

Towards Demography-based Integrative Modelling of Ecosystems and the Biosphere across Scales and the Tree of Life

Abstract

Theoretical and empirical research have established a view of ecosystems and the biosphere as complex adaptive systems since the early 1990s. After half of a century of effort in modelling ecosystems and the biosphere interacting with the atmosphere, a premise remains of up-scaling biogeochemical processes without appreciating their complexity to capture self-organization and emergence. However, this prevailing and fundamental assumption, however feasible and impactful, is losing its grounds as anthropogenic disturbances facing ecosystems and the biosphere become more frequent and intense. The time comes of formulating a real integrative modelling framework that can transcend boundaries of scale and organism (especially plant and microbe, two major branches of the tree of life) and explain their high-dimensional interactions with the environment and march together with empirical research. Here, we propose a framework of Pattern, Diversity, and Process (PDP) for demography-based integrative modelling of ecosystems and the biosphere to contribute to this grand goal. These three interrelated components together shape dynamics and functioning of plant-based, microbe-based system, and the whole ecosystems across spatial-temporal scales, and should be factored into modelling in concert instead of just processes. Existing modelling frameworks of vegetation and microbiome in isolation speak to the heuristic value. This heuristic framework lays a basis for building an integrated demography framework with a balanced perspective of both vegetation and microbiome by ingesting two data streams of remote sensing and multi-omics. Thinking globally and acting locally, those extreme systems in general and the arctic system in particular offer unique opportunities for developing and testing such an integrated framework. Acknowledging no super model for the biosphere, we advocate for this dynamic, cross-scale, and interdisciplinary framework to play a role in stimulating further theoretical constructs of ecosystem dynamics and addressing daunting challenges in the context of frequent and intense disturbances.

1. Introduction

Disturbances of increasing frequency, intensity, and extent are a grand challenge facing ecosystems and the entire biosphere. As an intrinsic property, disturbances, as a source of opportunity and innovation, play important roles in population persistence, species coexistence, and ecosystem resilience (e.g., Turner 2010; Gunderson and Holling 2002). However, anthropogenic disturbances of increasing frequency and impact, as exemplified by increasing extreme events from, for instance, heat wave to flash drought to fire, pose a threat of deteriorating supplies of ecosystem services (e.g., Vitousek 1997; Chapin et al. 2000; Turner 2010; Mahecha et al. 2022; Albert et al. 2023). The resilience of ecosystems and the biosphere emerges from their tremendous complexity comprising vegetation and microbiome that are complex, interwoven, and adaptive (Levin 1998). For this grand challenge facing ecosystems and the biosphere, it is not a vegetation problem, a microbiome problem, a physiology concern, an ecology concern, a local, regional, or global concern; rather, it is a problem for all (e.g., Watt 1947; Schimel et al. 2007; Mahecha et al. 2022). To have any power of informing policy interventions with a predictive understanding, integrative modelling becomes complementarily essential of bridging

organizational levels of both plants and microbes across spatial-temporal scales to capture cross-scale and -system interactions in the biosphere.

Theories regarding organization and dynamics of ecosystems and the biosphere propelled by a non-equilibrium view with empirical supports are compelling for developing such integrative modelling. Ecosystems and the biosphere are complex adaptive systems hierarchically organized (Levin 1998). Legacies or memories formed from past disturbances induce self-organizations across space over time (Odum et al. 1988). However, because of the hierarchical organization, ecosystem composition, structure, functioning, and dynamics at larger scales emerge from complex cross-scale interactions among relatively smaller scales (Perry 1994; Levin 1998, 2005). Such self-organization and emergence shape historical contingency (or path dependency; Levin 1998; Wolf et al. 2008; Blount et al. 2018), a non-linear property intrinsic to ecosystem development in a form of hierarchical responses to and recoveries from disturbances (Slobodkin and Rapoport 1974; Simon 1974; Pickett et al. 1989; Levin et al. 2022). This historical contingency is the very source of resilience, thresholds, and alternate states of ecosystems and the biosphere facing constant disturbances of different regimes (e.g., Holling 1973; Levin 1998; Scheffer et al. 2001; Roger et al. 2022), which applies to vegetation (e.g., Hastings et al. 2018), microbiome (e.g., Fujita et al. 2023), and beyond (e.g., Rietkerk et al. 2021). In other words, the present environment itself cannot exclusively dictate what ecosystems can become, rendering modelling far from being sufficient based on an equilibrium view (e.g., Reuter et al. 2010). Rather, modelling of an integrative nature is needed to help realize self-organization by capturing diverse responses, cross-scale interactions, and recoveries (e.g., Loreau and Holt 2004; Reuter et al. 2010; Fulton et al. 2019; Peters 2019; Albrich et al. 2020).

However, integrative modelling across both scales and organisms remains rudimentary, although inquiries are not rare into solutions by generations of researchers. As early as in 1974, Eugene P. Odum (1974) advocated for ecology as an integrative discipline to have real applications. O'Neill et al. (1998) also argued that fast and slow and local and distant processes cannot be treated separately. More specifically, Wu & Loucks (1995) proposed a hierarchical patch dynamics paradigm to integrate spatial-temporal scales. The metacommunity concept proposed by Leibold et al. (2004) is another notable endeavor along this line. From advocate to specific concepts, the concrete models of ecosystems and the biosphere realized, however, still simplify the ecosystems and the biosphere (e.g., Willis and Bhagwat 2009; Newman et al. 2019). The prevailing paradigm remains pertaining to the big-leaf approach or the big-microbe approaches. Although we have seen models moving towards this direction (e.g., Cramer et al. 2001; Purves et al. 2008; Shugart et al. 2018), simplification prevails, let alone the isolated treatment of vegetation and microbiome. Vegetation and microbiome are studied and modelled separately without coordination, each with its own community of researchers and rich variety of models of different structural complexity (e.g., Cramer et al. 2001; Sulman et al. 2018; van den Berg et al. 2022). By contrast, economics, largely in parallel to natural systems in its non-equilibrium nature and in a certain sense inspired by ecological theories, has embraced and developed more integrative modelling (e.g., Peters 2019; Arthur 2021; Levin and Lo 2021). We need to identify obstacles towards integrative ecosystem modelling across scales and constituents.

Conceptual challenges become a dominant force behind this rudimentary integration in modelling ecosystems and the biosphere. The intellectual motivation of the current models was a result of catering for Global Climate Models in recognition of land surface influences (Sellers et al., 1986; Pitman 2003). In other words, it is a result of top-down thinking. Because of its simplicity, it gains tremendous popularity, but also creates huge obstacles for making efforts of

departure. When pursuing such integrative modelling, those easy-to-cite limitations are missing data intermingled with scale arbitrariness in empirical investigations (Zhou et al. 2012; Cavender-Bares et al. 2022). These hurdles, albeit arguably true, can be crossed, or at least should not dilute our confidence at all towards developing the integrative model. Indeed, as argued by Cavender-Bares et al. (2022) in the context of remote sensing, data and techniques are not as urgently needed as integrative frameworks. We concur with this view and believe that the biggest obstacle may be a conceptual challenge of lacking coherent integrative frameworks arising from a series of reasoning fallacies. First, fine scales are reasoned to be unimportant, which turns out to be a reasoning fallacy (Rocha et al. 2018). Take litter decomposition for example. Many litter decomposition studies de-emphasize the role of microbial composition in controlling soil carbon dynamics (e.g., Beugnon et al., 2021). This approach reflects the influential conceptual framework of hierarchical control of litter decomposition (e.g., Lavelle et al., 1993; Aerts, 1997). That is, litter decomposition is argued to be hierarchically controlled by climate, substrate, and microorganisms, with microbial community composition occupying the least important position. More recently, this hierarchical theory has been challenged with the argument that decomposers control litter decomposition beyond the local scale and that a more explicit consideration of microbial communities is warranted (Bradford et al., 2017). Second, even if being regarded important, many low and/or intermediate levels/scales are argued to be simply ignored by seeking universal scaling laws (e.g., the scale-free power law; Marquet et al. 2005; Hatton et al. 2015). These universal scaling relationships, though scientifically true and intellectually attractive for many cases approached from the perspective of fundamental physics and statistics, are challenged by widespread discontinuities uncovered in ecosystems (e.g., Holling 1992; Brock 1999; Allen and Holling 2008). Third, somewhere between but tightly interrelated with those two beliefs is invoking the classical idea of realism-simplicity tradeoff to push against making models more explicit. We assert that this third argument, though valid per se, is largely intellectual laziness. Apparently, by no means we should capture details infinitely; rather, we must base our development on empirical and theoretical grounds. From this perspective, we believe the time comes of crossing these conceptual hurdles to have a real integrative modelling framework that can march together with empirical research as a digital twin (e.g., Mahecha et al. 2022).

Here, we propose a framework for demography-based ecosystem modelling as an initial step to contribute to achieving this grand goal of integration. Framed in an intuitive way into Pattern, Diversity, and Process (PDP), this modelling-oriented high-level conceptual framework tends to appeal to both modellers and empiricists to bridge theoretical and empirical efforts. Considering the very core of demography about life histories from growth to mortality to reproduction (e.g., Griffith et al. 2016), we believe that an ecosystem model valuing demography but under this framework would offer the structure explicitly integrating cross-scale interactions. We also believe this framework offers a heuristic model for integrating organismal components of both plants and microbes (two core branches across the tree of life) of ecosystems and the biosphere. Together, perturbations from diverse disturbance agents to dynamics of ecosystems and the biosphere can be modelled more robustly. As opposed to the big-leaf/big-microbe paradigm in ecosystem modelling that overemphasizes biogeochemical processes but neglecting the organization of diverse individuals, we use the term demography to refer to an ecosystem model that capture these components.

The overarching objective is to argue for this conceptual framework of demography-based modelling of ecosystems and the biosphere. First, we explicate the three interrelated components, followed by an elaboration of theoretical foundations of its capability in bridging

across organizational levels and spatial-temporal scales of ecosystems and the biosphere. Then, demonstrations of existing modelling frameworks are adduced to illustrate this explication. Against the backdrop of the history of vegetation and microbiome modeling, these existing models, though speaking to the validity of the framework, point clearly to, among others, an outstanding deficiency of treating vegetation and microbiome separately. Constructing this heuristic model, in addition to highlighting the similarities between microbial and plant communities, intends to guide such integrative demography modelling. Accordingly, we discuss how to integrate the two core component systems while integrating observations. Thinking globally and acting locally, we discuss the unique challenges and benefits of application of this integrative framework to high latitude systems. We end up with addressing concerns about complexity, predictability, and evolution, as well as implications.

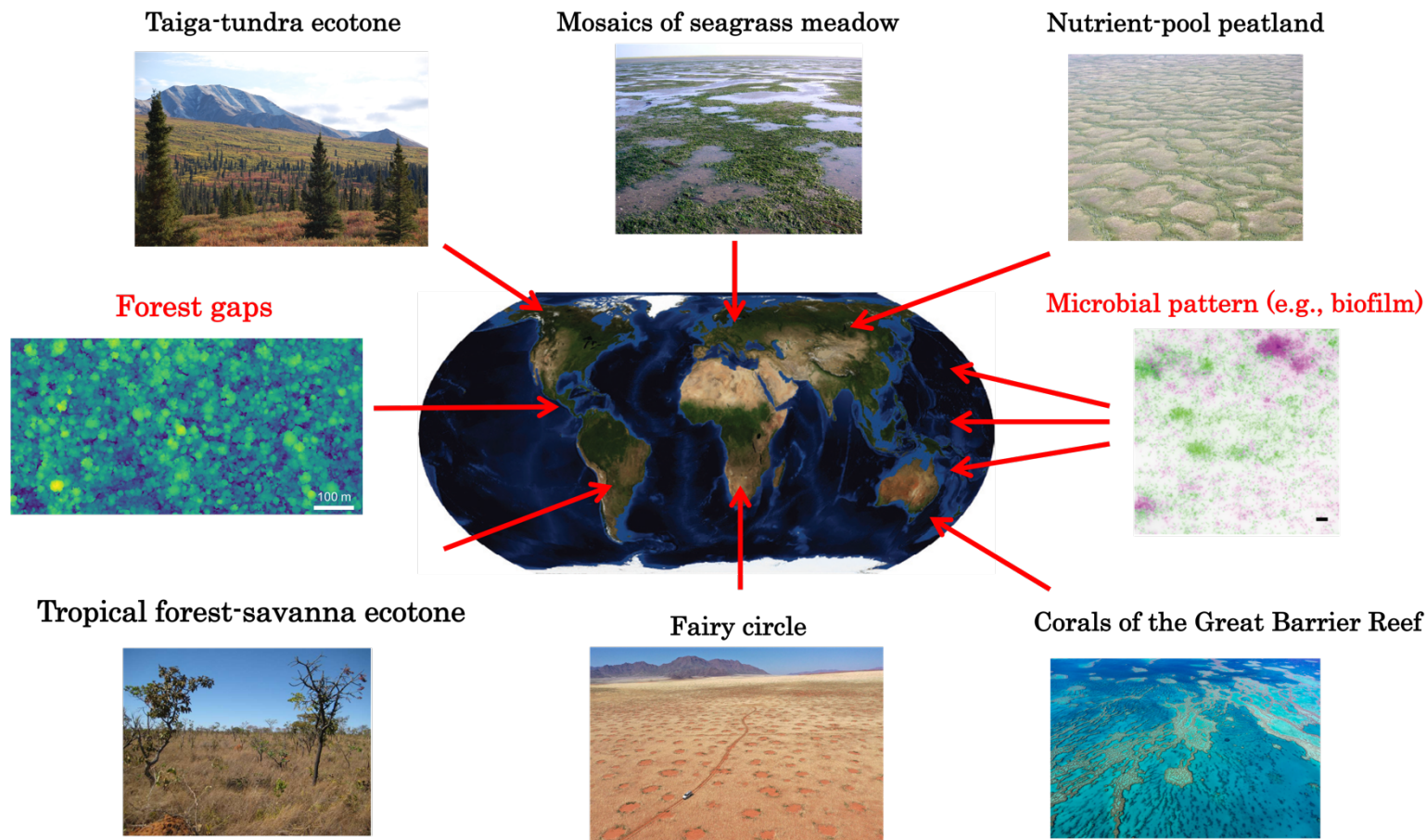


Fig.1 Spatial patterns of ecosystems across the biosphere. **Forest gaps:** a 1-m-resolution canopy heightmodel (CHM) derived from ALS data acquired over the 50 ha forest dynamics plot at Barro Colorado Island (BCI) in Panama (Jucker 2021). **Taiga-tundra ecotone:** Photo Credit: Bob Bolton. **Mosaic of seagrass meadow:** Uithuizerwad, The Netherlands (53°27'N, 6°41'E). **Nutrient-poor peatland:** in Siberia, Russia (56°16'N, 81°33'E). **Corals of the Great Barrier Reef:** Australia (18°17'S, 147°42'E). Image credit: imageBROKER / Alamy Stock Photo. **Fairy circle:** An April 2022 drone image in the NamibRand Nature Reserve (Credit: CNN). **Tropical-savanna ecotone:** Brazilian Cerrado with sparsely spaced trees (Credit: Simon Scheiter). All but the **microbial pattern** (fluorescence microscopy image of biofilm (scale bar: 10 μ m; Rossy et al. 2019) is associated with an actual location, for which multiple arrows are used to indicate its ubiquity across the biosphere.

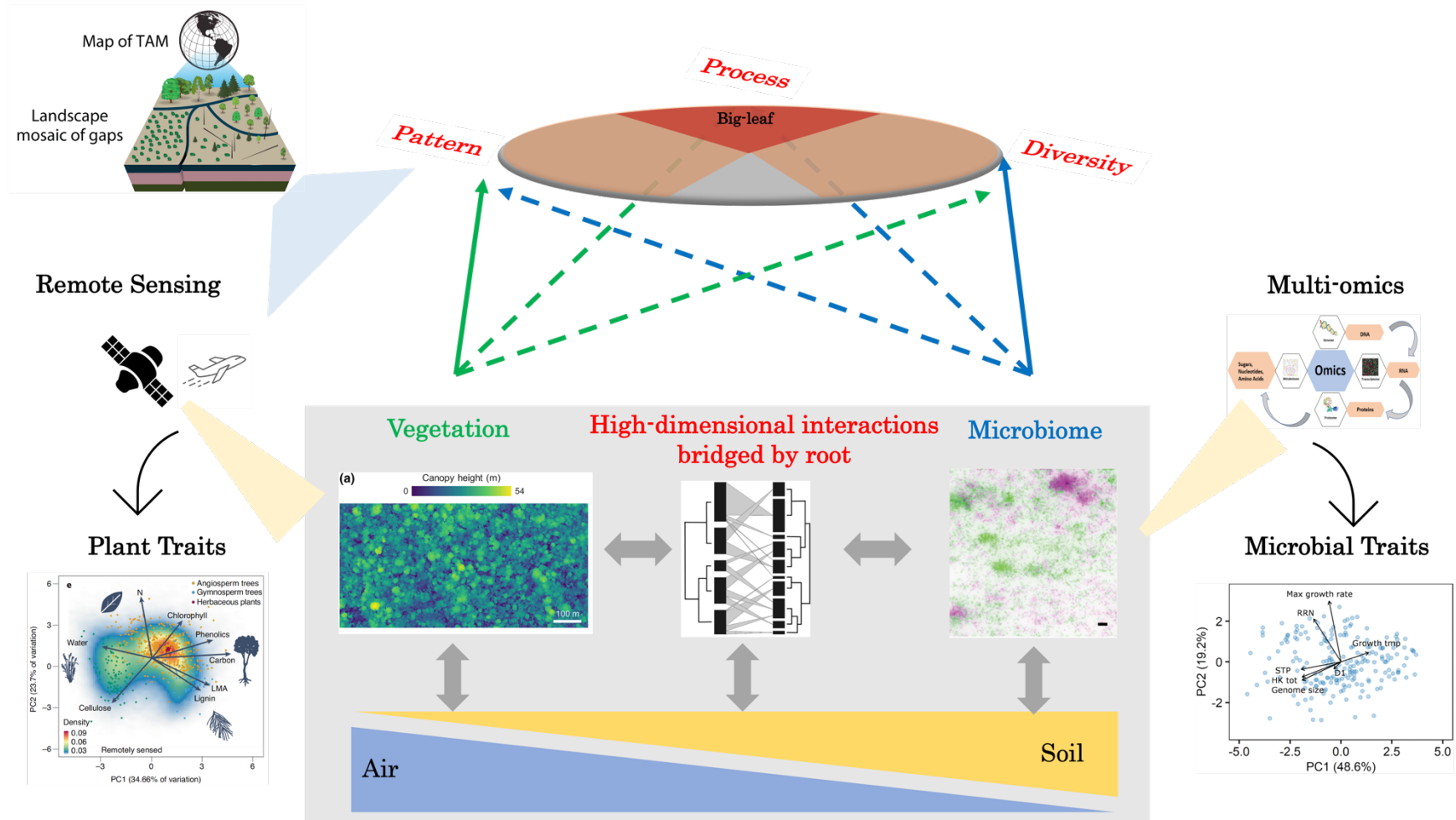


Fig.2 Framework of Pattern-Diversity-Process (PDP) for demography-based integrative modelling of ecosystems and the biosphere. The oval at the very top is inspired by Meron (2016). High-dimensional interactions between vegetation and microbiome PDP are mediated by the root system in general and the fine-root system (different orders with mycorrhizal fungi associations) in particular. The PCA of plant traits is from Cavender-Bares et al. (2022), and the microbial traits from Westoby et al. (2021).

2. Pattern, Diversity, and Process (PDP): a heuristic framework for demography-based modelling

'Species and individuals form different kinds of patches; these patches form a mosaic and together constitute the community. Recognition of the patch is fundamental to an understanding of structure. Patches are dynamically related to each other. But there are departures from this inherent tendency to orderliness. At any given time, therefore, structure is the resultant of causes which make for order, and those that tend to upset it. Both sets of causes must be appreciated.'

Alex Watt in his seminal work—Pattern and Process in the Plant Communities (Journal of Ecology;1947)—firstly discussed the idea of plant communities organizing as a mosaic of different patches by synthesizing seven examples of plant communities. Over the past half of a century with generations of scientists, the idea of patchiness has been discussed, proved, and extended with better data in more different ecosystems (e.g., Levin and Paine 1974; Paine and Levin 1981; Wu and Loucks 1995; Turner 2010; Rietkerk et al. 2021; Siteu et al. 2023; **Fig 1**). Moreover, this framework does apply not only to plant-based communities but also to microbial communities (e.g., Martinez-Garcia et al. 2022). Indeed, Alex Watt in ending his discussion also insightfully discussed the equally (if not more) important micro-organisms (Watt 1947). The two sub-systems and sub-spheres of ecosystems and the biosphere—vegetation and microbiome—share the pattern-process notion that, like structure and function in classical biology, pattern and process are portrayals of two mutually causal agents. From a perspective of modelling ecosystems and the biosphere, we make this pattern-process relationship explicit by proposing a 3-component framework of Pattern, Diversity, and Process (PDP) for demography-based ecosystem modelling (**Fig.2**). Embodying this framework is expected to formulate an ecosystem model simulating dynamics and functioning by integrating different organizational levels of plants and microbes across spatial-temporal scales. We elaborate below this framework and discuss its theoretical foundations in modelling the interplay of ecosystem composition, structure, and functioning across spatial-temporal scales interacting with various disturbances.

2.1 Pattern

Pattern is about spatial organization of organisms into patches. Though more intuitively being regarded as a result of dictation by external environmental heterogeneities at varying scales, this spatial pattern in terms of patches can be a result of self-organization without even spatial heterogeneity. In other words, self-organized pattern formation should be distinguished from those dictated by external environmental heterogeneities that is commonly dealt with in traditional spatial ecology (van de Koppel et al. 2008; Sheffer et al. 2013; Meron, 2016). Indeed, a premise of the discussion by Alex Watt is uniformity of external environment (Watt 1947). Dryland vegetation has become paradigmatic for discussing regular pattern formation resulting from scale-dependent feedbacks (i.e., Turing Pattern; Rietkerk et al. 2021; Walsh et al. 2023). In fact, self-organized pattern formation is common over a wide range of scales and levels of organization from vegetation (aboveground) to microbiome (belowground) patchiness, forming a myriad of self-organized spatial patterns including not only regular but also irregular ones (e.g., Pickett and White 1985; Wu and Loucks 1995; Rietkerk et al. 2004; Tarnita et al. 2017; Siteu et al. 2023; **Fig.1**). For instance, forest landscape is a mosaic of gaps (or patches) at different successional stages induced by exogenous and endogenous disturbances (e.g., Bormann and Likens 1979). As a result, forest

systems are argued to be structured both vertically by size and horizontally by age since the disturbance. Microbiomes share the pattern formation phenomenon, which, in fact, even provides a unique model system to study pattern formation because of their fast timescales and manageability (e.g., Martinez-Garcia et al. 2022). Self-organized microbial patterns (e.g., biofilm) has been revealed in both marine terrestrial environments (e.g., Momeni et al. 2013; Ratzke and Gore 2016; Ebrahimi et al. 2019; Rossy et al. 2019; You et al. 2021). In addition to influencing functioning (e.g., Meron, 2016; Ratzke and Gore 2016), self-organized pattern formation has been initially proposed as a key indicator for imminent catastrophic shifts in ecosystems (Rietkerk et al. 2004) and now as an adaptation of ecosystems evading dramatic changes (Rietkerk et al. 2021), acting as a hallmark of ecological resilience in the context of frequent disturbances (Peterson 2002; Cuddington 2011; Martinez-Garcia et al. 2022). These properties are conferred by different mechanistic details depending on the pattern and system (**Fig.1**; e.g., Rietkerk et al. 2004; Meron, 2016; Siteu et al. 2023). In general, self-organized patterns emerge from complex, high-order interactions among diverse individuals across scales through a rich array of processes.

2.2 Diversity

Diversity refers to different individuals grouped taxonomically. Studies, both theoretical and empirical, dedicated to its implications for functioning are historically rich and extensive. In particular, plant diversity and its importance have long been appreciated since at least the 1950s (e.g., Chapin et al. 2000), notably in grassland ecosystems with diversity manipulations (e.g., Grace et al. 2016). Though important in a broad sense, redundancy is an argument normally invoked against its importance or simplifying its treatment in functioning (i.e., grouped into a few functional types; Smith et al. 1997). This notion is especially true for microbiomes (e.g., Allison and Martiny 2008). Microbial diversity, due to cultivation-independent high-throughput sequencing (e.g., Pace 1997; Tringe and Rubin 2005), is revealed to be overwhelmingly high across the biosphere. Although relating microbial diversity to functioning relatively remains in its early stage, its importance is emerging as a big question (e.g., Bardgett and van der Putten 2014; Martiny et al. 2023). Simply emphasizing diversity *per se* (regardless of the measure) is not the whole story; how different organismal constituents (either plant or microbe) are spatially organized (as discussed above regarding pattern formation) matters as well (e.g., Zobel et al. 2022). Accordingly, forests are argued to be structured both vertically by size (height of different species) in each patch and horizontally by age (for different patches since disturbances; e.g., Kohyama 1993). Similarly, microbiomes, though not structured specifically by height like trees in each patch, form mosaic of patches consisting of individuals of different cell sizes at different life stages (e.g., Ratzke and Gore 2016). These spatial structures together with taxonomic diversity result in both within- (Walker et al. 1999) and cross-scale diversity (Peterson et al. 1998), which enables regeneration and renewal to occur following ecological disruption over a wide range of scales. Apparently, dynamics and functioning of ecosystems and the biosphere ultimately emerge from pattern and diversity interacting with processes under a fluctuant abiotic environment.

2.3 Process

Process tends to encapsulate any physiological and physio-chemical flow, storage, and transformation of matter and energy. Though used interchangeably with functions by many researchers (Jax 2005), the term process is used here in a very general sense to distinguish it from the two concepts above, and functioning is reserved to refer to the whole ecosystem (as has been used so far in this article). With demography, models need to capture basic demographic processes

from growth to mortality to reproduction (including dispersal) shared by plants and microbes, in addition to the usual biogeochemical processes ranging from vegetation-mediated processes (including carbon, nutrients, and water) to microbiome-mediated processes (including carbon and nutrients), as well as abiotic processes (e.g., non-microbial degradation and GHGs production; Wang et al. 2017) that shape the trajectories of carbon, nutrients, water, and other elements in the air and soil. Here, we do not exhaustively discuss further relevant details. On the one hand, we leave them to the rich literature in both empirical and modelling fields on plant and microbial physiology and soil physio-chemical processes. On the other hand, we intend to highlight the above pattern and diversity component that are still largely missing in models. Encapsulating these two, in addition to processes, in demography-based modelling to integrate organizational levels across spatial-temporal scales does not lack theoretical supports.

2.4 Theoretical Underpinnings

Rich theoretical constructs scattered in different fields or disciplines underpin the integrative capability of this demography-based framework. In fact, similar considerations have been discussed and practiced in social and economic systems likely because of a human-based origin of the demography notion and acute social-economic concerns (e.g., Jones et al. 2014; Arthur 2021). In formulating demography-based models of ecosystems and the biosphere with both plants and microbes, embodying those three components means capturing diverse life-history strategies but at different life stages structured spatially into a form of different patches from the above- to the below-ground at different spatial scales through not only environmental dictation but also their self-organizations. In other words, this means integrating different organizational levels of plants and microbes across space over time, in line with the hierarchy theory of ecosystem organization in general (Allen and Hoekstra 1990; O'Neill et al. 1998) and the more specific hierarchical patch dynamics theory (Kotliar and Wiens 1990; Wu and Loucks 1995) and the hierarchical disturbance notion (Pickett et al. 1989). In addition to biogeochemical fluxes, such an integrative nature makes possible capturing mechanisms from diverse responses to cross-scale interactions underlying stability and resilience of ecosystems and the biosphere (e.g., Pascual and Guichard 2005; Walker et al. 2023), making the resultant demography-based models more reliable in modelling dynamics and functioning facing disturbances. In fact, purely process-driven modelling with a minimum structural representation without diverse organisms and their patterning is far from being complete in capturing processes (Schröder 2006). A notable example is land surface models under the big-leaf modelling paradigm. Of course, various models under this paradigm do capture plant/microbial diversity by normally using a few functional types, which are fine as a simplification strategy. However, these models further prescribe spatial patterning of these PFTs at only regional and larger spatial scales dictated by climatic heterogeneities (Woodward 1987) without self-organized pattern formation, which makes the PFT approach worse. It is noteworthy that we do not intend to debunk the applicability of purely process-driven formulation of models that do not appreciate ecosystem structure, but rather to complement existing research and to reconcile the apparent gap between theoretical ideals and empirical realities. We believe the space of possible models is huge enough to allow coexistence of many different paradigms with different structures; that is, there is no 'super model' [in the sense of one ruling for all instead of the one used by Lorenz (1970)]. We certainly have empirical and theoretical supports to pursue this structure. Some of the claims of this demography-based modelling framework can be evidenced and illustrated by existing modelling frameworks.

3. Illustrations of this framework

Simulating demography is not a cryptic endeavor at all, but its coupling with ecosystem functioning that reflects the above framework remains in its infancy. Simulating population dynamics of different species has been ongoing at least since the 1940s, most of which, however, were limited to theoretical ecology in the population and community ecology setting, though available for both macro- and micro-organisms (e.g., Levins 1966; Sinko and Streifer 1967; Levins 1969). With a perspective of ecosystem ecology, integrating demography and biogeochemistry appeared notably much earlier in forests than in microbiomes with the concept of pattern appeared first in plant communities as discussed above. Since the 1970s (Botkin 1972), forest demography models have been under active development [see a review by Shugart et al. (2018)]. Demography modelling reflecting this notion in microbiome with a perspective of biogeochemistry did not appear until the 2000s (e.g., Widder et al. 2016). Without exhaustively writing about history and methodology (but see Wu and Loucks (1995) for a general account and van den Berg et al. (2022) for a microbial modelling focus), we detail below existing modelling structures to demonstrate the framework in forest and soil microbiome (**Fig.3**).

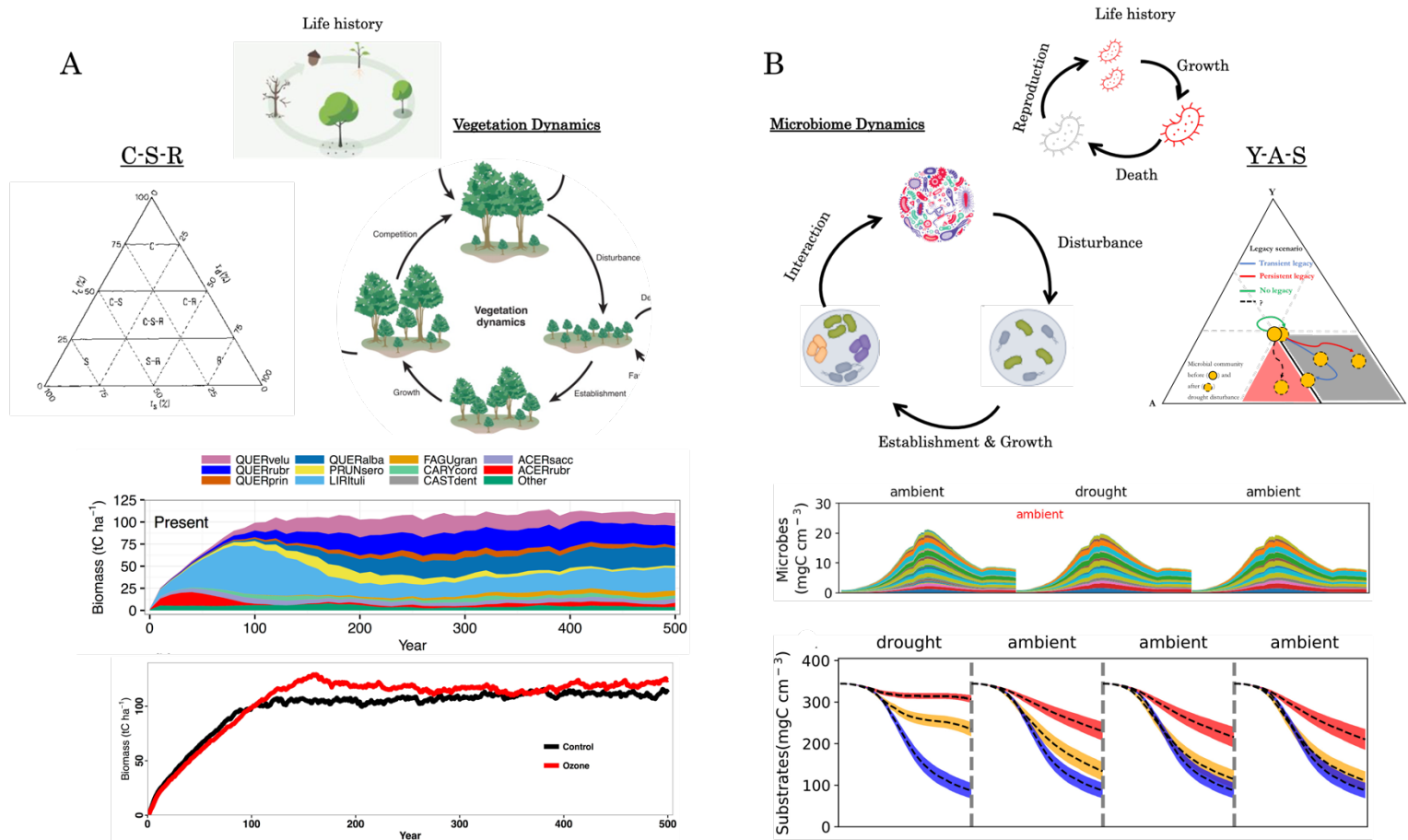


Fig.3 Demography-based simulation of forest and microbiome dynamics and functioning reflecting PDP. **A)** Simulated temperate forest dynamics after a clearcut in East Tennessee, USA with respect to composition and undampened biomass from ozone pollution. The biomass (tC ha⁻¹) are means of an ensemble of 200 simulations on a plot size of 500 m² to approximate a shifting-mosaic steady-state landscape using UVAFME-VOC [see Wang et al. (2016) for more details]. The triangle shows the C-S-R theory of plant life-history tradeoffs (Grime 1977). **B)** Simulated dynamics of a grassland litter microbiome system in Southern California, USA with drought disturbance with respect to composition (hypothetical taxa) and functioning (i.e., litter decomposition). The substrates and uncertainty are based on an ensemble of 40 independent runs of DEMENTpy (see Wang and Allison (2021) for more details). The triangle shows the Y-A-S theory of microbial life history tradeoffs (Malik et al. 2020).

3.1 Forest PDP

Forest demography modelling can be treated as a prototypical demonstration of the PDF framework (**Fig. 3**). Reflecting the view of shifting mosaic of patches/gaps as discussed above, forest demography models capture the PDP framework in forests to a maximum extent. The earliest gap models explicitly simulate growth, mortality, and reproduction of different individuals in an array of gaps at different successional stages arising from internal and external disturbances (e.g., Shugart 1984; Shugart et al. 2018). Modelling explicitly size and age of different species using an individual-based approach allows realistic light transfer within forest canopy and individual crown, enabling, for instance, dynamically simulating production and emission of secondary metabolites of Volatile Organic Compounds (VOCs) that are highly variable among species (Wang et al. 2017; 2018). Though conferring unique advantages (e.g., capturing better individual variation), such a strategy of simulating different species occupying a forest landscape can be simplified. By approximating the spatial and vertical structuring of vegetation without an explicit parameterization and simulation of different species, cohort-based models simplify the individual-based models by utilizing cohorts of like-sized plants without spatially explicitly simulating different patches (e.g., Levin and Paine 1974; Clark 1991; Kohyama 1993; Hurtt et al. 1998). Eventually, this approach was applied to the Ecosystem Demography model (Moorcroft et al. 2001) and the latest model FATES (Functionally Assembled Terrestrial Ecosystem Simulator) with more sophisticated algorithms of allometry and carbon-nutrient interactions (Fisher et al. 2018). Applications of these models reflecting the PDP are highly diverse, but an example that exemplifies the unique capability of forest PDP is challenging the long-held contention since the 1950s that tropospheric ozone pollution severely reduces on forest carbon sequestration (**Fig.3**). From appearance to simplification, the development and application of forest demography modelling illustrate why forest demography modelling is regarded as a prototypical example of the PDP framework. However, these demography modelling efforts do not involve demography of the microbiome.

3.2 Microbiome PDP

Modelling microbiome demography reflecting the PDP framework is independently conducted (**Fig. 3**). This independence serves a purpose in the microbial ecology community of complimenting empirical investigations. Demography-based modelling of dynamics and functioning of microbiome are challenging with their tremendous diversity, micro-scale patterns, and richness of processes (Kreft et al. 1998; Hellweger et al. 2016; Falkowski et al. 2008; Wu et al. 2022). We take for example the state-of-the-art trait-based modelling of litter microbial systems (Allison 2012; Wang and Allison 2021). In essence, it is a lattice-based model of different microbial taxa decomposing leaf litter. The diversity is approached using a trait-based approach to simulate hypothetical individuals. Then, a series of metabolic and demographic processes ranging from turnover to degradation are simulated. Therefore, functioning in terms of litter decomposition and other associated processes is simulated as a self-organization mechanism under the constraint of moisture and temperature, as well as litter inputs. The power of this model reflecting PDP can be exemplified by its application to drought disturbance and litter decomposition (**Fig.3**). Legacies of drought disturbances in litter decomposition were revealed to be contingent on intensity and dispersal, leading to different trajectories of microbial system development and decomposition that can be explained by 3-way life-history tradeoffs (Wang and Allison 2021; 2022). However, unlike the ED/FATES model, this microbial model is still applying a spatially explicit approach of every hypothetical taxon without a similar cohort-based approach to simplify the spatial and size-

based structuring into patches. Nevertheless, it does satisfyingly help reveal coarse-graining of organic matter degradation by soil enzymes in microbe-enzyme-decomposition systems (Wang and Allison 2019). Though speaking to the heuristic value of the framework together with the forest-based example, these demonstrations clearly show an outstanding gap of missing integration of vegetation and microbiome.

4. Integrative modelling of vegetation and microbiome

It is imperative to develop integrative modelling that holds a balanced perspective of both vegetation and microbiome PDP. Vegetation and microbiome are two complex adaptive systems that are coupled but do not synchronize. In other words, an integration means simulating two interactive self-organizing complex adaptive systems, each with a certain degree of autonomy, interacting with fluctuating environments. Vegetation PDP (or aboveground PDP indeed in the current state of research) clearly involves belowground mechanisms related to the PDP regulated by the complex microbiomes (e.g., Schimel et al. 2007; Callaway and Meron 2021). This belowground concern is especially true for systems beyond the forests (**Fig. 1**), in which the above-ground competition for light may become subordinate and complex interactions with the belowground microbiome dominant. Some arguments, though not against plant-microbe integration in general, would disavow an integration in a fashion like PDP. For instance, Yang et al. (2023) recently argued that free-living microbial communities do not vary meaningfully in functional potential within most ecosystems on time scales relevant to climate change. However, the need to integrate in an explicit way to avoid linear thinking is undisputable (e.g., Battiston et al. 2022), considering the highly non-linear, multilayered, high-dimensional interactions between vegetation and microbiome, especially as disturbances tighten vegetation-microbiome feedbacks (**Fig. 4**). Such a non-linear property is what the big-leaf and big-microbe paradigms or a pair of demography-based vegetation model and a big-microbe model cannot capture. The heuristic framework offers an umbrella under which we can appreciate the differences between vegetation and microbiome and their interactions for integrative modelling with empirical support.

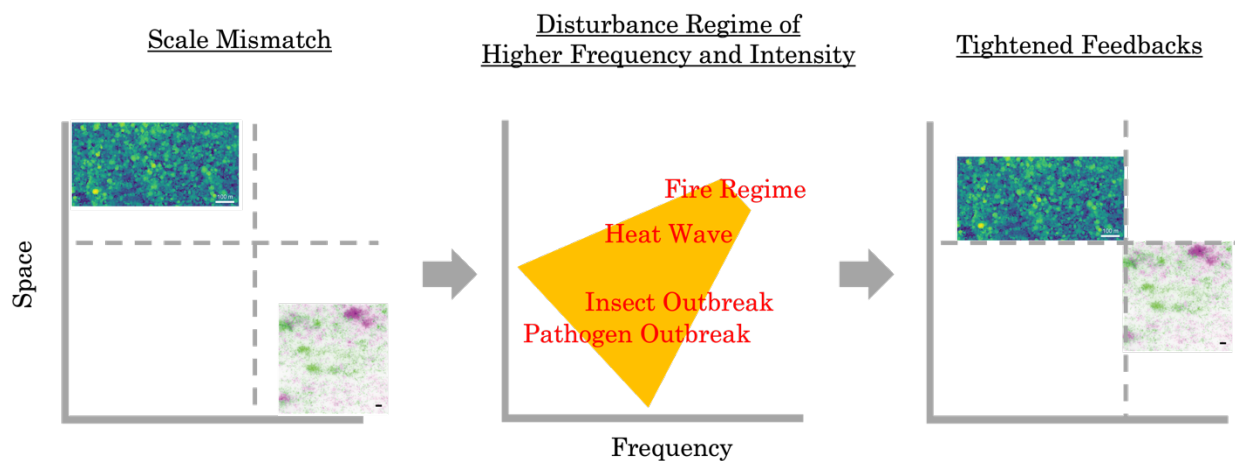


Fig.4 Relative operation scales of vegetation versus microbiome PDP reduced by increasingly frequent and extensive disturbance events. Vegetation is represented by a mosaic of canopy gaps derived from LiDAR measurements of canopy height (scale bar: 100 m). Microbiome is represented by fluorescence microscopy image of biofilm (scale bar: 10 μ m; Rossy et al. 2019).

Among the many external disturbance agents (e.g., fire, heat wave, insect outbreak, and pathogen outbreak), their relative positions in the space-frequency plane are only loosely distinguished.

The differences complicating such an ambitious initiative of balanced perspective can be coherently organized under the thread of scale mismatch (**Fig.4**). At the spatial scale of a self-organized vegetation pattern, tremendous environmental heterogeneity still exists for microbial communities, which, together with spatial self-organization, shape pattern, diversity, and processes of microbial community. For instance, a mosaic of forest gaps/patches on a homogeneous land would have different microbial systems (e.g., Griffiths et al. 2022). Microbial communities are diverse in the complex soil matrix of horizontal and vertical heterogeneity, rendering the scope of just modelling microbiomes spacious enough for more exploration. Decomposition regulated by microbiomes involves compartments from aboveground litter to root systems to bulk soils at different depths, which holds huge physic-chemical heterogeneity (e.g., Wang et al. 2019). Root systems (**Fig.2**), especially the fine-root systems (comprising different orders and mycorrhizal fungi), play a central role connecting these different parts; our recent discussion around TAM-based modelling could be treated as a starting point or point of departure (Wang et al. 2023). With these huge differences, a unified approach accommodating both vegetation and microbiome with data support would make the integration feasible.

4.1 Trait-based modelling as a unified stepping stone

Trait-based modelling, though not an ultimate solution to embody fully the PDP framework, can be a unified stepping stone (**Fig.2**). Trait-based approach is about assembling relevant traits (from morphological to functional) forming a huge space for either plants or microbes without traditional taxonomical identity (e.g., Clark 2010; REFs). More importantly, one fundamental aspect of which would be uncovering spectrums and tradeoffs (e.g., Wright et al. 2004; REFs). Trait-based modelling may prescribe these tradeoffs into the models to simplify the formulation across spatial-temporal scales, or instead treating these tradeoffs as emergent constraints. This approach has been applied firstly to vegetation (e.g., Rüger et al. 2020) and then to micro-organisms (e.g., Follows et al. 2007). Though challenges remain at large in assembling those traits for the belowground in general (e.g., FRED; Colleen et al. 2017; Colleen and McCormick 2021) and microbes in particular (e.g., Westoby et al. 2021), no real efforts have been made to integrate plants and microbes under the trait-based modelling approach. To integrate, we need empirical data from integrated assessment of whole ecosystems (e.g., Keith et al. 2022), which, however, is still lacking because of an analytical approach in ecology (see a review by Ohse et al. 2023). It is noteworthy that trait-based modelling does not mean blindly applying it to all components of all systems; for systems that are low with plant diversity, it can still be applied to the microbiome component but with the brute force approach of formulating and parameterizing constituent species for the vegetation directly. Still, coordinated data of all are needed. These data needs can be met by leveraging two major data streams from the aboveground to the belowground, in addition to traditional field and lab investigations into causal relationships.

4.2 Tapping into remote sensing and multi-omics

This framework offers the intuition and feasibility of leveraging two major data streams: remote sensing and multi-omics (**Fig. 2**). The way we structure this framework is a result of keeping in mind bridging modelling and empirical research. The pattern and diversity component

can benefit from the remarkable progress of remote sensing in acquiring data of biodiversity at an increasing resolution from sensors to algorithms (Pettorelli et al. 2016; Cavender-Bares et al. 2022). For instance, LiDAR (Light Detecting and Ranging; Lefsky et al. 2002) and RaDAR (Radio Detecting and Ranging; Hall et al. 2011; Le Toan et al. 2011) instruments can distinguish the vertical, horizontal, and 3-D structure of forests (Shugart et al. 2015; Torresani et al. 2023; Yang et al. 2023). Hyperspectral imaging spectroscopy can quantify leaf-and-species-level chemical and functional traits (Asner et al. 2012). A belowground equivalent of remote sensing for vegetation is multi-omics for microbiomes including shotgun metagenomics, single-cell genomics, metatranscriptomics, metaproteomics, and targeted and non-targeted metabolomics (e.g., Rondon et al. 2000; Li et al. 2004; Tringe and Rubin 2005; Eberwine et al. 2023). Together with increasingly advanced imaging advances, e.g., microfluidic and nanofabrication tools [see a review by Hol et al. (2014)], these -omics techniques will help reveal microbial pattern, diversity, and process in the soil matrix (e.g., Fierer et al. 2014). These data sources, complimented with accumulation of long-term observations (e.g., Inchausti and Halley 2001; Mechenich et al. 2023; FRED; TRY; FIA) and augmented by data-based modelling from machine learning to deep learning (e.g., Chen et al. 2021) to observational causal inference (e.g., Runge et al. 2019; Golan and Harte 2022; Correa-Garcia et al. 2023), will help the formulation and evaluation of the integrative modelling. Thinking globally, we stay in a huge high-dimensional space on many axes that can be categorized into different ecosystems (**Fig. 2**), and we can leverage the two data streams to develop an integrative biosphere model capturing their interactions. Acting locally, we believe that those systems holding unique but extreme positions in the global space would make developing and applying such an integrative structure a highly rewarding first step in the sense of laying a foundation for global integrative modelling and to understanding local mechanisms and addressing regional concerns.

5. Going to the extreme—Integrative modelling of the Arctic with PDP

The arctic system, holding a uniquely extreme position, can be a highly rewarding candidate for developing such integrative modelling. These systems span from peatland to boreal forest to tundra, and the PDP framework proposed above applies to the arctic system as well (**Fig.1**). Indeed, Alex Watt (1947) briefly discussed applicability of the pattern concept to the arctic systems. We now have rich empirical evidence to support this notion (e.g., Foster et al. 1983; Chapin et al. 1989). Biological diversity is relatively much lower for both plants and microbes (Jansson and Taş 2014). This relative simplicity makes tackling the diversity component much easier, as has been argued for microbial ecology in extreme environments (e.g., Denef et al. 2010; Shu and Huang 2022). Although the arctic involve unique physical and chemical processes (e.g., permafrost), we expect the application of this framework to the arctic to test and in turn inform the framework. More importantly, this integrative modelling is ever more urgently needed towards understanding and addressing challenges facing the arctic. The arctic is experiencing different disturbance regimes as the climate warms (e.g., Foster et al. 2022; Rantanen et al. 2022); for instance, wildfire is becoming bigger (e.g., Scholten et al. 2022), and permafrost is thawing (e.g., Smith et al. 2022). Changes in vegetation (e.g., shrub expansion; Frost and Epstein 2014) and microbiome (e.g., exit of dormancy; Jansson and Taş 2014; Heijmans et al. 2022; Nelson et al. 2022) entails and challenges the development of integrative models discussed here to understand and predict biogeophysical feedbacks and resilience of the arctic. However, the arctic is still understudied in general because of, e.g., low feasibility and accessibility (Griggs 1934), as reflected in the discussion above limited to forest and water-limited systems where relevant

concepts were initially conceived, later developed, and mostly discussed. This is even more so with respect to modelling and model-data integration. Though demography-based boreal forest modelling does exist (e.g., Bonan et al. xxxx; Shuman et al. 2010), demography-based integrative modelling in general is largely missing, let alone the taiga-tundra ecotone. From theoretical constructs to applied challenges, the arctic approached with the PDP framework is expected to be a rewarding inquiry.

6. Discussion

6.1 Embracing Complexity

One immediate and primary concern may be model complexity and predictability arising from this integrative framework. We acknowledge the complexity incurred compared to the current models we are familiar and bond with, especially those under the prevailing paradigm of big-leaf or -microbe models. However, we do not see complexity as a concern at all, at least not a concern that should preclude us from making models more explicit. We need models to catch up with empirical evidence and more explicit theories, which makes possible modelling staying ahead to sharpen hypotheses, a true beauty and power held by modelling over empirical investigations. Although we fully embrace the idea of making models simple (e.g., Edmonds 2000; Transtrum et al. 2015), we assert the space remains huge to make our models complex. Organismal components and their PDPs not yet considered are abundant (e.g., invertebrates), although we boast about integrative modelling across the tree of life. More importantly, we do not yet discuss at all evolution, the ultimate strategy of the biosphere as a complex adaptive system to self-organize to stay resilient while facing frequent and intense disturbances.

6.2 Missing Evolution

Although we do not touch on evolution, the framework here offers the backbone for incorporating evolution. Demography is central to understanding evolution (e.g., Metcalf and Pavard 2007; Jones et al. 2014). As paraphrased by James W. Vaupel of Dobzhansky's classical statement, "nothing in biology makes sense except in light of evolution, nonetheless, nothing in biology makes sense except in light of demography". Indeed, predicting evolution has been explored extensively (e.g., Lässig et al. 2017). Unlike those previous works limited to the theoretical ecology setting, the framework we have discussed warrant more integrative explorations of evolutionary implications of both plants and microbes (e.g., Flack 2017). In general, it allows us to explore the relative importance of contingency and determinism involving evolution (Blount et al. 2018; Vahsen et al. 2023). Notably, microbial evolution can happen simultaneously with ecological processes (Traverse 1998; Pelletier et al. 2007; Martiny et al. 2023), making essential incorporating both evolution into ecological and biogeochemical dynamics. Nevertheless, building such a modelling framework even temporally without evolution will contribute to Ecosystem and Earth System sciences.

6.3 Contributing to Earth System Science

This integrative framework in a bottom-up way contributes to understanding and predicting how dynamics and functioning of ecosystems and the biosphere self-organize in the Earth System. It brings together a series of concepts and approaches scattered in different disciplines or communities spanning biology, community ecology, ecosystem ecology, landscape ecology, and Earth System modelling, as well as data and computational sciences. This synergy

creates the challenge and meanwhile brings about all the excitement as we strive to address urgent and daunting challenges. Leveraging two main data streams of remote sensing and omics, the dynamic, cross-scale, and interdisciplinary framework will stimulate further theoretical constructs of and empirical investigations into dynamics and functioning in response to frequent and intense disturbances by testing hypotheses holistically around, e.g., soil and ecosystem carbon dynamics across spatial scales over especially long-time scales. If this framework and the resultant models are any impactful, it is because of its integrative nature, as there is no ‘super microbe’, ‘super plant’, or ‘super ecosystem’ to the daunting problem we have created for the biosphere and the whole Earth system. It is really a problem for all, just as how Alex Watt ended the 1947 article:

‘...to have the ultimate even if idealistic objective of fusing the shattered fragments into the original unity is of great scientific and practical importance; practical because so many problems in nature are problems of the ecosystem rather than of soil, animals or plants, and scientific because it is our primary business to understand.’

7. Conclusions

Despite a consensus on integrative research in general, integrative modelling in particular falls short of our needs to contribute to addressing a daunting challenge of frequent and intense disturbances facing ecosystems and the biosphere. Reasoning fallacies of diverse angles make relevant efforts fall behind, although theories of ecosystems and the biosphere as complex adaptive systems have been in place for decades. Demography-based modelling of ecosystems and the biosphere, we believe, is on the right track to approach this grand challenge. To this end, we propose a PDP framework for demography modelling by synthesizing from an array of fields concepts, theories, and models for both vegetation and microbiome. We marshal arguments complemented with specific modelling examples of both forest and microbiome separately. With solid theories (for a not short history) and available data (if not readily), we argue against likely concerns about model complexity and predictability by discussing the yet included evolution and the outstanding role of this framework in marching together with empirical research. To understand and predict the urgent and daunting challenges facing the biosphere overwhelmed by human, we advocate for the role of this demography-based integrative modelling effort.

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Appendix