New insights to be gained from a Virtual Ecosystem

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Abstract

The myriad interactions among individual plants, animals, microbes and their abiotic environment generate emergent phenomena that will determine the future of life on Earth. Here, we argue that holistic ecosystem models – incorporating key biological domains and feedbacks between biotic and abiotic processes – capable of predicting emergent phenomena are required if we are to understand the functioning of complex, terrestrial ecosystems in a rapidly changing planet. We argue that holistic ecosystem models will provide a framework for integrating the many approaches used to study ecosystems, including biodiversity science, population and community ecology, soil science, biogeochemistry, hydrology and climatology. Holistic models will provide new insights into the nature and importance of feedbacks that cut across scales of space and time, and that connect ecosystem domains such as microbes and animals or above and below ground. They will allow us to critically examine the origins and maintenance of ecosystem stability, resilience and sustainability through the lens of systems theory, and provide a much-needed boost for conservation and the management of natural environments. We outline our approach to developing a holistic ecosystem model – the Virtual Ecosystem – and argue that while the construction of such complex models is obviously ambitious, it is both feasible and necessary.

Keywords

Ecosystem complexity; Emergent phenomena; General ecosystem model; Organismal physiology; Temperature

Introduction

Terrestrial ecosystems are complex systems replete with emergent phenomena that challenge our understanding and defy prediction. Part of the problem is a mismatch between the goal of ecology, to understand ecosystems, and the approach of ecologists to that goal, which is largely reductionist. Fifteen years ago, Drew Purves made the bold statement that it's "time to model all life on earth," (Purves et al. 2013), and went on to lead a team that made a valid claim to having achieved this ground-breaking feat (Harfoot et al. 2014). Yet even this audacious project embedded compromises: it focussed on describing processes at global scales, used a highly representation of plant dynamics, and omitted microbes, and so necessarily did not simulate the local dynamics and cycles of a complete ecosystem. In the decade since these studies were published, the planet has been assailed by global catastrophes of drought, floods, epidemic and unprecedented levels of climate warming. There is an urgent need to develop process-based models that can predict ecosystem responses to these catastrophic phenomena. This is no easy task: ecosystems have been described as "more complex than the space station, and more connected than the internet" (Andrew Young, *pers. comm.*). We need models that capture this complexity and connectivity, and rise to the challenge of predicting how ecosystems will fare in a rapidly changing world.

Ecosystems arise through the interactions of plants, animals, microbes and the abiotic environment. The actions of individual organisms are driven by their physiology under the dictates of natural selection, and when connected through a web of interactions give rise to a complex system with self-regulating and self-maintaining properties. Describing this complexity through empirical observation is an unrealistic goal, as it would require simultaneous observations of all species, all facets of the abiotic environment, and all biotic interactions. Even if such data were available, they would still be unable to give insight into emergent phenomena arising from non-linear feedbacks and multiple stable states. Simulation using models provides an alternative, and more tractable, route to examining these complex features of complex systems, and hence a better understanding of their consequences.

Despite rapid advancements in the construction of detailed ecological models for terrestrial ecosystems (Clark et al. 2011, Harfoot et al. 2014, Fatichi et al. 2019, Geary et al. 2020), these are not yet fully holistic. Our definition of 'holistic' encompasses two key aspects: one is the breadth of processes being incorporated, and the other is the diversity of users that might benefit from such models. First, holistic ecosystem models should simultaneously encompass the domains of plants, animals and soil microbes, along with the abiotic drivers that impact those domains (such as temperature, hydrology and soil chemistry). The closest models that currently exist are the "end-to-end" models that have been used to simulate marine environments for several decades (Christensen and Walters 2004, Fulton et al. 2011), and have more recently begun to emerge in freshwater environments (Janssen et al. 2015, Janssen et al. 2019). These models seek to capture the breadth of components and processes that an ecosystem encompasses (Fulton 2010, Geary et al. 2020), but they focus mainly on the biological components of the ecosystems and do not yet allow for feedbacks where the biotic world influences the abiotic. Such feedbacks are common in terrestrial environments (e.g. trees controlling microclimate (Hardwick et al. 2015) and microbes modifying soil chemistry (Philippot et al. 2024)), necessitating their inclusion in holistic ecosystem models for terrestrial environments. The end-to-end models for marine and freshwater environments have demonstrated a broad suite of powerful applications (Plagányi 2007, Geary et al. 2020), and have set a benchmark for terrestrial ecologists to emulate.

The second feature of terrestrial holistic ecosystem models is the wide base of users whose demands can be satisfied from a single, unified framework (Box 1). Such models could simultaneously help systems ecologists to examine density- or frequency-dependent feedbacks, disturbance ecologists to predict ecosystem resilience to disturbance, and resource managers to optimise their management plans. They would have extraordinary potential to deliver new insights into the structure, function and emergent properties of natural ecosystems. For example, holistic ecosystem models may present the most viable route to exploring feedbacks across larger temporal and spatial scales and/or across ecosystem domains, and to test hypotheses about the origins of ecosystem stability, resilience and sustainability. These models could supercharge field research by directing attention towards key processes and data gaps, and would be an invaluable tool for guiding the management of natural environments.

Inspired by modelling approaches in the marine and freshwater environments, and building on existing knowledge of simple ecosystems and individual ecosystem domains, we are developing a terrestrial Virtual Ecosystem that replicates the many connections among individual organisms and their complex interactions with the abiotic environment. Here, we outline our approach to developing such a holistic ecosystem model, and illustrate the key ecosystem processes being simulated and the ecosystem states being predicted. We argue that such models need to be based on organismal physiology, with an emphasise on environmental temperature as a driving abiotic factor. We argue that holistic ecosystem models can reveal the emergent properties of ecosystems that data alone cannot, and highlight new insights that could emerge. Despite the apparent bewildering level of complexity required to develop such models, we make a positive case for achieving this ambitious goal.

The Virtual Ecosystem

We are developing a holistic ecosystem model that is designed explicitly to elucidate ecosystem-level emergent phenomena from the perspectives of a wide variety of users and disciplines: the Virtual Ecosystem (Box 1; Virtual Ecosystem Project Team 2024). This model is designed to replicate the basic physiological processes that determine the birth, growth, reproduction and survival of microbes, plants and animals, and the physical processes that determine microclimate and hydrology, which in turn affect, and are affected by, the biotic domains (Figure 1). The Virtual Ecosystem attempts to simultaneously balance the budgets for energy, water, carbon, nitrogen and phosphorus, which will emerge from cycling of matter through plant, animal and microbial functional groups. Organismal physiology, including the dependence of vital rates (e.g. birth, death, metabolism) on temperature and body size (Gillooly et al. 2001, White et al. 2006), drives the biotic domains of the model, with stoichiometry – the balance of carbon, nitrogen and phosphorus within organisms (Sterner and Elser 2002, Agren 2008, Cherif and Loreau 2013) – also playing a central role. There is close coupling between the biotic and abiotic world, and abiotic processes like the movement of heat and water are based on first-principles physics (Maclean and Klinges 2021). Finally, we focus on replicating processes across the spatial and temporal scales defined by our set of user stories (Box 1). These mandate a spatial extent encompassing the typical area of natural area management that range from 1 to 40,000 ha (UNEP-WCMC and IUCN 2024), and time scales that run the gamut from short-term management windows (≥ 1 year) to the long-term data series of decades that are needed to adequately detect changes in ecosystem resilience (Boulton et al. 2022).

We represent the plant, animal and microbe domains as functional groups, as defined by trophic interactions, which provides a tractable means of capturing the myriad species interactions that characterise complex terrestrial ecosystems. We do so because what matters in terms of ecosystem dynamics and the resulting emergent phenomena is not the taxonomic identity of a species, but rather the role it plays in ecosystem dynamics be it a primary producer, a consumer or a decomposer. Use of functional groups rather than individual species is routinely considered a necessary trade-off when integrating biodiversity into complex ecosystem models (Geary et al. 2020). Ultimately, it will be computational constraints that limit the diversity of functional groups that can be incorporated into the model, as the number of among-group interactions that need to be replicated increase combinatorially with the number of groups. Where appropriate for a user (Box 1), one or more functional groups can be narrowed down to reflect a target species of interest (Rüger et al. 2020), allowing for species-specific questions to be addressed within the Virtual Ecosystem. Moreover, neutral models can be used to estimate the diversity and abundance distributions of species within functional groups (Fernandes et al. 2022), enabling the Virtual Ecosystem to address biodiversity questions from a species perspective.

Our first Virtual Ecosystem model is based on the Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al. 2011), located in the tropical rainforests of Sabah, Malaysia. Researchers at SAFE have generated open-access data that encompasses large swathes of the ecosystem (https://zenodo.org/communities/safe), from the relative abundance and ecosystem energetics of plant (Both et al. 2019, Döbert et al. 2019), animal (Fayle and Ewers 2018, Sharp et al. 2018, Heon et al. 2020, Mitchell et al. 2020) and microbial taxa (Tin et al. 2017, Robinson et al. 2020, Elias 2021), to ecosystem processes (Ewers et al. 2015, Riutta et al. 2019, Mills et al. 2023) and the abiotic environment (Nainar et al. 2012, Hardwick et al. 2018, Riutta et al. 2020, Drewer et al. 2021).

Our larger goal is to generalise the Virtual Ecosystem once it is tested and validated with the SAFE data. The basic set of ecosystem processes that drive tropical rainforests are shared in common with other complex ecosystems. The vital biological processes (e.g. growth, survival and reproduction) underly the trophic interactions that form the fundamental building blocks of all communities, the allometries that connect those processes to body size, and abiotic drivers such as temperature and hydrology, are all universally applicable to all terrestrial ecosystems (Fig. 1). Similarly, the basic functional groups in a tropical forest are no different to those of other ecosystems. We define functional groups in terms of trophic interactions (producers, primary consumers and secondary consumers) and shared organismal characteristics based on taxonomy (e.g. plant *vs.* invertebrate *vs.* vertebrate), physiology (ectothermic *vs.* endothermic) and morphology (small *vs.* large bodied). Theis equivalence of processes and functional groups ensures the basic structure of the Virtual

Ecosystem will apply across other ecosystems in different geographic locations. That basic structure would need expanding to encompass large environmental differences: by working in a lowland tropical forest we have no need to simulate processes related to snow, ice and frost tolerance, for example. For ecosystems whose dynamics are adequately encompassed by the set of processes modelled in the Virtual Ecosystem, parameterising them with location-specific biotic and abiotic data should capture the fundamental similarities and differences among different ecosystem types (Harfoot et al. 2014, Slevin et al. 2015).

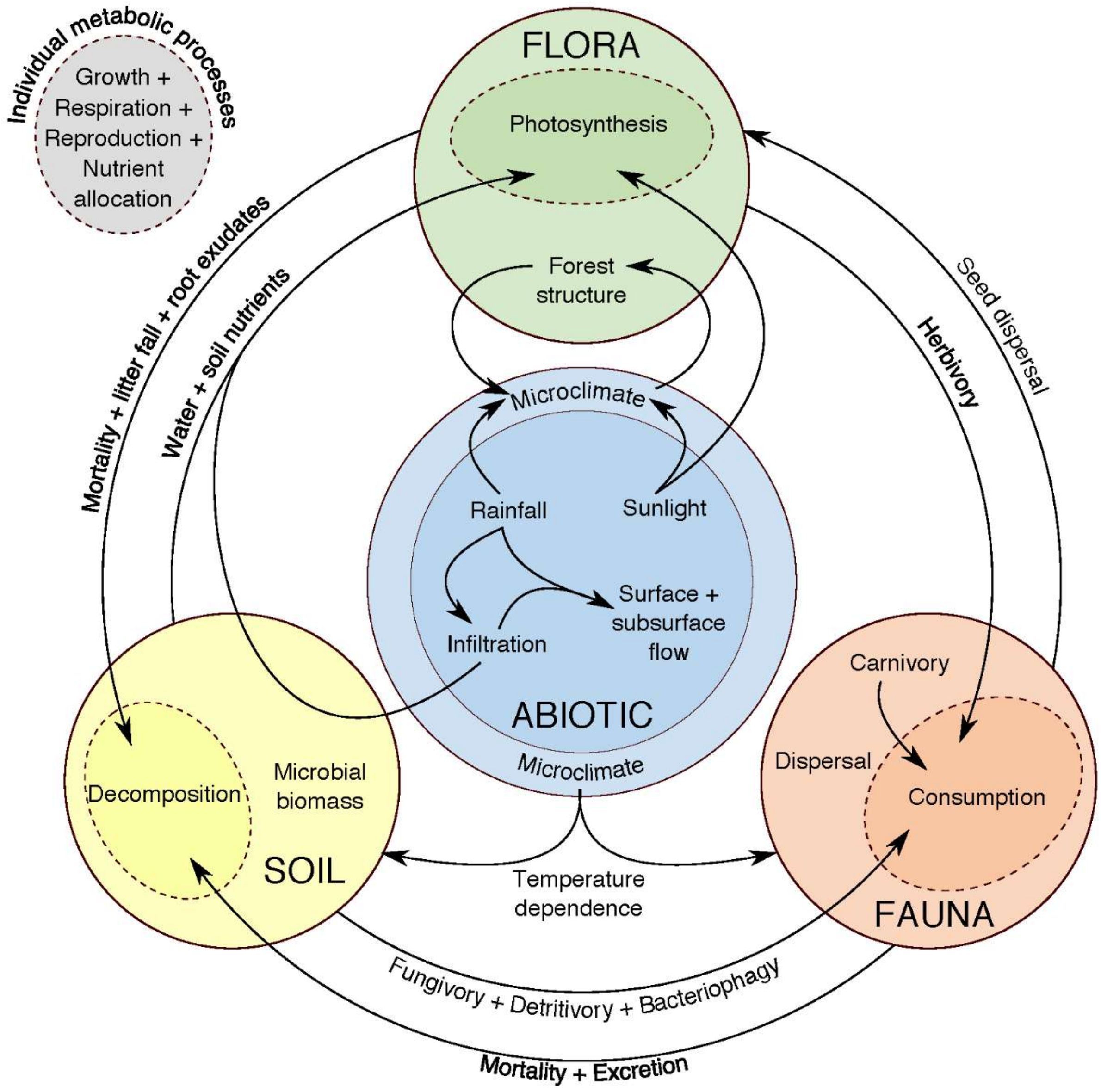

Figure 1. The key processes incorporated into the Virtual Ecosystem. The model replicates the ecosystem dynamics in four ecological domains, each constructed as a separate module generating the dynamics of plants, animals, soil and the abiotic environment respectively. The key metabolic processes that operate at the scale of individual organisms – plants, animals and microbes – are incorporated into the plant, faunal, and soil modules respectively. Modules will be dynamically connected through the transfer of matter and energy.

The Virtual Ecosystem implements a map of the key states and processes that both describe and drive complex ecosystems. Our understanding of ecosystem-level connections is an adaptive one, meaning this map is a continuously evolving thought experiment that is routinely updated in response to feedback we receive from colleagues and reviewers, and our own learning as we progress step-by-step through the process of converting the map into code. We use a pattern-oriented modelling approach to ensure we incorporate the minimum number of processes required to adequately replicate the ecosystem-level patterns being investigated (Grimm et al. 2005, Grimm et al. 2017). Currently, we have identified roughly 100 state variables that can be measured and validated, and that are targets for the model to predict. These state variables encompass physical variables like soil temperature and light intensity, and biological variables like canopy height, the abundance of animal functional groups, and the ratio of bacteria to fungi in soil. Because the Virtual Ecosystem is a circular system, each state variable and functional group is both a dependent variable that responds to changes in downstream parameters and functional groups, and also an input for state variables and functional groups connected upstream.

The Virtual Ecosystem has approximately 100 processes characterised by that many state variables (representing variables such as the abundance and biomass of functional groups, and resource pools such as the quantity of faeces in the soil), through which water, energy and nutrients are either converted in form or passed from one functional group or resource pool to another. Example processes include denitrification, surface runoff, resource acquisition and animal dispersal. Finally, our thought experiment identifies more than 300 edges connecting the model states to processes. While daunting, this complexity is manageable for two reasons. First, there is a formidable body of knowledge that directly examines the large majority those state variables, processes and their connections, both individually and in combination, giving a theoretical basis to build from. Second, ecologists have discovered some universal, first-principle rules – such as the scaling of vital rates with body size and temperature (Brown et al. 2004) – that allow us to represent this complexity in a tractable way.

Our modelling framework has a modular structure that largely aligns with the four key domains of an ecosystem (plants, animals, soil microbes and the abiotic environment; Figure 1) in a spatially and temporally explicit framework. This modular structure allows users to substitute particular modules with alternative formulations geared towards a particular ecosystem of interest, should they wish. We have developed the Virtual Ecosystem using the Python programming environment (Van Rossum and Drake Jr 1995), an open-source software that is freely available and widely used within our anticipated user community, and is well-suited to rapid development and adaptation. We use industry-standard Python coding practices, including enforcing static-type checking (‘mypy’) and code quality (via ’ruff ’) using the ’pre-commit’ framework. We run comprehensive unit testing using ’pytest ’ to ensure consistent behaviour of code updates. All new code is accepted through peer-reviewed pull requests to the development branch that must pass quality checks. The code is publicly available from GitHub (https://github.com/ImperialCollegeLondon/virtual_ecosystem) to facilitate community engagement with model development.

Box 1

User stories are a project management tool used to help define what would constitute success for a project. Here, we list eight example user stories of equal importance that would define success for a holistic ecosystem model. For the model to be considered fully successful, the requirements of all user stories would need to be met.

1. As a systems ecologist, I will be able to identify any core components and sub-networks that exert strong control over the full system dynamics, so that I can understand the mechanisms underlying ecosystem stability.
2. As a disturbance ecologist, I will be able to track the attenuation of external perturbations through the system, so that I can understand the mechanisms underlying ecosystem resilience.
3. As a sustainability scientist, I will be able to calculate the rate at which ecosystem services are provided, so that I can make predictions about the long-term sustainability of the ecosystem.
4. As a biogeochemist, I will be able to track the flow of carbon, nitrogen and phosphorus through the ecosystem, so that I can quantify elemental balances and residence times.
5. As a hydrologist, I will be able to predict the frequency and magnitude of flood events, so that I can design downstream flood defences.

6. As a field ecologist, I will be able to identify knowledge gaps that significantly impair our ability to predict ecosystem dynamics, so that I can prioritise future data collection activities.
7. As an applied ecologist, I will be able to examine the impact of climate change and extreme climatic events on ecosystem dynamics, so that I can predict the likely future state of the ecosystem.
8. As a resource manager, I will be able to predict the outcomes of competing sets of management strategies, so that I can make informed decisions about implementing cost-effective management actions.

First principles, organismal physiology and environmental temperature

Our goal is to build a holistic ecosystem model based on first principles: replicating ecological processes to predict empirically observed patterns, and to predict how these patterns may change under ongoing anthropogenic perturbations (e.g. climate change, habitat destruction, and logging). This approach ensures the Virtual Ecosystem is rooted in ecological theory and provides a strong basis for predicting future outcomes under hitherto unobserved environmental conditions (Evans et al. 2012, Connolly et al. 2017). Moreover, a process-based modelling approach can help avoid the potential problems with overfitting that can arise when models are parameterised using empirical data and subsequently validated with the same data (Schuwirth et al. 2019, Dittmer et al. 2023). Overfitting represents an extremely pervasive and difficult problem when dealing with large and complex systems (San Miguel et al. 2012, Dittmer et al. 2023), which terrestrial ecosystems undoubtedly are.

We argue that a holistic ecosystem model building from first principles must start with the physiology of individual organisms – the “elementary particles of all ecological systems” (Evans et al. 2012). A common set of processes – photosynthesis, respiration and metabolism – underlie all life, and it is these processes that we collectively refer to as “physiology.” The survival, growth and reproduction of any individual organism is ultimately driven by its ability to meet their metabolic, energetic and stoichiometric – i.e. their physiological – needs. These basic physiological processes therefore underpin all trophic (consumer-resource) interactions that take place in the ecosystem and can, in turn, become a dominant cause of mortality. Physiology, then, drives the interactions among organisms and functional groups, which in turn gives rise to population and community dynamics, and ultimately the emergent properties of ecosystems. These basic principles apply regardless of which life domain an organism belongs to.

The biochemical processes such as reaction kinetics and enzyme activation that underlie organismal physiology are all temperature-dependent. Endotherms regulate their body temperature to ensure their biochemical process rates are largely decoupled from the environmental temperature in which they exist. But ecosystems are dominated by ectotherms rather than endotherms (Bar-On et al. 2018), and the biochemistry and physiology of ectotherms *are* strongly linked to environmental temperature (e.g. Kern et al. 2015), Moreover, endotherms are indirectly affected by temperature due to their interactions with ectothermic resources, mutualists and natural enemies. Temperature, therefore, must also play an integral role in a holistic ecosystem model. The single word "temperature," however, hides a world of variation. Soil scientists focus on soil temperature, plant ecophysiologists on leaf temperature, and invertebrate ecologists on ground- or litter-layer air temperature. Moreover, to understand soil microbial respiration rates, what matters is the mean and distribution of soil temperatures (Liu et al. 2018), whereas invertebrate development rates are more commonly linked to cumulative temperatures and degree days (Quinn 2017), and mortality of larger organisms is more likely driven by extreme temperatures (Ratnayake et al. 2019). In the Virtual Ecosystem, then, we have chosen to model microclimate – temperature and humidity – from the top of the canopy to below the ground as part of the holistic ecosystem model, ensuring the model predicts all elements of environmental temperature that matter for organismal physiology.

From general ecosystem models to holistic ecosystem models

There have been a number of general ecosystem models developed since Odum's (1957) groundbreaking effort to study the Silver Springs aquatic ecosystem – the first general ecosystem model. A number of general ecosystem models have since been developed (e.g. Fitz et al. 1996, Kimball et al. 1997, McKane et al. 1997, Clein et al. 2000, Childress et al. 2002, Harfoot et al. 2014). There is an even larger set of models have been developed to investigate ecosystem dynamics without claiming to be general ecosystem models (e.g. Dickinson and Henderson-Sellers 1988, Harris et al. 2004, Best et al. 2011, Clark et al. 2011, Fatichi et al. 2012, Maxwell and Condon 2016). The problem, however, is that all of these modelling attempts omit one or more of the key domains of terrestrial ecosystems: plants, animals, microbes and/or the abiotic environment.

There are examples of ecosystem models that encompass each of the domains of plants, animals, soil microbes and the abiotic environment. For example, basic physiological principles have been used to replicate patterns of animal biomass and trophic structures (Harfoot et al. 2014), the enzymatic processes that generate soil microbial respiration have been modelled (Sihi et al. 2018, Fatichi et al. 2019), and there are multiple examples of microclimate (Kearney et al. 2014, Maclean and Klinges 2021) and hydrological models (Paniconi and Putti 2015). The most recent crop of general ecosystem models have begun to connect these pieces. These models focus on investigating tree dynamics while incorporating tree physiological, hydrological and biogeochemical processes (e.g. Best et al. 2011, Clark et al. 2011, Fatichi et al. 2012, Fyllas et al. 2014, Christoffersen et al. 2016, Maréchaux and Chave 2017, Rödig et al. 2017), although they still mostly ignore the role of animals (Harfoot et al. 2014) and soil microbes (Crowther et al. 2019). This void exists despite newly emerging evidence that animals may consume as much as half of net primary productivity (Malhi et al. 2022), and that microbes may control rates of soil organic matter turnover (Crowther et al. 2019) and even plant species composition (Yan et al. 2022). Ecosystems are efficient nutrient recyclers and everything that lives must eventually decompose (Wardle 2002). However, even advanced ecosystem simulators routinely gloss over the decomposition half of the dynamics that drive an ecosystem.

Encouragingly, progress is being made in connecting those domains, albeit largely in a pairwise fashion. Examples include the use of optimality theory (Prentice et al. 2014) to connect microclimate with plant ecophysiology (Joshi et al. 2022), linking evapotranspiration to hydrological regimes (Sandoval et al. 2023), connecting hydrological and biological dynamics above- and below-ground (Childress et al. 2002), and tying hydrometeorology to the carbon cycle (Paschalis et al. 2015). At the other extreme, heavily simplified ecosystem models have been generated that connect the domains of plant, animal and soil microbes to biogeochemical cycles (Zou et al. 2016, Rizzuto et al. 2024). To date, however, these provide only highly abstracted representations of real-world systems, investigating the connections among domains without considering processes occurring within those domains. If we are to understand the workings of complex ecosystems and predict their future in an ever-changing world, we need realistic depictions of the key biotic interactions and their feedbacks with abiotic drivers.

We argue that holistic ecosystem models like the Virtual Ecosystem hold the promise for developing a more universal modelling framework above and beyond that provided by the current generation of general ecosystem models. Such a framework will focus on how physiological processes at the organismal level translate into higher level processes driven by the interactions among organisms and ecosystem domains. It will encompass a broader set of processes within each domain, building on basic physiological processes to connect them with the demographic processes of birth, growth, reproduction and mortality, and the interactions such as predation, competition and mutualism that drive population and community dynamics. The holistic approach will track the movement of matter within and among domains, balancing the budgets for energy, water and carbon, as well as key nutrients such as nitrogen and phosphorus. Moreover, those biogeochemical cycles will be directly connected to the demography of the living organisms that consume, store and process those nutrients. By necessity, this will require the movement of matter among domains, such as the consumption of plants by animals, and the recycling of nutrients through the decomposition of dead organisms in the soil.

Novel insights to be gained from holistic ecosystem models

Unifying perspectives and getting the right answer for the right reason

The questions that theoretical and applied ecologists ask are as varied as the systems they study. Ecologists are an extraordinarily diverse group of scientists, encompassing biodiversity scientists, population and community ecologists, soil scientists, biogeochemists, hydrologists, climate scientists and everything in between (see Box 1). Members from every corner of this diverse group of researchers could all descend on the same ecosystem at the same time, collect their data and, based on their understanding of their particular domain, generate defensible conclusions about how the system works and what the most important parts of the system are. A whole system understanding needs to unify their answers, and should make it impossible to get the "right" answer for the "wrong" reason. If we can accurately predict population dynamics of key species, for example, but doing so leads to a predicted nitrogen budget that is wildly imbalanced, then our system-level understanding is incomplete. We argue that all of these perspectives on an ecosystem should be reconcilable because they are, after all, describing exactly the same system at exactly the same time.

A holistic ecosystem model should encompass the needs of the diverse group of scientists that wish to study a given ecosystem. Each of our different user groups (Box 1)may have different opinions as to what "matters" in an ecosystem, and all of these focal points are important: none are more right or more wrong than any other. What does matter, however, is that ecology delivers a framework that allows these diverse viewpoints on a single system to be reconciled within a common framework. Holistic ecosystem models like the Virtual Ecosystem constitute a key step towards achieving this goal.

The role of cross-scale and cross-domain feedbacks

Any ecosystem has thousands upon thousands of individual interactions among organisms and their environment operating simultaneously at any given time, and the web of connections among those interactions generates positive and negative feedback loops. Stable ecological systems typically arise when positive feedbacks are dampened (Coyte et al. 2015) and negative feedbacks are strengthened

(Landi et al. 2018), but exactly what are the feedbacks in complex ecosystems and how does the balance of negative and positive forces emerge?

Feedbacks in complex ecosystems arise from biotic interactions within and between functional groups, which themselves occur within and between domains. Abiotic factors cannot in themselves generate these density- and frequency-dependent feedbacks, but can alter their strength and magnitude. For example, interactions between non-linear feedback loops and environmental variability at the scale of a functional group or domain can lead to the emergence of new phenomena. These new phenomena cannot be predicted solely by the lower scale functional group or domain dynamics in the absence of environmental variability at those lower scales. This is the idea of scale transition (Chesson 2012) that underpins the cross-domain and cross-scale feedbacks that abound in complex ecosystems. Complex ecosystems have myriad, non-linear feedback loops, the net outcome of which determines the overall system dynamics. The advantage of holistic ecosystem models such as Virtual Ecosystem is that the focus on the key biotic interactions and abiotic drivers ensure that these feedbacks arise naturally and are resolved as they transition from one spatial and/or temporal scale to another. As a result, these models can reliably characterize the overall ecosystem dynamics, as well as predict how these dynamics may change under altered environmental conditions.

Indeed, examples of cross-scale and cross-domain feedbacks abound. Bacteria operate at temporal and spatial scales that are orders of magnitude smaller than those of elephants, which in turn are orders of magnitude smaller than those of long-lived tropical trees, and yet there are strong, pairwise feedbacks between these domains (Coyte et al. 2015, Beugnon et al. 2021, Li et al. 2022, Ong et al. 2023). Other closely coupled feedbacks occur at very high frequency, such as the connection between photosynthesis in the canopy domain and soil moisture in the soil domain (Joshi et al. 2022). Consumer-resource feedbacks can similarly operate in concert, despite clear biological differences between interacting functional groups. For example, the fractal scaling of body sizes ensures large animals can feed simultaneously with small animals (Holling 1992), causing high frequency resource competition among functional groups whose physiology varies over multiple orders of magnitude in body size. At larger spatial and temporal scales, low level resource flows across habitat compartments can increase the stability of food webs (Huxel and McCann 1998), suggesting functional groups that serve to connect ecosystem domains – such as those that forage both on the ground and in the canopy – might be key determinants of ecosystem stability. Finally, the connections of the nitrogen and phosphorus cycles among the domains of plants, soil and soil microbes are poorly described, yet the fact that those connections exist (Čapek et al. 2018) means the underlying cross-domain feedbacks must also exist.

There are often substantial knowledge gaps in how individuals, energy and matter interact across scales and between ecosystem domains, but these have potential to generate powerful feedbacks and emergent phenomena (e.g. Knight et al. 2005, Kamaru et al. 2024). If we are to understand emerging ecological patterns, we have to be able to elucidate the sign and magnitude of cross-scale and cross-domain feedback loops. This is because the characteristic signatures observed at larger scales invariably result from processes acting at smaller scales. For example, root-microbe interactions that operate belowground and at hourly time scales can determine aboveground carbon storage in trees over decadal time scales (Jevon and Lang 2022). The same scale transition is observed when non-random patterns of seedling mortality at ground level on the scale of days and months (Engelbrecht et al. 2007, Comita et al. 2010) might result in seemingly neutral coexistence of adult trees in a forest canopy on the scale of centuries (Hubbell 2001), because density-dependence has already operated on the seedling stage and is no longer apparent when adult trees are studied in isolation. These hidden feedbacks that cross scales and domains can represent powerful forces that determine the structure and dynamics of ecosystems, and models that replicate those processes across similarly diverse scales and domains will be required to gain insight into their actions.

Mechanisms of stability, resilience and sustainability

Natural environments generate ecosystem services through the combined actions of millions of interacting individual plants, animals and microbes all growing, respiring and reproducing simultaneously. This web of interactions in turn determines the stability (Tylianakis et al. 2006, Karp et al. 2011), resilience (Karp et al. 2011, Ewers et al. 2015) and sustainability (Fontaine et al. 2005, Wagg et al. 2014) of those ecosystem services. Yet exactly how the physiological processes underlying individual growth, survival and reproduction translate into ecosystem services, and whether this transition can continue to occur unimpeded in a changing world, are questions that defy easy answers (Wagg et al. 2014).

Field experiments can reveal the dynamical outcomes of individual ecological processes within a habitat, but experiments to understand emergent system properties are seldom tractable (Fayle et al. 2015). Yet many of the desired traits for ecosystems are emergent phenomena such as stability, resilience and sustainability, all of which arise from the non-linear feedbacks that occur within and between different ecosystem components. Holistic ecosystem models like the Virtual Ecosystem provide a way to integrate behaviour from individual processes into a virtual environment, and thereby provide a more pragmatic tool for exploring what controls the emergent properties of complex ecosystems (Peck 2004). This will open the door for using systems theory to test explicit hypotheses about the origins and maintenance of stability, resilience and sustainability (Figure 2). For example, systems theory suggests that highly connected actors within complex systems can form core networks that exert strong control over emergent system properties (Kitano 2002, Mariani et al. 2019), but are there any such core actors in ecosystems (Fig. 2b)? Moreover, how does this complex systems concept of core actors relate to ecological concepts such as ecosystem engineers (Jones et al. 1994), keystone species and keystone communities (Mouquet et al. 2013)? Similarly, do ecosystems buffer the impact of external perturbations by diffusing their impacts through the many actors and organisational layers that comprise the system (Mariani et al. 2019), and can this explain the origin of ecosystem resilience (Suweis et al. 2015) (Fig. 2c)? And finally, to what extent can ecosystems sustainably deliver ecosystem services in the face of external environmental pressure (Fig. 2d)? Questions of this nature cannot be answered through the collection of empirical data alone, or through models that cannot realistically capture the many feedbacks and cross-domain processes that connect real-world ecosystems. They can, however, be tackled with the tools provided by holistic ecosystem models.

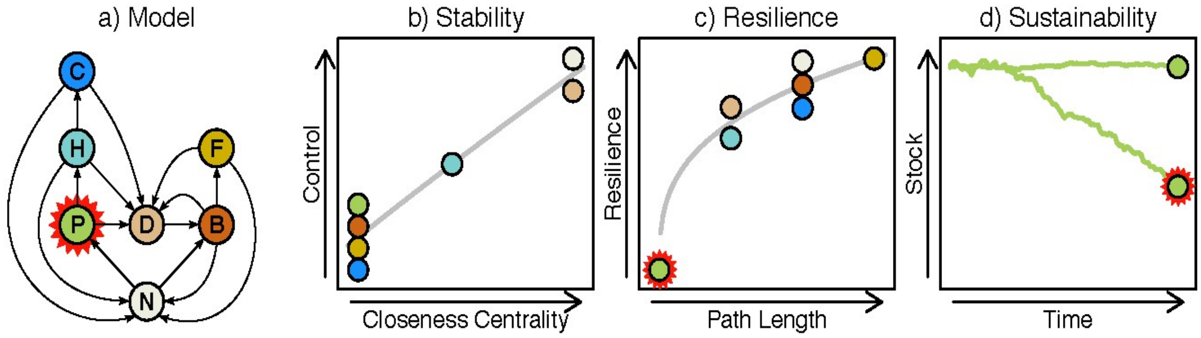

Figure 2. Three hypotheses about the emergent properties of rainforest ecosystems that can be tested using holistic ecosystem models. (a) A representation of a simplified ecosystem model adapted from Zou et al. (2016). Circles represent mineral nutrients (N), primary producers (P), herbivores (H), carnivores (C), detritus (D), decomposers (B) and the predators of decomposers (F). Black arrows indicate the flux of nutrients between system components. Red sunburst indicates a direct impact of an environmental perturbation on one component, illustrated here as an impact of climate change on primary producers. (b) Connected components – quantified by metrics such as closeness centrality (Jordán et al. 2007) – exert stronger control over system stability. (c) Components that are more distantly linked – quantified by metrics such as path length (Fath et al. 2019) – to environmental perturbations have increased resilience to that perturbation. (d) Stocks of ecosystem services are sustainable in a steady state system, but become unsustainable in perturbed ecosystems.

Better understanding is a prerequisite for better conservation

Holistic ecosystem models have the potential to become a powerful tool for managing natural environments. Conservation may often focus on single species or single threats (Geary et al. 2020), but by ignoring the many interactions, feedback loops and dependencies among species and ecosystem domains, the resulting conservation actions can generate perverse ecological outcomes (e.g. Zavaleta et al. 2001, Buckley and Han 2014, Skern-Mauritzen et al. 2016, Geary et al. 2020). Holistic ecosystem models present the opportunity to implement whole ecosystem management through *a priori* adaptive management: running a virtual experiment on a set of feasible management strategies and choosing the most cost-effective one to implement, without waiting for years for field results before improving the existing management plan. Understanding the likely impact of a conservation intervention before committing to that intervention represents a bottleneck in conservation planning that empirical data is struggling to fill (Christie et al. 2020). Moreover, many experiments must run for years or even decades to get the results needed to inform decisions that must be made now (Cusser et al. 2020, Naidu et al. 2022). The fact that they can be experimented on makes a holistic ecosystem model a powerful tool in adaptive management (Geary et al. 2020). Simulation experiments, conducted in the virtual world rather than the real world, can get results faster and cheaper than matching field experiments, and without running into ethical concerns about experimenting with threatened landscapes or species (Crozier and Schulte-Hostedde 2015).

In silico experiments on system models have been used to great effect in aiding decision making in economics (Burgess et al. 2013) and healthcare (Marshall et al. 2016), including guiding responses to the COVID-19 pandemic (McBryde et al. 2020), and have long been a central component of public and policy discussions around climate change (Steffen et al. 2020). We anticipate similar benefits could be obtained from holistic ecosystem models. Examining model outcomes in response to potential conservation interventions can give insight into the likely effectiveness of those interventions, potentially saving time and money by identifying ineffective actions before implementing them. This approach will also empower adaptative management approaches (Westgate et al. 2013), particularly in time-sensitive situations involving highly threatened ecosystems where we lack time to implement and then learn from a set of conservation actions. Similarly, holistic ecosystem models are more likely to predict how indirect effects might cascade through an ecosystem (Kamaru et al. 2024), helping avoid unintended outcomes from conservation interventions (Zavaleta et al. 2001, Larrosa et al. 2016, Pearson et al. 2022), and thereby preventing the solution to one problem from becoming the origin of another. Finally, models could be used to aid complex management decisions about how to optimise the value of an ecosystem when that ecosystem provides multiple values which might trade-off against each other (Rodríguez et al. 2006). Dynamic simulations using carefully parameterised, holistic ecosystem models provide a viable and tractable tool for predicting the optimal combinations of management actions to guide the behaviour of complex systems such as natural environments towards a desired, future state.

History tells us holistic ecosystem models are feasible

There is no doubt that constructing a holistic ecosystem model, like the Virtual Ecosystem, is an ambitious goal. But is it feasible? The history of modelling complex systems gives us cause to believe that it is. Across the breadth of the natural sciences, the trajectory has been clear: systems of ever-increasing complexity have been tackled and successfully replicated in computer models, and complex models that were once considered impossible have been successfully constructed. For example, the modelling community that first attempted to construct global digital vegetation models (e.g. Prentice et al. 1992, Neilson and Marks 1994, Foley et al. 1996) endured numerous conversations in which they had to defend the feasibility of their goals (Colin Prentice, *pers. comm.*), and yet these are now a standard component of global climate models (e.g. Drüke et al. 2021, O'ishi et al. 2021). Similarly ambitious attempts have been made to construct the first models of soil microbial systems (Fatichi et al. 2019) and to replicate the basic patterns of animal life at planetary scale (Harfoot et al. 2014). And finally, the class of general ecosystem models that has emerged over the past decade has begun to successfully tie together multiple ecosystem domains, knitting plant ecophysiology with microclimate (Joshi et al. 2022), hydrology (Sandoval et al. 2023), biogeochemistry (Paschalis et al. 2015) and soil microbial processes (Sihi et al. 2018, Fatichi et al. 2019). It remains now to tie all of these ecosystem domains together into a single, unified ecosystem model. We see holistic ecosystem models as a logical next step, and the history of pushing the limits of what can be done, and of having succeeded when pushing those limits, gives us confidence that this next step is achievable.

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