


Blowin' in the wind: Wind directionality affects wetland invertebrate metacommunities in Patagonia

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Abstract

Aim: To assess the relative importance of wind intensity and direction in explaining wetland invertebrate metacommunity organization.

Location: Seventy-eight wetland ponds in Patagonia (Argentina) covering a study area of 3.5×10^5 km².

Time period: Ponds were sampled once between 2006 and 2014.

Major taxa studied: One hundred and fifty-eight taxa of wetland aquatic invertebrates.

Methods: We generated two beta diversity matrices (based on flying and non-flying invertebrates) and six predictor matrices, including three environmental distance matrices, a topographic distance between ponds, and two wind pairwise matrices differing in wind speed. Using Moran spectral randomization of Mantel (MSR-Mantel) tests (which account for spatial autocorrelation), we assessed the relationship between the response and the predictor matrices. We used a network-constrained version of the nestedness metric based on overlap and decreasing fill (NODF), to assess if wind anisotropy (i.e., direction-dependent) affected community nestedness among ponds. **Results:** Flying dispersers' dissimilarity was significantly explained by environmental variables, whereas non-flying invertebrates' dissimilarity was not significantly explained by any of the distances tested. When wind direction was ignored, wind speed had a negligible effect on both types of communities, whereas when it was considered a consistent nested pattern emerged, with the eastern ponds (downwind) communities being subsets of those from the western ponds (upwind).

Main conclusions: We found that the invertebrate communities were mainly assembled by a combination of environmental factors and wind directionality, although this depended on the dispersal ability of the organisms.

KEYWORDS

anisotropy, beta diversity, dispersal, environmental distance, landscape, network-constrained NODF calculation, ponds, topographic distance, windborne

1 | INTRODUCTION

Freshwater habitats, and particularly lakes, wetlands and ponds, can be considered as islands organized in patches surrounded by a terrestrial matrix. To disperse among them, freshwater invertebrates use a variety of strategies broadly categorized as active (i.e., ability to fly) or passive (i.e., aquatic obligate) (Bilton et al., 2001). The dispersal of passive dispersers (hereafter referred to as 'non-flying') is driven by abiotic forces such as water flow or wind (Brendonck & Riddoch, 1999; Vanschoenwinkel, Gielen, Vandewaerde, et al., 2008; Waters, 1972), and also by biotic vectors like insects, amphibians, fishes, birds and mammals (Batzer & Boix, 2016; Beladjal et al., 2007; Vanschoenwinkel, Waterkeyn, et al., 2008). The dispersal of active dispersers (hereafter referred to as 'flying') mostly depends on wing morphology and behavioural traits (Sarremejane et al., 2020) but it can also be favoured by wind (Drake & Gatehouse, 1995). Overall, flying dispersers tend to track environmental conditions more effectively and show weak spatial structuring, while non-flying dispersers usually show strong spatial structuring and are less controlled by local environmental factors (Bonada et al., 2012; Heino, 2013; Juračka et al., 2019). However, dispersal is not only determined by the species intrinsic characteristics (e.g., dispersal type and dispersal rates), but also by extrinsic conditions like biotic interactions (e.g., phoresy), landscape connectivity and the spatial grain and scale considered (Cañedo-Argüelles et al., 2015; García-Girón et al., 2020; Thompson et al., 2020; Tonkin et al., 2018; Viana & Chase, 2019).

Metacommunity ecology provides a useful theoretical and methodological framework to study the role of dispersal in shaping regional biodiversity (Leibold & Chase, 2018; Tonkin et al., 2018). In this regard, although wind can significantly determine the dispersal of aquatic invertebrates (Frisch et al., 2012; Moreno et al., 2016; Vanschoenwinkel, Gielen, Seaman, et al., 2008), it has been rarely considered in metacommunity studies. Thus, the potential effect of wind on the exchange of species between communities is difficult to predict according to the available information. For example, some studies performed in temporary wetlands found that the wind-driven dispersal of the resistant eggs of microcrustaceans was restricted to a few hundreds of metres (Siriani, 2017; Vanschoenwinkel, Gielen, Vandewaerde, et al., 2008), whereas others found that wind storms could transport them across hundreds of kilometres (Rivas et al., 2019). Also, some studies have shown

that flying dispersers can use wind to increase their dispersal range (Chapman et al., 2011; Drake & Gatehouse, 1995), and others found that they could disperse flying against the prevailing wind direction (e.g., Huestis et al., 2019). The few metacommunity studies that have included wind as a factor affecting wetland invertebrates' dispersal showed that wind direction can modulate the relative importance of dispersal and environmental conditions on metacommunity assembly processes (Bertin et al., 2015; Horváth et al., 2016).

Here, we evaluate how invertebrate metacommunities are affected by wind intensity and direction in Patagonian wetland ponds (hereafter 'ponds'). Ponds are ideal systems to test the relative contribution of local and regional processes to metacommunity organization, since these systems are relatively small, typically discrete in space, and often cover wide ranges of environmental conditions (Cottenie et al., 2003; Hill et al., 2017). At the same time, there are two reasons that make the Patagonian region especially well suited for this study. On the one hand, the region experiences among the strongest winds on Earth (Figure 1a,b), with year-long persistent and strong westerly winds (Kling & Ackerly, 2020). On the other hand, Patagonian ponds are relatively little impacted by human activities (Epele et al., 2018), thereby providing an ideal setting for testing wind effects at a regional scale without the interference of potentially confounding human impacts. Here, we divided taxa according to their dispersal strategy (i.e., flying and non-flying dispersers) and assessed the relative importance of the local environment (pond and water characteristics, pond surrounding land cover and vegetation, and climatic data), the topography, and the wind intensity and direction in explaining metacommunity organization. We hypothesized that (H_1) wind would be the main factor explaining community dissimilarity of non-flying invertebrates, whereas that of flying dispersers would be mainly explained by local environmental conditions. Non-flying dispersers are expected to be more affected by wind intensity than flying dispersers because their propagules are easily transported by wind and by birds, which tend to follow favourable wind corridors (Erni et al., 2005; Liechti, 2006). In addition, as wind direction in Patagonia is predictable and constant throughout the year (i.e., westerly winds), we also hypothesized that (H_2) the anisotropic (direction-dependent) connection by wind paths would increase community nestedness from western to eastern ponds. At the same time, very strong Patagonian winds (i.e., average wind speed of 36 m/s; Labraga, 1994) could lead to stochastic invertebrate dispersal, therefore, we hypothesized that (H_3) nestedness would be higher when ponds are connected through lower wind speed paths.

2 | METHODS

2.1 | Study area and site selection

The Argentinian Patagonia region is located in southern South America, extending about 1,800 km from north to south (36°–55° S) and covering an area of approximately 800,000 km². Defined as temperate or cold-temperate, this region is between the subtropical

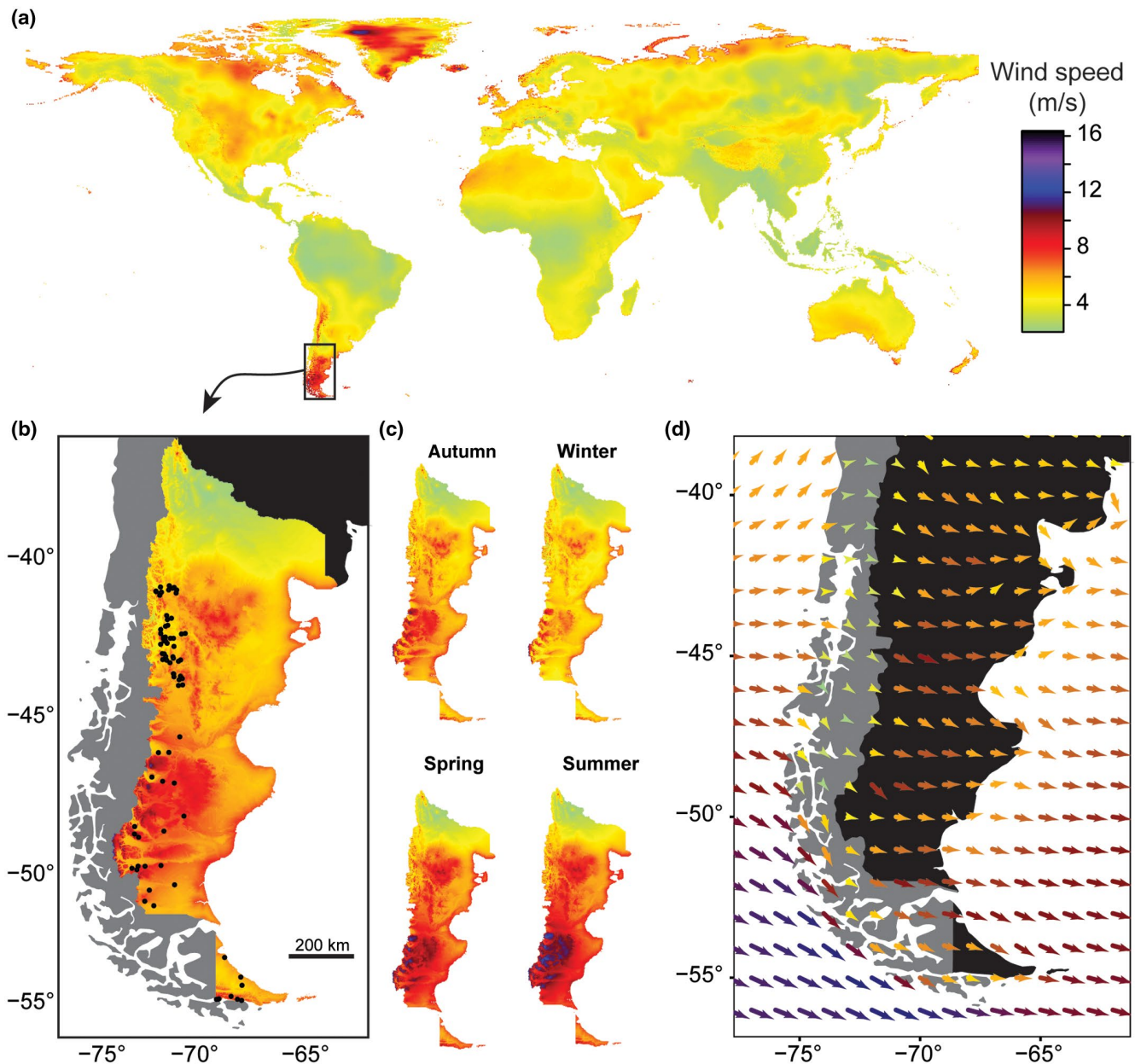


FIGURE 1 Wind speed (m/s) maps: (a) global mean annual wind speed (WorldClim v2.1; 10-s resolution); (b) Patagonia mean annual wind speed (WorldClim v2.1; 0.5-s resolution). Black dots represent the 78 study ponds; (c) Patagonia seasonal wind speed (WorldClim v2.1; 0.5-s resolution), autumn (April–June), winter (July–September), spring (October–December), summer (January–March); (d) mean daily wind speed and direction between 2011–2014 (National Oceanic and Atmospheric Administration (NOAA)/National Centers for Environmental Prediction (NCEP), Global Forecast System Atmospheric Model; 5-km² resolution)

high pressure (30° S) and the subpolar low pressure (60° S) systems (Prohaska, 1976). Consequently, it is greatly affected by the Southern Hemisphere westerly winds, which are characterized not only by their persistence throughout the year but also by an intensity rarely recorded in other regions of the world (Figure 1a). The annual distribution of the wind speed shows a maximum between September and January (spring–summer) and a minimum during winter (Figure 1c).

The north–south distribution of the Andes mountains is an important barrier for humid air masses coming from the Pacific Ocean, resulting in a strong west–east gradient of precipitation across

the Argentine side. The combination of these climatic factors (low precipitation, high evapotranspiration and strong westerly winds) induces the dominant arid conditions of Argentinian Patagonia (Burkart et al., 1999; Paruelo et al., 1998).

The study included 78 freshwater Patagonian ponds, ranging from small geographically isolated to well-connected systems associated with rivers and streams. To ensure that the sampled ponds were representative of the Patagonian climatic heterogeneity, sites were located from north (41°52' S) to south (54°52' S) covering the west–east rainfall and wind gradient (Figure 1b,d), and the main areas suitable for wetlands (Crego et al., 2013). Given the large size of the Patagonian region,

conducting representative sampling accounting for its spatial variability within a single year was not possible for us. Therefore, for this study we merged comparable datasets (i.e., collected by the same team of researchers and following the same methods) collected between 2006 and 2014. Each pond was sampled once, distributed as follows: 15 sampled in December 2006, 14 in December 2007, 3 in December 2009, 3 in December 2011, 12 in December 2012, 31 in January 2014. No significant climatic events occurred during the sampling period (see Supporting Information Appendix S1).

2.2 | Invertebrate data

We swept a dip net (500- μ m mesh size) from four to eight times (depending on pond area), from the margins to the centre of the pond, to collect invertebrates associated with epibenthos, nekton and pleuston. Such sampling effort allows species to be obtained from most of the habitats within the pond (Epele et al., 2019). We collected three samples per pond, which were later pooled together for statistical analyses. We fixed invertebrates in the field with 5% formalin, sorted them in the laboratory, and stored them in 70% ethyl alcohol. We performed identifications to the lowest taxonomic level possible (usually species or genus, except for some Diptera and Oligochaeta that were identified to family level) using regional keys (Hamada et al., 2018). We classified aquatic insects whose adults are able to fly as flying dispersers, and other invertebrates not able to fly as non-flying dispersers.

2.3 | Environmental data

2.3.1 | Pond and water characteristics

We measured pond area and mean depth using geographical information systems (GIS; Garmin Etrex10 or Google Earth Pro software) and a calibrated stick, respectively. In the field, and using multiparameter probes [Hach sensION156/OAKTON PCS Testr 35/YSI Pro 20, Hach sensION156 (HACH), OAKTON PCS Testr 35 (OAKTON), YSI Pro 20AQ19 (YSI)], we measured conductivity (μ g/L), pH, and dissolved oxygen (mg/L). In addition, we collected water samples for nutrient analysis and preserved them frozen. We analysed nitrate + nitrite (μ g/L), ammonium (μ g/L) and soluble reactive phosphorus (μ g/L) from field-filtered water samples (Sartorius, cellulose acetate filter).

2.3.2 | Land cover and terrestrial vegetation

We calculated the moderate resolution imaging spectroradiometer (MODIS) normalized difference vegetation index (NDVI), and land cover in a 100-m perimeter around each pond. The NDVI is produced at 16-day intervals and at 250 m \times 250 m pixels (MOD13Q1). After averaging NDVI values from January 2000 to each sampling date, we used mean values to account for the forest and steppe differences. We measured land cover using satellite imagery (GOOGLE

EARTH PRO, 2015), combined with field surveys, classifying them in 10 categories: (1) bare soil, (2) rocks, (3) agriculture, (4) steppe grasses, (5) wetland, (6) shrubs, (7) forest, (8) water, (9) urban (including roads and buildings) and (10) bog. Before analysis, we deleted those land cover categories with zeros in more than 60% of sites (i.e., rocks, agriculture and bog; Epele et al., 2018).

2.3.3 | Climatic variables

We used eight bioclimatic variables retrieved from the WorldClim v2.1 database for the 1970–2000 period (1-km² resolution; Fick & Hijmans, 2017): mean annual temperature ($^{\circ}$ C), maximum temperature of the warmest month ($^{\circ}$ C), minimum temperature of the coldest month ($^{\circ}$ C), temperature seasonality (values between 0–100), temperature annual range ($^{\circ}$ C), annual precipitation (mm), precipitation of wettest month (mm) and precipitation seasonality (coefficient of variation).

2.4 | Statistical analyses

We performed statistical analyses in two steps (Figure 2). The first step consisted of the generation of two beta diversity (based on flying and non-flying invertebrates) matrices and six predictor matrices to assess the effect of environmental and spatial factors on meta-community organization (H_1 : wind intensity). In the second step, we used two increasingly complex approaches to test each hypothesis (H_2 : anisotropic connectivity, H_3 : wind speed).

2.4.1 | Beta diversity calculation

Since spatial beta diversity can be adequately described using common species (Heino & Soininen, 2010) and rare taxa could be related with sampling errors and/or biases, we removed taxa occurring at a single pond prior to beta diversity analyses. Then, we determined beta diversity of flying and non-flying dispersers (separately) based on presence–absence data and using the positive matching index (PMI, Dos Santos & Deutsch, 2010). The PMI is a similarity index that was transformed into a dissimilarity index to allow comparisons with other studies (i.e., $1 - \text{PMI}$ results). The index, which ranges between 0 and 1, represents the mean proportion of positive matches relative to the complete list of taxa that could occur at a site (Dos Santos & Deutsch, 2010). It was calculated using the *PMI* function in R software (R Development Core Team, 2020) (R codes available on figshare: <https://figshare.com/s/741fbcf879581936ae8a>).

2.4.2 | Predictor matrices

We calculated three environmental distance matrices based on eight pond and water characteristics (hereafter 'local variables'), eight land

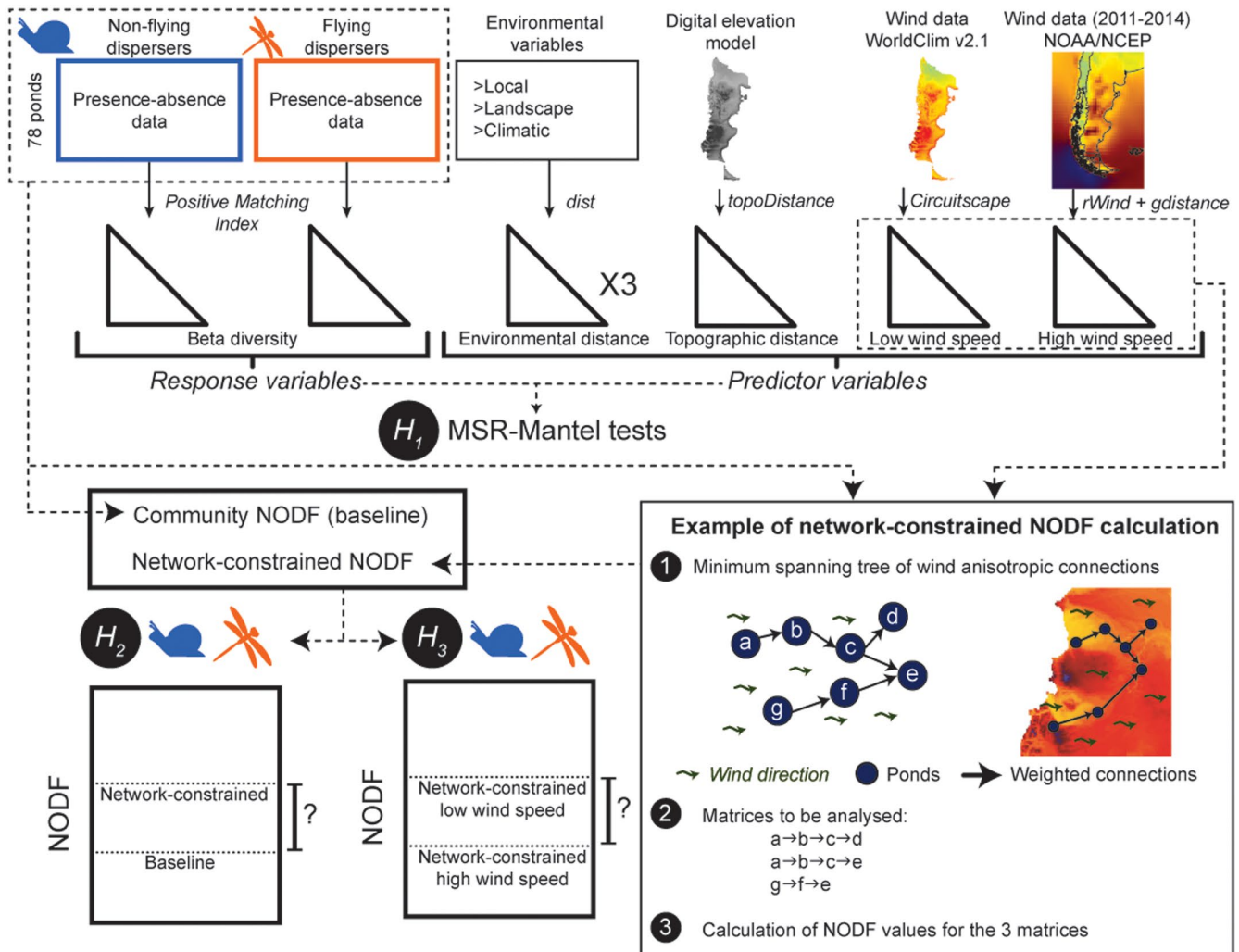


FIGURE 2 A flow chart of the statistical analyses used for invertebrate metacommunities sampled across 78 ponds surveyed in Patagonia (Argentina). For our first hypothesis we investigated non-flying and flying beta diversity patterns in relation to environmental variables, topographic distance between ponds and two wind matrices obtained to compare low and high intensity effects, using Moran spectral randomization of Mantel (MSR-Mantel) tests. For the second and third hypotheses, we used community presence-absence data to first calculate the nestedness metric based on overlap and decreasing fill (NODF) and then, the NODF of wind anisotropic (direction-dependent) connections between ponds, called network-constrained NODF. We are providing an example for the network-constrained NODF calculation using seven hypothetical ponds. *dist* = function of 'ade4' R package; Circuitscape is the software use to process WorldClim data; *topoDistance*, *rWind* and *gdistance* are R packages used for matrix pairwise calculations; H = hypotheses (see the main text); blue colour and the snail are used for non-flying dispersers; orange and the adult dragonfly are used for flying dispersers. NOAA, National Oceanic and Atmospheric Administration; NCEP, National Centers for Environmental Prediction

cover and terrestrial vegetation (hereafter 'landscape variables') and eight climatic variables. To do this, we separated the variables into local, landscape and climatic variables, and performed three principal component analyses (PCAs) to scale and standardized them. We calculated environmental distances as the Euclidean pairwise distances between 20 PCA axes. We used the *dudi.pca* and *dist* functions in the 'ade4' R package (Dray, Dufour, et al., 2020).

To account for landscape elevation, we measured the overland distance between ponds, creating a fourth distance matrix named 'topographic distance'. This distance assumes that dispersal occurs along lower altitude landscape paths, like rivers or glacier valleys.

To calculate the shortest weighted topographic distances, we used a digital elevation model (DEM) raster map (3-s resolution). As sea pixels are set to NA (no data), we coarsened the DEM's resolution (2-min resolution) until continental Patagonia was connected with Tierra del Fuego Island, allowing topographic distance assessment. We performed all calculations in the 'topoDistance' R package (Wang, 2020), using the *topoDist* function and a weight of 1,000 to be applied to the elevation (z) distances relative to the horizontal (xy) distances.

To account for wind anisotropic effects (our second and third hypotheses), we used two approaches to calculate the wind pairwise

matrices: (a) *low wind speed*, accounting for mean annual lowest wind speed paths in order to test if they promote a deterministic organization of the metacommunity; and (b) *high wind speed*, to test if strong winds lead to stochastic metacommunity organization.

To assess the effect of low wind speeds on metacommunity organization, we calculated a pairwise resistance matrix using 30 s (roughly 5 km²) mean monthly wind speed (m/s) raster maps from WorldClim v2.1 (Fick & Hijmans, 2017). We extracted two raster maps, averaging monthly wind speed into annual wind speed and summer wind speed (December–March). Then, we used both raster maps as input into the program *CIRCUITSCAPE* (McRae, 2006) to calculate landscape resistance to dispersal due to wind force between each pair of sites. Pairwise resistance values were calculated as the mean of the resistances of pixels between sites, allowing for multiple pathways between them. Thus, lower pairwise resistance values would indicate higher connectivity between ponds. We tested summer wind resistance assuming that most dispersal would occur during that season (i.e., mean monthly wind speeds from December to March), in coincidence with stronger winds. However, after comparing mean annual and summer wind resistance matrices, no significant differences were found between them, and all subsequent calculations were performed using the former matrix.

To assess the effect of high wind speed on metacommunities, we calculated a pairwise connectivity matrix, using mean wind speed from 2011 to 2014. We obtained daily wind speed and direction data from the National Oceanic and Atmospheric Administration (NOAA)/National Centers for Environmental Prediction (NCEP) Global Forecast System Atmospheric Model using the 'rWind' R package (Fernández-López & Schliep, 2019). As the resolution of these data was too coarse (roughly 50 km² per pixel), we interpolated the wind intensity and direction between pixels to reach a pixel resolution similar to that used for low wind speed (5 km²) using the open source *QGIS 3.12.1* software (QGIS Development Team). Finally, we computed the pairwise connectivity matrix as the least cost paths between ponds following highest wind speeds, using the 'gdistance' R package (van Etten, 2017).

2.4.3 | Relationship between community dissimilarity and predictor matrices

We used the Moran spectral randomization of Mantel (MSR-Mantel) test to assess the relationships between pairwise community dissimilarities (flying and non-flying beta diversity) and the six distance matrices: three environmental distance matrices, the topographic distance and the two wind speeds. Partial Mantel tests are widely used to assess relationships between distance matrices (controlling for spatial distances with a Euclidean distance matrix), but the MSR-Mantel test demonstrated better results in terms of addressing spatial autocorrelation and reducing its associated type I error rate when distance matrices are spatially structured (Crabot et al., 2019). To perform the MSR-Mantel tests, biological distance matrices were transformed using the *quasiEuclid* function in the 'ade4' R package

(Dray, Dufour, et al., 2020). Then, a total of 12 simple Mantel tests were performed using the *mantel.randtest* function of this package (with six predictors and two response variables) and MSR analyses were performed using the *msr* function in the 'adespatial' R package (Dray, Bauman, et al., 2020) with 999 permutations. The function uses Mantel test results and pond coordinates, correcting statistics and *p*-values for spatial autocorrelation.

2.4.4 | Nestedness across sites enmeshed in an anisotropic connectivity system

The nestedness concept is used to characterize a particular organization pattern in site-by-species incidence matrices. Nestedness occurs whenever the set of species inhabiting sites with lower richness represents a subset of the species pool from the sites with higher richness. Almeida-Neto et al. (2008) proposed the nestedness metric based on overlap and decreasing fill (NODF) to measure the degree of nestedness exhibited in sites by species matrices. The original definition of the NODF index depends on how the rows and columns are ordered, and to calculate NODF the input matrix is frequently ordered according to row and column marginal totals (Britton et al., 2016). NODF ranges from 0 (no nestedness) to 100 (perfect nestedness) when the marginal total of a row (column) further away from the most filled row (column) is lower than the one before. The final score is thus dependent on the ordering of items across both the rows and columns. In fact, nestedness analysis requires an ordering of rows and/or columns of the incidence matrix according to some predefined criterion (Ulrich et al., 2009). Other analytic strategies include the arrangement of sites according to an environmental gradient hypothesized to generate the nested pattern (Lomolino, 1996). In this last instance, comparisons are performed against null scenarios involving permutations of sites. Null models are commonly used to make statistical inferences about the degree of nestedness (e.g., random generation of incidence matrices by preserving both the row and the column marginals). Here, we propose a network-constrained NODF calculation to estimate nestedness on pre-ordered sites by species matrices depending on how sites are sequentially arranged in an anisotropic connectivity network.

First, we produced a funnel-like plot for NODF statistics using sub-matrices embedded into the global incidence matrix. Sites in sub-matrices are pre-arranged using information on paths in the underlying ecological network where they are embedded (i.e., low or high wind speed; see the basics in Figure 2). Then, we obtained the anisotropic connections between ponds by extracting the minimum spanning tree (MST) from the full matrix of pairwise distances (i.e., all connections allowed). Wind anisotropic connections are those going from western to eastern sites, as westerly winds are dominant in Patagonia. Then, we extracted all the maximal simple paths lying on the MST. Each of these low cost paths results in a sequence of sites that are used to calculate the NODF. Therefore, the sub-matrix subtended by the path (sequence of sites and their occurring taxa) is then used to calculate the NODF. Sites (rows) are arranged according

to their sequence in the low cost paths, whereas taxa (columns) are arranged by their decreasing marginal totals.

After enumerating all the maximal simple paths for both flying and non-flying dispersers, we calculated the respective network-constrained NODF (i.e., order of sites dictated by the paths themselves). Baseline NODF was also calculated as a reference for statistical comparison. Baseline NODF was obtained through random sampling of as many sites as included in the paths. It is measured with the standard procedure of ordering both rows and columns by their marginal totals. Finally, we performed paired *t* tests to assess the departure of low and high wind speed network-constrained NODFs from the baseline condition, and one sided *t* tests to compare low and high wind speed NODF within each dispersal type. The data and the R code used for the analyses are available on figshare (<https://figshare.com/s/741fbcf879581936ae8a>).

Given that 62% of the study ponds were located between 41° and 44° S, we repeated these analyses using only this subset of ponds to test the potential effect of a spatially unbalanced design on NODF patterns (Supporting Information Appendix S2). Also given the potential relationship between NODF and the geographical distance between ponds (i.e., the closer two ponds are the higher the NODF), we tested the effect of the geographical distance on NODF from subsets of randomly sampled ponds (Supporting Information Appendix S3).

3 | RESULTS

We recorded a total of 158 invertebrate taxa from 16 orders and 66 families (Supporting Information Appendix S4). Total taxa richness per pond varied from 2 to 39 (18.2 ± 7.16), with *Hyalella* sp. (Dogielinotidae, Amphipoda) and *Lancetes* sp. (Dytiscidae, Coleoptera) being the most frequent taxa (recorded in 62 and 60 ponds, respectively). Rare taxa (i.e., recorded only at one site) composed 23% of the total richness. Ponds exhibited considerable variation in their local water characteristics, surrounding landscape and climatic variables (Supporting Information Appendix S5), with some of them being significantly correlated (see Supporting Information Appendix S6). After the exclusion of rare taxa, flying and non-flying dispersers were composed of 84 taxa (1–22 taxa per pond) and 37 taxa (1–14 taxa per pond), respectively. No significant differences in total beta diversity were found between flying and non-flying dispersers (PMI values = $.73 \pm .16$ and $.72 \pm .22$, respectively).

According to MSR-Mantel tests, the community dissimilarity of flying dispersers was significantly explained by local, landscape and climatic variables (Table 1, Supporting Information Appendix S7), but not by topography and wind ($p > .05$). Regarding non-flying dispersers, none of the distance matrices could significantly explain beta diversity (Table 1).

The anisotropic connections between ponds obtained by extracting the minimum spanning tree for low and high wind speeds are shown in Figure 3. From the full matrix of pairwise distances, the NODF obtained after allowing all possible pond connections

TABLE 1 Moran spectral randomization of Mantel (MSR-Mantel) test correlation between flying and non-flying beta diversity and six distance predictors from 78 ponds across Patagonia, Argentina

Distance predictor	Flying dispersers beta diversity		Non-flying dispersers beta diversity	
	<i>r</i>	<i>p</i> -value	<i>r</i>	<i>p</i> -value
Local	.139	.032	.054	.248
Landscape	.274	.001	0	.986
Climatic	.216	.003	.025	.367
Topography	.079	.191	.024	.380
Low wind speed	0	.658	0	.724
High wind speed	.071	.248	.058	.253

Note: Significant relationships ($p < .05$) are shown in bold.

(referred to as the 'baseline') was significantly higher for non-flying dispersers ($M = 29.99$, $SE = 0.13$) than for flying dispersers ($M = 26.66$, $SE = 0.08$; $t(1,539) = 21.25$, $p = 2.2 \times 10^{-16}$) (Figure 4a). In contrast, the means of low and high wind speed network-constrained NODF values were almost equal for flying and non-flying dispersers (Figure 4b,c,d; $p = .81$ and $p = .61$, respectively). The mean NODF of flying dispersers was significantly higher than that expected at the baseline (random) when this value was calculated using either low ($M = 37.29$, $SE = 1.72$; $t(36) = 4.57$, $p = 5.5 \times 10^{-5}$) or high wind speeds connections ($M = 35.85$, $SE = 1.90$; $t(43) = 3.12$, $p = .003$). Regarding non-flying dispersers, low wind speed network-constrained NODF values were significantly higher than the baseline ($M = 37.89$, $SE = 2.18$; $t(36) = 4.202$, $p = .0001$), but the difference was weak for high wind speeds ($M = 34.40$, $SE = 2.44$; $t(43) = 1.98$, $p = .054$). In contrast to our expectations, the low and high wind speed NODF values were not significantly different in any case (i.e., flying and non-flying invertebrates; Figure 4c,d). We found similar results using a subset of 49 northern Patagonia ponds (Supporting Information Appendix S2). Finally, we found that NODF was not significantly related to the geographical distance between ponds for flying dispersers, and significantly but very weakly related for non-flying dispersers (Supporting Information Appendix S3).

4 | DISCUSSION

Our results suggest that the distribution of flying invertebrates in Patagonian ponds is significantly explained by environmental variables at the local (i.e., water chemistry and habitat characteristics) and the regional scales (i.e., landscape and climatic variables), partly supporting our first hypothesis. This is not surprising, since many studies have shown that local environmental conditions (species sorting) are the main drivers of freshwater invertebrate metacommunity organization, frequently overriding the effect of spatial connectivity (Cañedo-Argüelles et al., 2020; Cottenie, 2005; Hill et al., 2017; Thornhill et al., 2017). Also, this finding aligns with previous

Wind anisotropic spatial ordination

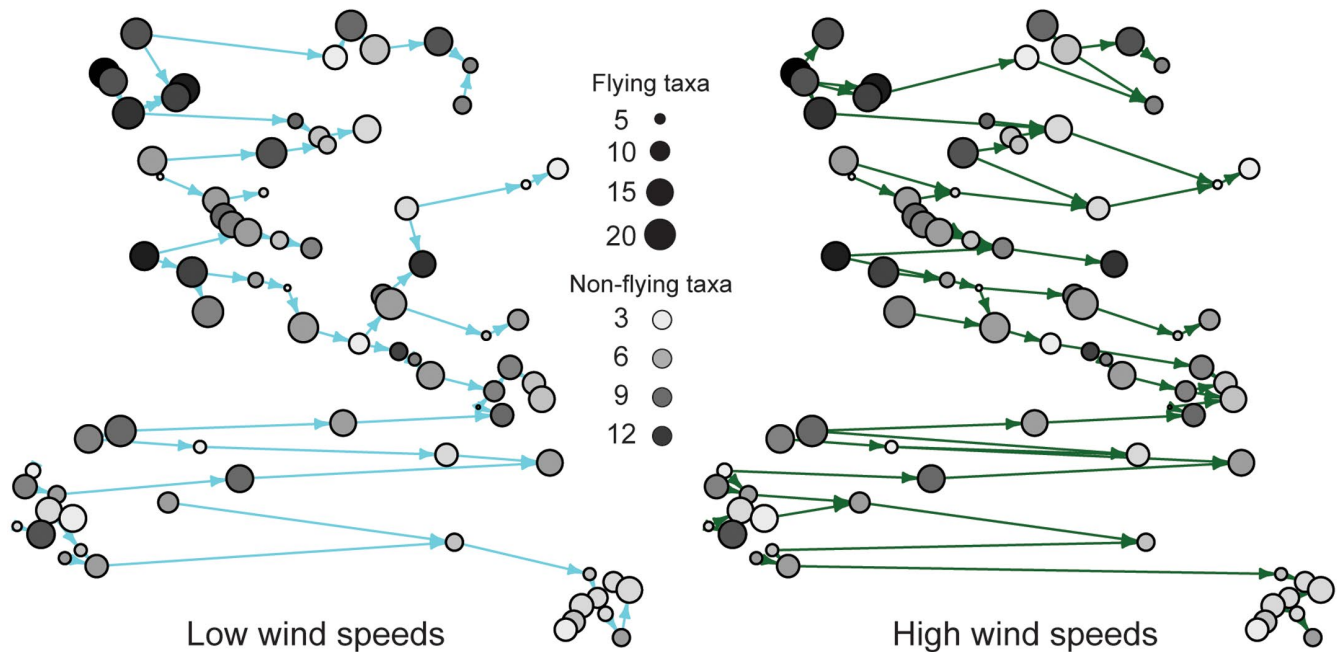


FIGURE 3 Wind anisotropic ordination (minimum spanning tree) of 78 Patagonian ponds. Ponds are ordered based on their longitude from west to east. Circles represent each sampled pond, with greyscale colour and circle size reflecting taxonomic richness of non-flying and flying dispersal communities, respectively. Low and high wind speeds were calculated by weighting ponds' connections based on WorldClim v2.1 mean annual wind speed and 2011–2014 daily wind speed and direction data from the National Oceanic and Atmospheric Administration (NOAA)/National Centers for Environmental Prediction (NCEP), Global Forecast System Atmospheric Model, respectively

investigations showing that intermediate dispersers (like most flying insects considered in this study) tend to track environmental gradients occupying their preferential niches and being mainly assembled through species sorting mechanisms (Heino et al., 2015). However, it is important to note that density-dependent biotic interactions (which we did not assess in our study) could be promoting the importance of species sorting mechanisms (García-Girón et al., 2020; Thompson et al., 2020).

According to previous studies, higher wind speeds should promote passive dispersal of aquatic invertebrates (Incagnone et al., 2015; Vanschoenwinkel, Gielen, Vandewaerde, et al., 2008). However, when wind direction was not considered, we found negligible effects of wind speed on flying and non-flying invertebrate community dissimilarities. This could be partly explained by the hydroperiod of the ponds sampled in our study (more than 6 months), and the fact that we did not consider zooplankton. Most previous studies tested wind effects on zooplankton assemblages from ephemeral pools or ponds, where resistant eggs and propagules are transported by wind during the dry phase (Frisch et al., 2012; Horváth et al., 2016; Pinceel et al., 2020; Rivas et al., 2019; Sirianni, 2017; Vanschoenwinkel, Gielen, Vandewaerde, et al., 2008). However, in ponds with longer hydroperiods or permanent waters like the ones sampled in this study, the main dispersal vectors of passive dispersers would be animals such as birds and large mammals (Allen, 2007; Vanschoenwinkel, Waterkeyn, et al., 2008) that are weakly affected

by winds or, in the case of many bird species, able to track favourable wind conditions in space and time (Erni et al., 2005). Moreover, some studies testing the wind speed and ignoring its direction found contrasting wind effects on the community assembly of flying dispersers. For example, in Patagonia, Grech et al. (2019) found that the probability of finding the world's most austral species of mosquito (*Aedes albifasciatus*) was positively associated with high wind speeds. In contrast, Magnussen (2010) found a negative effect of wind speed on aerial dispersal of Brachycera (Diptera) and Hymenoptera in the arctic region of Svalbard. Thus, the negligible effects of wind speed on metacommunity organization according to distance decay relationships in our study could have resulted from neglecting wind direction. This assumption was confirmed when we incorporated wind direction into our analyses.

To test our second and third hypotheses, both depending on the anisotropic wind connectivity (direction-dependent), we used a network-constrained NODF calculation. Two studies found anisotropic wind effects on invertebrate dispersal, one on zooplankton communities of temporary soda pans in the Seewinkel region (Austria and Hungary; Horváth et al., 2016), and another one on aquatic macroinvertebrates in high altitude Chilean wetlands (Bertin et al., 2015). Both studies used a methodology aimed at studying spatial distributions generated by directional physical processes, called asymmetric eigenvector maps (AEM; Blanchet et al., 2008). This method and other eigenfunction-based spatial filtering methods, such as

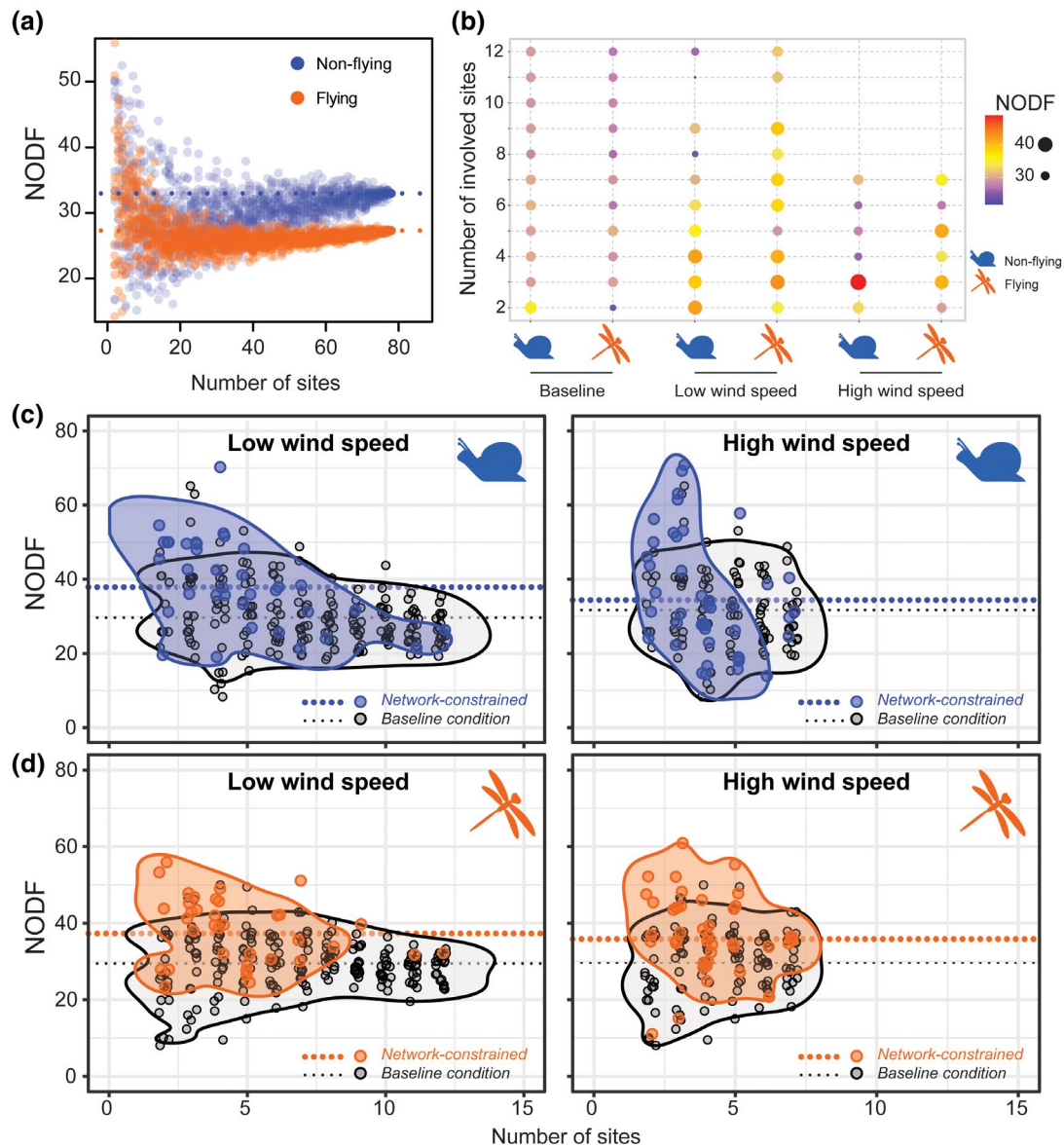


FIGURE 4 Nestedness variability depending on the data tables (sites-by-taxa) used as inputs, with non-flying dispersers distinguished from flying ones. Regarding sites (ponds), tables were constructed with the sites present in either (i) low cost paths embedded in wind networks or (ii) random sampling from the overall set of available sites. This last procedure is referred to as the baseline condition. (a) Funnel plot of nestedness based on overlap and decreasing fill (NODF) associated with the baseline condition for non-flying (blue) and flying (orange) organisms. Dotted lines represent the convergence scores for NODF as the number of sites approaches the total. The overlap of the NODF values increases as more sites are included in the calculation. (b) Average NODF values under different scenarios of allowed connections among ponds. Both size and colour of dots (graphical references alongside the plot) reflect the magnitude of NODF. Note that the network-constrained NODF for flying dispersers is consistently higher than the baseline condition in which sites are randomly selected. (c-d) Scatterplots of NODF versus the number of sites underlying its calculation. The 95% confidence envelope has been outlined using kernel density estimation. Scores of network-constrained NODF for each combination of wind speed and dispersal mode of taxa are represented, along with the baseline condition

Moran's eigenvector maps and principal coordinates of neighbour matrices, use the respective eigenvectors as covariables in regression models. In other words, they offer a way to calculate indices of spatial relationships among sites based on the configuration of their connections. However, in order to deal with a synthetic measure of metacommunity organization such as NODF (a quantitative attribute of a set of sites, not individual sites), network paths represent a

more realistic approach than the spectral decomposition of linkages. The network-constrained NODF calculation allowed us to study the behaviour of one of the most widely used metrics of nestedness (Aspin et al., 2018; Baselga, 2012) across ponds connected by winds and coded through cost-distance matrices, which capture dispersal processes (Cañedo-Argüelles et al., 2015; Fernández-López & Schliep, 2019).

We found a relatively consistent nestedness pattern for both communities, with westerly winds leading to impoverished eastern pond communities that were subsets of those from the western ponds. Interestingly, communities of non-flying invertebrates exhibited higher nestedness than those of flying ones (i.e., comparing baseline NODF), but we found the opposite pattern when ponds were connected following the wind direction (i.e., comparing network-constrained NODF). Furthermore, differences between baseline NODF and network-constrained NODF were stronger for flying than non-flying dispersers. This suggests that wind direction significantly modulated aquatic invertebrate biodiversity, exerting a stronger effect on flying than on non-flying dispersers (Bertin et al., 2015; Juračka et al., 2019), probably because non-flying invertebrates rely on animal vectors to disperse (Incagnone et al., 2015). Adult flying insects could be well adapted to strong winds (Magnussen, 2010) that, despite generating some stochastic dispersal (e.g., lowland insects found in high mountain snowpacks, L. B. Epele, personal observation), could increase their dispersal range (Drake & Gatehouse, 1995). Moreover, flying dispersers might be able to disperse using low wind paths during calm days or low speed hours (L. B. Epele & M. G. Grech, personal observation), tracking local environmental variation.

We did not find significant differences between low and high wind speed network-constrained NODF. Although it is possible that differences in wind speed do not result in differences in invertebrate dispersal rates, this is quite unexpected given the wide range of wind speeds covered by our study (regional mean for the 1960–2000 period = 5.77 ± 1.48 m/s; minimum = 2.08 m/s; maximum = 16.86 m/s). Future studies should consider not only using more precise wind models than the one used here (resolution = 5 km²), but also testing wind effects experimentally (Cáceres & Soluk, 2002).

Many studies found that invertebrates' wind anisotropic dispersion would be more effective over short distances (i.e., hundreds or thousands of metres; Cáceres & Soluk, 2002; Cohen & Shurin, 2003; Sirianni, 2017; Vanschoenwinkel, Gielen, Vandewaerde, et al., 2008), but recent findings are revealing that wind connectivity could reduce the dispersal limitation (e.g., geographical barriers), promoting even larger spatial dispersions than tested in our study. For example, in the last decade studies have claimed that Antarctica is ecologically connected with other continents through windstorms (jointly with ocean currents) that would override the southward dispersal barriers (see Fraser et al., 2018), leading to dispersions of thousands of kilometres in magnitude. Therefore, the effect of anisotropic factors (such as wind) on species dispersal could affect the relative importance of local (i.e., abiotic conditions and biotic interactions) and regional (i.e., climatic and landscape attributes) factors on metacommunity assembly. Thus, we encourage future studies on biodiversity (e.g., assessing species range shifts) to incorporate the anisotropic nature of some abiotic variables determining landscape connectivity, like for example upslope and downslope (Etherington, 2016), upstream and downstream (Dong et al., 2016), or upwind and downwind (Fernández-López & Schliep, 2019). As a recent study on wind dispersal effects in a global context (Kling

& Ackerly, 2020) suggested: it is not only important to consider 'where to go' (i.e., environmental filters) but also 'how to get there' (e.g., wind speed and direction). Overall, we think that incorporating wind dispersal into metacommunity studies can yield interesting results for many groups of organisms (e.g., from passive dispersers like diatoms to active dispersers like flying insects) and can help to explain biodiversity patterns at regional and global scales. This might become especially relevant in the context of climate change, which is already affecting global wind patterns (Kling & Ackerly, 2020; Pryor et al., 2020).

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AUTHOR CONTRIBUTIONS

L.B.E., D.A.D.S., R.S., M.G.G., N.B. and M.C.-A. wrote the manuscript. D.A.D.S. developed the network-constrained NODF calculation. L.B.E., R.S. and M.C.-A. contributed to statistical analyses. L.B.E., M.G.G., P.A.M., L.M.M. and M.L.M. carried out the collection and identification of samples.

DATA AVAILABILITY STATEMENT

Data used in this publication can be downloaded from Figshare (<https://figshare.com/s/741fbcf879581936ae8a>).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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