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Forest ecosystem properties emerge from interactions of structure and disturbance

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Forest structural diversity and its spatiotemporal variability are constrained by environmental and biological factors, including species pools, climate, land-use history, and legacies of disturbance regimes. These factors influence forest responses to disturbances and their interactions with structural diversity, potentially creating structurally mediated emergent properties at local to continental spatial scales and over evolutionary time. Here, we present a conceptual framework for exploring the emergent properties that arise from interactions between forest structural diversity and disturbances. We synthesize and present definitions for key terms, including emergent property, disturbance, and resilience, and highlight various types and examples of emergent properties, such as (1) interactions with species composition, (2) interactions with disturbance frequency and intensity, and (3) evolutionary changes to communities. Although emergent properties in forest ecosystems remain poorly understood, we describe a foundation for study and applied management of forest structural diversity to enhance forest restoration and resilience.

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Climate, species, and land-use history each affect spatiotemporal variations in forest structural complexity (Ehbrecht *et al*. 2021). Forest structural diversity – defined as the volumetric capacity and physical arrangement of biotic components within ecosystems (LaRue *et al*. 2023) – has consequences for ecosystem function and resilience. Forest structure is often quantified with metrics including tree diameter and height, stand density, biomass, or basal area, whereas structural diversity integrates three-dimensional (3D) forest structure and species diversity. Accurate forecasts of forest *resilience* – an ecosystem's capacity to recover fundamental structures, processes, and functions after disturbance (Chambers *et al*. 2014) – and *resistance* – an ecosystem's capacity to maintain fundamental structures, processes, and functions despite disturbances (Chambers *et al*. 2014) – depend on the generalizability of interactions and feedbacks between forest structural diversity and disturbance.

In a nutshell:

- Forest structural diversity emerges from past and present environmental and biological factors
- Disturbances affect forest ecosystem structure and function at multiple spatial and temporal scales, and forest structure can alter disturbance characteristics
- Structure–disturbance interactions can result in unique, emergent properties of forest ecosystems and disturbance feedbacks with structural characteristics can be better anticipated through cross-system comparisons
- Evolutionary processes can change forest emergent properties for both forests and species via complex feedback loops
- Understanding emergent properties in forest ecosystems provides a foundation for management of forest structure to increase ecosystem resilience

Of particular importance is the consideration of emergent properties, defined here as novel ecological properties that develop in a nonlinear and often cross-scale manner in response to spatial variation in, or temporal change to, forest structural diversity (Panel 1; WebTable 1). Detailed information about emergent properties is lacking for most forests because (1) they are difficult to predict from knowledge of independent components or from lower hierarchical levels alone (Odum and Barrett 1971); (2) they vary in space and time (Davies and Asner 2014; Atuo and O'Connell 2017); and (3) insufficient pre-disturbance measurements and the role of contingent and stochastic factors in ecosystem responses make connecting structural diversity–disturbance and dynamics–ecosystem relationships challenging (Fukami 2015; Burton *et al*. 2020). Here, we synthesize recent findings from new technology and research to scaffold our knowledge, better frame future scientific questions, and equip scientists and managers to anticipate emergent effects of forest structural diversity.

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As constrained by broad-scale factors (including environment, biota, and historical legacies), interactions between physical structure and disturbance can give rise to emergent properties in forests (Figure 1). Forest structural diversity mediates how environmental and biological factors interact in 3D space (Shugart *et al*. 2010). Structurally diverse forests support faunal communities with diverse taxonomic compositions, trophic guilds, and niche specializations (Campos-Silva and Piratelli 2021), thereby shaping the functional organization of forest ecosystems (Figure 2) (Shugart *et al*. 2010). Forest structural diversity is spatially and temporally variable and routinely modified by natural and anthropogenic disturbances, including windstorms, fire, floods, silviculture, invasive species, insect outbreaks, and land development. We define a disturbance (WebTable 2) as a discrete event that alters organisms' abundance or spatial distributions and changes the structure of a population, community, or ecosystem (Panel 1) (White and Pickett 1985; Paine *et al*. 1998). Therefore, forest structural diversity is determined by environmental and biological factors, and the spatiotemporal legacies of disturbance events and recovery.

Although forest structure responds directly to disturbance, structural diversity may influence ecosystem resilience and resistance by mitigating or amplifying disturbance effects (Figure 3; WebTable 3). For disturbances like hurricanes, structure shapes how force is transmitted through forests at multiple spatial scales, from individual trees to stands and regions, which in turn influences the magnitude of tree mortality at those scales (Kim *et al*. 2020). Structure also mediates disturbances like insect outbreaks through temporal synchronization of tree sizes, health, and stand density (Jactel and Brockerhoff 2007), or spatially via fuel continuity of contagious disturbances like fire (McWethy *et al*. 2014). Forest structural diversity can therefore act both as a limiting factor and as a catalyst of disturbance (Burton *et al*. 2020).

In this synthesis, our goals are to (1) summarize the drivers and constraints of forest structural diversity that influence disturbances and emergent properties, (2) outline interactions between forest structure and disturbances, and (3) examine how structure–disturbance interactions may result in emergent properties. Although we recognize that soil, coarse woody debris, understory vegetation, and other structural

Panel 1. Structure–disturbance–resilience relationships

Definitions

Structure: the size, quantity, and arrangement of vegetation and related features.

Structural diversity: the volumetric capacity and physical arrangement of biotic components within ecosystems (LaRue *et al*. 2023).

Disturbance: a discrete event that alters spatial distribution or abundance of organisms leading to substantial changes in the structure of an ecosystem, community, or population (White and Pickett 1985; Paine *et al*. 1998).

Emergent property: a novel ecological property that develops in a nonlinear and often cross-scale manner in response to spatial variation in, or temporal change to, forest structural diversity. For example, numerous lineages of vertebrate gliders in Borneo emerged over millions of years as an interaction of stable climate, low disturbance, and species pools that fostered the structural diversity of its tropical dipterocarp forests (Figure 2).

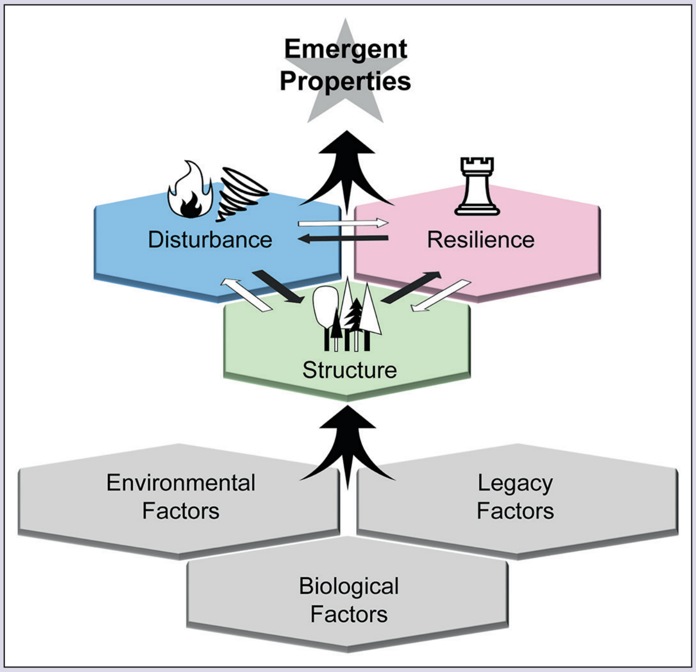

Figure 1. Conceptual diagram of how emergent properties arise from interactions between forest structure, disturbance, and resilience, while constrained by environmental, biological, and legacy factors.

Approach

Structure is just one of many measurable characteristics of a forest ecosystem, and it influences and is influenced by the system's disturbance regime and resilience. Here, we examine the emergent properties that arise from the complex interactions of structure, disturbance, and resilience. These three factors are also influenced by many other ecosystem constraints and conditions, including environmental factors, species present in a given biological community, and ecological legacies. Describing emergent properties requires understanding both their contextual drivers (discussed in the "Environmental, biological, and legacy factors constrain forest structural diversity" section) as well as the emergent properties themselves (discussed in the "Forest structural diversity and disturbance interact through time" and "Structure–disturbance interactions lead to emergent properties" sections).

characteristics influence disturbance dynamics, we focus on overstory vegetation structure because most studies are conducted at this level. This framework will facilitate the study of properties that emerge from interactions between structural diversity and disturbances, underscoring the need to quantify these processes for supporting predictive models of ecosystem response and resilience.

Environmental, biological, and legacy factors constrain forest structural diversity

Forest structural diversity is constrained not only by its abiotic context, regional species pool, and historical contingencies that contribute to regional assemblages (Figure 3) (Fukami 2015) but also by climate and by topographic influences on those climatic constraints. Evolutionary adaptations to climate include variability in forest stratification, size (eg basal area by species), canopy architecture, and foliage characteristics (Gratani 2014). For instance, short vegetation stature, sparse crown volume, and smaller leaf area are characteristics of tropical dry forests that minimize water loss, whereas the broad-leaved, discoid, and tall canopies characteristic of tropical humid forests increase sunlight interception (Terborgh 1985).

Forest structural diversity is a function of the taxonomic composition and life history traits provided by the regional species pool (Fotis *et al.* 2018). Canopy complexity determines patterns of light interception, photosynthetic capacity, and carbon sequestration potential of a stand (Hardiman *et al.* 2011). Altering light reflectance can change energy balances and constrain community composition through effects on soil chemistry and belowground function (Thompson *et al.* 2004). In some eastern North American forests, canopy height is a strong predictor of structural diversity (Gough *et al.* 2020) and correlated with greater stem density, temporal stability in canopy complexity, and aboveground net primary productivity (Fotis *et al.* 2018). Increased canopy complexity can reduce understory growth and vegetation stratification, which affects fuel loading and associated disturbances (Turner 2010). High species richness can create complex and diverse spatial structures and contribute to increased productivity, stability, and resilience to disturbances (Tilman *et al.* 2014). Historical variations in the order and timing of species establishment in a given community can also produce different forest structures. Early colonizers may reduce resource availability for late-arriving propagules and consequently limit their local abundance, alter niche properties to facilitate subsequent colonizers, or have a neutral effect on later arrivals. Early colonizers can direct communities toward alternative stable or transient states, even when regional species pools and environmental conditions are static (Fukami 2015).

Disturbance legacies include lasting biological, chemical, and physical effects that may interact with environmental and biological constraints to further shape forest structural diversity (Johnstone *et al.* 2016; Newman 2019). Disturbance legacies affect forest structure at various spatial scales and influence ecosystem feedbacks (Peterson 2002). Disturbances may leave remnant vegetation and propagules, alter soils, and restructure communities by modifying successional patterns (Cuddington 2011). The physical structures of forest ecosystems are both a product and driver of disturbances (Foster *et al.* 1998; Turner 2010) and influence communities for centuries. In low-intensity, high-frequency fire-dependent systems, such as those dominated by ponderosa pine (*Pinus ponderosa*) in the US Southwest, species composition and disturbance behaviors are moderated by the interplay between species traits, forest structural diversity, and disturbance processes (Covington and Moore 1994). However, these same relationships can be destabilized by nonlinear feedbacks associated with abnormally intense crown fires (Covington and Moore 1994), pest and pathogen outbreaks (Flower and Gonzalez-Meler 2015), storm damage (Xi *et al.* 2008), and prolonged droughts (Raffa *et al.* 2008). This spatial and temporal layering of disturbances creates a heterogeneous mosaic of structures (Newman 2019) mediated by regional species characteristics and their responses to disturbances, and by climatic differences in temperature and precipitation.

Forest structural diversity and disturbance interact through time

Conceptualizing how emergent properties result from ecosystem change requires understanding how structure is related to disturbance over space and time (Figure 1). In New Zealand, for instance, the arrival of humans ~ 750 years ago initiated a period of forest burning that facilitated a nonlinear and essentially permanent transition of nearly half the historical, structurally complex podocarp forests into connected, simple fuel structures of fire-prone shrublands and grasslands (McWethy *et al.* 2014). Understanding such relationships requires that we consider climate, species interactions, and disturbance histories.

Multiple emergent properties result from structure–disturbance interactions inherent to the logging of temperate deciduous forests in the northeastern and midwestern US during the 19th and 20th centuries. These disturbances shaped present forest structural diversity and transformed previously uneven-aged, structurally complex, old growth forests into relatively young, even-aged, structurally simple forests (Rhemtulla *et al.* 2009). Ecosystem properties, including canopy complexity and net ecosystem productivity, continue to shift in this region as these forests age. Consequently, spatially and temporally diffuse, low-impact disturbances (such as canopy damage from windstorms or lightning) have greater effect (Gough *et al.* 2016), promoting the emergence of properties otherwise hidden had these forests not been logged. For example, newly formed canopy gaps promote structural diversity by releasing shade-intolerant species and vertically stratifying vegetation (Gravel *et al.* 2010). Diverse structures may result in diverse functions, which can increase net ecosystem production and

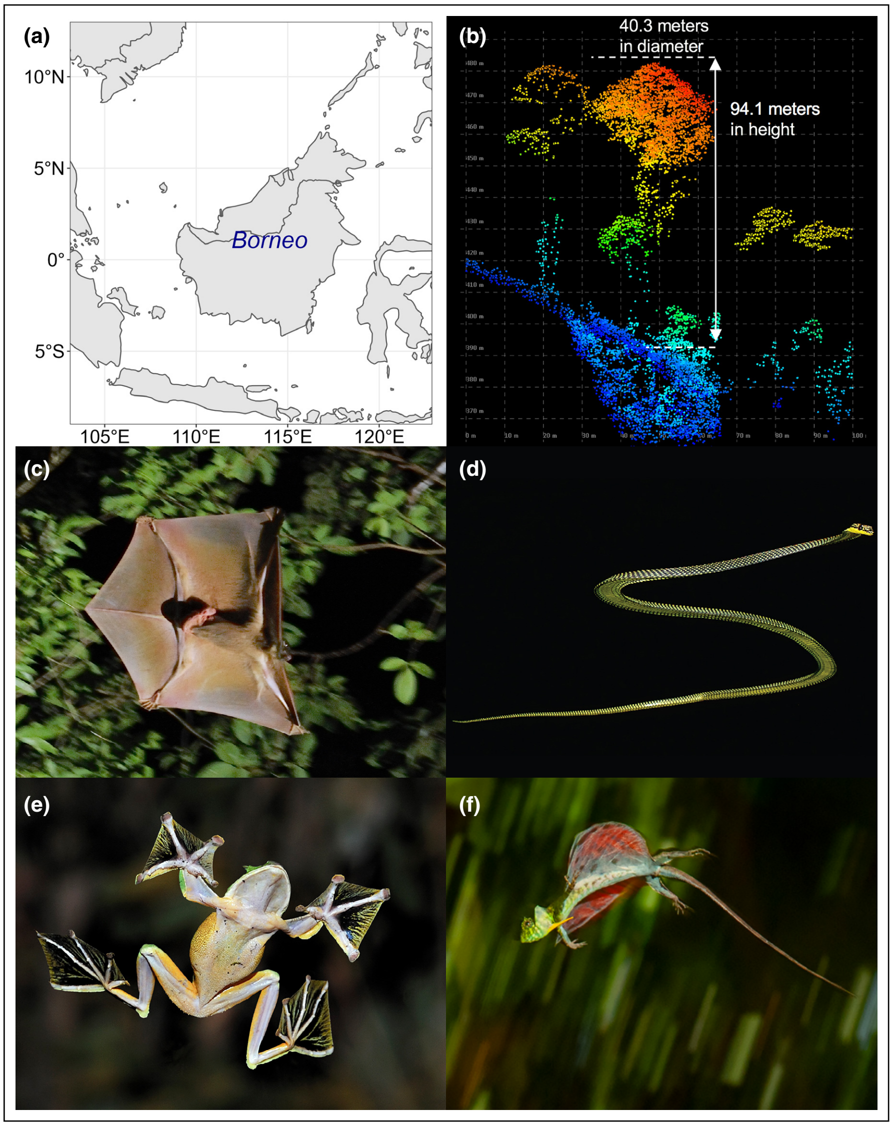

Figure 2. In Southeast Asia, the evolutionary emergence of vertebrate gliders within tropical forests reached its peak on (a) the island of Borneo, which hosts the tallest flowering plants in the world, (b) typified by a light detection and ranging (lidar) point cloud of a *Shorea faguetiana* (Dipterocarpaceae). Representing four of the eight lineages and more than 30 species extant in Borneo alone, (c) colugos ("flying lemurs"), (d) colubrid snakes, (e) rhacophorid frogs, and (f) agamid lizards evolved adaptations for directed aerial dispersal, or gliding, within the time period (50–20 million years ago) when dipterocarps emerged to dominate the tropical forests of Southeast Asia. Image credits: (b) NR Vaughn, Global Airborne Observatory; (c) C Prudente; (d) JJ Socha; (e) C Prudente; (f) C Prudente.

resilience by increasing resource use efficiency (Gough *et al.* 2016). Disturbance–structure interactions change as forests age and further influence forest structural diversity and associated processes.

Structure–disturbance interactions lead to emergent properties

Interrelationships between elements of forest structural diversity (dimensions, density, and arrangement of trees) and disturbances (origin, severity, intensity, frequency, and spatial distribution) may result in emergent disturbance events and ecosystem responses (Panel 1). Nonlinear changes in disturbance and forest recovery may emerge from changes in disturbance severity caused by the spatial and temporal variation in forest structural diversity (Scheffer and Carpenter 2003). Distinct structural signatures are created by disturbances of different types and severities, characterized by the extent and 3D arrangement of forest damage and by the structural patterns emergent during recovery. Severe, infrequent disturbances often kill most trees within a well-bounded area (Foster *et al.* 1998), but moderate disturbances, including windstorms, ice storms, mixed-severity fires, and pest and pathogen outbreaks, often damage specific structural components. For instance, defoliating insects often target one tree species or genus, thereby influencing present and future canopy composition through selective damage and mortality (Atkins *et al.* 2020). Disturbances can influence forest regeneration patterns, which shape future effects of disturbances on ecosystem structure and function. Novel disturbances, or events with cumulative effects greater than those of multiple isolated incidents, also affect structure and subsequent disturbance–structure feedback cycles (Paine *et al.* 1998; Buma and Wessman 2011). In the following sections, we provide examples of structure–disturbance interactions that lead to emergent properties in forest ecosystems.

Emergent properties mediated by disturbance effects on species composition and interactions

Forest structural diversity is largely determined by the dominant plants but is also affected by plant and animal species interacting via competition, herbivory, disease, pollination, and seed dispersal (Anderson *et al.* 2011; Ramirez *et al.* 2018). Species interactions, including mycorrhizal–tree associations or pollination and seed dispersal by insects, birds, or mammals, can hasten recovery of pre-disturbance structure, maintain high biodiversity, and contribute to ecosystem resilience (Anderson *et al.* 2011; Kaiser-Bunbury *et al.* 2017). Patterns of seed dispersal and subsequent forest regeneration by some frugivorous vertebrates depend on the density of species and nonrandom movement of individuals (Westcott *et al.* 2005). Thus, it is the species, their spatial and temporal interactions, and the properties of their

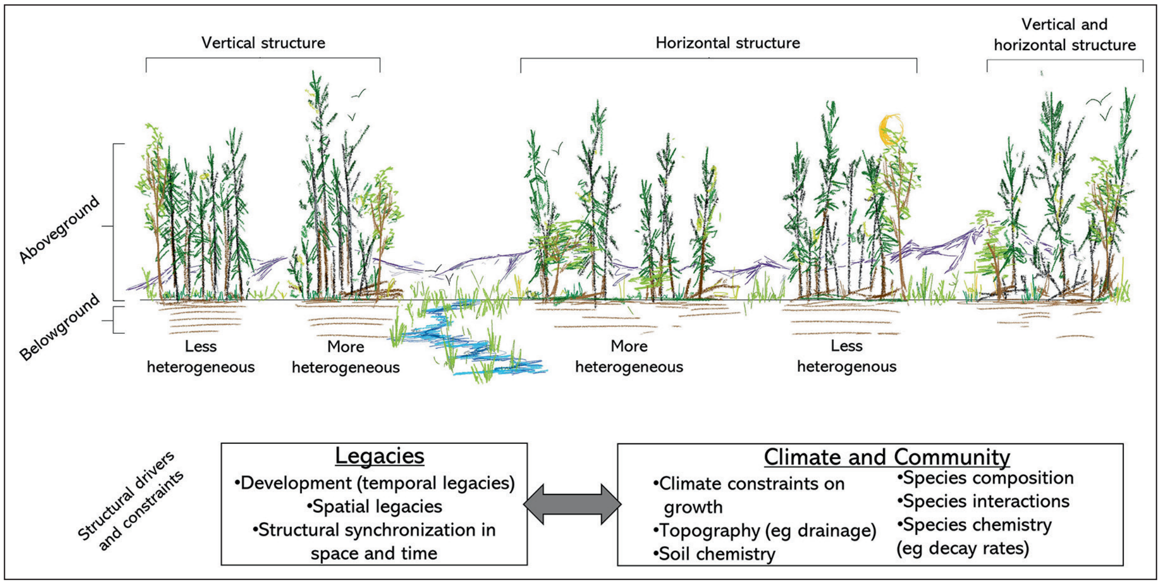

Figure 3. In regard to disturbance behavior and ecosystem response, structural heterogeneity can be divided into vertical and horizontal components, or a combination of the two. Forest structural diversity is generated by the species pool (community), climatic and topographical context, the spatial and temporal legacies associated with the disturbance itself, and site history.

disturbances and post-disturbance legacies that determine forest structural diversity, the resilience of that structure to disturbance properties, and the unique properties that emerge.

Mixed-species forests may recover from disturbances more quickly than single-species forests because they are typically more structurally diverse (Figure 3) and may therefore be more resilient to disturbances such as fire, drought, wind, and insect and pathogen outbreaks (Figure 4). Emergent properties of ecosystem resilience and resistance can arise from combinations of plant community composition and insect outbreak dynamics (Jactel and Brockerhoff 2007). For example, in stands of comparable basal area, black spruce (*Picea mariana*) forests were more resistant than balsam fir (*Abies balsamea*) stands to spruce budworm (*Choristoneura fumiferana*) outbreaks; however, when mixed with deciduous tree species, balsam fir stands became more resilient to budworm outbreaks (Sánchez-Pinillos *et al*. 2019). Ecosystem fragmentation contributes to increased landscape-scale heterogeneity, which can limit the spread of pest-controlling parasitoid populations, ultimately increasing the severity of pest outbreaks and decreasing forest resilience (Roland and Taylor 1997). These examples illustrate emergent properties of forest resilience through complex structure–disturbance and biotic interactions.

Emergent properties of structural patterns and alterations to disturbance regimes

Spatial distributions of forest structure affect disturbances, and small changes in structural continuity can have outsized influence on the behavior of a disturbance event, depending on disturbance type and tendency to spread. For example, highly continuous surface-fuel loads following windstorms subsequently affect the distribution of high-intensity fires, as they follow the shape and distribution of previous structural disturbances. Altering that continuity influences the patchiness of lower severity fire, which illustrates how structure can mediate disturbance dynamics (Buma and Wessman 2011). Spatial heterogeneity or homogeneity of structure across the landscape strongly influences the extent and effect of disturbance processes, and can be an indication of both past disturbance events and outcomes of future disturbances (Foster *et al*. 1998).

As with space, structural change over time can constrain or amplify disturbance characteristics. The relationship between reduced future fire probability as a result of reduced fuel from previous fire (Buma *et al*. 2020) is used in prescribed burning to reduce fire occurrence and intensity. The development of structure is often temporally synchronized, which can produce rapid transitions in disturbance intensity. For example, contiguous areas of forest simultaneously maturing into beetle-susceptible size classes can rapidly create the potential for epidemic-level pest outbreak conditions. Similarly, a healthy forest stand may be relatively resistant to beetle attack but can become vulnerable if surrounded by a contiguous stretch of drought-stressed trees, which are known to foster outbreaks (Raffa *et al*. 2008). Spatial and temporal variations in forest structural diversity combine within stands and across landscapes, and new and reshaped ecosystem dynamics emerge through interactions with disturbances.

Structure–disturbance interactions can also modify the frequency or magnitude of disturbances already present, or may even produce novel, unprecedented disturbance patterns (Kim *et al*. 2020). For example, timber harvesting alters remaining root density and structure; if the scale of

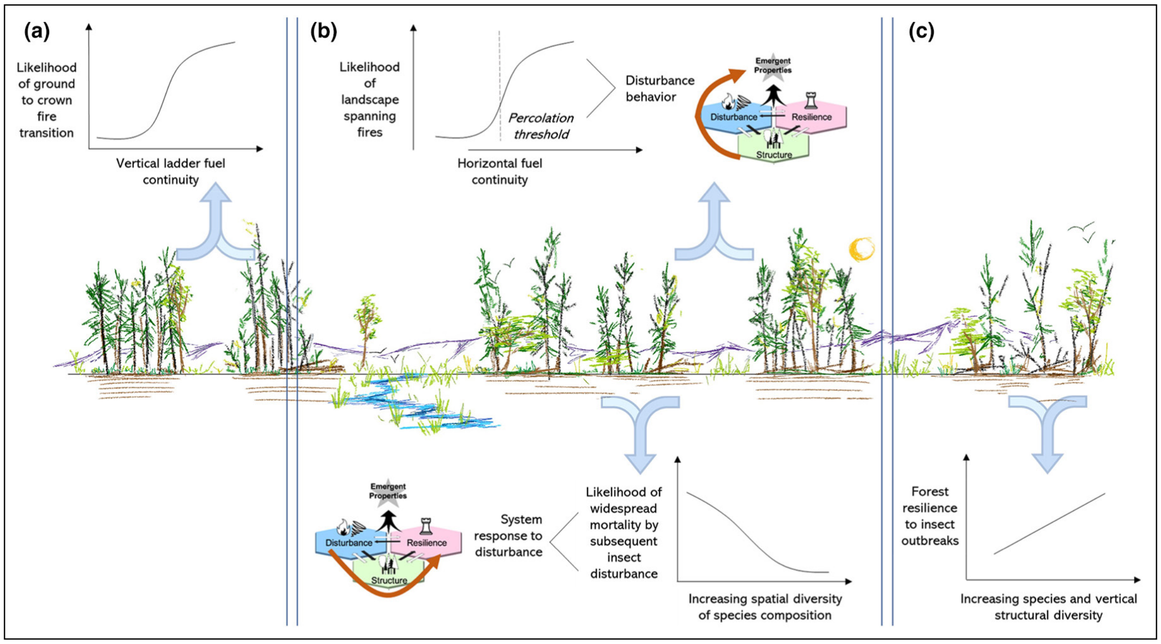

Figure 4. Forest structural diversity affects cross-scale and nonlinear emergent behaviors in, as well as ecosystem responses to, disturbance. For example, increasing vertical continuity (a) can create ladder fuels and cause rapid increases in ground-to-crown fire transitions (Peterson *et al*. 2005). Horizontal structural continuity (b) in fuels can cause quick transitions from small fires to contiguous, landscape-spanning fires and is hypothesized as one mechanism for commonly observed spatial coverage patterns of forest and grassland in savanna ecosystems globally (Abades *et al*. 2014). Spatial heterogeneity (c) caused by post-fire regeneration can reduce mortality caused by insect outbreaks (Seidl *et al*. 2016).

harvesting matches the scale of landslide initiation, the likelihood of landslides increases until those structures regrow (Goetz *et al*. 2015). Disturbances creating large barren areas may diminish recovery by some species and functional groups via seed dispersal limitations (Johnstone *et al*. 2016), which can directly affect structural reorganization following disturbance. Novel disturbances may create wholesale changes in forest structural diversity that can result in conversions between forest types. The introduction of emerald ash borer (*Agrilus planipennis*) to forested wetlands in midwestern and eastern North America resulted in widespread loss of ash (*Fraxinus* spp) trees, a regionally important genus, and in some cases conversion of forest to shrub wetlands (Slesak *et al*. 2014).

Forest structure–disturbance interactions and subsequent emergent properties can also manifest through adaptations to disturbance regimes. Decades of fire exclusion have effectively shifted the disturbance regime of many ponderosa pine-dominated ecosystems from frequent, low-severity surface fires to infrequent, large, high-severity fires that degenerate individual tree and forest resilience to insects, drought, and future fires (Covington and Moore 1994). The removal of frequent, low-severity surface fires from dry-mesic oak (*Quercus* spp)-dominated forests in the eastern US enabled invasion of shade-tolerant, mesic species that increase sunlight interception and prevent oak regeneration. Consequently, most open understory oak-dominated forests in the region have been replaced by mesic forests with dense canopies, dense understories, and moist litter layers that further inhibit burning (Nowacki and Abrams 2008). These wholesale changes to forest structural diversity have eroded the resilience of oak forests to such disturbances as windstorms, ice storms, and pest outbreaks, and have effectively converted them to fire-sensitive communities.

Emergent properties over an evolutionary time scale given absence of disturbance

Emergent properties deriving from forest structural diversity can also arise over evolutionary time scales, as illustrated by the convergent adaptation in forest canopies of more than 30 independent lineages of vertebrates and invertebrates to directed aerial dispersal, or gliding (Dudley *et al*. 2007). More than half of the world's gliding vertebrate species are found on the island of Borneo, which harbors numerous species of squirrels, colugos ("flying lemurs"), colubrid snakes, agamid lizards, rhacophorid frogs, and three independent lineages of geckos (Figure 2) (Emmons and Gentry 1983). Dial *et al*. (2004) proposed that this phenomenon evolved on Borneo as a consequence of the towering and heterogeneous structure of Dipterocarpaceae-dominated forest canopies, which have open understories occupied by few lianas and understory trees. As with temperate forests containing even taller species (eg *Sequoia* spp, *Eucalyptus* spp), other tropical regions in Africa and South America are similarly rich with ancient species pools, but lack comparable numbers of glider lineages (Emmons and Gentry 1983; Dial *et al*. 2004).

Evidence suggests long-term temporal climatic stability, with minimal disturbances from fire or major storms, fostered the emergence and dominance of dipterocarps in pace with the evolution of glider lineages (Heinicke *et al.* 2012). Borneo has been sheltered from open ocean by island arcs and the Asian continent for 30 million years (Hall 2013), which likely minimized destructive wind-shear events that select for shorter forest stature and enabled the evolution of extreme tree height (Jackson *et al.* 2021). The efficient dispersal of dipterocarps' winged, wind-dispersed seeds is reinforced by canopy architecture that towers above an expansive and otherwise open forest (Malhi *et al.* 2018). As canopy height and forest volume increased, so too did the maximum launch heights of vertebrate gliders and the selective value of gliding traits. Dorsoventral flattening, elaborate skin flaps, and other traits associated with these gliding lineages reduce time and energy expended in travel and increase the horizontal distance of locomotion in the canopy (Socha *et al.* 2015). Thus, considerable evidence supports the hypothesis that convergent adaptations of vertebrate gliding emerged from interactions of environmental, biological, and legacy factors (Panel 1), collectively maximizing Borneo's vertical forest structure and conferring selective advantages to gliding.

Discussion and conclusion

Forest structural diversity and disturbance can interact in unexpected ways to produce emergent properties, which in turn can affect community and ecosystem characteristics, including species interactions, resource provisioning, and vulnerability or resilience to future disturbances. Forests are inherently valuable to humans; their high biodiversity and the essential ecosystem services they provide warrant recognition of emergent properties and nonlinear responses to global change. Emergent properties are difficult to identify and measure, and recent sensory and analytical tools, such as light detection and ranging (lidar) and ecological network analysis, present promising opportunities to extend the utility of the emergent properties concept. Our work contributes a scaffold to frame rapid increases in the detection and research of emergent properties and disturbance behaviors that result from forest dynamics of structural properties and their complex interactions with climatic drivers and disturbance regimes.

Variation in forest structure and function may be better quantified with improved metrics of forest structural diversity (Schimel *et al.* 2015). Distributions of tree size, canopy complexity, and overall structural diversity influence forest resilience and responses of forest ecosystems to climatic and anthropogenic change. Advancements in plot-level metrics and large-scale structural diversity measurements will equip dynamic ecosystem models to better incorporate properties that emerge from changes in forest structures over time, disturbance, and other considerations (LaRue *et al.* 2019). Such metrics can fill the gaps in understanding 3D niche space that are currently unaddressed with traditional forest mensuration (Marselis *et al.* 2020). Active remote-sensing techniques (such as lidar) have revolutionized the study of forest structure and help quantify spatial distributions of structure and biomass, elucidating the heterogeneity of canopy composition from local to regional scales. The launch of the Global Ecosystem Dynamics Investigation (GEDI), a full-waveform spaceborne lidar system mounted on the International Space Station, will vastly improve global mapping of forest structural diversity and biodiversity predictions (Dubayah *et al.* 2020). Development of additional methods to explore forest characteristics that produce emergent properties will help reveal their importance.

In addition to technological limitations, there remain several knowledge gaps in identifying the emergent properties that arise from interactions of forest structural diversity and disturbance. Notably, our understanding of forest structural diversity and its role in ecosystem resilience stems primarily from data describing overstory structure and aboveground biomass (McElhinny *et al.* 2005). As compared with forest overstory communities, forest understory communities contribute more to overall species richness but less to total forest biomass, and therefore have been historically overlooked in research on forest ecosystem and disturbance dynamics. Notably, information about the roles that root and soil systems play in forest structure and disturbance dynamics is lacking. Robust measures of both understory and belowground structural diversity will enhance our ability to detect and understand forest emergent properties.

Assessments of emergent properties require work across diverse scales, ecological conditions, and disturbance regimes. The hierarchical organization of ecosystems means that disturbances can exert pressure at any ecosystem level, and resulting reverberations can manifest, amplify, or subdue disturbances throughout the hierarchy in unpredictable ways (Odum and Barrett 1971). Because understanding and identifying emergent properties depends on accurate descriptions of forest structural diversity, metrics must therefore be integrated across multiple spatial and temporal scales and across hierarchical levels (population, community, and ecosystem). The ecological hierarchy present and the scale at which processes are measured should be accounted for in evaluations of emergent properties, especially considering climatic change (Heffernan *et al.* 2014). Assessments should also include natural disturbances, anthropogenic activities, and their interactions, as these may create cause-and-effect feedback loops that could affect system resilience (Turner 2010).

An increasingly common goal of ecosystem management within a changing climate is to focus on resilience and adaptation (Johnstone *et al.* 2016). To that end, we further suggest that ecologists adopt an expansive view of resilience that includes processes contributing to it, and the emergent properties that develop from interactions of resilience with structural diversity and disturbances. To apply the concepts described above, managers should consider how forest structure may influence emergent disturbance dynamics and ecosystem responses for the species, ecosystems, and natural processes they prioritize. Such considerations could include observing how species use structural features, mapping disturbance patterns, using new tools to quantify forest structures, or a combination of approaches (LaRue *et al*. 2023). Emergent properties may originate from the interface of vegetative structures, or, as in Borneo, from the absence of disturbance. As such, we challenge practitioners and policy makers alike to expand investigations of emergent properties across ecosystem types and spatiotemporal scales.

Despite challenges in assessment, we can predict emergent properties of forest ecosystems through careful consideration of interactions between structural diversity and disturbance dynamics, whether resulting from species interactions, structural patterns, or evolutionary mechanisms. Developing this framework further provides the potential to hindcast current emergent properties from previous interactions between forest structural diversity and disturbance. Serving as starting points for investigations and models, structure–disturbance interactions may be later used in management and conservation decisions to forecast future structure–disturbance interactions and predict forest resilience. By articulating these relationships within a conceptual framework, we gain a valuable perspective on the emergence of forest resilience, as well as how ecologists and managers can measure and forecast ecosystem processes more broadly.

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Data Availability Statement

No data were collected for this study.

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Supporting Information

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FrontiersEcoPics

Are pelagic mussel stages chemically attracted to barnacle stands for settlement?

These photographs show dense aggregations of juvenile mussels (*Mytilus* spp) growing on intertidal barnacle stands (*Semibalanus balanoides*) on the Atlantic coast of Nova Scotia, Canada.

In wave-exposed habitats on this coast, extreme environmental events can lead to widespread mortality of intertidal organisms, resulting in large clearings on the rocky substrate. Typically, barnacles are the first macroscopic organisms that recolonize such areas. Once those barnacles attain a certain size, pelagic mussel stages settle upon them and become benthic recruits. These new additions to mussel populations occur substantially more often on barnacle patches than on bare rock. In the complex microtopography of barnacle beds, mussel recruits benefit from increased moisture during low tides and greater protection from waves during high tides. As mussel recruitment progresses, with later recruits concentrating around the first recruits, mussels achieve high densities and outcompete barnacles as they grow, ultimately becoming the dominant species.

What attracts young mussels to such areas? The surface rugosity and particular water flow that characterize barnacle beds aid pelagic mussel stages to find suitable settlement sites. Adult barnacles, however, are known to attract settlement-seeking conspecific larvae and even larvae of predatory nudibranchs through chemical cues. Therefore, is it possible that pelagic mussel stages may also be chemically attracted to barnacles? Chemical attraction of a superior competitor might be an interesting refinement of the facilitation model of succession, which currently considers abiotic improvements by pioneer species as the main mechanism triggering species replacement.

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