a) based on  $\alpha = 0.05$  and the adjusted  $R^2$  of the full model. For the subsequent analyses, only the combination of season (spring or summer), weight type (WD, WS, WT), function and exponent explaining the greatest portion of the variation in the composition of the assemblages (highest adjusted  $R^2$ ) was considered and tested for significance. Significance of the selected RDA model was evaluated by permutation tests using 9999 randomisations (Peres-Neto *et al.*, 2006).

### *Modelling symmetric spatial processes considering Euclidean-based schemes*

To model spatial processes according to the geographical distance only, we carried out Moran eigenvector map analyses (MEM, Dray *et al.*, 2006). This method allows modelling of bidirectional (symmetric) processes. The spatial variables are derived through the spectral decomposition of a symmetric connectivity matrix, which was constructed in the present case by considering connectivity schemes based on Euclidean distances: Delaunay triangulation, Gabriel graph, the relative neighbourhood and the minimum spanning tree (Dale & Fortin, 2010). Intensities of the connections were set by applying the same concave-down or concave-up functions used for WD and WT with  $d$  representing the Euclidean distances among sites. Selection of the model tested for significance and used in subsequent analyses was performed as above, by only considering the season, connectivity scheme, function and exponent combination providing the highest adjusted  $R^2$ . However, for these analyses, spatial linear trends (broad scale gradients) in the response variables were first checked and controlled for when present (Dray *et al.*, 2006).

### *Graphical visualisation of the modelled spatial structure*

To visualise at what geographical scale spatial structure occurred, the spatial distribution of the groups detected by the spatial models was mapped. To do so, we carried out a hierarchical clustering (the average linkage method, UPGMA) on the fitted scores of the significant RDA axes when significant spatial structure was detected. The number of groups was determined based on the elbow criterion, that is by setting the optimum number of clusters at the point where the percentage of adjusted variance explained in the fitted scores by the cluster groups levelled off in spite of the addition of new groups.

### *Environmental effects*

Partial least squares (PLS) regressions were carried out to analyse and explore the influence of environmental factors on macroinvertebrate assemblages. PLS regression consists of the linear regression of the dependent matrix on PLS components, that is linear combinations of the original predictor variables calculated to maximise the covariance between the predictor and response variables (Martens & Naes, 1989; Mevik & Wehrens, 2007). PLS regression offers the advantage of being suitable for

situations where the number of predictor variables is high compared to the number of observations (Mevik & Wehrens, 2007). The influence of the environmental data on macroinvertebrate composition was evaluated separately for the flying and non-flying assemblages. Model fitting was performed using a leave-one-out cross-validation procedure (Mevik & Cederkvist, 2004). To avoid over-fitting, the optimal number of components was determined by identifying the first local minimum of the root-mean-squared error calculated from the leave-one-out cross-validation predictions and then the variance in assemblage composition explained by environmental factors was assessed by performing RDAs including the retained PLS components as independent variables.

#### Variation partitioning and interpretation of the fractions

Both full and partial RDAs were carried out to partition the variation explained by the selected spatial variables and environmental PLS components. The fraction shared between environmental and spatial descriptors might result from induced spatial dependence (due to the influence of spatially structured abiotic factors). The fraction of the variation explained by the spatial variables after controlling for environmental effects may be caused either by spatially structured environmental factors not included in the analysis or by spatial processes occurring over the landscape (Legendre & Legendre, 1998). It is thus the fraction that accounts for the

effects of dispersal. Significance of the full and partial RDA models was evaluated by permutation tests using 9999 randomisations (Peres-Neto *et al.*, 2006).

## Results

### Spatial structure

Both macroinvertebrate assemblages showed significant symmetric and asymmetric spatial structure (Table 1). In both cases, spatial structure was most strongly driven by wind flows than by Euclidean schemes. The asymmetric spatial models leading to the highest adjusted variance were obtained using the wind connection diagram containing more edges, which was obtained from the spring season. It was identical to the summer connection diagram with the exception that it included two additional edges. The best set of AEM variables was produced considering wind distance and speed (WT) for the flying group and only wind speed (WS) for the non-flying group. The best symmetric spatial models were generated using the relative neighbourhood and Gabriel graph schemes (Table 1). These two Euclidean schemes considered few connections between sites (average number of edges per site 1.9 and 2.0, respectively), and in fact only differed in one connection between sites 2 and 4 (present in the Gabriel graph and absent in the relative neighbourhood scheme; see Fig. 1 for the geographical location of the sites).

**Table 1** Variance in macroinvertebrate assemblage composition explained (adjusted  $R^2$ ) separately by spatial and environmental descriptors according to redundancy analyses

| Macroinvertebrate assemblage | Tested effect   | Weight and function used in best model | Selected variables | $R^2_{adj}$ | F   | d.f.num <sub>v</sub> | d.f.den | P      |
|------------------------------|---|--|--------------------|-------------|-----|----------------------|---------|--------|
| Flying                       | Asymmetric spatial structure – wind direction               | $1 - (WT_{ij}/WT_{max}(WT_{ij}))^2$    | V5, V3, V7         | 0.25        | 3.2 | 3, 17                |         | 0.004  |
|                              | Symmetric spatial structure – Euclidean scheme              | $RN - 1 - (d_{ij}/d_{max}(d_{ij}))$    | V1, V5             | 0.18        | 3.2 | 3, 22                |         | 0.002  |
|                              | Environmental effects                                       |  | PLS1, PLS2         | 0.28        | 4.8 | 2, 18                |         | <0.001 |
|                              | All effects together (Environmental and spatial predictors) | See above                              | See above          | 0.43        | 3.2 | 7, 13                |         | <0.001 |
| Non-flying                   | Asymmetric spatial structure – wind direction               | $(WS_{ij}/WS_{max}(d_{ij}))^2$         | V6, V5             | 0.16        | 3.0 | 2, 18                |         | 0.002  |
|                              | Symmetric spatial structure – Euclidean scheme              | $GG - 1/d_{ij}^\alpha$                 | V10                | 0.06        | 2.2 | 1, 19                |         | 0.024  |
|                              | Environmental effects                                       |  | PLS1, PLS2         | 0.22        | 3.8 | 2, 17                |         | <0.001 |
|                              | All effects together (environmental and spatial predictors) | See above                              | See above          | 0.33        | 2.9 | 5, 15                |         | <0.001 |

Spatial variables were produced through asymmetric eigenvector map (asymmetric spatial variables) and Moran eigenvector map (symmetric spatial variables) analysis and selected using a forward selection strategy. PLS refers to components produced through partial least square regression (see methods). RN and GG stand for relative neighbourhood and Gabriel graph, respectively.

As expected, the greatest levels of spatial structure were observed for the flying macroinvertebrate assemblage (Table 1); the asymmetric and symmetric spatial structures of this group were, respectively, 1.5 times and 3 times that of the non-flying assemblage. Moderate to high correlations (i.e. >0.4) between taxa abundance and spatial variables were observed with 62.5% of the flying assemblage taxa including some Coleoptera (Elmidae), Ephemeroptera (Baetidae, Leptophlebiidae), Diptera (Athericidae, Ceratopogonidae, Chironomidae, Dolichopodidae, Empididae, Ephydriidae, Simuliidae, Stratiomyidae, Tabanidae) and Trichoptera (Hydrobiosidae, Leptoceridae, Limnephilidae). In contrast, such correlations were observed for only few non-flying taxa (i.e. 33.3%) involving flatworms (Dugesiiidae), annelid worms (Naididae and Glossiphoniidae), amphipods (Hyaellidae) and ostracods. Finally, differences were detected between the two assemblages regarding the geographical scale at which spatial structure occurred. For the flying assemblage, the selected eigenvectors described broad (V1–V3) to medium (V5–V7) scale patterns (Table 1), while for the non-flying group, they included eigenvectors from medium (V6–V5) to fine geographical scale (V10). These differences in spatial structure scale are well illustrated by the geographical maps of the clusters obtained from the fitted values (Fig. 1). Indeed, for the flying macroinvertebrates, both dendrograms (Fig. 1a,c) separated the communities into two geographically distant groups, one composed of the 10 northern sites (from the Copiapó and Huasco basins) and the other one of the 11 southern sites (from the Elqui, Limari and Choapa basins). Within each of these subsets, the communities then aggregated into groups including two to four geographically close communities (Fig. 1a,c). Thus, both the asymmetric and symmetric spatial analyses primarily modelled broad-scale variation in the flying macroinvertebrate assemblage, and to a lesser extent medium- to fine-scale spatial structures. No large-scale separation was identified for the non-flying assemblage (Fig. 1b,d). In contrast, the communities aggregated into groups mainly composed of one to three geographically close communities (Fig. 1b,d), indicating that spatially structured variation only arose at a medium to fine geographical scale. In fact, the symmetric spatial analysis suggests a very local effect, since only one community was differentiated from the rest.

#### *Environmental effects*

For both macroinvertebrate assemblages, the leave-one-out cross-validation predictions indicated that two

PLS components optimally predicted the abundance of most macroinvertebrate taxa. In both cases, the selected components together accounted for about 45% of the variation of the environmental data and explained relatively similar levels of the variation in composition of the flying and non-flying assemblages (i.e. 28 and 22%, respectively, Table 1). For the non-flying group, the environmental factors contributing most to the two PLS regression axes only involved water characteristics, including chemical and physical parameters (water concentration of magnesium, calcium, sodium, potassium and chloride, dissolved solids, water turbidity and conductivity, water concentrations of sulphate, phosphate and carbonate ions) and habitat characteristics (the proportion of stones and of aquatic vegetation). For the flying group, the contributing variables included the same set of water physical-chemical parameters as well as wetland altitude and average yearly precipitation.

#### *Variation partitioning*

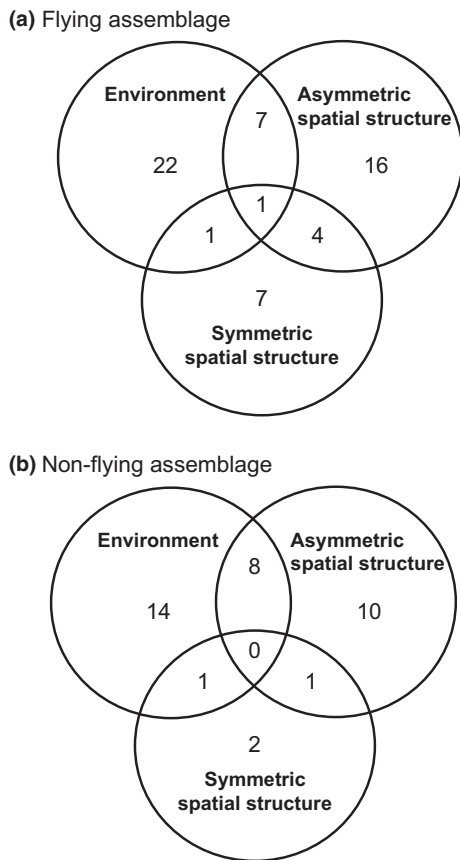
The environmental effects and spatial structure together accounted for 33–43% of the variation in composition of the two macroinvertebrate assemblages (Table 1). In both cases, more than half of the explained variation was attributed to environmental variables (Fig. 2). The shared fraction between environmental factors and spatial predictors only represented 25 and 40% of the spatial structure detected in the flying and non-flying assemblages, respectively (Fig. 2). The remaining fraction was accounted for by significant unique spatial patterns ( $P = 0.02$  in both cases) predominantly given by wind flows. The asymmetric spatial structure represented 74 and 84% of the unique spatial effects of the flying and non-flying assemblage, respectively (Fig. 2). Overall, the estimated spatial structure of the flying assemblage after controlling for environmental effects was twice that of the non-flying group. In both groups, the partial asymmetric component remained significant ( $F_{2,15}$  and  $F_{3,15} = 2.63$  and  $2.86$ ;  $P < 0.01$ ). This was only true with the symmetric spatial components for the flying group ( $F_{2,16} = 2.28$ ,  $P < 0.01$  for the flying group and  $F_{1,16} = 1.53$ ,  $P > 0.05$  for the non-flying group).

## **Discussion**

### *Importance of environmental and spatial processes in relation to dispersal mode*

Because the dispersal of species plays a pivotal role in their distribution, life-history and ecological traits that





**Fig. 2** Venn diagrams of the variation partitioning of macroinvertebrate composition explained by environmental factors for (a) flying and (b) non-flying assemblages. Asymmetric spatial variables derived from wind flows and symmetric spatial variables based on Euclidean schemes. Values represent adjusted  $R^2$  (%).

affect the ability of species to disperse can be expected to influence community composition and diversity (Cottenie, 2005; Flinn *et al.*, 2010). Empirical evidence indicates that dispersal mode (e.g. active versus passive) is a particularly important determinant of community structure (Cottenie, 2005). Its impact on aquatic organisms has mostly been investigated in patchy but highly interconnected systems and at relatively small spatial scales (Pinelalloul, Niyonsenga & Legendre, 1995; Cottenie *et al.*, 2003; Van De Meutter, De Meester & Stoks, 2007; Vanschoenwinkel *et al.*, 2007). By contrast, little attention has been paid to aquatic communities in fragmented and strongly isolated ecosystems such as the ones studied here.

In agreement with earlier studies on other freshwater ecosystems (Pinelalloul *et al.*, 1995; Cottenie & De Meester, 2003; Cottenie *et al.*, 2003; Van De Meutter *et al.*, 2007; Vanschoenwinkel *et al.*, 2007; Vanormelingen *et al.*, 2008; Declerck *et al.*, 2011; De Bie *et al.*, 2012; Heino *et al.*, 2012), our results suggest that high Andean

wetland macroinvertebrate assemblages are predominantly influenced by environmental predictors, regardless of their ability to fly at the adult stage. The amount of variation in taxonomic composition accounted for by environmental conditions was relatively high (c. 25% of adjusted variation, that is 30–35% of the unadjusted variation) and was probably underestimated, as other factors such as biotic interactions may play a significant role in community structure (Heino, 2011; Pigot & Tobias, 2013) and account for some unexplained variance. The importance of niche processes in community structure has been postulated to depend on the ability of species to track environmental changes and thus to be contingent on dispersal mode and spatial scale (Heino *et al.*, 2012; Heino, 2013). Our results do not support this assumption. Despite the relatively large geographical scale of our study, the environmental effects remained prevalent, matched levels reported for freshwater studies at the metacommunity scale (Table S1 in Cottenie, 2005), and were of relatively similar amplitude for both assemblages. However, the importance of present-day processes in shaping communities might be blurred at large scales, as broad ecological gradients and historical and evolutionary processes may come into play (Buckley *et al.*, 2010) and contribute to community–environment relationships. The environmental factors most strongly influencing taxa composition differed somewhat between the two assemblages. Whereas the non-flying assemblage was exclusively driven by aquatic characteristics, the flying assemblage was also influenced by wetland altitude and average yearly precipitation. This finding may reflect the fact that benthic macroinvertebrates experience different selective pressures depending on their dispersal mode, a key life-history trait when most of the non-flying taxa have an entirely aquatic life cycle, whereas all the flying dispersers have an aerial adult stage.

Our results suggest that spatial processes also contribute to the biogeography of the high Andean macroinvertebrate assemblages, as pure spatial structure was detected for both groups. Pure spatial effects bear the imprint of current and historical dispersal limitation, with weak dispersers usually being expected to show greater spatial autocorrelation than strong dispersers (Shurin, Cottenie & Hillebrand, 2009; De Bie *et al.*, 2012; Heino, 2013). Our results are inconsistent with this expectation, as we observed the highest levels of pure spatial structure for the flying assemblage, which we postulated to be the more vagile group. It is improbable that passive dispersers would travel greater distances than the flying taxa. Because our sampled wetlands

belong to different river basins, they lacked direct upstream–downstream hydrological connections. Wetland connectivity was thus mostly confined to overland routes. Aerial movement of aquatic macroinvertebrates can be achieved by passive dispersal by wind or animal vectors (Bilton *et al.*, 2001; Vanschoenwinkel *et al.*, 2008) and may have contributed to the spatial structure of the non-flying assemblage. This is supported by the fact that non-flying taxa, which show the highest degree of spatial structure, display features that increase survival during aerial movement such as diapause stages in ostracods or egg resistance to desiccation in flatworms and annelid worms (Moss, 2013). Nevertheless, while passive mechanisms may confer great dispersal potential to some taxa (Bohonak & Jenkins, 2003), their stochastic nature is associated with high risks of reaching unsuitable habitats (Bilton *et al.*, 2001), thus limiting dispersal success at medium and large scales. Moreover, the high mountain ridges between river basins of north-central Chile may restrain passive dispersal among basins. In contrast, flying species might overcome geographical barriers more readily (Townsend *et al.*, 2003). The ability of some flying taxa (mayflies) to disperse between river basins is supported by population genetic data from a study in north-central Chile spanning one of the basins included here (Sabando *et al.*, 2011). In our study, the importance of flight in structuring the flying assemblage is suggested by the fact that the majority of the taxa with spatially structured abundance preferentially dispersed via active flight (Verdugo, 2014), and their greater dispersal aptitude is substantiated by the broad-scale spatial pattern that we detected for this group. This contrasts with observations for the non-flying assemblage, which only showed small- to medium-scale spatial structure. This finding suggests that dispersal limitation occurred at larger scales in the flying taxa and is consistent with results reported by De Bie *et al.* (2012) showing that actively flying insects displayed more spatial structure at the largest spatial scale over Belgian territory (30 000 km<sup>2</sup>) than passive dispersers with similar sized propagules. In our high Andean sites, the spatial structure of the flying assemblage demonstrated a sharp discontinuity between northern and southern wetlands at the level of the Huasco and Elqui catchments. No concordant break was observed for the non-flying group or for the environmental variables found to influence specifically the flying assemblage (i.e. wetland altitude and annual precipitation). The observed discontinuity may thus indicate the existence of a past or current geographical barrier to aerial dispersal in this zone. It is noteworthy that the assemblage divergence occurs in the

area of highest slope values. In sum, we argue that our results are concordant with previous findings that flying/active aquatic invertebrates disperse more efficiently over greater distances than their passively dispersing counterparts (Van De Meutter *et al.*, 2007; Vanschoenwinkel *et al.*, 2007; De Bie *et al.*, 2012), even though the highest levels of pure spatial structure were observed for this group. This unusual trend agrees with experimental studies showing that dispersal effects on community composition strongly depend on the connection regime (Cadotte, 2006a) and illustrates the importance of landscape configuration and scale on spatial structuring.

#### *Wind as a driver of spatial structure in high-altitude wetland macroinvertebrate communities*

The recent development of methods capable of modelling asymmetric directional spatial processes (Blanchet *et al.*, 2008b) has opened up opportunities for quantifying the impact of directional forces in shaping ecological communities. Our results illustrate well the relevance of considering such processes. The spatial variables that we generated according to prevalent wind directions allowed modelling of the composition of the two macroinvertebrate assemblages more efficiently than the non-directional Euclidean variables. According to our results, both biological processes inherent to the communities (e.g. dispersal) and spatial dependence may have contributed to this wind-driven organisation. Wind-mediated dispersal was suggested in both assemblages by significant fractions of the variation in composition uniquely explained by the asymmetric spatial variables. However, in the two assemblages, part of the asymmetric spatial pattern was also explained by environmental characteristics. The fractions of a variation partition involving environmental and spatial variables are usually considered to reflect spatial dependence (Borcard *et al.*, 2010). Wind-driven spatial dependence may occur from induced spatial dependence if the factors structuring biological communities are themselves influenced and spatially structured by wind. In fact, aeolian transport and deposition can be expected to alter and generate spatial structuring of the physical–chemical properties of water, and as a consequence may produce non-random spatial patterns in aquatic communities irrespective of their ability to disperse aerially, as was observed for the non-flying assemblage. In contrast, the common effects of the wind-derived spatial variables and topographic elements likely reflect the effects of wind flows themselves influenced by the topography. The fraction of the flying assemblage structure jointly

explained by altitude and the asymmetric spatial structure thus most likely results from spatial processes such as windborne dispersal rather than from spatial dependence.

Euclidean spatial structure independent of environmental variation was found for the flying assemblage, which may indicate that some flying taxa also use other dispersal pathways (e.g. phoretic dispersal). Other dispersal routes are actually likely to be important and may account for the detected Euclidean spatial structure and/or some of the unexplained variation. Nevertheless, despite the predominant role of environmental factors, the potential role of alternative dispersal pathways, biotic factors and evolutionary history, the wind-mediated spatial structure in both groups accounted for a significant fraction of the variation in taxa composition. This finding demonstrates that Euclidean land models alone do not provide an accurate estimate of the functional connectivity between habitats for benthic macroinvertebrates, even for species capable of flight, as already highlighted by single-species landscape genetics studies with a wide range of taxa (Schwartz *et al.*, 2009; Cook *et al.*, 2011; Kormann *et al.*, 2012). Our results thus highlight the importance of considering wind routes, in addition to environmental features and Euclidean distances, to produce a more reliable picture of the processes underlying community assembly in high-altitude Andean wetlands. While the effects of wind flow on aquatic invertebrate communities have long been considered, they have always been envisaged in the context of passive transport and at relatively small spatial scales (Cáceres & Soluk, 2002; Cohen & Shurin, 2003; Vanschoenwinkel *et al.*, 2007, 2008, 2009). Our study indicates that, by assisting the dispersal of flying organisms and by impacting the spatial organisation of environmental proxies, the structuring role of wind flow on freshwater communities probably encompasses meso- to macro-scales as well.

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### Supporting Information

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

**Table S1.** List of the taxa included in the flying and nonflying macroinvertebrate assemblages.

**Figure S1.** Example of a wind flow map.

**Figure S2.** Wind connection diagram for the spring season.

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