Integrative disturbance theory for ecosystem ecologists: a primer with commentary

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Abstract

Understanding what regulates ecosystem functional resistance – the ecosystem-wide capacity to withstand process change following disturbance – is essential in this era of global change. However, many guiding theories relevant to ecosystem ecologists were developed prior to rapid global change and before tools were available to test them. In light of new knowledge and conceptual advances across biological disciplines, we summarize four disturbance theoretical frameworks relevant to ecosystem ecologists: a) the directionality of disturbance response; b) functional thresholds; c) disturbance-succession interactions; and d) diversity-functional resistance relationships. Our brief viewpoint and synthesis considers how knowledge, theory, and terminology developed by several biological disciplines, when integrated, can enhance how ecosystem ecologists analyze and interpret ecosystem-scale disturbance responses. For example, frameworks considering thresholds and disturbance-succession interactions should incorporate regime change, typically the domain of population and community ecologists. Similarly, the interpretation of ecosystem functional responses to disturbance requires analytical approaches that recognize disturbance can promote, inhibit, or fundamentally change ecosystem functions such as primary production. Moreover, embracing an encompassing definition of biological diversity is critical to identifying the ecosystem properties that confer high functional resistance to disturbance. We suggest that, moving forward, cross-disciplinary, integrative knowledge is essential to advancing and refining knowledge in the area of ecosystem functional resistance to disturbance.

Abstract:

Understanding what regulates functional resistance – the ecosystem-wide capacity to withstand process change following disturbance – is essential in this era of global change. However, many guiding theories were developed prior to rapid global change and before tools were available to test them. In light of new knowledge and conceptual advances across biological disciplines, we consider four disturbance theoretical frameworks relevant to ecosystem functional resistance: a) the directionality of disturbance response; b) functional thresholds; c) disturbance-succession interactions; and d) diversity-functional resistance relationships. We discuss how knowledge, theory, and terminology developed by several biological disciplines, when integrated, could modernize and increase the utility of disturbance theory to ecosystem ecology. For example, ecosystems-oriented theoretical frameworks considering thresholds and disturbance-succession interactions should incorporate regime change, typically the domain of population and community ecologists. Similarly, the interpretation of ecosystem functional responses to disturbance requires analytical approaches that recognize disturbance can promote, inhibit, or fundamentally change ecosystem functions such as primary production. Moreover, embracing an encompassing definition of biological diversity is critical to identifying the ecosystem properties that confer high functional resistance to disturbance. We conclude that cross-disciplinary, integrative knowledge along with creative, orthogonal thinking are essential to advancing and refining knowledge in the area of ecosystem functional resistance to disturbance.

Key words: disturbance ecology, ecosystem ecology, ecological theory, succession, resistance, resilience, stability, ecosystem functioning, net primary production

Introduction

Disturbances are processes relevant to all biological disciplines, occurring at every scale and level of organization. However, disturbance-focused studies are generally guided by discipline-specific theories, terminology, and literature. In ecosystem ecology, prominent theoretical frameworks emphasize disturbance effects on mass and energy pools and fluxes over time and space (Bormann & Likens, 1979; Odum, 1969; Whittaker et al., 1974). While the influence of these theoretical constructs endure (Corman et al., 2019), their inception preceded accelerating global change. Further, many conceptual models were not testable when proposed because of technological limitations. However, empirical tests of ecosystem disturbance theory have accumulated in recent decades as tools for measuring mass and energy fluxes became broadly available (Baldocchi, 2008; Novick et al., 2018).

Now, following decades of observations from multiple ecosystems along with the development of intersecting theory from other disciplines, we reconsider a subset of disturbance theories and concepts applicable to theories of ecosystem *functioning* , a primary research emphasis of ecosystem ecologists. By conceptually integrating advances from a variety of fields, we aim to reduce fragmentation among parallel disturbance literatures and leverage disparate findings and concepts to accelerate understanding of functional ecosystem ecology. Because short-term responses to disturbance are relatively well-studied, we emphasize functional *resistance* or the magnitude and direction of system-wide process change immediately following disturbance, while acknowledging that disturbance responses are dynamic and multidimensional (c.f. Mathes et al., 2021). Rather than exhaustive, our commentary is intended to stimulate discussion and promote integration across ecological disciplines.

Disturbance may stimulate, reduce, or create new ecosystem functions, all at the same time

With the origins of disturbance theory rooted in population and community ecology, conceptual and analytical frameworks for interpreting the magnitude and directionality of disturbance response have historically emphasized structure rather than function. For example, White and Pickett's (1985) often-cited definition describes disturbance as a discrete event in time and space "that disrupts the*structure* of an ecosystem, community, or population, and changes resource availability or the physical environment". While this definition does not explicitly exclude ecosystem functioning, its emphasis underscores foundations outside of ecosystem ecology.

As a consequence, most conceptual and analytical models assume an automatic negative ecological response to disturbance relative to a control or baseline. In nature, however, different disturbances have different impacts on ecosystem processes, and different functions may have different responses to the same disturbance. For example, disturbance source and severity have variable effects on processes regulating forest carbon uptake and emissions (Clay et al., 2022; Gough, Atkins, et al., 2021; Shabaga et al., 2022). Over timescales relevant to forest succession, disturbance may stimulate some functions at the expense of others by increasing nitrogen leaching and decreasing nitrogen-limited primary production (White et al., 2004). While disturbances generally do reduce population sizes of dominant species and may drastically alter community structure (e.g., by reducing biodiversity, Hillebrand & Kunze, 2020), the reallocation of function-limiting resources such as light, nutrients, and water may also increase whole-ecosystem resource-use efficiency. For example, wood-boring disturbances that killed only a fraction of trees and reduced species richness increased carbon-use efficiency and, consequently, enhanced the primary production of a temperate forest (Gough, Bohrer, et al., 2021). Moderate severity or partial disturbances from fire, wind, or thinning that reduce competition and liberate growth-limiting resources may similarly increase the production of temperate and tropical forests, especially in the context of changing climates (Buma & Schultz, 2020; Kweon & Comeau, 2019; Munoz et al., 2021; Nunes et al., 2018). Thus, there is no consistent impact of disturbance on the directionality of ecosystem functioning.

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Frameworks that accommodate the multiple responses of ecosystem functioning to disturbance have been proposed and are described in detail elsewhere (Figure 1, Mathes et al. 2021). While not yet widely embraced by ecosystem ecologists, the use of such analytical frameworks could help address a number of knowledge gaps in the realm of disturbance ecology, including: to what extent structure and function are coupled following disturbance; initial responses to disturbance predict long-term change; and disturbance regimes and sources deplete versus enhance structure and function.

Figure 1. By definition, disturbance effects are generally assumed to be negative, resulting in low ecosystem functional resistance. Ecosystem functioning, however, may increase in response to some sources and severities of disturbance. The initial functional response, or degree of resistance, may be positive or negative and vary in magnitude. This ecosystems-oriented response departs from the general expectation that disturbance categorically decreases the populations of dominant species.

Functional thresholds and the erosion of limiting resources are related

Ecologists have long-considered how ecosystem functions respond to disturbance. For example, the effects of different disturbance drivers (e.g., fire, insects, wind) on carbon cycling processes, including primary production, have been examined in several ecosystems (Amiro et al., 2010). Theory and simulation models generally assume that for most functional processes studied, the magnitude of change is inversely proportional to disturbance frequency, severity, or duration (Anderegg et al., 2015; Bond-Lamberty et al., 2015). For example, wood boring insects killing 50% of all trees within a forest stand are expected to reduce primary production by a similar amount, a logical hypothesis that is sometimes observed in nature (Hicke et al., 2012). However, some ecosystems experience substantial disturbance without commensurate changes in ecosystem functioning, exhibiting non-linear *threshold*responses to more frequent, severe, or longer lasting disturbances (Flower & Gonzalez-Meler, 2015; Stuart-Haentjens et al., 2015).

The concept of non-linear thresholds and the statistical tools for their detection (Jiang et al., 2018; Toms & Lesperance, 2003) are widespread across ecological disciplines (Briske et al., 2005; Groffman et al., 2006; Johnston et al., 2021), but underutilized by ecosystem ecologists. Ecological thresholds include non-linear changes in populations, community and landscape structure, and ecosystem processes following disturbance (Groffman et al., 2006), but the published literature contains relatively few studies emphasizing ecosystem-scale functioning. For example, a *Web of Science* key word search (on 09-20-22) yielded 146 articles referencing “threshold” and “ecosystem function*”, while substituting the latter for “communit*” and “population*” returned 2,918 and 2,005 articles, respectively. Moreover, population and community – rather than ecosystem – ecologists have generally led advances in the conceptualization of ecological thresholds, including the data visualization and quantification of nonlinear behavior (Jentsch & White, 2019; Seidl et al., 2016) and the application of basin attractor analogies (Holling, 1973; Huisman & Weissing, 2001; van Nes & Scheffer, 2007).

When integrated, population- and community ecology-originated theory provides a basis for interpreting the mechanisms underlying ecosystem functional resistance. For example, disturbance processes have non-random impacts depending on frequency, severity, type, and duration, and this leaves differential biotic (e.g., species abundances) and abiotic (e.g, nutrient capital) legacies. These ecosystems may maintain pre-disturbance functioning, but are frequently more fragile as a result, leading to threshold behavior in functioning if additional stressors or disturbances occur (Johnstone et al., 2016; Peterson, 2019). Similarly, slow and lasting “press” disturbances such as prolonged drought may incrementally exhaust compensatory material legacies at broad scales until a more abrupt “pulse” disturbance, like extreme weather events or insect mortality, pushes the system beyond its limit, resulting in threshold change and potential reorganization into new stable dynamics (Harley & Paine, 2009; Renwick et al., 2016). Merging these concepts, thresholds in ecosystem functioning can be illustrated as a basin attractor model, in which a loss of limiting resources or material legacies lowers resistance, and reduces the barrier to permanent functional regime change (Figure

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Figure 2. Drawing from theoretical frameworks developed by community ecologists and recent observations of ecosystem processes, functional thresholds can be conceptualized as an abrupt non-linear transition from one functional regime to another resulting from press or pulse disturbance (a) and using a basin attractor analogy (b). Press disturbances, such as sustained drought or gradually rising temperatures, may push a function closer to its threshold by eroding function-limiting resources, including material legacies, and priming the system for greater sensitivity to subsequent pulse disturbance.

Disturbance gives rise to multiple successional pathways

The interplay between ecological succession and disturbance has been an object of theoretical and empirical study for over a century (Shelford, 1912), with ecosystem ecologists considering functioning in this context by the middle 20th century (Odum, 1969; Whittaker, 1960). Initial theoretical models and observations emphasized a single axis of successional change, with disturbance partially or fully resetting succession, depending on the degree of severity (e.g., Tansley, 1935, Figure 2a). Some conceptions were dominated by primarily a single trajectory, while others allowed for alternative trajectories depending on initial conditions, but disturbance still played a "resetting" role (Young et al. 2001). In this general model, primary production increases rapidly in young, aggrading ecosystems as pioneer plant species with little competition and an abundance of resources populate an area and grow rapidly; eventually, primary production stabilizes as mortality and replacement achieve steady state. In some ecosystems, retrogression emerges as declines in nutrient availability or other constraints begin to limit productivity (Peltzer et al., 2010). With recognition that there are exceptions to this general trajectory (Pulsford et al., 2016), observations show that primary production, in the absence of disturbance, aligns with theory and progresses over timescales of decades to centuries in a relatively predictable and conserved way (Luyssaert et al., 2008; Pregitzer & Euskirchen, 2004).

Early theorists and empiricists, however, generally formulated their understanding in the absence of novel disturbance regimes and rapid climate change. Moreover, they typically assumed that disturbance categorically reset – partially or fully – ecosystem functioning. Indeed, a Google search (10-19-22) of "ecological succession" and "ecological succession and disturbance" yielded only textbook illustrations of linear, single-axis change and, when depicted, disturbance without exception rewound the successional clock (Figure S1).

Outside of ecosystem ecology, however, examples of "accelerated" succession and even full ecological regime change abound and inform a more nuanced model of succession-disturbance interactions. For example, moderate severity disturbances causing only partial mortality can promote microclimatic conditions that favor shade-tolerant late successional, rather than pioneer, species (Abrams & Scott, 1989; Fahey et al., 2015; Jenkins & Parker, 1998; Meigs & Keeton, 2018; Trammell et al., 2017). Severe or frequent (Calder & Shuman, 2017; Johnstone et al., 2020), linked or compounding (Buma, 2015; Crausbay et al., 2017), or novel disturbances (Dijkstra et al., 2017) can redirect community successional dynamics altogether into new regimes, giving rise to separate axes of functional resistance and, possibly, stable long-term change (Buma, Harvey, et al., 2019; Jasinski & Payette, 2005; Williams et al., 2011). Examples of functional regime change, while less documented, include coral reef shifts from coral to algal dominated systems, with concurrent changes in productivity and nutrient status (Nystrom et al., 2000), shifts from forests to grass dominated systems (Buma & Wessman, 2011), or major changes in hydrological functioning associated with fire in fire-naive forest ecosystems, leading to waterlogging and subsequent conversion to bog-like landscape (Diaz et al., 2007). In some cases, disturbances restructure ecosystems, making them more functionally resistant to emerging climate conditions (Buma & Schultz, 2020; Thom et al., 2017). These examples demonstrate the potential for disturbances to push ecosystems along multiple axes over long timescales – not only the "traditional" forward or backwards on a pre-defined successional continuum but also in alternate and novel directions.

We suggest the adoption of an updated functional-successional framework that acknowledges that disturbances can reset or enhance functioning or redirect successional trajectories all together. While the original model of succession (Figure 3a) may be valid under some conditions, this updated framing is more realistic in an era of global change and shifting disturbance regime (Figure 2b). Moreover, an updated model of disturbance-succession interactions should acknowledge the "accelerating" effects of some disturbances, particularly those that reduce or eliminate early successional species and produce greater biological and structural complexity.

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Figure 3. Early community ecology-driven successional theory posited and often observed partial to full resetting of plant community development in response to disturbance (a). Observations of plant community and ecosystem functioning dynamics suggest that disturbance can alternatively advance or change axes of succession altogether, and site degradation can lead to retrogression. Disturbance may enhance some elements of ecosystem functioning, while reducing others. For example, within the same north temperate forested landscape, different neighborhood-scale disturbance-succession interactions caused variable initial responses in net primary production (NPP), net ecosystem production (NEP), soil respiration (Rs), gross primary production (GPP), and ecosystem respiration (ER). -, =, and + indicate negative, neutral, and positive responses; [1]Gough et al. 2007;[2]Gough et al. 2021; [3]Scheuermann et al. 2018; [4]Clay et al. 2022;[5]Stuart-Haentjens et al., in review;[6]Gough et al. 2021.

Big "D" diversity supports functional stability, mostly for the same reasons

Biological diversity plays a key role in the stabilization of cellular to landscape processes, and is therefore central to functional resistance across scales of biological organization. For example, functionally redundant gene products provide "functional buffering" at the cellular level; response mechanism diversity (Elmqvist et al., 2003) and genetic diversity (Schippers et al., 2015) provide analogous landscape-scale resistance to disturbance processes. While the mechanistic basis for functional resistance is conceptually similar across scales, scale-centric biological disciplines approach diversity from different perspectives.

Moreover, while the interplay between structural, genetic, trophic, trait, and other aspects of diversity which give rise to ecosystems' functional redundancy are debated in the literature (Eisenhauer et al., 2019), the controlling variables are tightly intertwined in nature. For example, inter- and intraspecific genetic diversity, species diversity, and structural diversity are correlated in forest communities (Gough et al., 2020), suggesting that the isolation of a single controlling influence is impossible in natural (but perhaps not constructed) ecosystems. Attempts to identify the effects of single metrics of diversity on functioning are likely insufficient, and may miss important covariates or potentially confound unmeasured causes with measured correlates (Buma, Bisbing, et al., 2019). Therefore, we suggest that models considering diversity's effects on ecosystem functioning incorporate a multivariate perspective with input from a variety of disciplines, including molecular biologists focused on genetic diversity, community ecologists emphasizing species diversity, and ecosystem ecologists studying structural diversity.

Conclusions : Disturbances are changing in frequency, intensity, and type worldwide (e.g. in forests: Weed et al. 2013, Seidl et al. 2017; grasslands: Joyce et al. 2016; coral: Vercelloni et al., 2020). In addition to advancing fundamental knowledge, updated and more integrative theories relevant to ecosystem functioning are needed to guide disturbance management, and better anticipate and simulate ecosystems' responses to disturbance in this era of rapid global change. While disturbance occurs at all scales of biological organization, disciplinary science has resulted in disparate rather than integrative theories, terminology, and concepts. Comprehensively updating ecosystem disturbance theories requires outside-of-the-disciplinary-box thinking, and such thinking necessitates reading, discussion, and research that spans disciplines. While not exhaustive, Table 1 provides a sampling of literature from biological disciplines outside of ecosystem ecology that is relevant to the four theoretical areas discussed in this commentary. We invite your contributions to this list via https://osf.io/a5zvp/.

Table 1. Disturbance theoretical frameworks originating outside of ecosystem ecology with applicability to ecosystem functioning. We invite additional recommendations from the community here: https://osf.io/a5zvp/.

Theory	Origin	What it said:
Multidimensional stability	Population & community ecology	There are multiple, quantifiabl
Intermediate disturbance hypothesis	Community ecology	Moderate intensity disturbanc
Disturbance legacies	Population & community ecology	Traits and adaptations, as wel
Tipping points, thresholds, and alternate stable states,	Population & community ecology	High intensity or frequency dis
Diversity and resilience	Community ecology	Diverse communities respond t
Landscape dynamics	Landscape ecology	Spatially and temporally asyn
Functional buffering	Cellular biology	The functional redundancy of

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