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Review

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Natural microcosms in ecology: fulfilling the promise of model systems?

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Natural microcosms (NMs) have been proposed as model systems for ecology based on their ubiquity, ease of study and natural context. We assess whether this potential has been met by examining 824 studies of six NMs (bromeliads, moss patches, nectar microbiomes, pitcher plants, rockpools, treeholes). Of these, we judged 314 studies to use NMs as model systems, testing a broad range of ecological theories. Although these theories spanned large biological, spatial and temporal scales, most studies concentrated on community-level niche processes occurring at local scales and within a generation—especially trophic control theories. However, metacommunity theory, which integrates over spatial and temporal scales, was also commonly studied. NMs were particularly effective in studying environmental stressors, often in combination with multitrophic effects or responses. While NMs have many advantages as model systems, there are limits to which theories can be tested due to specific life-histories of their inhabitants, uniqueness of certain ecosystem processes and frequency of disturbance. Particularly under-represented were tests of behavioural and ecosystem theory, long-term processes and impacts of invasive species. Greater use of molecular methods, community science and collaborative research networks could enable NMs to reach their full potential as model systems.

This article is part of the theme issue 'Life in natural microcosms'.

1. Introduction

A model system is one that is tractable, realistic and generalizable, enabling efficient testing of theoretical predictions. Biology is replete with examples. In evolutionary biology, *Drosophila* flies and *Arabidopsis* plants provide rapid generation times and enable fast selection of traits. In molecular biology, *Caenorhabditis elegans* nematodes and *Escherichia coli* bacteria provide small

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and tractable genomes. In developmental biology, axolotl embryos and eggs of *Xenopus* toads are easily reared year-round. Model systems provide common, standardized biological templates that facilitate experimental manipulations to study specific processes. Multiple research groups explicitly use the same model system in order to enable replication of experiments and scaffolding of knowledge between groups. It is often highly instructive when a theory fails to be supported in a model system, as understanding why can suggest which processes are missing from the theory. Yet, ecology has no such tradition of model systems. Instead, it focuses on iconic systems, where research on one particular system becomes identified with a particular ecological process, such as intertidal communities and keystone predation [1]. Iconic systems, unlike model systems, were not explicitly developed to facilitate replication and scaffolding of experiments among distant research labs. It could be argued that this focus on iconic rather than model systems reflects the context-dependence of ecology, where the unique history and environment of each system determines its dynamics [2]. However, the goal of all science is to discover general principles that apply across systems, even if contextual factors must be integrated into the theory [3]. Arguably, the use of model systems in ecology could accelerate progress towards this goal.

Natural microcosms (NMs) have been proposed as a model system for ecology [4]. By a natural microcosm we refer here to a small, naturally contained ecosystem whose inhabitants interact with each other over at least one life stage. Unlike a laboratory microcosm, the species in NMs have a long evolutionary history with each other and their habitat. This means that processes detected in NMs through experiments can be readily linked to patterns observed in nature. The sampling of NMs can be both fast and exhaustive, and their quick response to manipulations contrasts with the slower response times of macrocosms (e.g. fish in cattle tanks). Ecosystem-level manipulation in large systems (e.g. forests, rivers, lakes and oceans) are difficult to perform and nearly impossible to replicate, making it challenging to test causal mechanisms *in situ* at relevant spatial scales. Conversely, small and highly replicated NMs are easily manipulated and sampled, offering impressive statistical power to test hypotheses. Finally, the high regional representation of NMs enables the replication of experiments or observations across geographic space (e.g. [5,6]).

A number of studies have built the case for NMs being an ecological model system, perhaps starting with a highly cited review in 2004 [4]. Since then, there have been calls for using specific NMs as model systems, such as bromeliads [7], moss patches [8] and nectar microbiomes [9], pitcher plants [10], rockpools [11] and treeholes [12]. The primary goals of this review are to determine whether this potential of NMs as model systems has been met and when NMs can—and cannot—be used as model systems. To do so, we ask five questions: (i) how often are NMs used as model systems?; (ii) are NMs generalizable?; (iii) which theories have most often been tested with natural microcosms?; (iv) which theories are under-studied by NMs (and why)?; and (v) how have NMs contributed to the two theories most often studied with NMs: metacommunity and trophic control theory? We end by considering what unrealized opportunities may exist for using NMs to test theory.

2. How often are natural microcosms used as model systems?

We identified 824 English-language studies on six common NMs published from 1940 to 2024 (see electronic supplementary material). These six focal NMs included the aquatic micro-ecosystems within bromeliads, pitcher plants, treeholes and rockpools, terrestrial micro-ecosystems in moss patches, and the microbiomes in floral nectar. Publications on these six NMs have increased over time, with increases since 2005 particularly marked in bromeliads, nectar microbiomes and rockpools (figure 1b). The majority of NM studies do not consider NMs to be model systems, instead reporting on specific attributes of the system such as species occurrence, natural history or importance to humans (e.g. disease vectors, honey production). For the remainder of this review, we focus on the 314 NM studies that explicitly use NMs as a model system to test theory. The proportion of NM studies that use NMs as a model system has generally increased over time, in the last decade varying between a quarter to a half of studies (figure 1c).

3. Are natural microcosms generalizable?

To paraphrase Levins [13], model systems should be tractable, realistic and generalizable. We have already argued that NMs offer many advantages in terms of tractability and realism [4,10]. For NMs to reach their full potential as model systems, they must also be generalizable, bridging the gap between theoretical models and the larger ecosystems for which predictions are needed. Theoretical models focus on a subset of possible processes in order to increase tractability and interpretation. Model systems enable us to externally validate a theory, establishing if it has included enough processes and accurately captures their causal relationships to make predictions that hold true in nature. To then apply the validated theory to larger systems than the model system, we must be confident that both the model system and the larger systems are structured by similar processes. Do NMs meet these criteria of generality?

We start by comparing the structure of five phytotelmata (i.e. plant-formed container habitats) NMs to those in larger systems. In general, the five NMs analysed by Ellison & Gotelli [10] have lower species richness than most systems ('nodes' in figure 2). As NMs are small, low species richness is expected simply based on species–area relationships. Species richness may be further depressed in NMs if their unique abiotic conditions result in a narrow and endemic suite of inhabitants [14]. For example, nectar yeasts are dominated by a few species in one genus, *Metschnikowia* [9]. While low species richness can facilitate understanding mechanisms, it reduces representativeness. As NMs are small, most organisms living in NMs are also small, such as macro- and micro-invertebrates and microorganisms. These organisms can differ from larger organisms, such as vertebrates, in traits that may affect their ecology, including physiology, size and stoichiometry [15,16]. Despite these

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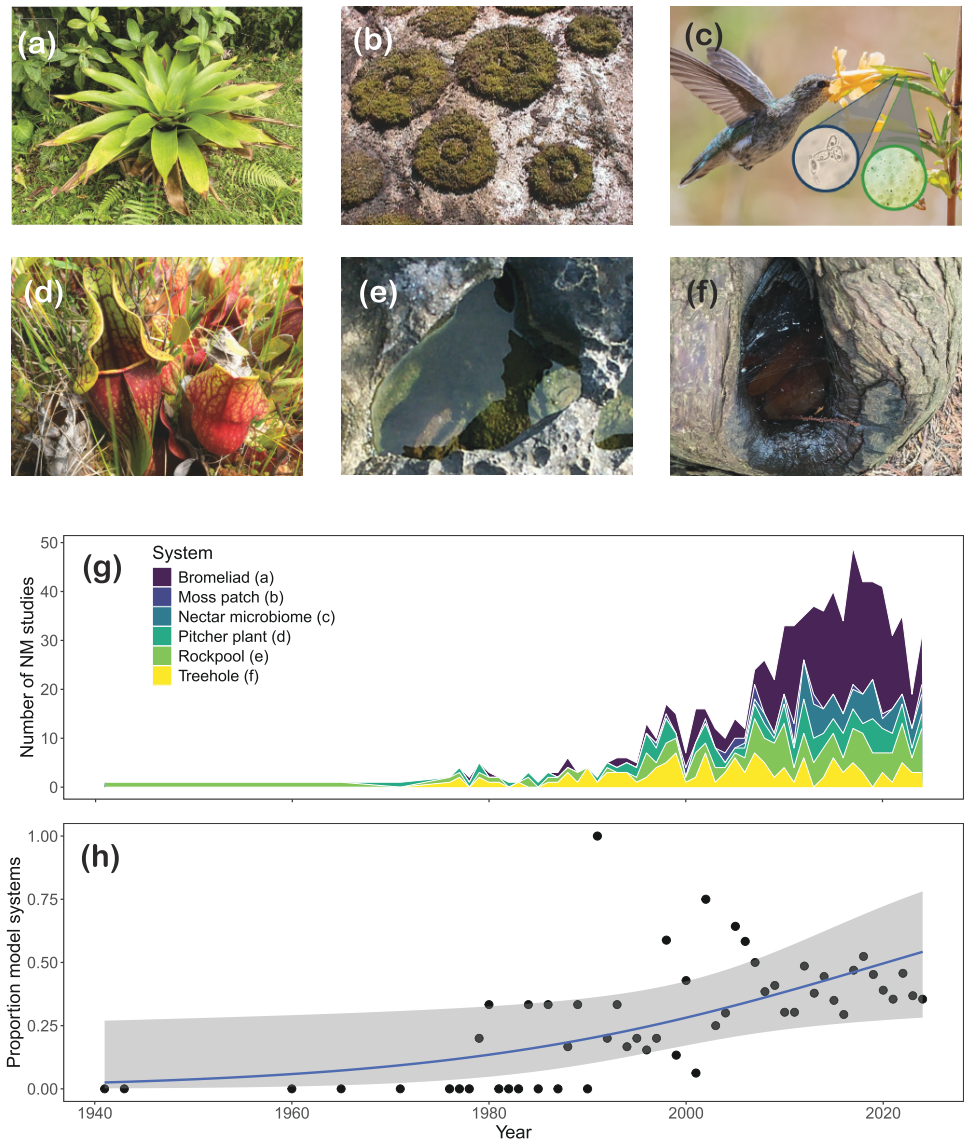

Figure 1. (a–f) Six focal natural microcosm (NM) systems that we considered in our search of studies from 1940 to 2024. (g) The number of studies on these six focal NMs has increased through time. (h) The proportion of NM studies that use NMs as model systems has generally increased through time. Photo credits: (a,b,f) D. Srivastava, (c) large photo: Rick Morris, insets: Rosa McGuire, (d) N. Gotelli, (e) J. Kolasa.

differences, metrics related to food web complexity seem broadly comparable between phytotelmata NMs and larger systems (figure 2). For example, connectance—which measures the proportion of potential links that are realized—is between 0.1 and 0.2 in both NMs and other systems (figure 2). Trophic depth and ascendancy refer respectively to how energy flows through trophic levels and within subsets of the network, and while values vary between NM types, they are typical of all systems (figure 2). These results are echoed by a comparison of intertidal rockpools with larger systems that shows connectance and mean trophic level to be broadly similar, despite lower species richness in rockpools [17].

A second way to examine the generalizability of NMs is to ask whether similar processes dominate NMs as in systems that may be larger and more permanent. There are reasons why NMs may fail this criteria of generalizability. The small size of NMs predisposes them to frequent disturbance, selecting for either disturbance-tolerant or rapidly developing taxa. Consequently, species in NMs may be more resistant to environmental changes than those in larger systems, potentially dampening trait–environment relationships. Additionally, under such a disturbance regime, stochastic processes may be particularly influential in NMs, as suggested by several studies [18,19], complicating their use in testing deterministic theory. To escape frequent disturbance, many organisms in freshwater NMs exhibit complex life cycles that span ecosystem boundaries—e.g. aquatic larvae that emerge as terrestrial adults [20]. Such cross-boundary exports of biomass are likely to constitute a large fraction of the energy budget of NMs, influencing their dynamics. For example, bromeliads have 2–5 times more secondary production (i.e. aquatic-to-terrestrial biomass flux through emerging insect adults) per unit surface area than lakes and rivers [21].

The counter argument to such direct comparisons is that model systems are intended to test the general structure of a theory rather than serve as a miniaturized version of a larger system. For example, the same mechanism—cross-community asynchrony of taxa—stabilizes communities across clusters of rockpools or lakes, even though community variability is an order of magnitude higher across rockpools [18]. Once a theory is validated, it must be appropriately parameterized before being applied to other systems. For example, Bradshaw & Johnson [22] assert that, 'The ecology of *W[yeomyia] smithii* development in leaves of *S[arracenia] purpurea* is analogous to that of amphibian development in bodies of water where the persistence of the

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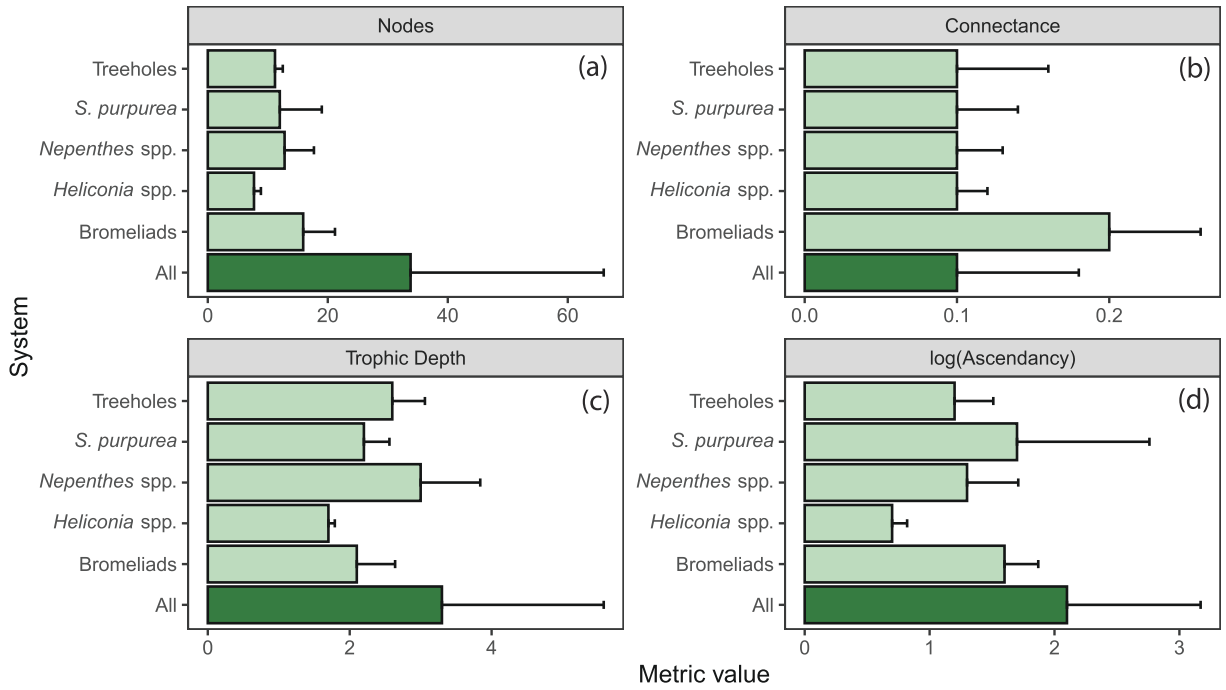

Figure 2. Food web metrics (a–d) from five types of phytotelm (i.e. plant-contained) NMs compared with mainly larger systems ('all'). The phytotelm NMs include treeholes, bromeliads, *Heliconia* spp. floral bracts, and pitchers of either *Nepenthes* spp. or *Sarracenia purpurea* plants. Data extracted from Lindo & Gonzalez [8]; see electronic supplementary material. Means and SEs are plotted of four food web metrics described in the text.

habitat or resource has a duration approximating that of individual larval development'. The key to such comparison is scaling the process in biologically relevant units—here, the duration of larval development relative to disturbance frequency—and framing the expected outcome as a testable hypothesis.

4. Which theories have most often been tested with natural microcosms?

Our analysis of the literature reveals that NMs have been used to test a wide variety of theories across all ecological, temporal and spatial scales (figure 3). NMs have explored contemporary issues in ecology, such as the impact of climate change on natural systems, and classical theories, such as assembly rules for ecological communities. We identified a total of 28 ecological theories tested by NMs. We suggest that NMs are most effective as model systems when the temporal and spatial scale of the ecological theory matches the natural history of the NM.

NMs are by definition naturally contained, and so often hold their inhabitants captive—at least for part of their life cycle. This facilitates manipulations of community structure, including changing the presence or absence of taxa, and even assembling the entire macroscopic community *de novo*. Such manipulations enable tests of many niche-based theories in community ecology (all theories in figure 3 except 12, 14, 16, 19, 21), such as those predicting competition, trophic control or biodiversity–ecosystem function relationships (respectively theories 3, 28, 1 in figure 3). Indeed, the most tested theory in our analysis was trophic control theory (theory 28 in figure 3), encompassing bottom-up and top-down control, trophic cascades and productivity–diversity relationships. Many of these community niche theories can be tested at limited spatial and temporal scales (lower left quadrant of figure 3), that is, within an ecosystem and at either a point in time (i.e. in a survey) or over a short window of time (i.e. in a short manipulative experiment).

For the organisms in NMs, the small habitat comes with risks of disturbance or change, whether the drying out of a bromeliad, the phenological death of a *Nepenthes* pitcher, or extreme temperatures in an exposed moss patch. To persist over multiple generations, inhabitants of NMs need an escape strategy. The smallest organisms may be carried by the wind or phoretically [11,23], whereas larger organisms may have complex life cycles, such as many aquatic insects that disperse terrestrially [24,25]. Given the importance of dispersal in NMs, these systems are well-suited to test theories about how dispersal affects individuals (habitat selection theory: theory 16 in figure 3), populations (metapopulation theory: theory 21 in figure 3) and communities (metacommunity theory: theory 20 in figure 3) [12]. In general, any community theories that combine or contrast niche and neutral processes (theory 24 in figure 3) require information across multiple temporal and spatial scales. At the ecosystem level, dispersal is one of the key cross-ecosystem fluxes, and tests of cross-ecosystem theory (theory 4 in figure 3) are enabled by the straightforward quantification of fluxes of organisms and resources into and out of NMs [20,21].

Time series are often essential to understanding eco-evolutionary dynamics (theory 5 in figure 3). This is possible with microscopic taxa that have many generations within individual NMs, such as yeasts in floral nectar (table 1). For larger organisms that spend less than a generation within NMs, there is still potential to examine the phylogenetic history of contemporary communities to understand the evolution of behaviour, niches, genes and species interactions (theories 12, 23, 14, 13 in figure 3).

As the environment of NMs can be easily measured and manipulated, they are particularly well-suited to testing the effects of stressors. Roughly half of NM-model system studies tested theory related to specific stressors (figure 4). The broad

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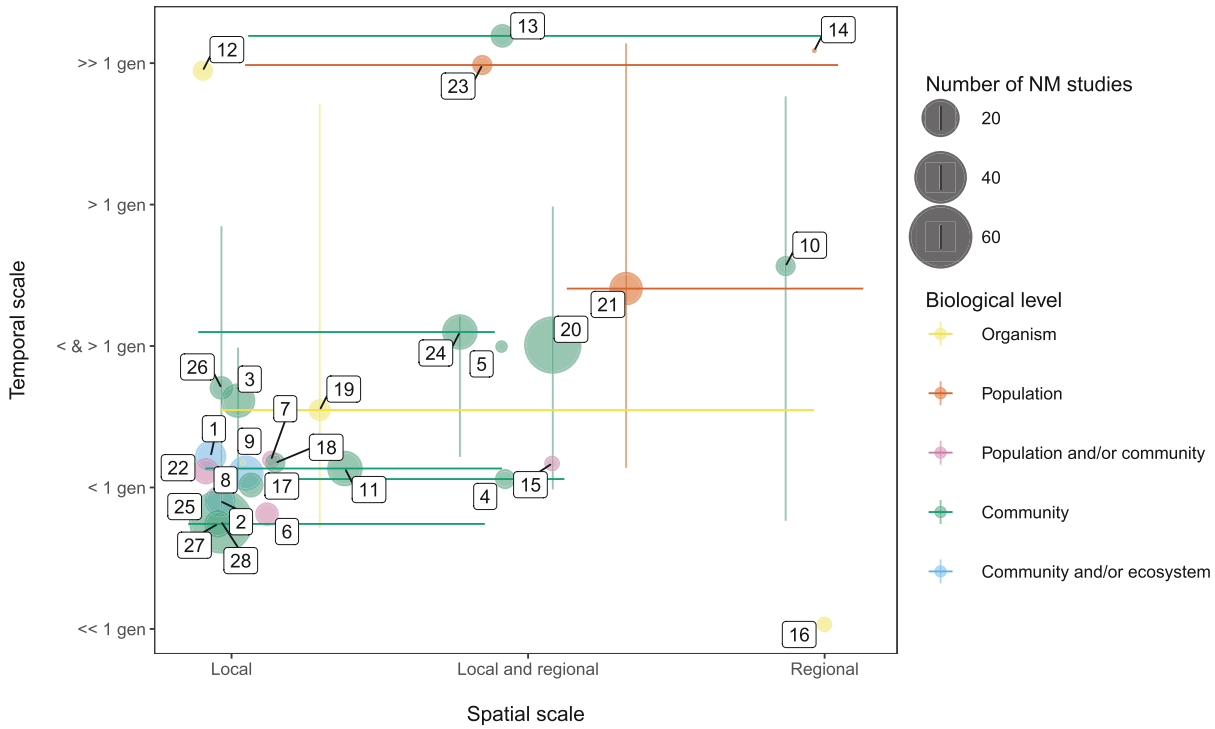

Figure 3. Theories examined by 314 studies that use NMs as model systems. Each theory is represented by a circle scaled by the number of studies and placed at the theory's dominant spatial and temporal scale. When the theory can be examined at multiple scales, whiskers indicate the extent of these scales. Temporal scale is in generations ('gen') of the focal taxa. Spatial scale is 'local' (processes within a patch or community), 'regional' (processes between multiple patches or communities) or requiring both 'local and regional' processes. The labels on each of the 28 theories correspond to the theory IDs in table 1.

geographic extent of many NMs enables surveys over climate gradients, such as those associated with latitude and elevation (theory 10 in figure 3), or over land use gradients, such as those associated with urbanization (figure 4). The small size of NMs facilitates simulations of climate impacts, showing that drying or warming of aquatic NMs can alter species interactions (theory 2 in figure 3). NMs have long been used to examine questions related to habitat geometry, including habitat size, complexity and isolation. Such approaches rely on the ease of measuring habitat geometry in NMs, such as the connectivity of rockpools [11,23], or changing it, such as by carving isolated patches out of continuous moss [26]. At the level of individual NMs, resource inputs can also be controlled by adding nutrients or detritus.

Finally, the trophic complexity of many NM communities, especially in the tropics, facilitates examining multitrophic mechanisms and responses. In fact, half (49%) of the studies we examined were explicitly multitrophic, describing mechanisms related to predation or distinguishing responses by trophic level (figure 4).

5. Which theories are under-studied by natural microcosms (and why)?

We found that NMs are rarely used to test theory related to behaviour, ecosystem models, long-term change or introduced species. Theories related to individual behaviour, such as evolution of behaviour (theory 12) and optimal habitat selection (theory 16), may be under-studied in NMs due to practical constraints on observing behaviour of benthic or microscopic organisms, especially *in situ*. The few studies investigating behaviour have been conducted *ex situ* using species that co-occur in NMs but in an artificial or lab setting [27,28]. However, emergent technologies, such as miniaturized cameras combined with video analysis using artificial intelligence, offer promising tools for analysing *in situ* behaviour.

Testing theories at the ecosystem level (theories 1, 4, 6, 9 in figure 3) can be challenging in phytotelmata where plants affect the contained water by taking up nutrients, altering water chemistry and adding or removing oxygen on a diurnal cycle. Nutrient uptake adds an additional export from the aquatic ecosystem to consider—and one that lacks a direct analogy in larger ecosystems. These interactions between the plant host and the micro-ecosystem may be partly responsible for complex and hysteretic responses of pitcher plants to nutrient addition [29]. The emergence of adult life stages (insects, frogs) from some NMs also represents an export of biomass and nutrients often not considered in standard energy or elemental balance models—but well-suited to informing the new field of meta-ecosystem ecology. Finally, many of the NMs we reviewed are 'brown' food webs, dominated by allochthonous rather than autochthonous resources. While this makes such NMs poorly suited to testing ecosystem theories related to primary production, they can be useful models of detritus-based systems.

We found few tests of long-term change. Long-term studies needed to test evolution (theories 12, 13, 14, 23 in figure 3) have been challenging in NMs formed by short-lived plants or their parts. In such cases, macroscopic taxa often do not complete their life cycle within the plant and so evolutionary change occurs at a larger spatial scale than the NM. By contrast, evolution of microscopic organisms has been successfully evaluated through time series [30,31]. Repeated sampling can also be precluded by destructive sampling of NMs, sometimes required to extract all organisms from complex plant structures. These challenges

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Table 1. Number of studies using each of six natural microcosms as a model system to test a specific theory. The ID code for the 28 theories in this table correspond to those used as labels in figure 3.

ID	theory	bromeliad	moss patch	nectar microbiome	pitcher plant	rockpool	treehole
1	biodiversity–ecosystem function	3	0	1	5	2	2
2	climate mediation by species interactions	10	0	0	3	0	0
3	competition theory	0	0	9	1	0	6
4	cross-ecosystem linkages	4	0	0	0	0	1
5	eco-evolutionary dynamics	1	0	0	0	0	1
6	ecological energetics theory	1	0	0	0	3	3
7	ecological indicators	1	1	0	1	1	0
8	ecological resilience	4	0	0	5	7	1
9	ecological stoichiometry theory	1	0	0	0	0	0
10	elevation or latitudinal gradients in diversity	1	0	0	2	2	0
11	environmental determinism of community structure	9	0	1	4	1	2
12	evolution of behaviour	0	0	0	0	2	3
13	evolution of species interactions	1	1	2	1	1	1
14	evolutionary genetics	0	0	1	0	0	0
15	global variation in climate impacts	1	0	0	0	2	0
16	habitat selection	0	0	0	0	1	2
17	indirect interactions	2	0	1	0	0	5
18	land use effects on communities	1	0	0	0	1	3
19	life history theory	0	0	0	4	2	0
20	metacommunity theory	10	12	5	5	13	3
21	metapopulation theory	2	0	1	2	10	0
22	multiple stressor impacts	5	0	0	0	4	0
23	niche evolution	1	0	0	2	2	0
24	niche versus neutral theory	8	0	2	2	1	4
25	socioecological systems theory	0	0	0	0	0	1
26	temporal niche theory	2	0	0	2	3	0
27	trait-based ecology	8	0	0	0	2	0
28	trophic control theory	32	0	0	17	4	8

apply less to treeholes and rockpools, which have been repeatedly monitored over longer periods to understand phenology within a year (e.g. [32]), parasite richness over 16 years [33], and population genetics [34] and community composition [35] over 25 years. However, there is untapped potential to examine temporal change by sampling similar but not identical NMs over time, as exemplified by examining long-term effect of hurricanes on bromeliad communities [36].

The impact of introduced species is relatively unexplored in NMs (figure 4). Besides the ethical considerations of using potentially invasive species in field experiments, the highly specialized species pools of NMs may make biological invasions relatively rare, limiting opportunities to study them. However, a few studies have investigated invasive species in NMs, such as invasive seaweeds in rockpools [37], an invasive weevil of bromeliads [38], and invasive mosquitoes in treeholes [39]. We suggest that NMs hold promise for studying introduced species in urbanized areas [40], where invasions may be more common.

6. How have natural microcosms contributed to metacommunity and trophic control theory?

Of all the theories we examined, the most studied with NMs were metacommunity theory (15% of all studies, theory 20 in figure 3) and trophic control (19% of all studies, theory 28 in figure 3).

Metacommunity theory examines how the interaction between local and regional processes can explain ecological patterns across spatial and temporal scales [41]. Testing this multi-scale theory requires quantifying or manipulating dispersal, integrating information at local and regional scales and manipulating the structure of habitat patches [41]. These three requirements are relatively easily met in NMs. Dispersal of organisms into NMs occurs through defined pathways, which can be assessed through means such as traps [23] or population genetics [24]. Dispersal can be directly altered by adding colonists [42], excluding phoretic vectors [43] or mixing communities [44] and indirectly altered by connecting NMs with corridors [26]

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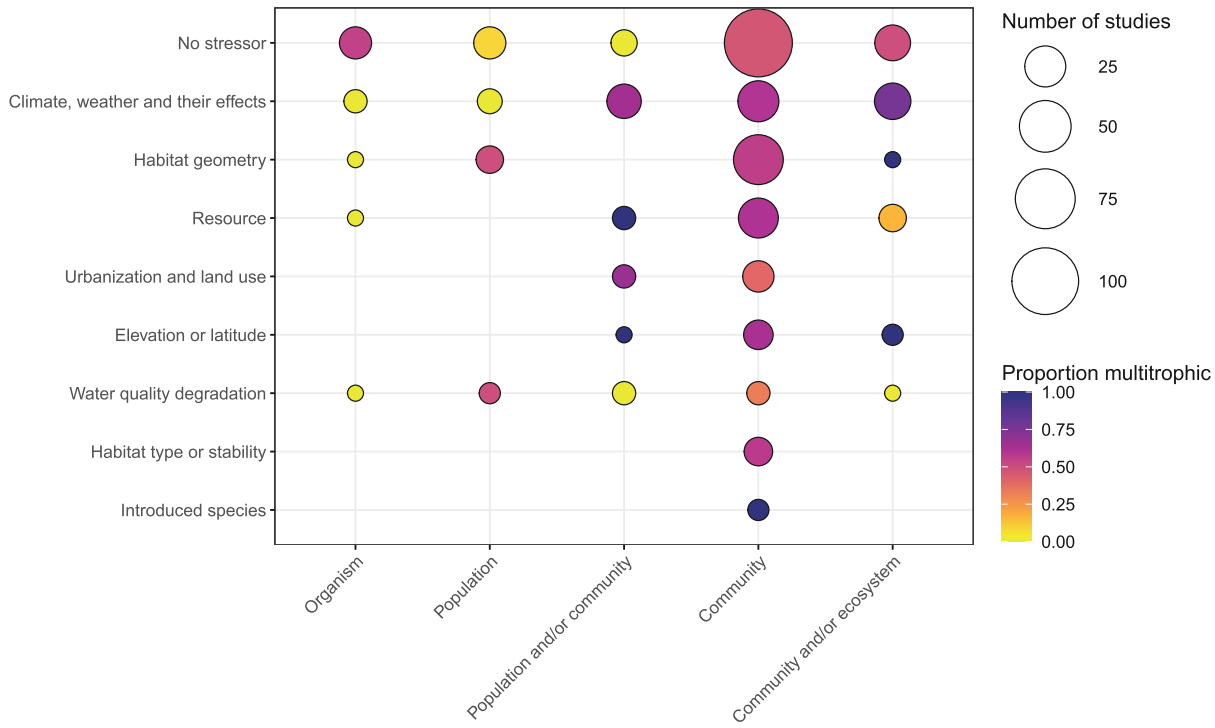

Figure 4. Distribution of 314 studies using NMs as model systems in terms of stressor type (vertical axis), biological level (horizontal axis) and whether they were multitrophic (colour). We defined studies as multitrophic if they either described mechanisms related to predation or distinguished responses by trophic level.

or reducing the pool of source NMs [45]. Assessment of ecological processes at multiple spatial scales is facilitated by the nested spatial structure of many NMs, such as clustered rockpools on isolated inselbergs [11]. Finally, the temporal patterning of disturbance within a metacommunity can also be altered, such as by experimental drying of aquatic NMs [46]. Such properties of NMs have enabled the testing of metacommunity processes such as priority effects [9,42,47], spatial insurance [46,48], dispersal–diversity relationships [44], invasion resistance [49], patch dynamic models [50] and competition–colonization trade-offs [51]. For example, because researchers can manipulate the order in which different yeast species colonize new flowers, nectar yeasts have proven to be particularly useful in understanding priority effects, elucidating their genetic basis [47] and their long-term impacts on the metacommunity [42]. Similarly, because dispersal between pitcher plants can be simulated by moving aliquots of pitcher water between plants, and predators can be added experimentally, pitcher plants have provided useful real world tests of metacommunity models that consider the interaction between dispersal and trophic processes [44,50]. It is perhaps not surprising, therefore, that two new frameworks for metacommunity theory—incorporating either trophic interactions or dormancy [52,53]—both include NMs as empirical case studies.

The role of trophic processes in controlling community structure and relative biomass has been a prominent research focus in ecology [1], yet many aspects of trophic control theory are still unresolved [54]. For example, some of the earliest debates in trophic control theory concerned the relative importance of top-down and bottom-up control [55]. Answering this question requires simultaneous manipulations of resources and predators. This is often practical in phytotelm NMs, where increasing resources may be as simple as adding dead plant or animal matter, and adding predators may simply require dropping in a particular invertebrate. Through such manipulations in pitcher plants, for example, top-down and bottom-up processes have been shown to interact, with the top-down effects generally stronger [56–58]. The broad geographic distribution of NMs then allows experiments and observations to be replicated over latitudinal and climate gradients, revealing important dependencies in the strength and depth of top-down effects. In bromeliads, geographic variation in trophic structure can be explained by predator traits, detrital traits, habitat size and climate [59–61]. In pitcher plants in North America, densities of a top predator are greatest at southern latitudes, depressing microbial prey diversity and generating an unusual inverse latitudinal gradient [6].

A second debate in trophic control theory concerns the importance of non-consumptive effects. Although it is well-established that fear of predators can drive the spatial distribution of prey, it has been argued that there is a 'dearth of evidence' for effects on prey densities and ecosystem processes [62]. NMs offer an opportunity for high replication of treatments with and without caged predators, allowing for powerful tests of effects on prey densities and ecosystem processes. In bromeliads, fear of predacious damselflies have been shown to halve the density of their invertebrate prey, increasing microorganisms and affecting nutrient cycling or CO_2 emissions [63,64]. Such non-consumptive effects even extend well beyond the bromeliad with the predator, with an unknown volatile compound from predatory *Toxorhynchites* mosquitoes affecting oviposition in neighbouring predator-free plants [65].

A final debate concerns the relative importance of ecological and evolutionary mechanisms in top-down control. Experiments of simplified communities in chemostats have shown the potential for predator–prey dynamics to be affected by evolutionary processes (e.g. [66]), but it is challenging to test if this actually occurs in natural, co-evolved communities. The short generation times of protozoans in pitcher plants enable such tests. In the absence of competitors, *Colpoda* protozoans evolve to escape mosquito predation within 12 days [30]. However, in diverse communities, mosquitoes also reduce competitor

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densities, resulting in opposing selection on *Colpoda* sp. traits and consequently no net effect of mosquitoes on *Colpoda* [31]. This example illustrates how NMs can pinpoint gaps in theory that may be missed by studies with artificial communities.

7. Conclusion: unrealized opportunities and recommendations

We have shown that there are both advantages and limitations of using NMs as model systems in ecology. While there are areas of theory for which NMs are not well suited, there are many areas of theory where NMs have made substantial contributions—and are likely to contribute more. So what, then, is the future of NMs as model systems for ecological research? There is still unrealized potential. New methods like metabarcoding and metagenomics are enabling fast assessment of species compositions and hidden interactions like parasitism [14]. In tropical NMs, much of the diversity is in undescribed species, but through sequencing we can place this diversity on a phylogeny to understand the evolutionary context of ecological processes. There is also substantial power in organizing collaborative research networks around particular NMs, such as the Bromeliad Working Group. This has enabled the combination of community data from geographically extensive sampling of bromeliads with data on traits, stoichiometry and climate to test the universality of patterns and processes [5,67]. Such collaborations can be extended to the public through community science initiatives [40]. In a rapidly changing world, NMs can also act as indicator systems for global change given their ubiquity and known responses to stressors [7]. As ecologists race to develop theory relevant to changing environments, the combination of indicators and models in one system could prove to be very powerful.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. We invite readers to explore and reuse the data and R scripts for this submission, archived on Borealis, the Canadian Dataverse Repository, at [68].

Supplementary material is available online [69].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. D.S.S.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, visualization, writing—original draft; M.K.T.: conceptualization, investigation, validation, writing—original draft, writing—review and editing; J.S.P.: conceptualization, investigation, validation, writing—original draft, writing—review and editing; R.C.: conceptualization, investigation, validation, writing—original draft, writing—review and editing; V.F.F.: conceptualization, investigation, validation, writing—review and editing; A.P.F.P.: conceptualization, investigation, validation, writing—review and editing; A.L.G.: conceptualization, investigation, validation, writing—review and editing; P.K.: conceptualization, investigation, validation, writing—review and editing; P.M.d.O.: conceptualization, investigation, validation, writing—review and editing; N.J.G.: conceptualization, investigation, software, validation, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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