

NEWS AND VIEWS

PERSPECTIVE

At least some protist species are not ubiquitous

DIEGO FONTANETO* and
JOAQUÍN HORTAL†

*Institute of Ecosystem Study, National Research Council (CNR), Largo Tonolli 50, 28922 Verbania Pallanza, Italy;

†Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales (CSIC), C/José Gutiérrez Abascal 2, 28006, Madrid, Spain

Body size is one of the main regulators of the ecological characteristics of living organisms, including their biogeography. The ‘ubiquity hypothesis’ for microorganisms states that they are widely distributed, if not cosmopolitan, due to their small size that allows passive dispersal, in contrast to large organisms that are limited by geographical barriers in their active dispersal. Such idea, summarized in the tenet ‘Everything is everywhere, but the environment selects’, has driven most of the research in biogeography for microscopic organisms in the last decades, spurring a debate on whether there are fundamental differences in the biogeography of small and large organisms or not (Fenchel & Finlay 2004; Foissner 2008; Hortal 2011). The strong focus on the ubiquity hypothesis may have been often abused to provide a rationale for otherwise descriptive work on the spatial distribution of microscopic organisms; nevertheless, such focus also provides a framework to understand the mechanisms originating and maintaining biodiversity in space. The reliability of the analyses on unknown and understudied organisms is improving, and Heger *et al.* (2013) is a splendid example on small unicellular eukaryotes of what should be done to overcome the major problems and ambiguities that heated the debate on the ubiquity hypothesis.

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The main problem hampering the evaluation of the ubiquity hypothesis is philosophical, for it cannot be explicitly and directly tested, as absence of evidence is not evidence of absence. Thus, only a large amount of undisputable information may provide the basis for reliable inference and generalizations. Moreover, for such analyses on microscopic

organisms, three major problems still exist, namely unreliable taxonomy, limited knowledge on the relative effects of environment vs. dispersal and how to identify the Grinnellian (i.e. abiotic) niche (Fontaneto 2011).

Taxonomy

Morphological features of small organisms may not be enough to identify the actual units of diversity. Thus, the very broad geographical ranges of most species may be an artefact due to the presence of species complexes composed of several cryptic species that are geographically more restricted. The use of DNA taxonomy is the only avenue to overcome such problems. Heger *et al.* (2013) exemplify a great use of tools in DNA taxonomy: they approached the problem of taxonomic units by applying three different methods supporting each other: (i) the DNA barcoding method, with a fixed threshold in genetic distances (Hebert *et al.* 2003), set at 1% for COI in the analysed group; (ii) a less subjective method to find the optimal threshold of genetic distances within and between species, the Automatic Barcode Gap Discovery (Puillandre *et al.* 2012); and (iii) a method based on the shift in the branching rate from a phylogenetic tree, the Generalized Mixed Yule Coalescent model (Fujisawa & Barraclough 2013). These methods provide support for the identification of the units of diversity, and the DNA sequence information that has been gathered could be used for finer analyses of the shape of the correlation between genetic and geographical distances and for more sophisticated approaches to estimate migration rates. Heger *et al.* (2013) found evidence for 12 cryptic species within one morphological species. If this is a common scenario for other protists, the taxonomic inflation due to DNA taxonomy in unicellular eukaryotes could be massive.

Environment vs. dispersal

Passive dispersal of resting stages in microscopic organisms is indeed different from the dispersal mechanisms of larger organisms and depends on (i) population size: the higher the number of individuals, the higher the chances that some of them could be passively dispersed; (ii) resting stages: the longer such stages can survive desiccated, the higher the chances that some of them could act as proper propagules for dispersal; (iii) size of the dispersing stages: the smaller and the lighter, the easier to be moved around by wind; (iv) niche width: the wider the ecological needs, the higher the chances of finding a suitable place.

The effects of these factors interact with the environment—which presents a distinct structure in space—in a spatially explicit way, giving place to spatial patterns that are

Correspondence: Diego Fontaneto, E-mail: d.fontaneto@ise.cnr.it



Fig. 1 *Hyalosphenia papilio* (bottom right) is abundant in Northern hemisphere *Sphagnum*-dominated peatlands, such as this peatland near Knob Lake (Alaska, USA). *Sphagnum* moss: bottom left. Photograph credits: *Sphagnum* moss and landscape: Edward Mitchell (University of Neuchâtel, Switzerland); *Hyalosphenia papilio*: Thierry Heger (University of British Columbia, Canada).

hard to separate from those caused merely by the environmental requirements of the species (see below). Heger *et al.* (2013) disentangled these effects using recently developed statistical tools such as Moran's Eigenvector Mapping (Diniz-Filho & Bini 2005), formerly called principal coordinates of neighbour matrices (Borcard *et al.* 2011). The results of Heger *et al.* (2013) suggest that dispersal limitation probably has little to do with biogeographical patterns in the analysed taxon.

Grinnellian niche

Identifying the environmental conditions suitable for microscopic organisms is not trivial, and very little is actually known about them. The Grinnellian niche is the part of the fundamental niche that describes the abiotic conditions that allow positive population growth rates for the species—as separate from the Eltonian niche, which describes the fundamental biotic interactions that allow species survival (Soberón 2007). The potential distribution of the species is thus the subset of the Grinnellian niche that is actually available at a given space and time, and the realized niche is what comes out after the effect on the potential distribution of additional constraints by biotic interactions (i.e. Eltonian niche), and historical –biogeographical– processes (Hortal *et al.* 2012).

Some of the characteristics of microscopic organisms make it extremely difficult to determine the potential distribution. On the one hand, the realized niche can extend out of the bounds of the Grinnellian niche, and thus of the potential distribution, in the cases when some sink populations, where population growth rate is negative, are maintained by propagules coming from large source populations placed in suitable areas (Soberón & Nakamura 2009). This is likely to

be common for most microscopic organisms; they produce massively viable resting stages that disperse easily through long distance (Fontaneto 2011), so they can be found in unsuitable areas. Such difference may result in overestimating the Grinnellian niche, especially when using environmental sequencing, which will not distinguish between active or dormant stages. On the other hand, many microscopic organisms are able to monopolize entire landscapes; the combination of high dispersal rates with high population growth rates, short generation times and capacity to produce dormant stage banks result in a great advantage of the resident population over new colonizers (De Meester 2011). This may restrict species distributions at the global scale (Fontaneto & Hortal 2012), preventing them to occupy their whole potential distribution despite their easy dispersal.

What we know now

In the debate between the ubiquity hypothesis and the moderate endemism hypothesis for protists, Heger *et al.* (2013) find an intermediate scenario: isolation between continents exists, but then there is little effect of geography within each continental mass, where environmental features explain most of the variability in the spatial patterns. Here, note that the problems to measure the Grinnellian niche from distributional data highlighted above prevent from identifying all spatial processes that may cause the departure of the realized niche of the species from its potential distribution. But overall, Heger *et al.* (2013) support the idea that the geographical distribution of protists and other microscopic multicellular eukaryotes has much in common with that of large plants and animals (see also Hortal 2011), even if microscopic eukaryotes usually have wider ranges and a higher proportion of true cosmopolites.

The future

Heger *et al.* (2013) already investigated an unusual taxon in an unusual habitat, arcellinid testate amoebae (Amoebozoa) in *Sphagnum* bogs (Fig. 1), but for several groups of protists from various habitats almost nothing is known. Most research should also focus on the use and calibration of next-generation sequencing (Tang *et al.* 2012), which may be the key to obtain a large amount of reliable data to explore the diversity of freshwater, marine and terrestrial habitats. More studies are also needed on organisms other than protists, including prokaryotes and viruses on the smaller side and microscopic multicellular eukaryotes on the larger side, and across a gradient from common to rare habitats. Surely, the most important advance of the interest on biogeography of microscopic organisms, including prokaryotes, protists and small animals, is in experimental biogeography (Hortal 2011). Such avenue may be really important to test several hypotheses and ideas in biogeography, using protists and other microscopic organisms in carefully designed experiments to evaluate the theory developed from the observation of spatial patterns in large and small organisms.

References

- Borcard D, Gillet F, Legendre P (2011) *Numerical Ecology with R*. Springer, New York.
- De Meester L (2011) A metacommunity perspective on the phylo- and biogeography of small organisms. In: *Biogeography of Microscopic Organisms. Is Everything Small Everywhere?* (ed Fontaneto D), pp. 324–334. Cambridge University Press, Cambridge.
- Diniz-Filho JAF, Bini LM (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography*, **14**, 177–185.
- Finch T, Finlay BJ (2004) The ubiquity of small species: patterns of local and global diversity. *BioScience*, **54**, 777–784.
- Foissner W (2008) Protist diversity and distribution: some basic considerations. *Biodiversity and Conservation*, **17**, 235–242.
- Fontaneto D (2011) *Biogeography of Microscopic Organisms. Is Everything Small Everywhere?* Cambridge University Press, Cambridge.
- Fontaneto D, Hortal J (2012) Microbial biogeography: is everything small everywhere? In: *Microbial Ecological Theory: Current Perspectives* (eds Ogilvie LA, Hirsch PR), pp. 87–98. Caister Academic Press, Norfolk.
- Fujisawa T, Barraclough TG (2013) Delimiting species using single-locus data and the Generalized Mixed Yule Coalescent (GMYC) approach: a revised method and evaluation on simulated datasets. *Systematic Biology*, **62**, 707–724.
- Hebert PDN, Cywinska A, Ball SL, deWaard JR (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B*, **270**, 313–321.
- Heger TJ, Mitchell EAD, Leander BS (2013) Holarctic phylogeography of the testate amoeba *Hyalosphenia papilio* (Amoebozoa: Arcellinida) reveals extensive genetic diversity explained more by environment than dispersal limitation. *Molecular Ecology*, **22**, 5172–5184.
- Hortal J (2011) Geographical variation in the diversity of microbial communities: research directions and prospects for experimental biogeography. In: *Biogeography of Microscopic Organisms. Is Everything Small Everywhere?* (ed Fontaneto D), pp. 335–356. Cambridge University Press, Cambridge.
- Hortal J, Lobo JM, Jiménez-Valverde A (2012) Basic questions in biogeography and the (lack of) simplicity of species distributions: putting species distribution models in the right place. *Natureza & Conservação*, **10**, 108–118.
- Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology*, **21**, 1864–1877.
- Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.
- Soberón J, Nakamura M (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences USA*, **106**, 19644–19650.
- Tang CQ, Leasi F, Obertegger U, Kieneker A, Barraclough TG, Fontaneto D (2012) The widely used small subunit 18S rDNA molecule greatly underestimates true diversity in biodiversity surveys of the meiofauna. *Proceedings of the National Academy of Sciences USA*, **109**, 16208–16212.

D.F. is interested in using microscopic organisms to explore the generality of the known patterns in biodiversity. J.H. is a biogeographer with broad interests in macroecology, community ecology and biodiversity.

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