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Lakes and rivers as microcosms, version 2.0

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ABSTRACT

Limnology has been greatly influenced by The lake as a Microcosm *(Forbes, 1887), which described a holistic focus on the internal machinations of singular, island-like aquatic ecosystems. I consider three persistent influences of* The lake as a Microcosm*: as an organizing paradigm for the teaching of limnology relative to its practice; the idea that inland waters are like islands, and the replicability of types of inland waters. Based on inspection of recent peer-reviewed literature and 32 limnology texts, we teach limnology according to Forbes but do not practice it in that holistic context. Instead, we practice limnology as aquatic ecology. Based on novel analyses of species-area relationships for 275 inland waters and 392 islands, inland waters are more like continental habitat patches than islands; the island metaphor is poetic but not accurate. Based on a quantitative review of beta diversity (40 data sets representing 10,576 inland waters and 26 data sets representing 1529 terrestrial sites), aquatic systems are no more replicable than are terrestrial systems; a typological approach to limnology is no more justified than it is in terrestrial systems.*

I conclude that a former distinction between limnology and aquatic ecology no longer applies, and that we should define limnology as the ecology of inland waters. Also, we should not consider lakes and rivers as islands that represent other systems of the same type, but should consider them as open, interactive habitat patches that vary according to their geology and biogeography. I suggest modern limnology operates according to 3 paradigms, which combine to form 3 broad limnological disciplines and establish a basis for a plural, interactive view of lakes and rivers as microcosms. This model of modern limnology may help better connect it to ecology and biogeography and help limnology be even more relevant to science and society

Key words: limnology, aquatic ecology, biogeography, paradigms, species-area relationships, beta diversity.

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INTRODUCTION

> "*One finds in a single body of water a far more complete and independent equilibrium of organic life and activity than on any equal body of land. It is an islet of older, lower life in the midst of the higher more recent life of the surrounding region. It forms a little world within itself, - a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on so small a scale as to bring it easily within the mental grasp*."
>
> *S.A. Forbes (1887)*

A singular view

Few papers published in similarly remote outlets will have the long-term impact of Forbes' *The lake as a Microcosm*, first published in 1887 in the Bulletin of the Scientific Association (Peoria, IL, USA). It is well known because it has been reprinted in multiple formats, including as the first paper in the popular Foundations of Ecology (Real and Brown, 1991). It has been especially relevant in limnology but it also represents an early view of key and persistent concepts in ecology, including population, community, and ecosystem ecology.

Three important, interacting themes for limnology emerge from *The lake as a Microcosm* and are the subject of this paper:

i) The ecosystem concept is an organizing framework for limnology. Forbes' early description of a lake as a microcosm (note the singular of each) is important because it was the antecedent of the ecosystem concept's integrated view of interactive biota in a physicochemical context (McIntosh, 1986, Kingsland, 1991; Golley, 1996; NRC CIAE, 1996).
ii) A body of water is an island. Forbes' view fostered a focus on structure and processes *within* that islet rather than among islets. This internal focus was consistent with the ecosystem concept and remained wholly consistent with an assessment of limnology by limnologists in the 1990s (Lewis *et al.,* 1995; Golley, 1996). One consequence is that limnology has been stranded apart from other disciplines that study natural systems (McIntosh, 1986; Hairston, 1990; Kalff, 1991; ASLO CLC, 1995; Golley, 1996; Brezonick, 1996).
iii) Results of studies within one aquatic system represent other such systems. Forbes (1887) organized his discussion by summarizing his observations among lakes according to lake type (*e.g.*, floodplain lakes) and community (*e.g.*, plankton). In doing so, he established a descriptive, typological approach to limnology that persists today.

Here I review the literature regarding the three points above. I begin with a commonly applied and broad definition of limnology as the study of inland waters. I later modify that definition. I also start with Ringelberg's (1993) distinction between ecosystem-oriented limnology and organism-oriented aquatic ecology: *In ecology attention was and still is focussed on problems of individual organisms, populations and communities, thus on biological units at different integration levels. Consequently, ecology has always been an integral part of biology, which does not hold for limnology. Evolutionary thought, for instance, is central to ecology as it is in many other branches of biology. In contrast, limnology seems to manage to a large extent without Darwinian, evolutionary principles as is apparent from its textbooks.* This distinction reflects other contemporary evaluations of limnology (Hairston, 1990; Kalff, 1991; ASLO CLC, 1995). I return to this distinction later, with some ideas about limnology's future. And because it remains especially important that a historical perspective be retained amidst our exponentially-increasing literature (Graham and Dayton, 2002), I cite below some vital reviews and historical landmarks in limnology and aquatic ecology.

Is the ecosystem concept an organizing framework for limnology?

> "*One of the best ways to understand the progress of freshwater science is to compare the textbooks of the past few decades.*"
>
> *S.R. Carpenter, foreword in Brönmark and Hansson (1998)*

If the ecosystem concept serves as an organizing framework for limnology, then most limnological textbooks should convey that organizational, hierarchical framework. Also, limnological research should be conducted in a holistic, integrative context, in which biota and their physicochemical environment are studied as an interactive system. To test the above hypotheses, I evaluated the tables of contents for limnology textbooks and recent peer-reviewed literature.

The ecosystem concept descended from Forbes' lake-as-a-microcosm is a popular organizing framework for limnology textbooks (Supplement 1). In addition, the Forbesian singular, internal view of aquatic systems is repeatedly emphasized in most texts. Of the 32 texts I examined, many provide a physical (90%) and chemical (78%) context (sometimes in great detail), followed by summaries of biotic assemblages (*e.g.*, its biotic components, organized by habitat, taxon, or both). Interestingly, only 4 of 13 (31%) texts published before 1990 include chapters on ecosystem ecology, whereas 14 of 19 (74%) published since 1990 do so. Almost half (44%) of texts also explain geological context, and applied limnology is included in over half (56%) of the texts (Supplementary Tab. 1). In sum, limnology texts consistently follow Forbes' lead by describing internal components and interactions for a water body of a type, and ecosystem-scale processes are now commonly discussed in limnology texts. By comparison, relatively few texts evaluate heterogeneity and patterns *among* water bodies sufficiently to list that topic in a table of contents, and when they do, the content is always a small minority of content (Fig. 1A).

One symptom of an ecosystem-based approach in research would be a predominance of descriptive research rather than experimental approaches, as observed in *Limnology & Oceanography* 1980-1990 (Bourget and Fortin, 1995). Also, keywords such as *ecosystem ecology* should be used at least as often as keywords representing subsystems (*e.g.*, *plankton*, *benthos* or *littoral*) or concepts (*e.g.*, *population ecology* or *community ecology*). Alternatively, most limnological research may now take a reductionist view, in which experimental ecology is more common than descriptive ecology, and subsystems (*e.g.*, plankton) or targeted concepts (*e.g.*, population ecology) are discussed more often than ecosystem ecology.

I searched the 1991-2012 journal literature in ISI Web of Science using the keywords *aquatic OR freshwater* in combination with three sets of other keywords: i) *descriptive ecology* or *experimental ecology*; ii) *ecosystem ecology*, *plankton*, *benth**, or *littoral*; and iii) *ecosystem ecology* or *community ecology* or *population ecology*. I simply plotted the counts of papers identified with these keywords through time. I expected modern journal papers to be more often reductionist (*i.e.*, report on subsystems or component species) and experimental. If so, then practicing limnology typically defers its integration to textbook authors but does not necessarily apply the ecosystem concept in practice. I expected this outcome for a combined influence of four reasons. First, a complete ecosystem study is a daunting task for any given investigator (or team) over multiple years (*e.g.*, Likens, 1983; Schindler, 2006), especially in an era of specialization. Second, a comprehensive history (Golley,1996) discussed the wane of the ecosystem concept in favor of reductionist approaches that have enabled conceptual connections across habitats (*e.g.*, trophic interactions, adaptation, and phenotypic plasticity). This potential generality for any one topic has great appeal, though it differs from classic, holistic limnology that dwells in a singular body of water (Ringelberg, 1993; Brezonick, 1996; Lampert, 1997). Third, I expected limnologists have responded much like other disciplines to the unabated combination of a publish-or-perish approach and indolent accounting of scientific merit in academia (Fischer *et al.*, 2012). I expected this process would select against a comprehensive ecosystem analysis that counts as one paper, when an investigator might generate multiple least publishable units (LPUs; Broad, 1981) from the same data set. Of course, multiple papers on subsystems may eventually lead to an integrative overview paper for an especially compelling body of work (*e.g.*, Likens, 1983), but my first and second expectations reinforce the third. Finally, I expected that a reductionist approach is now entrenched generationally, where students of aquatic community or population ecologists are more likely to themselves conduct aquatic community or population ecology without considering their work reductionistic relative to molecular biology, *etc*. They are correct, but overall reductionism may still be at work.

The integrative ecosystem approach to inland waters presented in most texts is remarkably unaligned with the majority of our research practice. As practiced in journal publications, limnology is almost fully replaced by aquatic ecology (*sensu* Ringelberg, 1993), in that experimental approaches greatly outnumber the descriptive (Fig. 1B) and far more studies are conducted on subsystems (*e.g.*, populations, assemblages; Fig. 1C) or habitats (Fig. 1D) than on entire, integrative freshwater ecosystems. The results of my simple analyses of research literature and textbooks are consistent with my four expectations (above), though not a direct test of those expectations. At the least, there is a strong mismatch between how limnology is taught and how it is conducted. I must conclude that the ecosystem concept is an organizing framework for the teaching of limnology, but not for the conduct of it in practice.

What might this mean for limnology (*sensu* Ringelberg, 1993)? I think his characterization was accurate at the time, but that the difference between limnology and aquatic ecology in practice has since blurred; limnology is now equal to aquatic ecology, and distinctions of two decades ago no longer exist. If ecology is the interaction of organisms and their environment, then studies of the geomorphology, physics, and chemistry of aquatic ecosystems are nested within aquatic ecology and fully justifiable in their own scope, in the same way that studies of aquatic biota *in vitro* or *in silico* are part of aquatic ecol-

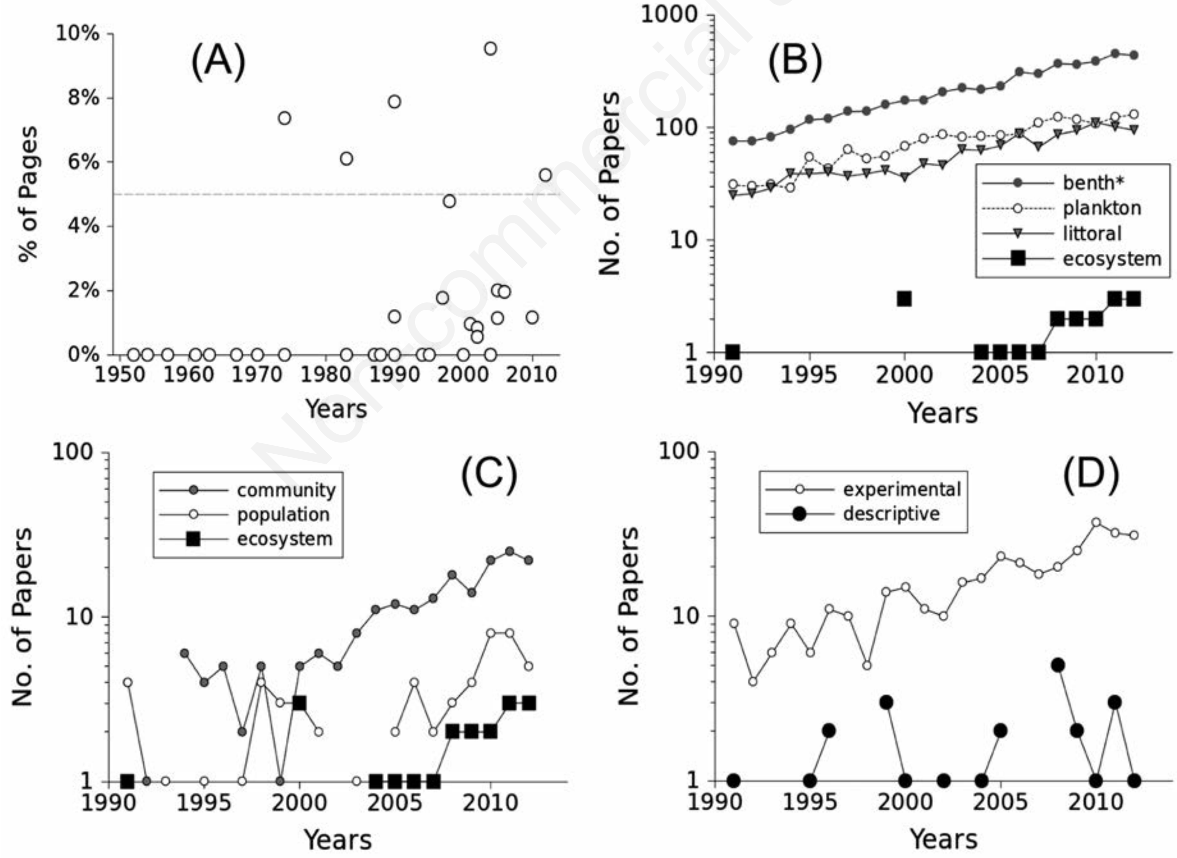

Fig. 1. Trends in limnology textbooks and peer-reviewed journals. Note that axes change among graphs and an exponential upward trend is expected. A) The estimated proportion of textbook pages dedicated to among-system patterns. More than 95% of texts typically focus within systems. B) Studies representing habitats relative to whole ecosystems. Benth* includes benthic and benthos. C) Studies representing component concepts relative to whole ecosystems. D) Studies using experimental and descriptive approaches in inland waters. Some trend lines are interrupted because values of zero cannot be plotted on a log scale.

ogy. If ecology includes hierarchical levels of organization from individuals to the biosphere, then limnology is wholly consistent for a set of Earth's habitats. If limnology was formerly targeted to the ecosystem level, it is now practiced at multiple hierarchical levels that ultimately integrate to the ecosystem. I see no reason now to maintain a distinction between limnology and aquatic ecology, and suggest that limnology be defined simply as the ecology of inland waters. I return to this theme in the last portion of this paper.

Are lakes and rivers like islands?

> "*The great intellectual fascination of limnology lies in the comparative study of a great number of systems, each having some resemblance to the others and also many differences. Such a point of view presupposes that each lake can in fact be treated as at least a partly isolated system*."
>
> *G.E. Hutchinson (1964)*

The idea that a lake is like an island has been a common refrain (*e.g*., Maguire, 1963; Hutchinson, 1964; Keddy, 1976; Fryer, 1996; Dodson, 1992; Arnott *et al.,* 2007). To be clear, an island-like system should be relatively isolated (*i.e*., more closed to biotic exchange than other systems) and relatively independent. To test the veracity of this metaphor we must consider patterns *among* systems and different kinds of systems, which differs markedly from the Forbesian within-system view.

A common analytical tool from island biogeography is a species-area relationship (SAR), which evaluates the number of species as a function of the habitat areas. A SAR is now considered one of the *laws* of ecology because SARs describe many fragmented sets of habitats, ranging from individual thistle plants to continents (MacArthur and Wilson, 1967; Brown, 1971; Schoener, 1976; Connor and McCoy, 1979; Ceballos and Brown, 1995). Because SARs are so common, a positively-sloped SAR with a high r^2 is not by itself definitive evidence of an island-like system (Connor and McCoy, 1979; Lomolino, 1989), though that inference is common in lake-as-island papers. Instead, I reasoned that if lakes and rivers are biotically analogous to islands, then lakes, rivers, and islands should be quantitatively similar in their SAR parameters. One may expect that lakes and rivers have already been quantitatively compared to islands (I did). In fact, the island metaphor inherited from Forbes (1887) is typically presumed; area and other factors are then analyzed as predictors of species richness without quantitative comparison to islands (*e.g*., Barbour and Brown, 1974; Connor and McCoy, 1979; Browne, 1981; Eadie *et al.,* 1986; Hugueny, 1989; Dodson, 1992; Oertli *et al.,* 2002; Stomp *et al.,* 2011). This approach reveals interesting pattern but does not actually test the island-like nature of lakes or rivers because SARs are so general (Schoener, 1976; Connor and McCoy, 1979; Lomolino, 1989). Here I analyzed SARs among lakes, rivers, and islands using appropriate regression techniques and then statistically compared regressions.

As one of the most widely discussed relationships in ecology and biogeography, the SAR literature is vast beyond the scope of this paper. I did not directly explore other factors (*e.g*., isolation, latitude, disturbance regimes, *etc*.) that may also affect species richness, though isolation effects can be inferred because SARs for more remote archipelagos have a lower intercept and a greater slope (Rosenzweig, 1995). Nor did I attempt to analyze for mechanisms (*e.g*., area-*per-se*, habitat heterogeneity, passive sampling, speciation) that have been proposed to explain SARs. As before, I expected that a sufficient number of values may represent actual patterns, but did not expect to obtain all values ever published. In addition, the long history of SAR research has generated much data without also adhering to analytical advances. As a result, technical problems arise but are not often addressed; perhaps these devils in the developing details are why I could find no quantitative comparison of SARs for lakes, rivers and islands using appropriate models.

A SAR is classically modeled as the power equation $S=cA^z$, where S is species richness, and *c* and *z* are coefficients. The power equation is infrequently applied; instead a SAR is sometimes modeled as a semi-log equation (*e.g.*, Drakare *et al.,* 2006) but far more commonly modeled using log-transformed data, in an ordinary least squares (OLS) linear regression; $\log_{10}(S)=\log_{10}(c)+z\,(\log_{10} A)$. Four problems arise to date:

1. OLS regression is actually designed to predict S given a specific A, in contrast to the purpose of SAR analyses - to describe the true relationship between all values of A and S. Evidence of the more general goal is the common practice of reporting *z* coefficients relative to a canonical (*i.e.,* general) value (Rosenzweig, 1995).
2. OLS regressions of SARs assume areas have no variance, when in fact, areas of lakes, watersheds, islands and most habitats are estimates with error (Connor and McCoy, 1979). This is especially apparent when one considers scale-dependence of coastline estimates (Mandelbrot 1983).
3. Though both the *c* and *z* coefficients affect the SAR shape (Lomolino, 1989), most studies only report and compare obtained *z* coefficients obtained by OLS regression (*e.g*., Rosenzweig, 1995; Drakare *et al.,* 2006). The *z* coefficients are not affected by the various units of area used among studies, but area units strongly affect the *c* coefficient. Thus, area must be standardized among studies to analyze and report both *c* and *z* coefficients.
4. A regression of $\log_{10}(S)=\log_{10}(c)+z\,(\log_{10}A)$ applies a

multiplicative error term and may not be the best fit (Xiao *et al.,* 2011).

As a result of the above complications, a simple tally of reported SAR regression coefficients is not sufficient to compare lakes, rivers, and islands. Instead, I computed SARs using standardized major axis (SMA) regression to resolve problems 1-3 above. SMA regression is also known as model II, geometric mean, or reduced major axis regression [but see Warton *et al.* (2006) on why these terms are inappropriate] and can obtain results that are substantially different from OLS regressions (Connor and McCoy, 1979; Eadie *et al.,* 1986; Warton *et al.,* 2006). Unfortunately, many papers do not provide original data and I found that SMA regression coefficients cannot be reliably estimated from reported OLS values, despite conversion formulae provided by Connor and McCoy (1979). I retained the log-log equation in (last point above) because it is so common in the literature and *generally sufficient* (Xiao *et al.,* 2011); results here should relate to the long history of SAR research and represent general comparisons among lentic and lotic systems and islands.

I gathered data in the literature for area and species richness among lentic and lotic systems and islands. I made no distinctions based on system size (*e.g*., lakes *vs* ponds, rivers *vs* streams). I limited analyses to fishes in aquatic systems and nonvolant mammals on islands. Among the limited reasonable choices (*e.g*., phytoplankton data exist for lakes (Stomp *et al.,* 2011) but not for islands), I expected fishes and nonvolant mammals to be most comparable in dispersal among habitats and well-documented. To check that comparability, I first compared the body mass – maximum dispersal distance regressions for fish (N=73) and nonvolant mammals (N=81) from data collected for Jenkins *et al.* (2007). The SMA regressions were not significantly different for slope (P=0.09) and intercepts broadly overlapped in 95% confidence intervals. I concluded that macroecological comparisons of fishes in lakes and rivers relative to mammals on islands may be fair for species-area relationships.

Positive and significant SARs have been observed among sites *within* a system (*e.g*., Angermeier and Schlosser, 1989; Oberdorff *et al.,* 1993), but I omitted such studies to avoid confounding results with *among*-system analyses. I distinguished between oceanic and landbridge islands because they differ in SARs (Lomolino *et al.,* 2010); thus I tested a subsidiary hypothesis that if lentic and lotic systems are like islands, then they would match more closely with landbridge islands than oceanic islands because oceanic islands are more isolated. Alternatively, lentic and/or lotic systems may more closely resemble continental habitat patches by having lesser *z* coefficients but a greater *c* coefficient than islands (*i.e*., be displaced above island SARs; MacArthur and Wilson, 1967; Rosenzweig, 1995). I also compared SARs for lentic and lotic systems and oceanic and landbridge islands within the Nearctic biogeographic realm (Holt *et al.,* 2013; Lomolino *et al.,* 2010), which was the only realm for which I could obtain data for all four types of systems. Preston (1960) also analyzed Nearctic SARs, but surprisingly, biogeographic spatial units are rarely used in SAR analyses. In sum, I conducted hierarchical tests of SARs: i) all inland waters *vs* all islands; ii) global lentic systems, lotic systems, landbridge islands, and oceanic islands; and iii) Nearctic lentic systems, lotic systems, landbridge islands, and oceanic islands. I standardized area estimates to km^2, and calculated SMA regressions of the equation $\log_{10}(S)=\log_{10}(c)+z(\log_{10}A)$ with the smatr 3 package in R 2.14.1 (Warton *et al.,* 2012; R Core Team, 2013), including tests of common *z* coefficients among lakes, rivers, and continental and oceanic islands. The *c* coefficients reported here were calculated as the antilog of $\log_{10}(c)$ solved for in regressions. I applied the Huber M estimator for robust regression estimates given that some data sets had outliers, and error variance was not necessarily homogeneous (Taskinen and Warton, 2011). I also applied Sidak corrections to P values based on multiple comparisons. Species and area data were obtained from the literature for 187 lentic systems, 88 lotic systems, 296 landbridge islands, and 96 oceanic islands (Tab. 1). In general, SMA regressions obtained strong fits to data; r^2 values ranged from 0.37 to 0.83, mean r^2=0.58. For nine of ten SARs estimated here, the simple relationship with area explained about one half or more of the variance in species richness, meaning that other factors (*e.g*., isolation, latitude, disturbance) are often secondary.

Globally, the SAR of freshwater systems was significantly different ($P<<0.0001$) from that of islands; freshwater systems had a much greater c coefficient but a lower z coefficient than islands (Tab. 1, Fig. 2A). Thus, global lentic and lotic systems are more consistent with continental habitat patches and are not equivalent to islands, likely related to greater island isolation (MacArthur and Wilson, 1967; Rosenzweig, 1995). At the next level of detail, lentic systems were not equivalent to lotic systems (Tab. 1, Fig. 2B). Likewise, pair-wise comparisons among global lentic systems, lotic systems, landbridge islands, and oceanic islands were all significantly different ($P\leq 0.05$) except for the *z* coefficients of rivers and oceanic islands (Tab. 1). That similarity is not sufficient to consider river SARs analogous to those of oceanic islands because *c* coefficients also affect SAR shape (Lomolino, 2000) and those were again very different (Tab. 1, Fig. 2B). Finally, patterns among Nearctic lentic and lotic systems, landbridge islands, and oceanic islands were generally similar to global patterns (compare Figs. 2B and 2C), but details differed importantly for statistical tests of regressions. Nearctic lentic and lotic systems had *z* coefficients that were not significantly different from landbridge islands, though *c* coefficients were very different (Tab. 1, Fig. 2C). All other pairwise comparisons were significantly different ($P \leq 0.05$).

Is a lake or river like an island? At all levels examined here, I must answer no. Instead, the SAR patterns for lentic and lotic systems are more similar to expectations for continental habitat patches than for islands (MacArthur and Wilson, 1967; Rosenzweig, 1995). Lakes and islands may share similar *z* coefficients, but this alone is not sufficient to claim equivalence because *c* coefficients differ markedly (Lomolino, 1989). Based on these analyses of fish and mammal SARs, there is no basis to consider lentic and lotic systems as islands. These results appear roughly consistent with those of Drakare *et al.* (2006), though their analyses were subject to problems 1-3 (above).

My conclusion carries several caveats and implications. First, fish and mammals may not be equivalent for the purpose of SARs and this difference may underlie the results, rather than the habitats. I addressed this possibility (above), but that potential complaint begs the question – if not these taxa, what can be used to fairly compare lakes and rivers to islands? Few other options exist because matching taxa do not exist in large numbers in both aquatic and terrestrial habitats, or because not enough data sets exist, or both. Thus, this potential complaint only adds to my conclusion – evidence to consider lakes as islands is wanting and will likely continue to remain so. It is worth reiterating that the mere presence of a SAR is not sufficient evidence that a set of habitats are islands (Connor and McCoy, 1979). Instead, analyses here differ from most prior work by using SMA regressions to statistically compare *c* and *z* coefficients of SARs among different systems. Also, it has been common practice to evaluate and report only *z* coefficients in SARs, though *c* coefficients affect SAR shape and vary more widely than *z* coefficients (Lomolino, 1989). Both coefficients need to be reported and analyzed with SMA regressions. This statement indicates that we still have much to learn about SARs among systems. In addition, biogeographic units (*e.g.*, the Nearctic) should be more commonly considered in limnological analyses. Future analyses for other biogeographic realms may differ in the details, but analyses presented here show that the comparison of lentic

Tab. 1. Summary of species-area relationships for fishes in lakes and rivers and for mammals on landbridge and oceanic islands. Standardized major axis (SMA) regressions were computed for the equation $\log_{10}$(species richness)=log(c)+z*$\log_{10}$(area).

Comparisons	Prob. of no overall difference in *z*	Modeled systems	*c* (±95% CI)	*z* (±95% CI)	r^2	N
Global (lentic and lotic systems= *vs* all islands=)	P<<0.0001	Lentic and lotic systems	10.179 (1.010)	0.20280 (0.01213)	0.66	275
		Islands	0.765 (1.134)	0.34393 (0.02399)	0.48	392
Global lentic systems *vs* lotic systems *vs* landbridge islands *vs* oceanic islands°	P<<0.0001	Lentic systems	10.571 (1.117)	0.19865 (0.02021)	0.50	187
		Lotic systems	3.879 (1.505)	0.30365 (0.04096)	0.69	88
		Landbridge islands	0.801 (1.131)	0.38273 (0.02595)	0.64	296
		Oceanic islands	0.525 (1.386)	0.28744 (0.04558)	0.37	96
Nearctic lentic systems *vs* lotic systems *vs* landbridge islands *vs* oceanic islands#	P=0.0002	Lentic systems	11.832 (1.114)	0.25046 (0.02980)	0.50	147
		Lotic systems	3.962 (1.504)	0.34800 (0.04729)	0.83	38
		Landbridge islands	1.083 (1.157)	0.29220 (0.03193)	0.60	94
		Oceanic islands	1.026 (1.205)	0.18435 (0.04471)	0.54	26

°*Global rivers and oceanic islands were not significantly different (P=0.997) for* z *coefficients but had significantly different* c *coefficients (as judged by 95% confidence intervals). All other pairwise comparisons were significant (P<0.05).* #*Nearctic lakes and rivers were not significantly different for* z *coefficients from landbridge islands (P=0.364 and 0.305, respectively). Nearctic lake* z *coefficients were also not significantly different from oceanic islands (P=0.256). All other pairwise comparisons were significant (P<0.05).*

and lotic systems to islands should be considered no more than a poetic metaphor (as in *all the world's a stage*); the comparison breaks down upon closer inspection. Instead, it is more appropriate to think of freshwater systems as being comparable to terrestrial habitat patches in their isolation. As a result, limnology is not so far afield from terrestrial ecology.

Are lentic and lotic systems replicates?

> "*A group of lakes confronts the investigator as a series of very complex physicochemical and biological systems, each member of which has its own characteristics and yet also has much in common with the other members of the group*."
>
> *G.E. Hutchinson (1957), pg. 1*

Forbes' (1887) lake-as-a-microcosm view emphasized research on a lake's characteristics that implicitly informs us about other lakes of the same type. This approach thus assumes lakes are, in part, independent replicates of a type. This view has persisted for nearly a century, as evidenced by the typological approach in limnology textbooks (Supplementary Tab. 1) and Hutchinson's encyclopedic *Treatise on Limnology* series (Hutchinson, 1957, 1967). Why did Forbes' categorical, deterministic view of lakes persist uncontested for about a century, while a colleague (Gleason, 1926) contested the same fundamental idea applied to terrestrial vegetation (Clements, 1916)? Is it because limnologists inherited the concept of lakes as being at least partly isolated, independent islets (to fuse the phrases of quoted Forbes and Hutchinson above)? Is it because organisms below the waterline are more removed from our direct observation than terrestrial vegetation? To my knowledge, limnology has followed ecology's lead in its recognition that both stochastic regional processes and deterministic local processes contribute to heterogeneity among inland waters (*e.g.*, Ricklefs, 1987; Jenkins, 1995; Jenkins and Buikema, 1998; Bohonak and Jenkins, 2003). Multiple studies now try to resolve regional (*i.e.*, dispersal) and local processes controlling various aquatic ecosystems (*e.g.*, Angermeier and Winston, 1998; Cottenie and De Meester, 2004).

Of course, others have questioned the typology of lakes that extends from the singular, internal focus inherited from Forbes. For example, Lindeman's famous paper on the trophic-dynamic concept (Lindeman 1942) was initially rejected, in part because Chancey Juday doubted the generality of the single-system view; *"According to our experiences, lakes are* rank individualists *and are very stubborn about fitting mathematical formulae and artificial schemes proposed by man*" (emphasis by Juday; Cook, 1977). Lindeman's paper eventually served as a conceptual foundation for much of ecosystem ecology and Juday's initial concern on lake individuality does not appear to have resurfaced explicitly. However, no-one expects that lakes or rivers are identical; instead, we know that they vary as a result of latitude, landscape position, drainage basin conditions, climate, morphometry, history, *etc*. This set of relationships is the basis for comparative limnology, which seeks to infer underlying causes of pat-

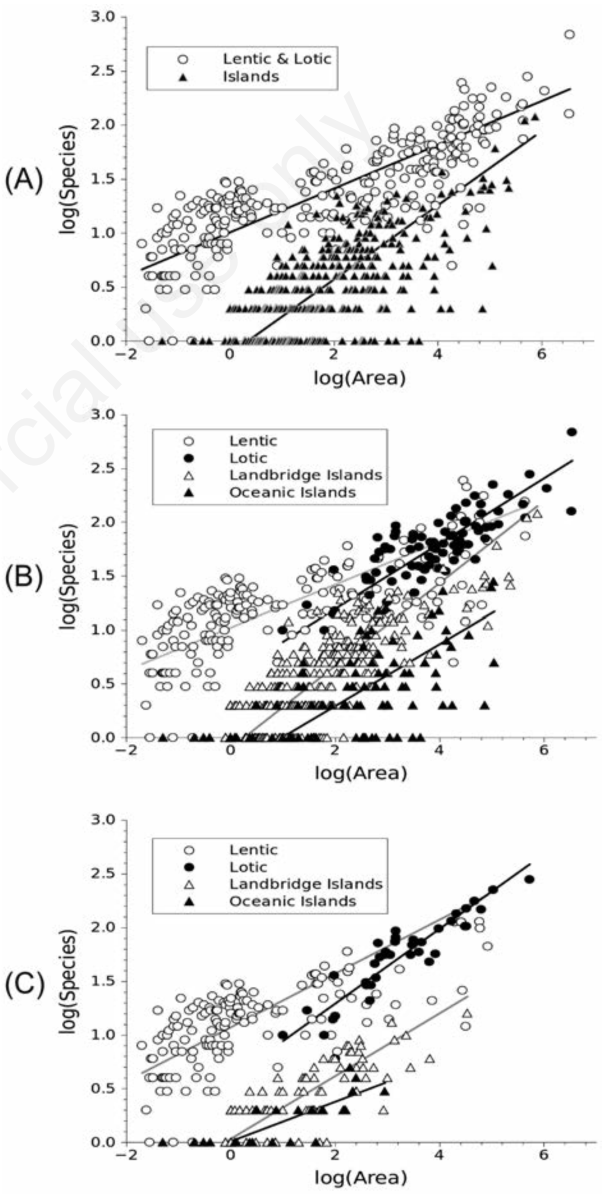

Fig. 2. Species-area relationships for A) [global lakes and rivers] relative to [global islands]; B) each of global lakes, rivers, landbridge islands and oceanic islands; and C) each of lakes, rivers, landbridge islands and oceanic islands in the Nearctic realm. See Tab. 1 for regression details.

terns among lentic or lotic systems (*e.g.*, Kratz and Frost, 2000; Wetzel, 2001). Instead of absolute replicability, I tested here for *relative* replicability by asking *Are lentic and lotic systems more replicable than terrestrial systems*?

I used beta diversity (β) as a measure of differences among various assemblages in lakes and rivers relative to those among terrestrial systems. Beta diversity measures are themselves quite diverse and debated, and the effects of different measures and scaling effects remain unknown (*e.g.*, Koleff *et al.,* 2003; Tuomisto, 2006; Baselga, 2010; Anderson *et al.,* 2010). Instead, I merely summarized an array of analyses and meta-analyses already conducted on β patterns, with the logic that repeated patterns by different measures will indicate generality. I emphasized distance-decay in similarity to compare among lentic, lotic, and terrestrial systems (Nekola and White, 1999; Soininen *et al.,* 2007). Distance decay in similarity is also described as spatial autocorrelation or beta diversity and is considered another *law* (Nekola and White, 1999). As above for SARs, salient questions then center on the general shape of the relationship (Fig. 3) rather than whether one exists. A diversity of similarity (or dissimilarity) measures have been studied by different sampling methods and at diverse spatial scales. As a result, equilibration of measures and quantitative evaluation of slopes and goodness of fit measures are not reliable (Koleff *et al*., 2003; Steinbauer *et al.,* 2012). Instead, I simply collected distance decay studies in the literature and recorded the general shape of the distance decay in similarity (Fig. 3) obtained if axes units were untransformed. I selected data sets that included multiple drainage basins to avoid confounding comparisons among and within systems. Also, I selected studies that used simple regressions of classic similarity measures and distance in order to capture more studies and maximize comparability.

Assemblage similarity may occur across distance in one of four general shapes. Similarity among assemblages may not significantly decay with distance (*i.e*., zero slope; Fig. 3A), but this is most likely due to a weak pattern (*i.e*., low r^2) than to a strong pattern (*i.e*., high r^2) across all distances. Alternatively, decay in similarity may be deferred to larger distances, so that assemblages at local to intermediate distances may be considered replicable up to a threshold, beyond which they rapidly become more different (Fig. 3B) or concave function of distance (Fig. 3D). Given that distance decay in similarity should be common, I hypothesized that lentic, lotic, and terrestrial systems should most commonly exhibit curves C or D, and that they should do so in similar proportions if they are all similar in replicability. I obtained 66 distance-decay relationships from the peer-reviewed literature (20 lentic systems, 20 lotic systems, 26 terrestrial systems). By far, concave decay curves (Fig. 3D) were most common among all systems (34 of 66 cases, or 52%), followed by linear decays (23 cases; 35%) and no significant decay (9

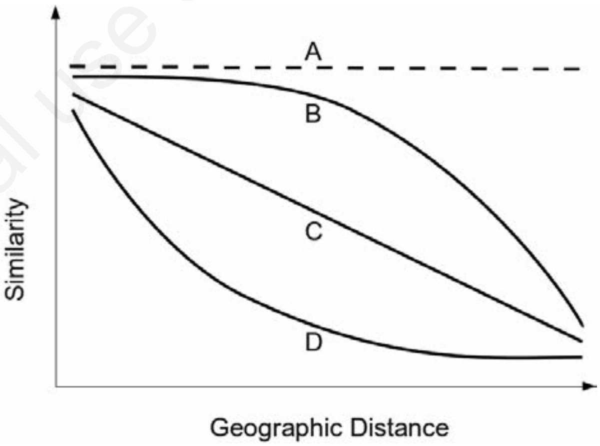

Fig. 3. Potential curve shapes of distance decay in similarity. A) An unlikely and generally high similarity across all distances would indicate inland waters are uniform replicates. B) A convex curve would indicate inland waters are replicates of spatial neighborhoods. More likely curves are: C) a linear or D) concave decay in similarity with distance, given general expectations (Nekola and White, 1999).

Tab. 2. Number (and percent) of studies among lentic, lotic, and terrestrial systems that reported a distance decay curve shape that had a nonsignificant decay (A), a convex curve (B), a linear decay (C), or a concave curve (D; also see Fig. 3). In order to standardize among studies, shapes were interpreted as untransformed axes in the relationship between geographic distance and similarity.

Curves	Lakes	Rivers	Terrestrial	Total
A°	4 (20%)	4 (20%)	1 (4%)	9 (13%)
B	0 (0%)	0 (0%)	0 (0%)	0 (0%)
C	8 (40%)	4 (20%)	11 (42%)	23 (35%)
D	8 (40%)	12 (60%)	14 (54%)	34 (52%)
Total	20	20	26	66

°*All data sets classified as shape A had low* r^2 *values (see Supplementary Tab. 2) and thus do not indicate high replicability across distance as suggested in Fig. 3.*

cases; 14%; Tab. 2). No cases were observed with a convex curve (Fig. 3B), consistent with a general absence of local to regional replicability or a threshold effect. I retained additional information for each data set (where possible) for further analyses (Supplementary Tab. 2).

I tested the hypothesis that lentic, lotic, and terrestrial systems have similar distance decay relationships using Fisher's exact tests. The systems differed overall in their proportions of curve shapes (P<0.001), due to differences between all pairs of lakes, rivers, and terrestrial systems (all P<0.05), including the difference between aquatic and terrestrial systems (P=0.01; Tab. 2). To better understand why these differences existed, I conducted a backward, stepwise model selection approach using stepAIC (in the MASS package; R Core Team, 2013), starting with a full factorial linear model of all variables obtained in Supplementary Tab. 2. Only spatial extent significantly (P=0.003) predicted model shape, and the stepwise AIC approach retained the correlated variables of spatial extent, number of taxa, and number of sites. In addition, spatial extent significantly (P=0.0002) varied among lentic, lotic, and terrestrial systems, where terrestrial systems were studied at far greater spatial extent than aquatic systems (Fig. 4).

In summary, lentic and lotic systems are not more replicable than terrestrial systems, and distance decay in similarity is a rule for lentic, lotic and terrestrial systems. However, lentic and lotic systems differ from terrestrial systems in the mix of distance decay relationships, where aquatic systems have a greater proportion of exceptions to the rule, related to smaller spatial scales of studies than among terrestrial systems. The few exceptions to the rule in aquatic systems do not indicate replicability because distance decay in similarity was highly variable (low r^2), indicating substantial variance among systems that is related to something other than simple distance measures.

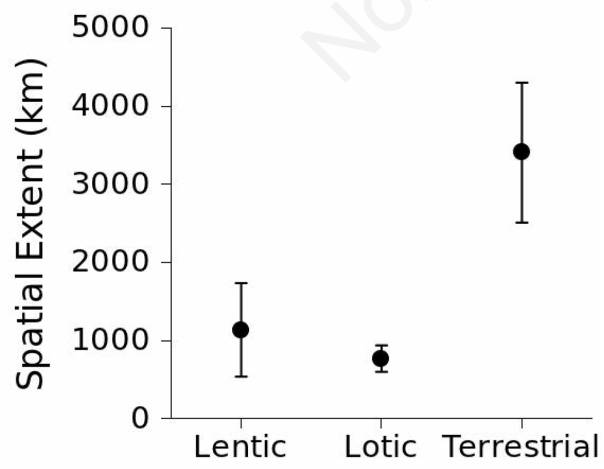

Fig. 4. Mean spatial extent of lentic (N=20), lotic (N=18), and terrestrial (N=15) studies on distance decay of similarity. Error bars are 95% confidence intervals. N differs here from Tab. 2 because some studies did not report spatial extent.

A plural view

> *"Studies of individual lakes have provided important insights into numerous basic limnological processes. For general understanding, however, limnologists must incorporate a comparative perspective that considers the diversity of conditions that occur across a range of lakes and the factors that generate them."*
>
> *T.K Kratz and T.M. Frost (2000)*

The holistic, internal focus on singular aquatic ecosystems advocated by Forbes over a century ago was important to limnology and led to rich knowledge about the structure and function of aquatic ecosystems. Forbes' view remains important today but may also influence limnology in unrecognized ways. I outlined above three such influences: we teach a Forbesian view as an organizing paradigm but rarely practice its full breadth; we often think of aquatic systems as islands when they appear to be more like continental habitat patches; and aquatic systems are no more replicable than are terrestrial systems. Recent paradigms offered for limnology are consistent with Forbes' lake-as-a-microcosm (ASLO CLC, 1995; Brezonick, 1996; Reynolds, 1998) or reflect expansion of that paradigm to include climate change (Walz and Adrian, 2008). Given that paradigms tend to evolve rather than shift wholesale (Graham and Dayton, 2002), I offer a modern conceptual model for limnology (Fig. 5) that attempts to maintain its continuity with the valuable research accrued to date while better connecting to current limnology as represented by papers in this volume. This model is based on three paradigms already in practice: the traditional lake-as-a-microcosm, multiple systems, and open systems. The intersections of these elements form the disciplines of comparative limnology, landscape limnology, and biogeographic limnology (Fig. 5). In combination, the three disciplines comprise a complete modern model of limnology.

Comparative limnology is a long-standing, plural form of limnology (Wetzel, 2001), without which analyses above could not have been conducted. The organization of lake districts fostered this approach (Kratz and Frost, 2000); other early examples, albeit on a small scale, include Brooks and Dodson (1965) and Dillon and Rigler (1974). Modern comparative limnology studies lakes-as-plural-microcosms in the same way that other ecologists study patches across a landscape or latitudinal gradients in diversity. I simply argue here that we more explicitly and more often express that plural view, consistent with a more useful, modern definition of limnology as the ecology of inland waters. This shift to a plural view does not mean limnologists have abandoned a detailed study of a system, but instead means that single-system research connects to other systems in concept and evidence. This is all the more possible with technological advances, including informatic approaches. Regional examples of limno-informatic efforts include a Long Term Ecological Research site (http://lter.limnology.wisc.edu/datacatalog/search) and the CSI Limnology project (http://csilimno.cse.msu.edu) – more such efforts are needed and would be all the more valuable if connected in a global database (*e.g.*, the Global Biodiversity Information Facility; http://data.gbif.org).

In addition, limnology now often studies inland waters as open systems (Fig. 5), meaning that the relative importance of the exchange of organisms, materials and energy among systems is of interest. For lack of an already established name, I call this discipline landscape limnology because it is related to landscape genetics (Manel *et al*., 2003) and occurs within the context of landscape connectivity, including interactions with terrestrial systems. An important part of this work is research about metapopulation, metacommunity, and meta-ecosystem concepts (*e.g*., Gotelli and Taylor, 1999; Forbes and Chase, 2002; Howeth and Leibold, 2008; Cottenie *et al.,* 2003; Van de Meutter *et al*., 2007; Larned *et al*., 2010, some papers in this volume).

Finally, limnology also takes a biogeographic approach (Fig. 5), in which it evaluates the interactions among multiple freshwater systems in space and time, including the effects of: the histories of plate tectonics, glaciation, and human resource use; isolation; and latitudinal and altitudinal gradients (*e.g*., Walker and Mathewes, 1989; France, 1992; Schindler *et al*., 1996; Koskinen *et al*., 2002; Schumm *et al*., 2000; Scheffer *et al*., 2006; Smol, 2008). A greater and more explicit recog-

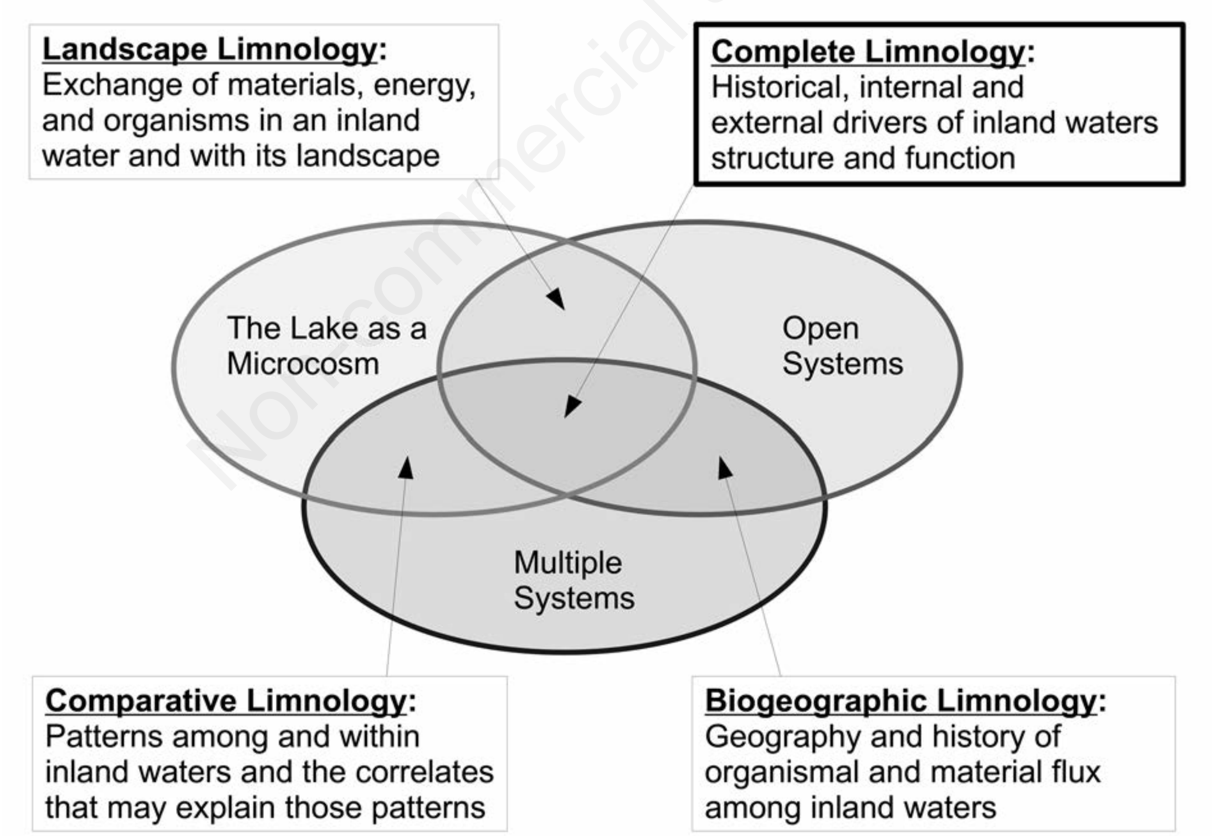

Fig. 5. A graphical representation of modern limnology. Ellipses represent paradigms, including Forbes' *Lake as a Microcosm* (1887), which led to the ecosystem concept and represents limnology's traditional focus *within* a system. Open Systems studies evaluate exchanges of materials and energy (*e.g.*, discharge, nutrient flux, allochthonous C), and organisms *among* systems. Multiple Systems evaluates spatial distributions and fundamental properties of inland waters (*e.g.*, glacial moraine lakes, tidal rivers). Interactions of these three paradigms represent modern limnological disciplines (in boxes) which combine to make a complete limnology.

nition of biogeography in limnology as it is taught and practiced will help limnology increase its relevance in the coming integration of ecology and biogeography (Ricklefs and Jenkins, 2011). If limnology more explicitly and widely recognizes these existing paradigms and disciplines as a foundation in limnology courses and research, it will more fully embrace a plural approach and become more fully related to studies of terrestrial and marine systems that also apply those conceptual frameworks (Fig. 6). Limnology has been internally-focused (Fig. 6A) and thus distinct from ecology and evolutionary biology for decades (Hairston, 1990; Ringelberg, 1993; ASLO CLC, 1995). To overcome this former segregation and gain broader relevance, limnology must continue to be more externally comparable (Fig. 6B) so results in lakes and rivers can be compared to those on land or in the oceans. For example, analyses presented here and comparing SARs and beta diversity *among* different kinds of inland waters, islands, and continental habitats appear to be far less common in the literature than analyses *within* each set. Comparisons within *and* among systems are needed (Fig. 6), but will not happen until limnology is conceptually linked to other disciplines in shared paradigms.

To conclude, I argue that limnology would do well to embrace a modern definition based on plurals: it is the ecology of inland waters, including the study of physical, chemical, and biological attributes and interactions in aquatic environments. Modern limnology also seeks to understand the importance of evolution, geography and history among multiple, open systems for current and future ecological conditions. Limnology should continue to be more plural and less singular in its work, including comparisons among different types of inland waters and with terrestrial and marine ecosystems. To do so will require that we more explicitly recognize the long-lasting influence of Forbes' *Lake as a Microcosm* (1887) on our thinking, be prepared to expand our view beyond that century-old viewpoint, and thus make limnology even more relevant to science and society.

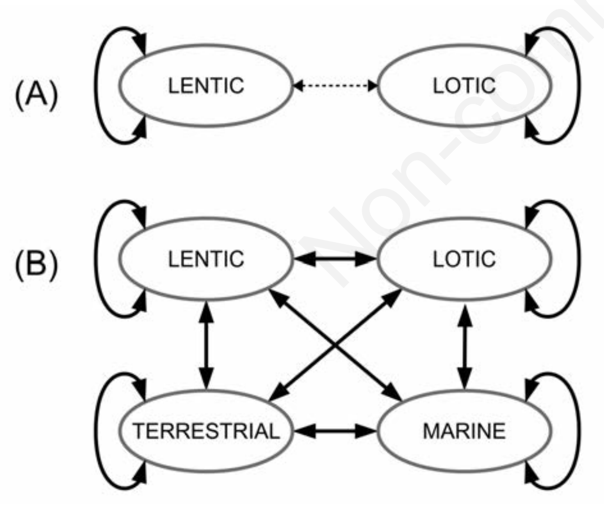

Fig. 6. Historical and potential approaches in limnology and beyond. A) Traditional limnology has historically focused *within* lentic systems or lotic systems (curved arrows) and has and rarely compared *among* lentic and lotic systems (thin dashed arrow); this made sense when the goal was to understand each of those systems. B) Future research may expand this view to maintain that historical approach while also comparing *among* lentic and lotic systems and terrestrial and marine systems (straight arrows); surprisingly, little progress has been made in this larger view.

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