

Perspectives on the use of lakes and ponds as model systems for macroecological research

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ABSTRACT

Macroecology studies large-scale patterns aiming to identify the effects of general ecological processes. Although lakes (and ponds) are particularly suited for macroecological research due to their discrete nature and non geographically-structured variability, the development of this discipline in lentic habitats is comparatively much smaller than for terrestrial environments. This is despite the interest of limnologists for large-scale phenomena, which results in the high level of development of some disciplines such as predictive limnology. Here we discuss how current state-of-the-art in macroecology may benefit from research in lentic habitats at five topics. First, by including an island biogeography analytical framework to incorporate the effects of lake origin and history on lentic biodiversity. Second, by studying local and regional effects on the latitudinal gradients of species richness. Third, by considering lakes and ponds altogether for the study of beta diversity and metacommunity structure, which is already common ground in limnological research. Fourth, by relating species traits with ecosystem structure and functioning; here we consider in particular the potential effects of body size-determined dispersal and competitive exclusion processes on lake-wide trophic organization. And fifth, by incorporating current research in functional (i.e., trait) and phylogenetic diversity to the study of community structure. We finally conclude that lentic habitats can be particularly important for the development of the most functional aspects of macroecology, due to the relative ease of studying the different biotic and abiotic components of the system separately, compared to most terrestrial systems. This can allow teasing apart many of the confounding factors that are characteristic of macroecological research, thus helping the development of future theoretical syntheses.

Key words: biodiversity gradients, body size, dispersal, ecosystem functioning, ecosystem structure, metacommunity.

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INTRODUCTION

Macroecology can be defined as large-scale ecology. As such, it aims to study the ecological and evolutionary forces that influence patterns in the abundance, distribution, traits and diversity of species (Brown and Maurer, 1989; Hawkins and Diniz-Filho, 2008). The essence of the macroecological research agenda involves studying ecological systems across spatial (and temporal) scales using a top-down approach, assuming that the unifying principles acting on biodiversity that are not unique to any particular local system will be easier to detect at large spatial (and temporal) scales. This transversal discipline now involves using analyses on data gathered at different spa-

tial and temporal scales to study current and past relationships between organisms and their environment (including other organisms), as well as temporal (i.e., macroevolutionary) trends (Hawkins and Diniz-Filho, 2008; Diniz-Filho *et al.*, 2013). Indeed, this discipline seeks processes that are general, unifying, and not specific to any particular system or location. This view is allowing us, for instance, to obtain a deeper understanding of current gradients in the diversity of species (Hortal *et al.*, 2011; Gouveia *et al.*, 2013), ecological traits (Diniz-Filho *et al.*, 2009) and species' distributions (Olalla-Tárraga *et al.*, 2011; Gouveia *et al.*, 2014). The imprint of macroecology (and macroevolution) on modern ecology is so

large that it recently led to Ricklefs' (2008) proposal of *disintegrating* the concept of local ecological community and favouring instead a more regional perspective on the effects and evolution of biotic interactions and environmental adaptations.

To date, macroecological studies have predominantly concerned terrestrial systems, and the organisms and communities inhabiting water bodies have been less studied from this particular macroecological perspective. However, it would be inaccurate to say that aquatic ecologists were blind to macroecological questions in the past. If we assume that a fundamental component of the macroecological research program roughly consists in analyzing a large number of *ecological particles* (*sensu* Brown and Maurer, 1989) over broad spatial and temporal scales in the search for patterns and explanations, then a number of examples can be cited. For instance, within a field known as predictive limnology¹ (Håkanson and Peters, 1995), a number of studies used data from dozens of lakes to predict aggregate community variables (*e.g.*, the biomass and cover of aquatic macrophytes) in function of environmental predictors (*e.g.*, lake size, underwater light and lake slope; Chambers and Kalff, 1985; Duarte *et al.*, 1986). More recently, the large collaborative project FADA (Freshwater Animal Diversity Assessment) compiled and described current knowledge on the worldwide coarse-grain distribution of animals and macrophytes from aquatic continental ecosystems (Balian *et al.*, 2008), providing the baseline knowledge for large-scale studies on c. 60 different taxa. Other recent examples include the study of large-scale biodiversity gradients (Griffiths, 2006; Hof *et al.*, 2008; Stomp *et al.*, 2011; Stendera *et al.*, 2012; Bruce *et al.*, 2013; Azevedo *et al.*, 2013; Griffiths *et al.*, 2014), or the conjecture that ponds and small lakes have a disproportionate importance for global biogeochemistry cycles (Downing, 2010). These and many other examples illustrate that the macroecological perspective has been an integral part of the study of inland waters, despite lentic habitats being somehow out of the macroecological research agenda. Importantly, data used in the studies cited above (both for the response variables, as species richness, or, for predictor variables, as nutrients) were mainly obtained in the field with comparable methods, instead of being compiled from atlases or from the use of remote sensing techniques. Therefore, they benefit from comprehensive, fine-grained datasets covering large spatial extents, a rare (and desirable) combination in macroecological studies (Beck *et al.*, 2012).

Given the above, the relative paucity of macroecologi-

cal studies on lake ecosystems when compared to terrestrial ecosystems is surprising and unfortunate. It is surprising because one of the earliest studies in macroecology was conducted on lakes (Barbour and Brown, 1974). It is unfortunate because lakes have some unique features (explained in detail below) that allow teasing apart hypotheses that typically cannot be evaluated using terrestrial systems. Studies on the biodiversity of lakes and other water bodies (herein lakes for short) have traditionally focused on local scales (*i.e.*, within a lake), paying particular attention to local dynamics, such as mixing regimes, trophic networks or local spatial gradients (*e.g.*, horizontal gradients in reservoirs). It was also through these local studies that the relationships of the biological component with environmental variables started to be understood (*i.e.*, the lake as a microcosm; Forbes, 1887; see the discussion in this issue by Jenkins, 2014), providing the roots of most modern ecological knowledge (Hutchinson, 1957; Odum, 1963; Margalef, 1984; see Colwell and Rangel, 2009). However, in many regions aquatic ecologists started to sample over large spatial extents only recently. For example, most studies on phytoplankton in Brazil are still local; while almost two thirds of the articles published by Brazilian limnologists are local, the proportion of works conducted at the regional scale is increasing (Nabout *et al.*, 2009, 2013; Wetzel *et al.*, 2012). A result of this traditional focus on the local scale is the paucity of macroecological knowledge on lakes; a restrictive search on Scopus² rendered only 13 studies of macroecology on lakes, and 39 additional works studied biogeographical gradients on lakes³. A thorough revision looking for evaluations of hypotheses about biodiversity gradients in freshwater habitats found a total of only 87 relevant studies for lakes (Stendera *et al.*, 2012).

Despite the lack of macroecological studies conducted so far, lakes are particularly suited for macroecological research. This discipline typically aims to characterize phenomena across large numbers of comparable ecological particles, and in fact very few ecosystems are so well delimited (in relative terms) as lakes, which constitute *islands* within an unsuitable matrix with relatively easy-to-measure characteristics. Lakes of various ages, sizes and physical, chemical and biological characteristics can be found at different climates (Margalef, 1983; Lewis, 1996; Wetzel, 2001; Elser *et al.*, 2010). Further, the correlation between lake temperature and productivity is, in general, not strong (Lewis, 2000). All these characteristics make lakes particularly suitable to disentangle the effects of different concurring factors that are often more correlated in terrestrial ecosystems. Nonetheless, the particular charac-

¹ A body of research that uses theories in limnology to describe, manipulate and control the environment (Peters, 1986).

² Search at <http://www.scopus.com/> on 01/10/2013, using the terms TITLE-ABS-KEY(lake* macroecol*).

³ Search at <http://www.scopus.com/> on 01/10/2013, using the terms TITLE-ABS-KEY(lake* biogeogr* gradient*).

teristics of lake biotas add an interesting dimension to macroecological studies. Apart from the distribution into trophic levels that is common to all ecosystems, lake biotas are segregated between spatially distinct habitats: the limnetic zone – the portion of the water body open to the photosynthetically active radiation penetration; benthos – the deepest part of the lake, normally the surface of the sediment; and littoral – the shallowest part of the lake shore. Two interacting communities are traditionally distinguished in the limnetic zone for operational reasons, the nekton (active swimmers) and the plankton (organisms suspended in the water column) (Lampert and Sommer, 2007). Depending on lake depth and transparency light can reach the sediment. In this case, both the littoral and benthos have a rich primary producer community; otherwise such communities are restricted to the littoral. This spatial and depth stratification effectively creates different ecological systems that will show differential responses to the same factors and stressors.

Importantly, the size of lentic habitats influences the levels of physical, chemical and biological interactions between limnetic and littoral zones, thereby determining the whole ecological dynamics of the lake. Water bodies with more than two hectares in area are generally considered lakes, while smaller ones are considered ponds (Biggs *et al.*, 2005). From a macroecological perspective lakes and ponds are discrete ecological particles that share the same spatial matrix. Further, although ponds are more numerous and smaller in size, most species have different discrete populations in each of them. While both lakes and ponds have traditionally been used for metapopulation and metacommunity studies (Jenkins and Buikema Jr., 1998; Cottenie *et al.*, 2003; Leibold and Norberg, 2004; Heino and Soinen, 2010; Logue *et al.*, 2011), lakes have been comparatively more studied from a biogeographical perspective (Verleyen *et al.*, 2009; Poquet and Mesquita-Joanes, 2011). However, the different ecological and biogeographical processes affecting species distributions and community diversity interact across scales in a hierarchically structured way (Rajaniemi *et al.*, 2006; Hortal *et al.*, 2010, 2012; Guisan and Rahbek, 2011). For example, lake communities may be more controlled by deterministic processes at larger spatial scales, while pond communities may be more influenced by stochastic factors at ecological time scales, as many ponds experience cyclic periods of drought (Chase, 2007). These scale-related changes can alter the concordance between the freshwater biotas of several groups (Paavola *et al.*, 2006). We thus believe that research on lentic communities from a macroecological perspective will benefit from considering the size-scaling between ponds and lakes explicitly in the analyses, at least for organisms inhabiting both types of habitats.

Here we examine how five major macroecological questions, namely island biogeography, geographical gra-

dients of biodiversity, metacommunities, species' trait variations and community structure, can be, and have been, investigated in lakes. We make it under the assumption that the observed patterns, and the process behind them, may change from the terrestrial to the lentic systems. If that is the case, current macroecological knowledge will be advanced. When, on the contrary, patterns and/or processes are similar, these studies will add support to the generality of particular aspects of current macroecological theory. Although the results of macroecological research can inform applied fields such as conservation management through the disciplines of systematic conservation planning (Margules and Pressey, 2000) and conservation biogeography (Whittaker *et al.*, 2005), we have deliberately excluded this aspect from the questions we discuss. We do this because a proper description of the state-of-the-art and its application to lentic habitats (such as in *e.g.*, Nel *et al.*, 2009) would require a detailed discussion that is certainly out of the eminently theoretical aim of our text. In sum, our aim is to provide a perspective rather than a comprehensive review, considering the benefits -and some caveats- of using lentic habitats as study systems for macroecological research, and highlighting several potential future lines of research. We will focus primarily on lakes, but we note that most (if not all) of the research questions we review can also be applied to ponds (see Boukal, 2014; De Meester and Pantel, 2014; Jenkins, 2014; Gravel *et al.*, 2014).

Lakes as islands within terrestrial seas

Researchers have long been interested in islands. Their isolate and discrete nature makes them the perfect natural experiments to study evolutionary and ecological patterns. Islands have in fact served as the foundations of several basic theories in different research topics (MacArthur and Wilson, 1963; 1967; Diamond, 1969, 1970; MacArthur *et al.*, 1972; Emerson, 2002; Gillespie and Roderick, 2002; Ricklefs and Bermingham, 2008; Whittaker *et al.*, 2008). The *Theory of Island Biogeography* (MacArthur and Wilson, 1963, 1967) is one of the most influential theories in modern ecology (Losos and Ricklefs, 2009). MacArthur and Wilson proposed that the number of species on an island tends to an equilibrium state resulting from the balance between immigration and extinction rates. Their model implies that the fundamental processes of dispersal and colonization should vary in a predictable way in relation to isolation and area. Immigration rate should decline with increasing isolation, and extinction rate should decline with increasing area (a general surrogate for the total carrying capacity of the island). Although many other factors can shape island diversity (*e.g.*, habitat diversity: Hortal *et al.*, 2009; island age: Whittaker *et al.*, 2008; species pool diversity: Santos *et al.*, 2011), the *Theory of Island Biogeography* is still one of the most empirically supported theories in ecology.

Islands have different sizes, shapes, geology, environments, and history, which make each one of them unique entities (Whittaker and Fernández-Palacios, 2007). One can think of islands not simply as pieces of land surrounded by water (*i.e.*, true islands), but also as a suitable habitat surrounded by a matrix of unsuitable habitats (Whittaker and Fernández-Palacios, 2007). Although lakes are not completely isolated from the terrestrial systems, they are easy to define spatially and present a clearly distinct biota from that of the surrounding systems. Therefore, lakes can also be perceived as *islands* within a *sea* of terrestrial landscapes (Keddy, 1976; Eadie *et al.*, 1986; Minns, 1989; Heino, 2011), having also its own size, shape, diversity and history, as any other *true* island. Although lakes could serve as good models to study island biogeography theory, relatively few works have done so (but see *e.g.*, Hubbard, 1973; Browne, 1981; Hockin, 1982; Brönmark, 1985; March and Bass, 1995; Harris *et al.*, 2011; Brooks and Colburn, 2012). Most of the tests of island biogeography theory in lakes focus on the relationship between species richness and lake surface area and/or isolation (March and Bass, 1995; Rolon *et al.*, 2008; Bagella *et al.*, 2010; Bosiacka and Pieńkowski, 2011; Brooks and Colburn, 2012). But when variables such as water quality (Rørslett, 1991) or lake history (*e.g.*, Minns, 1989; Lévêque *et al.*, 2008) are taken into account, they do show significant explanatory power. It is likely that research traditions are responsible for the study of variation in lacustrine species richness over large spatial scales being modelled by a different set of predictors in addition to lake area. Current theory of island ecology and biogeography introduces many aspects that could be directly applied to the study of lake diversity, particularly the influence of age, habitat diversity (Rolon *et al.*, 2008) or lake depth, that can be to some extent analogous to elevation on islands.

Geographical gradients of species richness

The decrease in species numbers from the equator to the poles is one of the most striking and best known patterns in nature (Hawkins, 2001), and despite notorious exceptions (see Rabenold, 1987; Kouki *et al.*, 1994; Mori *et al.*, 2010; Santos and Quicke, 2011), it is generally consistent regardless the geographic region, scale or taxon (Hillebrand, 2004). To date more than thirty hypotheses have been proposed to explain this pattern (see Willig *et al.*, 2003; and Hawkins, 2008 for a review), and according to Mittelbach *et al.* (2007) they can be grouped into three main types: i) ecological hypotheses focused on the maintenance of diversity, mainly due to higher energy input (or productivity) (Weyhenmeyer *et al.*, 2013); ii) historical hypotheses which sustain that the extent and duration of tropical climate on the Earth's history allowed longer time for the species to diversify and accumulate (Hawkins *et al.*, 2007); and iii) evolutionary hypotheses which propose higher diversification rates in the tropics (Allen and Gillooly, 2006).

Grouped within the historical hypotheses, the effect of Pleistocene glaciations on current richness gradients deserves an especial mention. Firstly, because it has been traditionally neglected (Francis and Currie, 2003) and secondly because of the increasing body of evidence documenting their effects on many groups (Svenning and Skov, 2007; Hortal *et al.*, 2011; Griffiths *et al.*, 2014). Lentic faunas are not an exception to this. Glacial waters host less diverse biotas (Gesierich and Rott, 2012), which would have caused massive extinctions in the glaciated areas. Hence, most temperate lakes host particularly species-poor fish communities due to limitations to post-glacial recolonisation and low diversification rates in cold waters (Minns, 1989; Amarasinghe and Welcomme, 2002). Although ecological explanations of the latitudinal gradient have been preponderant, during the last decade, historical and evolutionary explanations have gained relevance and some authors have gone further proposing them as the principal forces driving this pattern (Wiens and Donoghue, 2004; Hawkins, 2008). Yet, despite some attempts at reconciliation (Hortal *et al.*, 2011), the debate is still open.

One of the reasons for the lack of consensus comes from the fact that most studies exploring latitudinal gradients have been conducted over large landmasses, where potential explanatory factors are correlated and may interact synergistically (Willig *et al.*, 2003). In that sense, lakes constitute an excellent study system to evaluate the hypothesized mechanisms underpinning latitudinal richness gradients. On the one hand, most – if not all – freshwater organisms show latitudinal diversity patterns (see Collen *et al.*, 2013), although the generality and strength of these gradients in microscopic organisms is under debate (see contrasting views at Finlay *et al.*, 1996; Finlay and Esteban, 2007 and Heino *et al.*, 2011 compared with Vyverman *et al.*, 2007; Fontaneto and Brodie, 2011; Hortal, 2011; Fontaneto and Hortal, 2012, 2013). On the other hand, despite some general environmental influences, lake characteristics (such as area, age, temperature or productivity) are not necessarily correlated, or at least are not as spatially autocorrelated as the characteristics of terrestrial landscapes. These characteristics make direct hypothesis testing easier in lentic habitats, even though several factors can interact to affect diversity gradients in a non-linear way (see Matuszek and Beggs, 1988).

Despite their potential, few studies have explored the strength and potential mechanisms underlying the geographical diversity gradients in lakes. However, the ones that do so show offer valuable insights on the general characteristics of the geographic variations in diversity (see Barbour and Brown, 1974; Minns, 1989; Gillooly and Dodson, 2000; Amarasinghe and Welcomme, 2002; Lévêque *et al.*, 2008; Verleyen *et al.*, 2009; Stomp *et al.*, 2011; Stendera *et al.*, 2012; Pinel-Alloul *et al.*, 2013). Many variables, related to different ecological processes, can drive geographic gradients in lake species richness.

Recently, Stomp *et al.* (2011) found that local environmental variables such as water temperature, chlorophyll-*a*, lake area and depth had significant effects on phytoplankton diversity. Further, the availability of solar energy has been found to correlate with the species richness of pelagic crustaceans in a large cold temperate region (1665 Canadian lakes; Pinel-Alloul *et al.*, 2013). And while fish diversity of cold temperate lakes is affected by their glacial history (Minns, 1989), ancient lakes host disproportionately rich fish faunas (Lévêque *et al.*, 2008).

The geographical concordance of diversity patterns in different groups also offers valuable insights. Unsurprisingly, freshwater vertebrates and decapods show distinct global-scale patterns of species richness and threatened and rare species when compared to terrestrial mammals and birds (compare Figure 1 in Grenyer *et al.*, 2006 with Figure 1 in Collen *et al.*, 2013). Further, Griffiths *et al.* (2014) found differences in the responses of freshwater fish to climate variation between North American and European and between generalist and specialist species, as well as significant effects of historical predictors on the richness of migratory species. However, it is interesting to note that the patterns of decrease in diversity with latitude are similar for phytoplankton (Stomp *et al.*, 2011) and pelagic crustaceans (Pinel-Alloul *et al.*, 2013).

Recent works point to the convergence in the macroecological patterns among different freshwater groups (see Soinenen, 2012; Tisseuil *et al.*, 2013). Behind such general convergence, the disagreement among significant environmental variables also highlights the importance of the particular characteristics of each species group and their responses to lake characteristics as determinants of local diversity. This is in agreement to the perspective that no single mechanism is enough to account for the origin of geographical diversity gradients (Hortal *et al.*, 2011). Nonetheless, there is large body of evidence on the determinants of species diversity and community structure in lakes (Amarasinghe and Welcomme, 2002; Fallu *et al.*, 2002; Rosenfield, 2002; Hessen *et al.*, 2006; Lappalainen and Soinenen, 2006; Mehner *et al.*, 2007; Muylaert *et al.*, 2010; Olden *et al.*, 2010; Collen *et al.*, 2013; Weyhenmeyer *et al.*, 2013). Despite the multiplicity of hypotheses and groups, formal meta-analyses (or informal ones, such as Stendera *et al.*, 2012) may allow identifying the main general drivers of lake diversity.

Incorporating lakes into the macroecological research agenda can contribute to shed light to a problem that has intrigued scientists during two centuries. Of course, macroecological analyses of lake data is not free of problems. Temporal variations in the composition and diversity of lakes could affect the results of the analyses of diversity gradients, as the distribution and diversity of many groups are shifting with climate changes (Hallstan *et al.*, 2013). In addition, survey unevenness and incompleteness may com-

promise data quality (Hortal *et al.*, 2007; Straile *et al.*, 2013). However, additional studies are yet necessary to evaluate the relative importance of large-scale environmental gradients, watershed characteristics, historical factors, and local characteristics for lake diversity. These studies may incorporate large datasets from taxa or species groups of different trophic levels and detailed information on the origin and biogeochemical characteristics of lakes, in order to complement the existing knowledge.

Beta-diversity and metacommunities in lentic habitats

Given that lakes have discrete borders defining the extent of the aquatic habitat, a set of lakes in a large region is an ideal model to study compositional variation from a metacommunity perspective. That is, the perspective of multiple communities connected by dispersing organisms (Leibold *et al.*, 2004) that are affected by local and regional processes (see Ricklefs, 2008). Given that a major goal of community ecology is to describe and explain how and why the composition of biological communities varies in space and time, ecologists have made great advances recently in understanding beta-diversity – the spatial or temporal variability of species composition (Anderson *et al.*, 2011). Not surprisingly, the increase in the number of articles on metacommunities and beta-diversity in lakes accompanied the overall increase of the number of publications about the topic (Fig. 1; see also

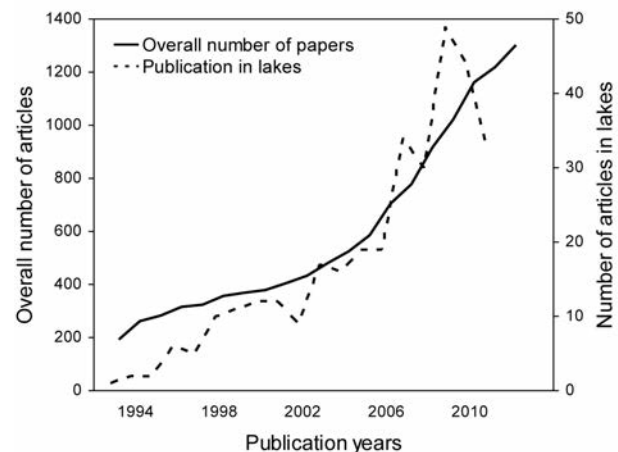


Fig. 1. Number of publications in the last 20 years (1992-2012) indexed in ISI web of science database about metacommunities or beta-diversity per year (left axis, $N=12,017$) and about the same topic only in lakes (right axis, $N=384$). Search conducted at <http://www.webofknowledge.com/> on 24/09/2013 using the terms TITLE-ABS-KEY("metacommunit*" OR "beta-diversit*" OR "beta diversit*") for overall number of articles, and TITLE-ABS-KEY ("metacommunit*" OR "beta-diversit*" OR "beta diversit*" AND "lake*") for number of articles about lakes.

Logue *et al.*, 2011). In fact, the study of a set of interconnected ponds made by Cottenie *et al.* (2003) is one of the first and most influential attempts to confront the relative role of local and regional processes on the spatial variation of zooplankton communities (but see also Warren, 1996). In another study, Beisner *et al.* (2006) showed that crustacean zooplankton and fish were more constrained by dispersal-based processes than bacteria and phytoplankton in a set of Canadian lakes. These results are in line with Nekola and White's (1999) prediction of steeper distance-decay relationship for organisms with lower dispersal abilities when compared to those organisms with higher dispersal abilities.

Lakes are a good model system to investigate the relationship between dispersal ability, landscape structure and metacommunity structure. One can, for example, compare the output of a variation partitioning analysis or the distance-decay relationship between weaker dispersers, such as fish, and stronger dispersers, such as the microbiota (Beisner *et al.*, 2006; Var der Gucht *et al.*, 2007). A deconstructive trait-based approach within each one of these broad categories can be also fruitful (Algarte *et al.*, 2013; Grönroos *et al.*, 2013). This debate has received much attention among macroecologists, given that the relative importance of niche- and dispersal-based processes varies across spatial scales (Hortal *et al.*, 2010). For example, Chase (2010) manipulated productivity in a set of experimental ponds and found that within-pond species richness in low and high productivity treatments were very similar after a 7-year experiment. He found, however, consistently high beta-diversity among high-productivity ponds (*i.e.*, at a within-region scale), in comparison with low-productivity ponds. Chase's study shows that deterministic processes predominate in low productivity ponds, making them very predictable, whereas stochastic processes predominate in high productivity ponds. In contrast, Van der Gucht *et al.* (2007) highlighted the power of species-sorting mechanisms on lake bacteria over a wide range of spatial scales. These authors demonstrated that bacteria have weak dispersal limitation and that, given their rapid grow rate, species sorting along environmental gradients drives bacteria metacommunity dynamics. However, many other groups present strong dispersal limitations. Therefore, modern bioassessment⁴ approaches must integrate niche, dispersal and biotic interactions (Heino, 2013). Given their discrete nature, lakes may constitute good model systems to determine the effects of landscape structure and complexity on the relative importance of neutral and niche-based processes (see Gravel *et al.*, 2014). These are just a few examples of how studies focusing on lakes can provide

theoretical advances of major importance for the understanding of community variations.

Species' traits, body size and ecosystem structure and functioning

Macroecologists are interested in characterizing how variations in physiological and functional traits represent the effects and evolution of the species' niche, through their relationships with environmental gradients and other species within the community. Studies showing evidences of local adaptation in species traits are abundant in aquatic ecology (see De Meester and Pantel, 2014 for a recent example). There are also studies showing geographical patterns in traits of freshwater organisms (Heino *et al.*, 2013). The strongest effects of environmental gradients have been found on traits related with biotic interactions such as predation (Hairston and Walton, 1986; Cousyn *et al.*, 2001), omnivory (González-Bergonzoni *et al.*, 2012) and parasitism (Ebert, 1994), as well as in traits that can be directly affected by climatic changes such as physiological adaptations to increasing water temperature. Amongst them, temperature-related adaptations have been found to prevent immigration success in zooplankton (Van Doorslaer *et al.*, 2009), to avoid habitat colonisation in fish (Ohlberger *et al.*, 2008), and to foster phenotypic divergence in amphibians (Richter-Boix *et al.*, 2010). Geographic gradients of temperature are also a key factor determining species distributions and affecting traits such as body size (Gillooly and Dodson, 2000). In fact, the ecophysiological constraints occurring at the local scale of a pond or a lake scale up to determine the evolution of the thermal niche of freshwater species, such as anuran tadpoles (Gouveia *et al.*, 2014).

One of the traditional assumptions of ecology is that the ecological role of the species varies according to their differences in a series of traits with functional significance (see Messier *et al.*, 2010). Ecosystem processes are known to depend on the range of species' traits present in each ecosystem (Tilman, 2001). One of the most important traits for understanding large-scale ecological patterns is body size. Alike land organisms, freshwater species show a negative relationship between abundance and body size (Jonsson *et al.*, 2005; Yvon-Durocher *et al.*, 2011). But most importantly, body size is related to dispersal ability of the species (Gillooly and Dodson, 2000; De Bie *et al.*, 2012), resulting in a wide range of differences in macroecological and biogeographic patterns (Fontaneto and Brodie, 2011; Hortal, 2011; Fontaneto and Hortal, 2012, 2013). At large scales, dispersal ability can sometimes be more important than

⁴ *Bioassessment*, or *biological assessment*, is an evaluation of the condition of a waterbody using biological surveys and other direct measurements of the resident biota in surface waters (Barbour *et al.*, 1999).

environmental variables (Heino *et al.*, 2012), although environmental gradients can also produce isolation between water bodies and promote rapid adaptive processes that result in niche differentiation (see De Meester and Pantel, 2014). Body size also determines the ecological role and niche position of aquatic organisms (Maly and Maly, 1974; Chase and Leibold, 2003), particularly for large-sized organisms. In large organisms such as fish, limiting similarity processes can exclude species of similar size from particular lakes, whereas the high dispersal capacity of small-sized organisms may counteract the effect of these processes (Fenchel and Finlay, 2004; but see Hortal, 2011; Fontaneto and Hortal, 2013). Due to this, the distributions of small-sized organisms would be more structured by large-scale geographical gradients and landscape-scale spatial processes and the large-sized organisms by within-lake niche-related processes (Martiny *et al.*, 2006; Soininen *et al.* 2011; see however De Meester *et al.*, 2002; De Bie *et al.*, 2012). Following the framework proposed by Hortal *et al.* (2010) the relative importance of scenopoetic⁵, biogeographic and occupancy dynamics factors will be higher for microorganisms, whereas bionomic⁶ factors will be most important for aquatic vertebrates inhabiting lentic habitats.

Here we argue that the effects of body size on biogeographic patterns (*sensu* Fontaneto and Brodie, 2011) may affect the ecological functions performed by guilds of organisms with different sizes. Trait diversity show a positive relationship between ecosystem functioning and resilience (Hooper *et al.*, 2005; Scherber *et al.*, 2010). Therefore, if large-sized organisms show less trait variability within a single lake than small-sized ones due to increasing strength of limiting similarity processes (see above), then the ecological functions performed by progressively smaller species groups will be enhanced and more resistant to environmentally-induced changes in lakes and other water bodies. As the major ecological guilds inhabiting lentic systems are also body size-structured, the differences in the biogeographic characteristics of macroscopic and microscopic organisms may have a significant effect in the trophic structure of lakes placed in different parts of the world. The reliance on body size as a major structuring factor does not mean that the incorporation of other traits would not be necessary to attain a better knowledge on aquatic food webs (Boukal, 2014). Also, the high density of large organisms in the higher

trophic levels leads to deviations from the typically triangular trophic pyramids. Particularly, a more asymmetric or even inverted pattern across trophic levels may occur (Jones and Jeppesen, 2007).

The introduction of predators such as fish is amongst the most important factors affecting community composition in lakes (Knapp *et al.*, 2001). Freshwater fish are one of the animal groups with higher number of invasive species (Hulme *et al.*, 2009). The weak resistance of lacustrine habitats to fish invaders (Irz *et al.*, 2004) results in within-lake alterations in trophic relationships and substantial effects on lake biodiversity (Vitule *et al.*, 2009). Since their impact is widespread and relatively well documented, the changes in trophic relationships in lakes associated with invasive species offer new opportunities to study the effects of trophic changes in different biogeographic regions (Brose *et al.*, 2004). If, as we hypothesize, the ecological performance of large species can be highly variable, global change effects such as the appearance of invasive species could produce large differences in the trophic structure of lakes located in the same climatic domains, breaking down the more consistent functioning of the lower trophic levels. Several studies on the impact of invasive fish and crustaceans provide evidence for disruptions of the ecological dynamics of lakes (Feroz Khan and Panikkar, 2009; Wahl *et al.*, 2011; Cucherousset *et al.*, 2012; Strock *et al.*, 2013), while others do not (Nilsson *et al.*, 2012; Jackson *et al.*, 2013). These mixed (though not necessarily contradictory) results may be due, among other things, to the wide variety of approaches used, or the influence of other global change stressors. For example, warming can cause changes on phytoplankton size that are uncoupled with changes in zooplankton, thus resulting in a reorganization of the biomass structure of the food web (Yvon-Durocher *et al.*, 2011) and generating strong changes in ecosystem functioning. Thus, further studies conducted in a standardized way are needed (Cucherousset and Olden, 2011). Although hypotheses similar to ours have been formulated recently (see Blanchet, 2012; Dick *et al.*, 2013), as far as we know they have not been formally evaluated to date. It thus seems worth investigating further their validity and the generality.

Functional and phylogenetic community structure

Community structure has been traditionally described using species richness. However, such approach presents

⁵ According to Hutchinson (1978), the environmental conditions that *set up the scene* for the basal growth rate of populations, for which competition is not relevant; they are commonly referred to simply as *conditions* in niche theory (see Soberón, 2007).

⁶ Also following Hutchinson's (1978) terminology, all factors related with species interactions and consumption of resources, either affecting competition and/or the impacts that consumers have on the resources (Chase and Leibold, 2003); they are commonly referred to as *resources* in niche theory (see Soberón, 2007).

important limitations, since it assumes that all species contribute equally to biodiversity (Magurran, 2004). As a result, the last 20 years have seen an increasing interest in studying other aspects of community structure, namely through the use of functional and/or phylogenetic diversity (Fig. 2). According to Tilman (2001), functional diversity describes the value and range of variation of the traits shown by the species present in the ecosystem, that influence ecosystem functioning. So, according to this definition, functional diversity links individuals with their traits (Violle *et al.*, 2007) and the functions they perform

in the ecosystems. Another way of assessing the patterns of community assembly and structure is through phylogenetic diversity, which measures the phylogenetic relationships between the species inhabiting the community (Magurran, 2004). Here, diversity will be higher in communities where species are phylogenetically most distinct. There are several methods for estimating functional and phylogenetic diversity (see Faith, 1992; Webb, 2000; Pausas and Verdú, 2010; Pavoine and Bonsall, 2011; Vamossi, 2014), each one of them conveying distinct facets of diversity.

Both functional and phylogenetic diversity can be used to ascertain the processes determining community assembly (Díaz *et al.*, 1998; Webb *et al.*, 2002; Schwillk and Ackerly, 2005; Pausas and Verdú, 2010). Regarding functional diversity, one way to do this is by comparing the distribution of functional traits of each community with that from a random assembly of species from the regional species pool. Communities with lower values of functional diversity than the null expectation (*i.e.*, functional clustering) are, in general, thought to be shaped by environmental filtering that allows the occurrence of only a reduced range of traits (Zobel, 1997). On the other hand, communities with higher values of functional diversity than the null expectation (*i.e.*, functional overdispersion) are shaped by limiting similarity processes, such as competition or facilitation, which select species presenting disparate functional traits (Weiher and Keddy, 1995). Again, lakes can be considered ideal models to study these facets of biodiversity as the delimitation of both local communities and regional species pools are facilitated. However, interpreting natural communities using this framework is not as straightforward as it may appear, particularly when incorporating the determinants of the phylogenetic structure of communities. Many concurrent evolutionary processes play a major role in determining the phylogenetic diversity of local communities. Due to this, processes that apparently would produce different communities, such as competition and environmental filtering, may produce similar phylogenetic (but not functional) structures (Losos, 2008; Mayfield and Levine, 2010; Hille Ris Lambers *et al.*, 2012; Adler *et al.*, 2013). Further, the spatial (and temporal) scale also plays a major role in the interpretation of community structure. While both convergence and divergence processes can shape functional diversity at the local scale, convergence typically predominates at larger scales, so regional assemblages tend towards trait redundancy (see De Bello *et al.*, 2009). As a consequence, community structure cannot be understood only from the functional patterns described above. Rather, it needs to incorporate information on whether trait values are either conserved or convergent across the tips of the phylogeny (Pausas and Verdú, 2010; Pavoine and Bon-

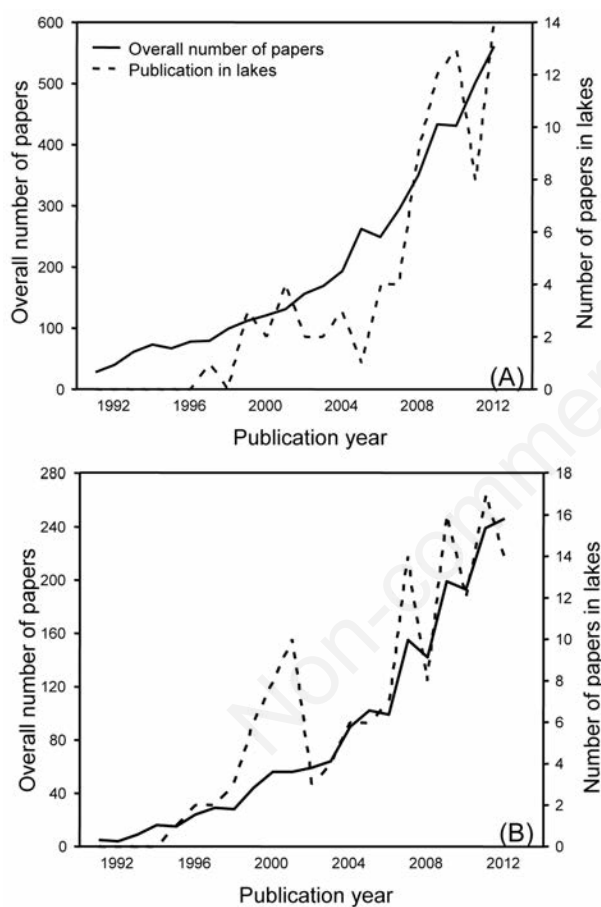


Fig. 2. Number of publications in the last 20 years (1992–2012) indexed in ISI web of science database about: A) functional diversity per year (left axis, $N=4908$) and about the same topic only in lakes (right axis, $N=92$). B) phylogenetic diversity per year (left axis, $N=2074$) and about the same topic only in lakes (right axis, $N=155$). Search conducted at <http://www.webofknowledge.com/> on 24/09/2013 using the terms TITLE-ABS-KEY (“functional diversity”) for overall number of articles; TITLE-ABS-KEY (“functional diversity” AND lake*) for number of articles in lakes; TITLE-ABS-KEY (“phylogenetic diversity”) for overall number of articles; and TITLE-ABS-KEY (“phylogenetic diversity” AND lake*) for the number of articles in lakes.

sall, 2011; Cadotte *et al.*, 2013), bearing in mind the spatial scale of the analysis (De Bello *et al.*, 2009; Hortal *et al.*, 2012).

The study of functional and phylogenetic diversity has increased exponentially during the last decade (Cianciaruso, 2011). Despite following the same trend, still very few studies in lakes focus on these aspects of diversity when compared to other environments (Fig. 2). The few limnological studies analysing functional and phylogenetic diversity were performed over regional scales. In the particular case of functional diversity, community structure has been assessed through the use of functional groups (Reynolds *et al.*, 2002), an approach that has been criticized for assuming too many arbitrary decisions and for perceiving species within groups as functionally redundant (Magurran, 2004; Petchey and Gaston, 2006; Carneiro *et al.*, 2010). In fact, several groups working on stream ecosystems have used trait composition and functional diversity metrics rather than functional groups to study community structure (Statzner *et al.*, 2004; Poff *et al.*, 2006; Feld *et al.*, 2013). Functional and phylogenetic diversity measure aspects of biodiversity that are not fully covered by species richness or evenness (see Longhi and Beisner, 2010; Litchman *et al.*, 2010). Changes in functional (and phylogenetic) community structure can alter completely the functioning of lentic ecosystems (Matsuzaki *et al.*, 2013). Knowledge on this research area is still scarce (Sternberg and Kennard, 2014; Vogt *et al.*, 2013). Therefore, additional efforts can provide significant developments on the conceptual body of modern limnology.

CONCLUSIONS

We identify a set of typical macroecological questions that are particularly suited to the use of lakes as study systems, such as the determinants of species diversity and community variation, or the effects of body size on ecosystem functioning. However, the use of lakes for macroecological research presents several caveats that need to be accounted for, or assumed explicitly in the study design. Within-lake habitat diversity can be a confounding factor for studies on groups whose species use different parts of the lake ecosystem. This problem can be easily solved by studying different groups (note that most species are habitat specific), by conducting standardized surveys that account for habitat diversity, and either study each habitat separately, or include habitat diversity explicitly in the analyses. Further, local factors (*e.g.*, physico-chemical variables) are of extreme importance for the structure and diversity of lentic communities. Hence, good-quality data on the geomorphology and origin of lakes should be included in the studies of diversity gradients or species' trait variations, together with other – generally used – environmental variables such as climate. As

the size of the lentic habitats determines the impact of diversity in ecosystem functioning (Korhonen *et al.*, 2011), the study of their macroecological patterns should include data and samples from water bodies across the whole ecosystem size gradient.

Given the discrete and isolated nature of lakes and ponds, it is not surprising that most studies on metacommunity were developed in aquatic systems. Results from these studies are, from one side, already using important concepts and methods from macroecology and, from another side, contributing to the advancement of this field in general. This is perhaps the best indicator of the potential gains in *wetting* macroecology or *spatializing* limnology at broad scales. The relatively easy measurement of some ecosystem properties related with its functioning (*e.g.*, biomass, eutrophication, productivity, *etc.*) allows studying the relationships between guild structure, species interactions and diversity and ecosystem functioning. We believe that lakes (and ponds) are particularly suited for the study of the most functional aspects of macroecology, because the different biotic and abiotic parts of the ecosystem can be examined, measured and controlled for relatively easily. This allows teasing apart many of the confounding factors that introduce noise in the outcomes of macroecological processes. Here it is necessary to take into account that many lakes have suffered the effects of climate change and substantial anthropogenic alterations such as eutrophication or the introduction of invasive species, which in most cases imply strong ecological changes. Therefore when using large lake datasets for macroecological studies it is also important to take into account these alterations, which in some particular cases might completely mask any global ecological pattern. Despite this unavoidable drawback (which is also common to most, if not all, ecosystems), lakes and ponds hold a great potential to foster the advance of macroecological theory, similarly to their prominent role in the origin of modern ecology.

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