

# Dispersal limitations matter for microbial morphospecies

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Geographic range restrictions are typical for macro-organisms. In contrast, many micro-organisms appear to have cosmopolitan distributions, an observation Baas-Becking formulated “everything is everywhere, but, the environment selects” (1). Finlay (2) argues that microbial biogeography is fundamentally different because vast population sizes drive ubiquitous dispersal. This hypothesis has been challenged by evidence of dispersal limitations. Taxonomists argue that they find endemic morphospecies—for example in the Yellowstone Lake diatom flora (3)—and genetic data demonstrate that microbial organisms can exhibit classical biogeographical patterns, such as provincialism and distance decay (4). Unfortunately, taxonomic uncertainties, undersampling, and different interpretations of the genetic variability frustrate unequivocal testing of the ubiquitous dispersal hypothesis with these types of evidence (2, 4, 5).

Understanding the rate of global dispersal is key to discriminating between these alternative views of microbial biogeography. Is dispersal so rapid that regional biota are homogenized into a single global metacommunity, or is it slow enough to allow signatures of regional-scale processes to develop? We address this question by exploring regional species richness–environment relationships. If dispersal is ubiquitous, all regions should share one underlying richness–environment relationship, governed by the global species pool. If dispersal is limited, regional-scale metacommunity processes (6), such as colonisation–extinction dynamics, will decouple regional species pools from the global pool, allowing richness–environment relationships to vary between regions. We predict that, if dispersal is limited, regional richness relationships will depend on regional habitat availability (Fig. 1A).

We tested this prediction by investigating lake-diatom species richness along pH gradients in 16 regional data sets from Europe and North America. Diatoms are a pH-sensitive, species-rich group of microscopic siliceous algae, common in freshwater lakes. By concentrating on richness patterns (Fig. 1), our analysis does not require taxonomic consistency between data sets, only that there are no pH-related biases in the richness estimates.

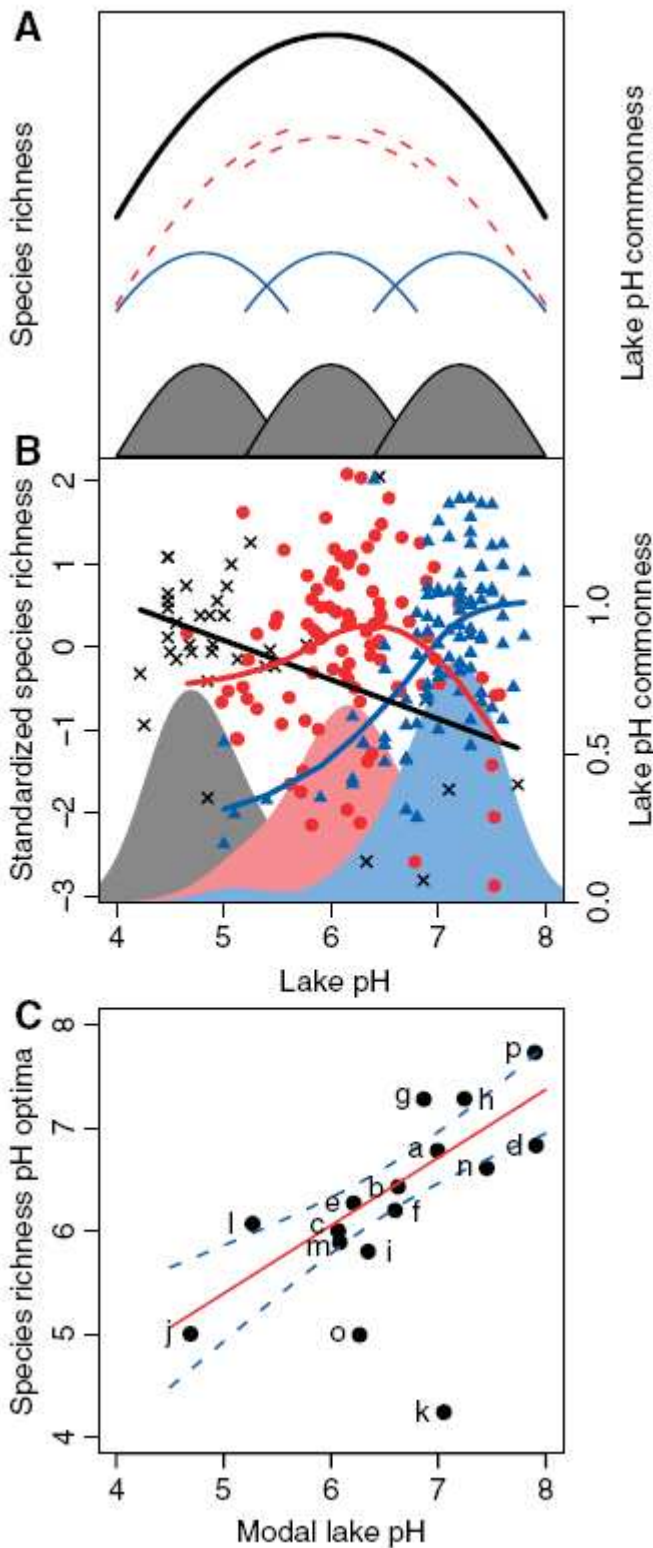


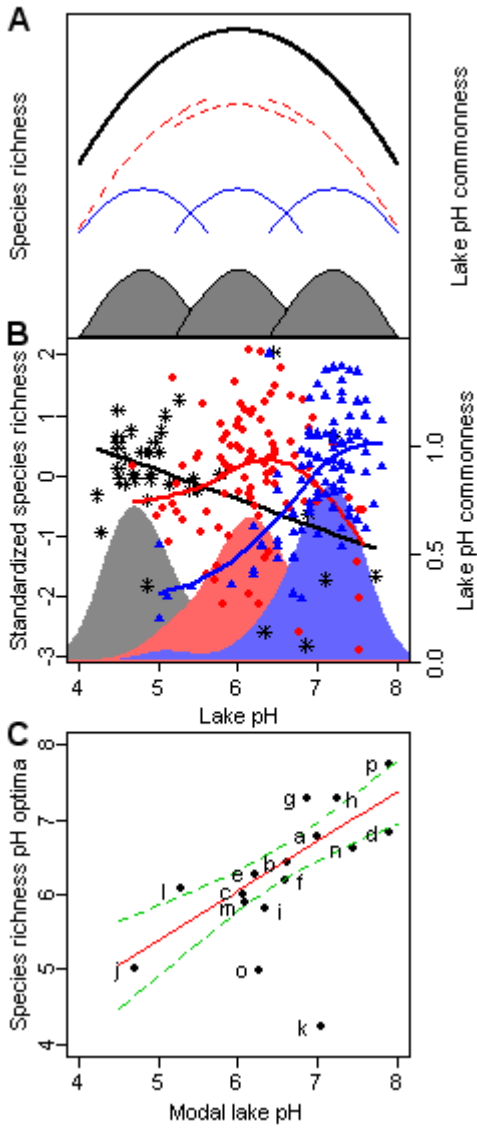
Figure 1. Predicted patterns of lake diatom species richness in relation to pH (**A**) for three regions with different pH availability (grey areas) if metacommunities operate at the regional (solid blue) or global (dashed red) scale. The thick black line shows a hypothetical global species richness. Observed lake pH availability and standardised rarefied species richness in individual lakes (**B**) for North Florida (black), South Norway (red) and Finnish Lapland (blue). Thick lines show trends in species richness estimated with generalised additive models. Species richness pH optima against modal lake pH (**C**) in 16 regional data sets (see supporting material) from Europe (a-i) and North America (j-p). Regions are labelled from south to north in each continent. The modal lake pH is estimated from the pH density. Species richness pH optima are estimated using LOWESS (span = 2/3). If richness reached a plateau rather than an optimum, the break of slope was used instead. The linear regression of richness optima on the most common lake pH (solid line with dashed confidence intervals) is highly significant ( $p < 0.001$ ; excluding two outliers, regions o and k).

The species richness–pH relationships differ markedly among regions (Fig. 1B and Fig. S1), and richness optima, which vary by 2.5 pH units, are strongly correlated with the regionally most common environments (Fig. 1C). Adjacent regions (e.g. within Fennoscandia) can have very different richness pH-optima, whereas latitudinal trends are weak (Fig. S2). This suggests that diatom metacommunities are regional rather than global in scale. Despite the enormous populations and high passive dispersal potential of diatoms, their dispersal at the global scale must be too slow to override regional metacommunity processes.

These results complement recent genetic work by demonstrating that dispersal limitation can affect microbial community assembly, even at the relatively coarse taxonomic resolution of morphospecies. Our results help reconcile the positions of the adherents and detractors of the ubiquitous dispersal hypothesis. Although many microbial species may indeed have a cosmopolitan distribution, it is probably attained slowly and incrementally. This allows time for regional genetic differences to develop and for endemic taxa specialising in rare or isolated habitats (3) to evolve as their probability of dispersal to suitable distant sites approaches zero. Dispersal limitations, which are so important in shaping the diversity and distributions of macro-organisms (6), also play a critical role in the microbial world.

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# Supporting online material for Dispersal limitations matter for microbial morphospecies

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## Material: Data set selection

Diatom data sets were selected from the European diatom database (S1), the Diatom Data Cooperative (S2), and directly from diatomists (Table S1). Data sets with fewer than 25 lakes, or a 95% interquantile pH range less than 1 pH unit, were excluded from the analysis. Data sets for which we lack an estimate of pH commonness, primarily because of severe augmented sampling at the acid end of the pH gradient, were also excluded.

Details on taxonomic and analytical procedures are given in the original publications. These procedures may differ slightly between data sets, but are consistent within each data set.

The region covered by each data set is determined by the objectives of the original research. Two observations were deleted from the S. Norway data set as they were ~1000 km from the remaining observation. The long axis of the regions range from <100 km to 1600 km. The median size is ~300 km.

## Methods

Species richness at each lake is estimated by rarefying the diatom count data to the minimum count sum in each data set. A locally weighted scatterplot smoother (LOWESS; span=2/3) is used to estimate pH of maximum richness. Richness in regions h and p (Finland and Arctic Canada) reaches a plateau rather than a unimodal maximum, for these regions the pH of break of slope is used instead.

The modal pH is estimated using a Gaussian kernel density with a bandwidth of 0.3 pH units.

## Table S1

Data sets used in the analysis. The codes refer to figures 1C, S1 and S2.

Code	Region	No. Lakes	Minimum count size	pH range	Reference
a	Pyrenees, Spain	28	492	5.5-7.5	<i>S1, S3</i>
b	Massif Central, France	28	463	4.9-8.2	<i>S1, S4</i>
c	Italian Alps	31	335	5.3-7.9	<i>S1, S3</i>
d	S. England	26	499	6.8-8.6	<i>S1, S5</i>
e	S. Norway	98	370	4.7-7.6	<i>S6</i>
f	N. Sweden	118	172	5.0-8.3	<i>S1, S7</i>
g	Swedish Lapland	100	394	5.8-8.1	<i>S8</i>
h	Finnish Lapland	98	495	5.0-7.8	<i>S1, S9</i>
i	Kola Peninsula, Russia	25	482	5.0-7.4	<i>S1, S10</i>
j	N. Florida, U.S.A	40	500	4.2-7.7	<i>S2, S11</i>
k	Pocono Mountain, Pennsylvania, U.S.A.	38	992	4.2-9.7	<i>S2, S12</i>
l	Great Lakes, U.S.A.	51	494	4.4-7.5	<i>S2, S13</i>
m	New England, U.S.A.	62	492	4.4-7.8	<i>S2, S14</i>
n	N.E. U.S.A.	241	407	4.3-8.7	<i>S15</i>
o	Labrador, Canada	48	500	5.0-7.3	<i>S2, S16</i>
p	Arctic Canada	62	610	7.0-8.6	<i>S17</i>

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Figure S1. Observed density distribution of lake pH and rarefied species richness in individual lakes for each data set. Thick lines show trends in species richness estimated with LOWESS, asterisks highlight the position of the optima.

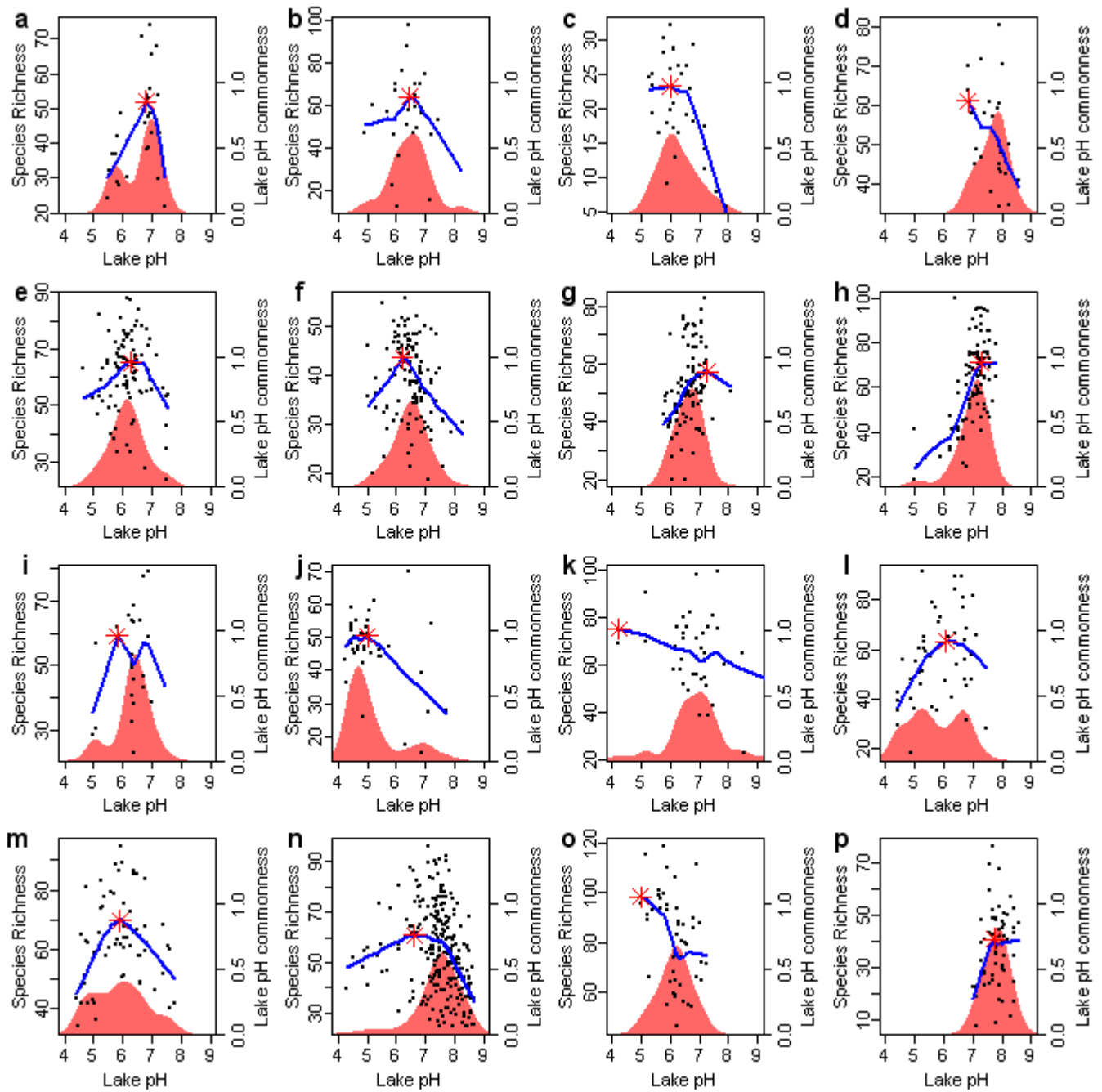
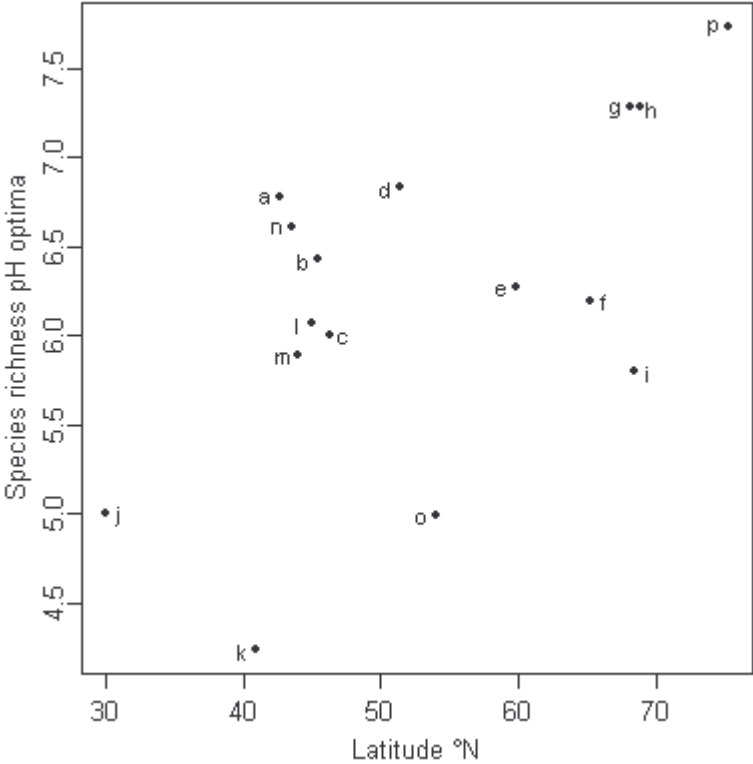


Figure S2. Species richness pH optima against the latitude of the data set.





## **Web Abstract**

In contrast to macro-organisms, whose geographical ranges are typically restricted, many microbial species appear to have cosmopolitan distributions. This has been explained as a consequence of ubiquitous dispersal due to the enormous population sizes of microbial species. Recently, this “everything is everywhere–the environment selects” theory has been challenged by the detection of considerable regional genetic variability within microbial morphospecies. We demonstrate that, contrary to what is expected under ubiquitous dispersal, evidence of regional scale metacommunity processes can be detected in microbial morphospecies. Our results imply that the microbial and macrobial world are structured by analogous processes.