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Disturbance ecology and the problem of $n = 1$: A proposed framework for unifying disturbance ecology studies to address theory across multiple ecological systems

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Abstract

1. Disturbances are a key part of ecosystem dynamics at multiple scales. They can maintain ephemeral habitat, alter local and landscape biodiversity, drive carbon balance changes and trigger whole ecosystem regime shifts. Yet, there are few theories and only limited frameworks underlying disturbance ecology by which scientists and practitioners can anticipate the impacts of novel disturbances or changes in disturbance regimes. Much of the challenge in developing and testing theories lies in the diversity of ecosystems and disturbance processes and the general inability to (a) properly replicate studies and (b) compare results across disparate systems, from bacterial communities to boreal forests.
2. General syntheses of disturbance processes have identified key aspects of disturbance impact and response—resource stock change, resource flux change, spatial dynamics and trait diversity—that should apply across systems. Yet, application and testing remain challenging due to a lack of a common set of metrics and baselines for comparisons across systems.
3. Here, I propose a discipline-wide effort to develop and publish standardized metrics (in addition to study-specific data) such that the field as a whole can build and test general theory that works across ecological systems. Ten metrics spanning event type, location/design data and biotic composition comprise this suite of 'minimum descriptors' and are directly derived from current disturbance ecology theory. Several examples of cross-system applicability, from bacterial studies to palaeoecological disturbances, are noted. These are example metrics, intended to open the conversation about the most appropriate and theory-based lines of commonality across the field, and they may be further refined through cross-disciplinary conversation.
4. The result of standardizing metrics will be a coordinated dataset that allows for inter-system testing of theory, meaning disturbance ecology studies can move past disparate, seemingly unique systems with little replication to integrated research. To phrase it in another way, disturbance ecology studies should be planned, in part, to contribute to future quantitative meta-analyses. If done, we (as a community) will be much better prepared to address the challenges of emerging

disturbances, novel ecosystems, and no-analogue changes in disturbance regimes which are anticipated with climate change and increasing human pressures.

KEYWORDS

disturbance, ecology, meta-analysis, synthesis, theory

1 | INTRODUCTION

> 'It came to pass that builders realized that they were sorely hampered in their efforts by delays in obtaining bricks...' BK Foscher (1963)

Disturbances are interesting ecologically because they rapidly catalyse ecosystem change (Allen et al., 2014; Rykiel, 1985), which can result in either recovery (for a resilient system; Holling, 1973) or a shift to some alternate regime, such as a hard coral-dominated reef to an algal-dominated ecosystem (Mumby et al., 2007; Muthukrishnan et al., 2016). Disturbance events have a relatively short duration compared to the life span of individuals in the ecosystem, but the effects can have long-lasting legacies and can strongly influence mean values of many ecosystem processes (Turner, 2010). From the perspective of an ecological system, a disturbance encompasses a series of dynamic processes of mortality and recovery, a process that makes energy available for new species, structures and organizations and that can potentially trigger a breakdown of the feedbacks and stabilizing processes that maintain an ecosystem in state. For example, disturbances trigger transient changes in energy or material flows to surrounding ecosystems and can maintain ephemeral, post-disturbance habitat for species in a larger spatial landscape (DeGraaf & Yamasaki, 2003). These events may be relatively short duration but are often of such a magnitude that they are significant even over long time-scales. Furthermore, novel disturbance processes (Buma, 2015; Newman, 2019) are emerging with little historical precedent to study. Given the intensification and emergency of new disturbance processes, and the long-lasting implications for ecosystem functioning, it is critical that we understand disturbance ecology generally so that predictions can be made with confidence.

Understanding disturbance dynamics is key to anticipating if ecosystems are generally stable to a given disturbance regime, prone to rapid transitions (to potentially desirable or undesirable alternate states), or highly uncertain. The answer to those questions is incredibly important for modelling climate change-biosphere dynamics, restoration questions, managing socioecological systems, ecosystem service maintenance and other goals.

This manuscript proposes that the field of disturbance ecology intentionally coordinate to test generalized theory via the inclusion of key, theory relevant data to address these challenges. The purpose here is to start the conversation, not to settle it, and so the datapoints suggested should be read in the spirit of proposed collaboration.

2 | UNIFYING THE STUDY OF DISTURBANCES

Disturbance ecology studies and ideas have made substantial contributions to the field of ecology overall. The intermediate disturbance hypothesis (IDH), for example, is a well-known example of a disturbance frequency versus biodiversity concept applied from forests to coral reefs. But there is no well-tested general theory of ecological disturbance, though various frameworks have been proposed (such as Clements, 1916; Gleason, 1927; Jentsch & White, 2019; Pulsford et al., 2016; White & Jentsch, 2001). It is worth noting that not all ecologists think general theories of ecology are even possible (e.g. Shrader-Frechette & McCoy, 1993).

There are certainly substantial challenges. Cross-system comparisons are hindered by the variety of disturbance drivers, such as fires, hurricanes, landslides and floods; the variety of ecosystems involved; and the unpredictability of the events themselves (making things like pre-event data collection difficult). But perhaps most of all, a general, unified theory is hindered by the simple fact that replication of many disturbance processes is essentially impossible. The independent sample size (*n*) is generally small for most disturbance studies, and especially for field-based investigations of disturbance ecology subjects such as disturbance intensity, severity or ecological resilience, where entire studies may take place within a single fire (for example) or perhaps over a few fire events. This makes generalization difficult for two, independent reasons.

First, the scale of inference is constrained by the locations and systems under investigation; extrapolation outside the surveyed conditions is necessary to make predictions about the impact of different disturbances. Each study location is unique, at the **event scale** (i.e. differing climates, differing edaphic conditions, differing species), **across spatial scales** (i.e. spatial heterogeneity in topography, cover type, disturbance extent and impacts) and **across temporal scales** (e.g. differing weather before, during and after a disturbance event). Multiple events can be studied, such as a series of fires or differing locations within an insect outbreak, but the statistical population of many disturbances typically dwarfs any attempt of any one person to gather a representative sample at global or even regional scales. Formal experiments (winching to replicate hurricanes, Cooper-Ellis et al., 1999; manufactured ice storms, Campbell et al., 2020 or in silico experiments on asteroid air bursts, Robertson & Mathias, 2019) are useful but similarly constrained by setting, often more suited to exploring phenomena within a given disturbance event (e.g. soil heating as a result of fire) rather than *across* ecosystems. Yet, cross-system comparisons have great value, such as between coral reef systems and forests (Connell, 1978; Epstein et al., 2003), which share similarities in terms of their reliance on their heterogeneous and complex structure for important functioning and traits, such as biodiversity and resilience (Muthukrishnan et al., 2016).

Second, generalization is difficult because investigators, questions and methods differ. Comparing across studies is fraught with differing definitions or metrics (resilience, Ingrisch & Bahn, 2018; resistance, Mori, 2016), or the use of semi-quantitative or qualitative measures like 'severity'. One study may report fire intensity as a function of flame length, others by scorch height, others by watts/m^2, depending on the question and goals of the researcher and on data availability. But those intensity metrics are not interchangeable nor independent from other important cofactors such as wind and fuel characteristics (Alexander & Cruz, 2012), which constrains future researchers' ability to combine different projects into more discipline-spanning, quantitative syntheses.

The purpose here is to make the focus the disciplinary scale, *disturbance ecology* itself, so that common data are communicated alongside the study-specific data required for other questions in any specific system. The goal is the establishment of specific commonalities on which future theory can be built (sensu Ioannidis, 2010). To phrase it in another way, disturbance ecology studies should be planned, in part, to contribute to future quantitative meta-analyses at the disciplinary level.

3 | EMPIRICAL SYNTHESES AND FIRST PRINCIPLES

The selection of standardized measurements is an empirical way to approach generality in theory (Velland, 2016). Empirical data can be considered a 'low-level', factor-oriented approach to generating theory, as opposed to theory based on 'higher-level' processes such as selection, drift or speciation. This higher level more directly approaches the 'first principles' needed to properly frame a general theory that can be applied to novel situations which have yet to be observed. While empirical data can provide the germ of theory, a challenge is that in a lower-level approach, the list of potential drivers of disturbance responses is nearly endless, from topography to climate to random chance (Jentsch & White, 2019). In disturbance ecology especially, the problem of study scale means localized factors are often evaluated directly, with little tie to the higher-level theory or first principles. But empirical data are still necessary and valuable, of course. For example, the aforementioned IDH (e.g. Connell, 1978) had its genesis in empirical observation but moved to higher-level organization: diversity and frequency. Empirical data are also necessary to test those theories, such as productive and thoughtful critiques of the IDH (Fox, 2013).

The tension between searching for generality in disturbance ecology via theoretical formulations versus empirical synthesis should be considered a positive (for a thorough discussion, see Huston, 2014). Unfortunately, the disturbance ecology literature is scattered with respect to those empirical, lower-level factors for the reasons described above. Unlike, say, fundamental physics, researchers are all studying unique systems with their unique factors (at least superficially; it must be assumed that there are underlying commonalities if there are to be fundamental theories). This poses a challenge to both the empirical/synthetic approach to generalization—few common factors to compare across—and the application of empirical data to theoretical, high-level theories due to the lack of broad-ranging, consistent data.

3.1 | Typical solutions

The challenge of looking beyond one or a few disturbance events is not a new one, and several methods are commonly used to address these limitations.

3.1.1 | Collaborations

Large-scale collaborations in disturbance ecology are becoming more common, which bring together multiple specialists. Collaborative methods are useful but inherently limited if they are retrospective. For example, a recent global synthesis of temperate forest disturbance agents and patterns spanned multiple continents (Sommerfeld et al., 2018). However, major components were limited to qualitative, expert-opinion data due to a difficulty mentioned above—differing metrics and methods. The NEON network is an example of a forward-looking attempt to capture standardized measures at scale, but application to disturbances is currently limited due to spatial mismatches between disturbance events and NEON installations.

3.1.2 | Remote sensing

Scaling of disturbance ecology is often addressed via remote sensing/GIS. By correlating ground variables relevant to disturbance questions with satellite reflectance, questions can be asked over a broader range of conditions. One of the strengths of remote sensing is the ability to make repeated measurements of a given location over time, and the archiving of data means pre-disturbance data is often available. From this, important information on regimes and trends can be derived (Buma et al., 2020; Lutz et al., 2011).

However, broad datasets that can be applied over multiple independent events (e.g. Landsat/Sentinel) are only available in relatively coarse resolution, unsuitable for questions like soil impacts or other fine-grained processes. Disturbance and ecological response variables often must be correlated through indirect linkages (Keyser & Westerling, 2017). Fundamentally, this technology is limited to relatively broad-scale processes, and thus ignores the strong contributions to disturbance theory from fields like microbial ecology.

TABLE 1 Minimum descriptive criteria for the disturbance study. Copying this table into disturbance studies will provide consistency across studies for community-level integration. Not all categories will be appropriate for some studies, and variability should be noted if possible, or reference made to gaps in knowledge

	Type/units	Notes
Event criteria		
Magnitude	Percent change	Include variability if possible
Extent	Percent of focal region	
Frequency	*f*	Reference to components of calculation if not directly measured (e.g. growth rate). Include variability if possible
Location and design criteria		
Location	Latitude/Longitude (if applicable)	Include coordinate reference system
Experimental Setup	Apparatus details (if applicable)	
Isolation	Unitless	May not be applicable to all studies
Biotic criteria		
Species richness	Count	Define focal range of species surveyed (designated pre-/post-disturbance)
Species diversity	Shannon's Diversity Index (SDI)	
Functional group richness	Count, with definition	Define how functional groups are defined (designated pre-/post-disturbance)
Functional group diversity	SDI, with definition	

3.1.3 | Co-opting general datasets

Some datasets exist for other purposes that can be repurposed for investigating multiple disturbance events. For example, the Pacific Reef Assessment and Monitoring Program run by NOAA collects data on coral reef health that has been used for disturbance resilience assessments (Jouffray et al., 2015). Similarly, the Forest Inventory and Analysis program in the United States offers a dense network of forest plots with basic ecosystem metrics measured on a regular basis. This dataset has been used in powerful studies of disturbance behaviour and trends (Shaw et al., 2017; Singleton et al., 2019). However, most ecological systems do not enjoy the scale and scope of repeat measures that these targeted programmes provide, and the metrics collected on those plots are not necessarily designed for theoretical questions.

3.1.4 | Syntheses

Combining published studies into new conceptual frameworks is common in many fields and can be very productive. For example, recent syntheses of disturbance ecology in the Anthropocene (Newman, 2019), restoration and disturbances (Jentsch, 2007), disturbance interactions (Buma, 2015; Burton et al., 2020), and management and terrestrial/aquatic linkages (Kreutzweiser et al., 2012) have all utilized cross-system comparisons. Generally, they are qualitative, taking a ‘conceptual framework’ approach to unifying the various pieces of research. Long-term ecological research sites (LTERs), where methods are frequently standardized, demonstrate the benefits of unifying the fields' approach across disparate ecosystem types (socio-ecological disturbances: Gaiser et al., 2020). But the diversity of ecosystems that experience disturbance dwarfs LTERs locations, and the field can do better than depend on those locations only for coordinated measurements.

3.1.5 | Meta-analyses

Meta-analyses link multiple studies to draw generalities from a diverse set of literature. (The focus here is somewhat analogous, encouraging practices such that future quantitative meta-analyses can be written at the scale of the discipline.) The value of such work is evidenced by system-specific meta-analyses, such as the analysis of pathogen and drought interactions (Jactel et al., 2012), or coral reef decline (Côté et al., 2005). The challenge with meta-analyses is the prodigious amounts of publications that must be explored to find a few with quantitative data that match the other publications, either due to different methods of measurement or different definitions (Mori, 2016). For example, Fedrowitz et al. (2014) reviewed >5,000 papers to find 78 with appropriate data for their question re: logging practices and species richness.

4 | LINKING METHODS WITH THEORY

Disturbance ecology would clearly benefit from the establishment of a minimal set of empirical metrics that would be reported in all (or most) published work, even if seeming tangential to the question being investigated. It does not mean all studies need similar methodologies, of course, but rather studies should include a small suite of standardized data that can stitch disparate work across systems together. I propose to call them the ‘minimum descriptive criteria (MDC)’, those fundamental variables which describe the basics of the disturbance event. Response variables are not necessarily included, of course; while all disturbance studies have a disturbance event, there is not a shared set of response variables of interest. Sub-disciplines may have additional metrics beyond those suggested here (e.g. resilience ecology; Ingrisch & Bahn, 2018).

These metrics (Table 1) are intended as a conversation opener, rather than a 'final word', and the field should think about alternative metrics that could accomplish the same goal, with the ultimate aim of commonality.

4.1 | MDC selection

Current 'first-principles' disturbance ecology theory, broad though it is, can provide guidance to variable selection. Jentsch and White (2019) highlight four postulates that capture the phenomena of disturbance and recovery, regardless of ecosystem: Changes in resources (space, time and rate), fluxes of energy in the system, spatial dynamics of the ecosystem and trait diversity in the ecosystem. They encompass more specific generalizations such as disturbance-driven landscape dynamics (Turner, 2010), generalized disturbance interactions and cascades (Buma, 2015), and biogeochemical trajectories (Kranabetter et al., 2016). The task is deriving a suite of empirical data that can be collected in any given system to provide standardized datapoints corresponding to those fundamental components.

There is a second consideration to this practically focused paper. To make this proposal practicable, the MDC must be (a) feasible for most researchers, (b) generally accessible (meaning they can be measured by most investigators, not just specialized laboratories) and (c) comprehensive, meaning they encompass key attributes of a disturbance at multiple scales—they must be applicable to systems ranging from bacterial communities to coral reefs.

The proposed MDC are broken into three groups: **Event scale criteria** describing the disturbance itself; **location and design criteria** describing the plots/laboratory setup and details relevant to disturbance impact/recovery; and **biotic criteria**, describing organismal conditions.

4.2 | Event criteria

First, basic disturbance characteristics should be listed—magnitude, extent and the regime in which the disturbance occurred. Magnitude can be defined as the relative change in resources (e.g. live biomass, number of live bacteria, available nitrogen) associated with a disturbance, with units dependent on the focal question, and is a function of the force of the disturbance, initial resource concentration and the fraction of the community resistant to that disturbance (modified from Jentsch & White, 2019):

$$\text{Magnitude} = R_{\text{initial}} \times F_{\text{event}} \times \left(1 - P_{\text{resistant}}\right),$$

where F is the force of the disturbance which modifies the initial condition (e.g. percent potential mortality), R_{initial} is the percent of total system exposed (if a whole landscape, then it would equal 1) and P is the fraction of the focal system resistant to the disturbance. This equation is equivalent to the impact of the disturbance scaled to pre-disturbance conditions, or percent change pre to post. For example, for a system entirely exposed ($R = 1$) to a low-intensity fire that kills approximately 50% of individuals ($F = 0.5$), and where 20% of the individuals are fire resistant ($p = 0.2$), the calculated relative magnitude would be 0.4.

Second, disturbances occur in space; explicitly as in a forest fire or abstractly, as in a mesocosm where all portions of the experiment may be exposed to the disturbance equally (disturbance extent is 100% of the study extent/landscape size). The extent of a disturbance strongly influences both the broad-scale impact and localized recovery at any given point (e.g. seagrass and shrimp; Castorani & Baskett, 2020). Extent must be normalized as a fraction of study extent.

Third, the event must be located in time. The regime should be reported based on the typical return interval and range of the disturbances under study relative to the growth rate/recovery rate of the system (species or other) under study. Arbitrary units, such as years or days, are less useful. For example, experimental studies on bacterial community responses to various intensities and return intervals often use days as the descriptor of the return interval (Berga et al., 2012; Jacquet & Altermatt, 2020), a metric that is not immediately scalable to other disturbance studies such as forest or coral systems, where return intervals are often measured in decades or centuries. Normalizing for growth rates takes the form of:

$$f = r/\text{disturbance interval}.$$

Essentially, f is the frequency of disturbances per unit time, where units of time are set to a generation time or time to reproductive maturity. $1/f$ therefore indicates time between disturbances in units of generations. As an example, a fire regime of 1 event per 200 years in a system where approximately 40 years to maturity is a reasonable approximation (such as a *Picea mariana* forest in the boreal) would equate to a system with an f of 0.20 (variability can be reported). Note that f will typically need to be defined based on the study species of interest in any given study, and if multiple species are involved then multiple f values are possible (note that time to seed bank recovery is not perfectly analogous to r in bacterial population growth, but functionally similar). This general formula could also be applied to the recovery time of disturbance-sensitive ecological functions like biogeochemical stocks (e.g. Kranabetter et al., 2016).

In some systems, growth rate is highly dependent on the surrounding community (in other words, interspecies interactions depress or enhance growth rates), using an adjusted growth rate, r^*, which compensates for growth rates in a community rather than a monoculture is potentially more appropriate (Arnoldi et al., 2019; Jacquet & Altermatt, 2020):

$$r^* = rN^*/K,$$

where N^* is the equilibrium population in the community under study, and K is the carrying capacity.

TABLE 2 Example of the metrics, contrasting across three independent studies, that highlight the utility in reference to frequency versus resilience questions: Hayes and Buma's study (2021) is a field-based multiple disturbance observational study, using recent (1940 to present) fires in the boreal and few treatments, which allows reporting of individual values; Jacquet and Altermatt's study (2020) is a laboratory-based study applying differing disturbance frequencies and intensities to microbial communities along a spectrum; Chileen et al.'s study (2020) is a palaeoecological study based on a sediment core from a lake in the subalpine forests of Colorado, USA, exploring fire history and vegetation in that location. Biotic criteria units are means (standard deviation in parentheses)

	Hayes and Buma (2021)		Jacquet and Altermatt (2020)		Chileen et al. (2020)	
	Number	**Note**	**Number**	**Note**	**Number**	**Note**
Magnitude	1	Complete mortality	0.1–0.9	Experimentally applied	Varies	Generally high, near 1
Extent	1	100% of study sites	1	Within disturbance treatments	Varies	
f	Range: 0.2–1.5 (mean: 0.9)	Dominant pre-disturbance species (30 years to seed prod.)	Range: 0.03–0.8 (mean: 0.2)	Relative to growth rates[a]	Range: 0.03–0.5 (mean: 0.08)[b]	Dominant species (10 years to seed prod.)
Location	65.69, −149.13 65.58, −145.02		Laboratory		40.33, −105.85	
Exp. setup	Field observations		Laboratory experiment		Field, sediment core	
Isolation (unitless)	0.2–1.3[c]		NA		NA	
Spp. rich (*SD*)	1 fire: 4.1 (1.7) 2 fires: 4.5 (0.7) 3 fires: 4.5 (1.4)	Trees only	Undisturbed: 4.9 (1.1) Disturbed range: 2–7 (mean 4.1)[d]		15	Genus or family level taxa, not species
Spp. div. (*SD*)	1 fire: 0.8 (0.3) 2 fire: 1.0 (0.2) 3 fire: 0.9 (0.3)	Trees only	Not reported		Varies	
Functional group richness	1 fire: 2 2 fire: 2 3 fire: 1.9	Deciduous conifers	3	Bacteria, Bact/predator, Bact/autotroph	3	Arboreal, shrub, herbaceous
Functional group div.	1 fire: 0.5 (0.2) 2 fire: 0.5 (0.2) 3 fire: 0.1 (0.1)	Deciduous conifers	Not reported		Not reported	

[a]Note this differs from the frequency as calculated in the original publication, which was per day, not relative to the population growth rate.

See Jacquet and Altermatt's (2020) supplementary data for growth rates.

[b]Reported in detail in Dunnette et al. (2014); seed production timing from Anderson (2003).

[c]Assuming 80 m dispersal for conifers, 500 m for deciduous, all plots >100 m from legacies (Burns & Honkala, 1990). Not reported in source paper.

[d]Based on supplementary data in original paper which combined some species together, example data only.

The salient point is that disturbance frequency, often measured in ecology studies, has no fundamental temporal unit (e.g. days or years). Setting the temporal unit for defining disturbance frequency as a generation time (or time to first viable reproductive event in iteroparous species) will standardize across studies. For example, short-interval disturbances are a growing topic in disturbance ecology currently (Burton et al., 2020), which is often defined as an interval less than the time required for species to recover, or $f > 1$ in the above formulation, and which will result in extirpation if M approaches 1, a result seen in several studies (Fairman et al., 2019). This approach has led to the ability to generalize across disparate species (Buma et al., 2013) and would be valuable if applied across disparate systems (qualitatively described in Paine et al., 1998) and if incorporated intentionally into future study designs. Note that combining growth rates (r) with regime magnitudes and frequencies also allows for system persistence thresholds to be calculated, useful when comparing resilience or stability of systems (including incorporating variability; Supporting Information 1).

4.3 | Location and design criteria

Location is a valuable multi-use datapoint, from which other metrics can be derived by future researchers, such as climatic conditions and topographical information. Another important benefit is the ability to incorporate time with repeat visits (Buma et al., 2019; Johnson & Miyanishi, 2008).

Second, it is well recognized that dispersal from undisturbed legacies is a key component of disturbance recovery (forests: Fastie, 1995, benthic invertebrates: Palmer et al., 1996, kelp: Fraser et al., 2018, coral systems: Gilmour et al., 2013). This spatial context must be captured here. Like the regime relativization, the terms must be scaled to be comparable. Calculation and reporting of location isolation, the median distance to surviving individuals/median dispersal distance allows for such a comparison:

$$\text{Isolation} = \frac{\text{Distance}_{\text{median distance to surviving legaices}}}{\text{Distance}_{\text{median dispersal distance}}}.$$

(Medians are suggested here over means, given the potential for 'fat tails' associated with rare long-distance dispersal events). Note that $\text{Dist}_{\text{median dispersal}}$ is, in reality, a dispersal kernel/probability density function (Nathan et al., 2012) and depending on study may have considerable spread and uncertainty; they may even be bimodal (Pansing et al., 2020). Studies may report isolation at a species or community level (if that makes logical sense), depending on the question and data resolution. For micro and mesocosm studies, isolation may be zero unless the apparatus has specific reservoirs and dispersal corridors.

4.4 | Biotic criteria

Disturbance events are mediated via interactions between organisms and their environment. Organismal influence may be relatively strong (e.g. hosts species are required for specific pest outbreaks) or negligible (e.g. volcanic eruptions, though at some distance species traits do become important; Adams et al., 1987). These interactions can be split into interactions significant at evolutionary versus ecological time-scales (Jentsch & White, 2019). At the evolutionary scale, there are fundamental theoretical questions regarding the direction of disturbance-related trait evolution (e.g. the evolution of flammability; Cui et al., 2020) and the role of genetic diversity across long-term disturbance gradients. These debates have clear relevance to more proximate, ecological time-scale theoretical questions, such as the stability and persistence of savannah–forest complexes (Newberry et al., 2020) and how resilience mechanisms shape species-level responses to novel disturbance events (Buma & Wessman, 2011).

The selection of MDC's for this important part of disturbance theory is a challenge, given the variety of ways that biodiversity can be defined and categorized. Leveraging expertise in other fields is vital. Gene banks can be valuable if species (and subspecies, if applicable) are identified (Wambugu et al., 2018), and recent calls for work on seed traits salient to disturbance and recovery identify seedbanks as key sources of data (Saatkamp et al., 2019). At the ecological scale, disturbance theory has long sought to link trait and species diversity to disturbance impact and response (microbial biofilms, Feng et al., 2017; theoretical history reviewed in Peterson et al., 1998). However, application of biodiversity–disturbance relationships remains difficult due to the non-equilibrium nature of most ecosystems (Mori, 2016).

Trait diversity and species diversity address the twin theoretical angles of evolutionary and ecological complexity. Reporting species richness and a standardized diversity metric, such as Shannon's Diversity Index, covers both the raw number of species and a simple measure of diversity. Some systems, like palaeoecological studies, will be challenged to report species richness values; others, like controlled microbial disturbance studies, may find it easier.

5 | IMPLEMENTATION

Building and testing theory in disturbance ecology requires linking disparate systems, which can be done quantitatively through shared metrics. This is not meant to replace study-question-specific measurements, but as a simple, direct and repeatable supplement. Nor will the proposed MDC's fit perfectly into all studies; certain systems may have a difficult time defining frequency or the regime, especially in low-disturbance areas. Other applications, like the disturbance ecology of biogeochemical species, may not have a sensible value to report for isolation. That is not a fundamental problem; this is meant as the beginnings of a conversation to move, as a field, into a coordinated future such that the major difficulty associated with testing and devising disturbance theory are intentionally addressed.

The format for MDC inclusion is a simple table, ideally incorporated directly so formatting is consistent across studies to facilitate simple data collection/data scraping for meta-analyses. Some values may be left blank if not applicable or not known; a notes column allows for reporting of uncertainty or underlying sources used to calculate the metric (e.g. dispersal distances for calculating isolation or growth rate estimates for calculating the r inequality).

6 | EXAMPLE

Working at this fundamental level highlights commonalities across disturbance studies that are not necessarily obvious. For example, consider the relationship between disturbance frequency and ecosystem resilience (defined as recovery to a similar state). Palaeoecological studies of disturbance regimes, such as forest fires (e.g. Chileen et al., 2020) are an excellent parallel to the microbial community disturbance studies mentioned above (e.g. Jacquet & Altermatt, 2020). Both look at community stability after a series of disturbance events in time, one over days, the other over centuries, but both are approximately matched in terms of their f values (approx. 0.03–0.8), based on growth rates of the various bacterial species (r; 0.7–2.2, measured in days and with disturbance experimental disturbance intervals ranging 3–12 days) and the time to substantial seed production in *P. contorta* (~10 years (Burns & Honkala, 1990) and a disturbance interval from 20 to 330 years). Comparatively, both systems demonstrate community stability except for high frequencies and magnitudes, an important commonality. Contrast with Hayes and Buma (2021), a similar multi-disturbance system in boreal forests with similar resilience mechanisms as Chileen et al., but where f values are >1. In that case, substantial ecosystem shifts were noted. One utility of the MDC's proposed here is that ability to calculate minimum growth rates for persistence under changing disturbance frequencies and/or magnitudes, as well as variability in each (see Supporting Information 1). For the entire set of proposed metrics for each, see Table 2.

It is true that not all categories fit as comfortably as others, depending on the study; for example, while functional groups are reported and interpreted in Chileen et al. (2020), they vary continuously across the time period. This makes reporting simple metrics like functional group diversity very difficult. However, these small complications should not hinder an attempt at integration, and these metrics that are shared highlight commonalities between seemingly disparate study systems and the potential for broad theory to encompass both.

7 | KEY CHALLENGES

The MDC ideas presented here are not without their limitations. The hope is that they spur discussion to address those challenges and expand their utility. For example, the use of median dispersal distances is intended to minimize the impact of 'fat tails' in distributions—but in some settings, those rare events can be consequential (Petrovskii & Morozov, 2009). Furthermore, the simple metric, rather than a more accurate but more involved metric like connectivity, is more easily understood across systems. Indeed, the extent to which medians are useful, or less so, in cross-comparing studies will be illustrative. Another significant challenge is magnitude and extent, which are defined by the study area being considered. Generally, the study area should be defined as appropriate to the question being asked (a central tenant of spatial ecology; e.g. Jackson & Fahrig, 2015; Weins & Milne, 1989). That theoretical pronouncement, however, hides real practical challenges which should not be minimized and the implications considered. At a more fundamental level, any discussion on refining/refocusing the MDC's towards commonalities across systems will be valuable, and these are only potential practical starting points. Simply by discussing the quantification of a common metric, the field will push forward on both theoretical definitions and practical implementation of unified research. Furthermore, explicit consideration of these generalizable metrics may aid in study design at the outset, such as matters of appropriate scale, which biota will be measured, and similar design decisions.

8 | CONCLUSIONS

Understanding the response of ecosystems to disturbances is increasingly critical as the climate warms and those catalytic events become more common. The generally difficult-to-predict nature of disturbance events makes their study challenging, as does the scale and scope of the events themselves. Experiments are difficult to scale, and so the field must rely heavily on unreplicated natural experiments, observations and correlative studies. Finding a way to efficiently link those studies is a prime challenge in unifying the field of disturbance ecology.

Here I have presented suggestions for a set of minimum quantitative descriptive criteria that could be included in all disturbance ecology studies. Not all metrics will be available for any given location, but those that are will (if reported in a standardized way) enable future researchers to combine results in powerful, quantitative ways. The descriptive criteria proposed here encompass fundamental disturbance descriptors and both the spatial and temporal context of the study. They were chosen to be 'minimal' to not add an unreasonable workload to the individual researcher while still enabling the widest potential use in the future as possible. By including these MDC's, any individual study will better fit into coherent, discipline-wide future research. The alternative for unification is one focused on description, a collection of analogous stories. This is much less powerful and constraints quantitative testing of theory across systems to mostly opportunistic settings.

This proposal is not meant to benefit any individual study or research project but rather the field of disturbance ecology as a whole. In the classic 'Chaos in the Brickyard', BK Forcher argued that strong structures (theory) are the result of the careful collection of specific and tailored bricks (data), bricks that fit together in a planned and thoughtful way. The creation of a theoretical edifice is the result of careful, coordinated brickwork and deep thought. Forcher goes on to lament that uncoordinated research can create too many ill-fitting bricks, a disorganized pile that obscures and even hinders the creation of structures—bricks do not fit into larger structures because they are not designed to fit. Modern disturbance ecology studies produce excellent bricks, and lots of them. But they are mostly uncoordinated.

This proposal is an attempt to tailor the creation of those datapoints such that disturbance ecology can more efficiently make those grand edifices. However, an endeavour of this size benefits from debate and so this proposal should be seen as the beginnings of a field-wide discussion, based in common theoretical frameworks, that will mature the discipline of disturbance/change ecology and benefit the wider ecological field. In the future, this could take the form of an online database for more rapid inclusion, searching and downloading of data. Initially, however, inclusion in papers (which we are already producing) is the likely easiest way to begin the habit of writing with future meta-analyses in mind.

The field and community will benefit immensely by coordinating its research in this fashion such that rather than a series of single, one-off studies with little to unite them we have a gradually building, cohesive network of studies that can provide deep, fundamental insights into disturbance ecology and ecosystem change.

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CONFLICT OF INTEREST

The author has no conflict of interests to declare.

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REFERENCES

Adams, A. B., Dale, V. H., Smith, E. P., & Kruckeberg, A. R. (1987). Plants survival, growth form and regeneration following the 18 May 1980 eruption of mount St. Helens. *Northwest Science*, *61*(3), 160–170.

Alexander, M. E., & Cruz, M. G. (2012). Interdependencies between flame length and fireline intensity in predicting crown fire initiation and crown scorch height. *International Journal of Wildland Fire*, *21*(2), 95–113.

Allen, C. R., Angeler, D. G., Garmestani, A. S., Gunderson, L. H., & Holling, C. S. (2014). Panarchy: Theory and application. *Ecosystems*, *17*(4), 578–589.

Anderson, M. D. (2003). *Pinus contorta* var. *latifolia*. In *Fire effects information system* [Online]. U.S. Department of Agriculture, Forest Service. Retrieved from https://www.fs.fed.us/database/feis/plants/tree/pinconl/all.html

Arnoldi, J. F., Loreau, M., & Haegeman, B. (2019). The inherent multidimensionality of temporal variability: How common and rare species shape stability patterns. *Ecology Letters*, *22*(10), 1557–1567.

Berga, M., Székely, A. J., & Langenheder, S. (2012). Effects of disturbance intensity and frequency on bacterial community composition and function. *PLoS ONE*, *7*(5), e36959.

Buma, B. (2015). Disturbance interactions: Characterization, prediction, and the potential for cascading effects. *Ecosphere*, *6*(4), 1–15.

Buma, B., Bisbing, S. M., Wiles, G., & Bidlack, A. L. (2019). 100 yr of primary succession highlights stochasticity and competition driving community establishment and stability. *Ecology*, *100*(12), e02885.

Buma, B., Brown, C. D., Donato, D. C., Fontaine, J. B., & Johnstone, J. F. (2013). The impacts of changing disturbance regimes on serotinous plant populations and communities. *BioScience*, *63*(11), 866–876.

Buma, B., Weiss, S., Hayes, K., & Lucash, M. (2020). Wildland fire reburning trends across the US West suggest only short-term negative feedback and differing climatic effects. *Environmental Research Letters*, *15*(3), 034026.

Buma, B., & Wessman, C. A. (2011). Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere*, *2*(5), 1–13.

Burns, R. M., & Honkala, B. H. (1990). Silvics of North America: 1. Conifers. In *Agriculture handbook 654* (Vol. 2, pp. 877). U.S. Department of Agriculture, Forest Service.

Burton, P. J., Jentsch, A., & Walker, L. R. (2020). The ecology of disturbance interactions. *BioScience*, *70*(10), 854–870.

Campbell, J. L., Rustad, L. E., Driscoll, C. T., Halm, I., Fahey, T. J., Fakhraei, H., Groffman, P. M., Hawley, G. J., Leuenberger, W., & Schaberg, P. G. (2020). Simulating impacts of ice storms on forest ecosystems. *JoVE*, *160*, e61492.

Castorani, M. C., & Baskett, M. L. (2020). Disturbance size and frequency mediate the coexistence of benthic spatial competitors. *Ecology*, *101*(1), e02904.

Chileen, B. V., McLauchlan, K. K., Higuera, P. E., Parish, M., & Shuman, B. N. (2020). Vegetation response to wildfire and climate forcing in a Rocky Mountain lodgepole pine forest over the past 2500 years. *The Holocene*, *30*(11), 1493–1503.

Clements, F. E. (1916). *Plant succession: An analysis of the development of vegetation* (No. 242). Carnegie Institution of Washington.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, *199*(4335), 1302–1310.

Cooper-Ellis, S., Foster, D. R., Carlton, G., & Lezberg, A. (1999). Forest response to catastrophic wind: Results from an experimental hurricane. *Ecology*, *80*(8), 2683–2696.

Côté, I. M., Gill, J. A., Gardner, T. A., & Watkinson, A. R. (2005). Measuring coral reef decline through meta-analyses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1454), 385–395.

Cui, X., Paterson, A. M., Wyse, S. V., Azharul Alam, M., Maurin, K. J. L., Pieper, R., Cubino, J. P., O'Connell, D. M., Donkers, D., Bréda, J., Buckley, H. L., Perry, G. L. W., & Curran, T. J. (2020). Shoot flammability of vascular plants is phylogenetically conserved and related to habitat fire-proneness and growth form. *Nature Plants*, *6*(4), 355–359.

DeGraaf, R. M., & Yamasaki, M. (2003). Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecology and Management*, *185*(1–2), 179–191.

Dunnette, P. V., Higuera, P. E., McLauchlan, K. K., Derr, K. M., Briles, C. E., & Keefe, M. H. (2014). Biogeochemical impacts of wildfires over four millennia in a Rocky Mountain subalpine watershed. *New Phytologist*, *203*(3), 900–912.

Epstein, N. R. P. M., Bak, R. P. M., & Rinkevich, B. (2003). Applying forest restoration principles to coral reef rehabilitation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *13*(5), 387–395.

Fairman, T. A., Bennett, L. T., & Nitschke, C. R. (2019). Short-interval wildfires increase likelihood of resprouting failure in fire-tolerant trees. *Journal of Environmental Management*, *231*, 59–65.

Fastie, C. L. (1995). Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology*, *76*(6), 1899–1916.

Fedrowitz, K., Koricheva, J., Baker, S. C., Lindenmayer, D. B., Palik, B., Rosenvald, R., Beese, W., Franklin, J. F., Kouki, J., Macdonald, E., &

Messier, C. (2014). Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology*, *51*(6), 1669–1679.

Feng, K., Zhang, Z., Cai, W., Liu, W., Xu, M., Yin, H., Wang, A., He, Z., & Deng, Y. (2017). Biodiversity and species competition regulate the resilience of microbial biofilm community. *Molecular Ecology*, *26*(21), 6170–6182.

Foscher, B. K. (1963). Chaos in the Brickyard. *Science*, *142*(3590), 339.

Fox, J. W. (2013). The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology & Evolution*, *28*(2), 86–92.

Fraser, C. I., Davies, I. D., Bryant, D., & Waters, J. M. (2018). How disturbance and dispersal influence intraspecific structure. *Journal of Ecology*, *106*(3), 1298–1306.

Gaiser, E. E., Bell, D. M., Castorani, M. C., Childers, D. L., Groffman, P. M., Jackson, C. R., Kominoski, J. S., Peters, D. P., Pickett, S. T., Ripplinger, J., & Zinnert, J. C. (2020). Long-term ecological research and evolving frameworks of disturbance ecology. *BioScience*, *70*(2), 141–156.

Gilmour, J. P., Smith, L. D., Heyward, A. J., Baird, A. H., & Pratchett, M. S. (2013). Recovery of an isolated coral reef system following severe disturbance. *Science*, *340*(6128), 69–71.

Gleason, H. A. (1927). Further views on the succession-concept. *Ecology*, *8*, 299–326. https://doi.org/10.2307/1929332

Hayes, K., & Buma, B. (2021). Effects of short-interval disturbances continue to accumulate, overwhelming variability in local resilience. *Ecosphere*, *12*(3), e03379.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, *4*(1), 1–23.

Huston, M. A. (2014). Disturbance, productivity, and species diversity: Empiricism vs. logic in ecological theory. *Ecology*, *95*(9), 2382–2396.

Ingrisch, J., & Bahn, M. (2018). Towards a comparable quantification of resilience. *Trends in Ecology & Evolution*, *33*(4), 251–259.

Ioannidis, J. P. (2010). Meta-research: The art of getting it wrong. *Research Synthesis Methods*, *1*(3–4), 169–184.

Jackson, H. B., & Fahrig, L. (2015). Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography*, *24*(1), 52–63.

Jacquet, C., & Altermatt, F. (2020). The ghost of disturbance past: Long-term effects of pulse disturbances on community biomass and composition. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20200678.

Jactel, H., Petit, J., Desprez-Loustau, M. L., Delzon, S., Piou, D., Battisti, A., & Koricheva, J. (2012). Drought effects on damage by forest insects and pathogens: A meta-analysis. *Global Change Biology*, *18*(1), 267–276.

Jentsch, A. (2007). The challenge to restore processes in face of nonlinear dynamics – On the crucial role of disturbance regimes. *Restoration Ecology*, *15*(2), 334–339.

Jentsch, A., & White, P. (2019). A theory of pulse dynamics and disturbance in ecology. *Ecology*, *100*(7), e02734.

Johnson, E. A., & Miyanishi, K. (2008). Testing the assumptions of chronosequences in succession. *Ecology Letters*, *11*, 419–431. https://doi.org/10.1111/j.1461-0248.2008.01173.x

Jouffray, J. B., Nyström, M., Norström, A. V., Williams, I. D., Wedding, L. M., Kittinger, J. N., & Williams, G. J. (2015). Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 20130268.

Keyser, A., & Westerling, A. L. (2017). Climate drives inter-annual variability in probability of high severity fire occurrence in the western United States. *Environmental Research Letters*, *12*(6), 065003.

Kranabetter, J. M., McLauchlan, K. K., Enders, S. K., Fraterrigo, J. M., Higuera, P. E., Morris, J. L., Rastetter, E. B., Barnes, R., Buma, B., Gavin, D. G., & Gerhart, L. M. (2016). A framework to assess biogeochemical response to ecosystem disturbance using nutrient partitioning ratios. *Ecosystems*, *19*(3), 387–395.

Kreutzweiser, D. P., Sibley, P. K., Richardson, J. S., & Gordon, A. M. (2012). Introduction and a theoretical basis for using disturbance by forest management activities to sustain aquatic ecosystems. *Freshwater Science*, *31*(1), 224–231.

Lutz, J. A., Key, C. H., Kolden, C. A., Kane, J. T., & van Wagtendonk, J. W. (2011). Fire frequency, area burned, and severity: A quantitative approach to defining a normal fire year. *Fire Ecology*, *7*(2), 51–65.

Mori, A. S. (2016). Resilience in the studies of biodiversity–Ecosystem functioning. *Trends in Ecology & Evolution*, *31*(2), 87–89.

Mumby, P. J., Hastings, A., & Edwards, H. J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature*, *450*(7166), 98–101.

Muthukrishnan, R., Lloyd-Smith, J. O., & Fong, P. (2016). Mechanisms of resilience: Empirically quantified positive feedbacks produce alternate stable states dynamics in a model of a tropical reef. *Journal of Ecology*, *104*(6), 1662–1672.

Nathan, R., Klein, E. K., Robledo-Arnuncio, J. J., & Revilla, E. (2012). Dispersal kernels: Review. In J. Clobert, M. Baguette, T. Benton, & J. M. Bullock (Eds.), *Dispersal and spatial evolutionary ecology* (pp. 187–210). Oxford University Press.

Newberry, B. M., Power, C. R., Abreu, R. C., Durigan, G., Rossatto, D. R., & Hoffmann, W. A. (2020). Flammability thresholds or flammability gradients? Determinants of fire across savanna–forest transitions. *New Phytologist*, *228*(3), 910–921.

Newman, E. A. (2019). Disturbance ecology in the Anthropocene. *Frontiers in Ecology and Evolution*, *7*, 147.

Paine, R. T., Tegner, M. J., & Johnson, E. A. (1998). Compounded perturbations yield ecological surprises. *Ecosystems*, *1*(6), 535–545.

Palmer, M. A., Allan, J. D., & Butman, C. A. (1996). Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in Ecology & Evolution*, *11*(8), 322–326.

Pansing, E. R., Tomback, D. F., & Wunder, M. B. (2020). Climate-altered fire regimes may increase extirpation risk in an upper subalpine conifer species of management concern. *Ecosphere*, *11*(8), e03220.

Peterson, G., Allen, C. R., & Holling, C. S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, *1*(1), 6–18.

Petrovskii, S., & Morozov, A. (2009). Dispersal in a statistically structured population: Fat tails revisited. *The American Naturalist*, *173*(2), 278–289.

Pulsford, S. A., Lindenmayer, D. B., & Driscoll, D. A. (2016). A succession of theories: Purging redundancy from disturbance theory. *Biological Reviews*, *91*(1), 148–167.

Robertson, D. K., & Mathias, D. L. (2019). Hydrocode simulations of asteroid airbursts and constraints for Tunguska. *Icarus*, *327*, 36–47.

Rykiel, E. J. Jr (1985). Towards a definition of ecological disturbance. *Australian Journal of Ecology*, *10*(3), 361–365.

Saatkamp, A., Cochrane, A., Commander, L., Guja, L. K., Jimenez-Alfaro, B., Larson, J., Nicotra, A., Poschlod, P., Silveira, F. A. O., Cross, A. T., Dalziell, E. L., Dickie, J., Erickson, T. E., Fidelis, A., Fuchs, A., Golos, P. J., Hope, M., Lewandrowski, W., Merritt, D. J., … Walck, J. L. (2019). A research agenda for seed-trait functional ecology. *New Phytologist*, *221*(4), 1764–1775.

Shaw, J. D., Goeking, S. A., Menlove, J., & Werstak Jr, C. E. (2017). Assessment of fire effects based on Forest Inventory and Analysis data and a long-term fire mapping data set. *Journal of Forestry*, *115*(4), 258–269.

Shrader-Frechette, K. S., & McCoy, E. D. (1993). *Method in ecology: Strategies for conservation*. Cambridge University Press.

Singleton, M. P., Thode, A. E., Meador, A. J. S., & Iniguez, J. M. (2019). Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. *Forest Ecology and Management*, *433*, 709–719.

Sommerfeld, A., Senf, C., Buma, B., D'Amato, A. W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L. E., Gutiérrez, Á. G., Hart, S. J., Harvey, B. J., He, H. S., Hlásny, T., Holz, A., Kitzberger, T., Kulakowski, D., Lindenmayer, D., Mori, A. S., Müller, J., … Seidl, R. (2018). Patterns and drivers of recent disturbances across the temperate forest biome. *Nature Communications*, *9*, 4355.

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, *91*(10), 2833–2849.

Wambugu, P. W., Ndjiondjop, M. N., & Henry, R. J. (2018). Role of genomics in promoting the utilization of plant genetic resources in genebanks. *Briefings in Functional Genomics*, *17*(3), 198–206.

White, P. S., & Jentsch, A. (2001). The search for generality in studies of disturbance and ecosystem dynamics. In *Progress in botany* (pp. 399–450). Springer.

Wiens, J. A., & Milne, B. T. (1989). Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology*, *3*(2), 87–96.

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SUPPORTING INFORMATION

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