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INNOVATIVE VIEWPOINTS

A multidimensional stability framework enhances interpretation and comparison of carbon cycling response to disturbance

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Abstract. The concept of stability is central to the study and sustainability of vital ecosystem goods and services as disturbances increase globally. While ecosystem ecologists, including carbon (C) cycling scientists, have long-considered multiple dimensions of disturbance response, our discipline lacks an agreed-upon analytical framework for characterizing multidimensional stability. Here, we advocate for the broader adoption of a standardized and normalized multidimensional stability framework for analyzing disturbance response. This framework includes four dimensions of stability: the degree of initial change in C fluxes (i.e., *resistance*); rate (i.e., *resilience*) and variability (i.e., *temporal stability*) of return to pre-disturbance C fluxes; and the extent of return to pre-disturbance C fluxes (i.e., *recovery*). Using this framework, we highlight findings not readily seen from analysis of absolute fluxes, including trade-offs between initial and long-term C flux responses to disturbance; different overall stability profiles among fluxes; and, using a pilot dataset, similar relative stability of net primary production following fire and insect disturbances. We conclude that ecosystem ecologists' embrace of a unifying multidimensional stability framework as a complement to approaches focused on absolute C fluxes could advance global change research by aiding in the novel interpretation, comprehensive synthesis, and improved forecasting of ecosystems' response to an increasing array of disturbances.

Key words: carbon; disturbance; ecosystem ecology; forests; resilience; resistance; stability; synthesis.

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INTRODUCTION

Quantifying ecosystems' functional response to disturbance is a long-standing focus of ecologists that has become more crucial in this era of unprecedented global change (Hicke et al. 2012, Cohen et al. 2016, Sommerfeld et al. 2018). Ecologists have long considered how disturbance affects ecosystem functions such as primary production, nutrient and water cycling, and carbon fluxes, recognizing both the multidimensional behavior of disturbance response and varying degrees of stability among ecosystems (Holling 1973; Box 1). For example, 20th-century theorists hypothesized a pattern of primary production decline and recovery following succession-resetting disturbance (Bormann and Likens 1979; Odum 1969, Vitousek 1982); empiricists used chronosequences and long-term observations to test this theory, documenting and comparing the stability of primary production following disturbance (Amiro et al. 2010, Hicke et al. 2012, Gough et al. 2013); and modelers used theoretical and empirical information to build, parameterize, and challenge earth system models' representation of disturbance responses (Cao and Woodward 1998, Dorheim et al. 2021). Following Holling's (1973) definition of resilience as the capacity of ecosystems to withstand and recover from perturbation (Holling 1973), ecosystem ecologists have also characterized the temporal dynamics and degrees of functional change that follow disturbances varying in scale, source, severity, and frequency (Turner et al. 1993, Goulden et al. 2011, Nave et al. 2011, Gough et al. 2021a).

Despite these advances, ecosystem ecologists, including carbon (C) cycling scientists, have not embraced the theories and analytical tools developed and applied by other disciplines for assessing the stability of ecological properties and processes following disturbance. *Multidimensional stability frameworks* (MDSFs) offer a conceptual and analytical basis for deriving and interpreting the many components of disturbance response, including the rate, magnitude, variability, and direction of compositional and functional change that proceeds disturbance (Box 1). These frameworks decompose absolute responses into discrete standardized and normalized components of stability, which can be compared against one another (i.e., to evaluate response trade-offs) and across ecosystems, fluxes, and disturbance sources (Harrison 1979, Peterson et al.1998, Donohue et al. 2016, Kéfi et al. 2019).

Applied broadly by population and community ecologists, MDSFs have been used to assess the multidimensional stability of populations or taxonomic composition following disturbance (Donohue et al. 2013, Kéfi et al. 2019). These studies have led to several new insights, including ecological and evolutionary trade-offs among short- and long-term disturbance responses (Stuart-Haëntjens et al. 2018; Cabrerizo et al. 2019; Hillebrand and Kunze 2020); differences in stability among disturbance types and spatial scales (Radchuk et al. 2019); the coupling of compositional and biomass change throughout disturbance recovery cycles (Gao et al. 2017); and recognition that—because dimensions of stability may relate to one another—initial changes in populations and communities could foreshadow long-term stability and the degree of full recovery (Hillebrand and Kunze 2020). However, despite the utility and widespread adoption of MDSFs

Box 1. Glossary of terms

Deconstructing "multidimensional stability framework" (MDSF)

Multidimensional: Necessarily characterized by multiple aspects of response behaviors, for example, with respect to functional change following disturbance.

Stability: The magnitude, direction, and rate of structural or functional change following disturbance(s).

Framework: Here, a conceptual foundation *and* analytical approach for assessing structural and functional responses to disturbance.

Other terms

Structure: Physical arrangement, quantity, and composition of vegetation in an ecosystem. Examples include leaf area index.

Function: Physical, chemical, and biological processes that move energy and material through ecosystem to sustain life. Net primary production, nutrient, and water cycling are examples.

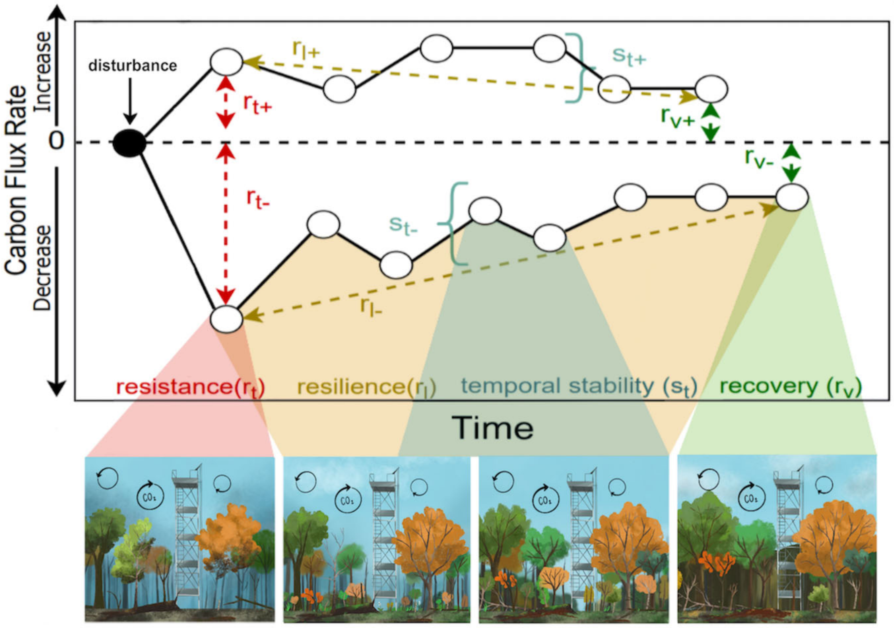
for assessing population- and community-level responses to disturbance, a meta-analysis found that none of the 508 studies utilizing these frameworks examined ecosystem-scale functions, including C fluxes, which are routinely characterized by ecosystem ecologists (Hillebrand and Kunze 2020).

In this *Innovative Viewpoint*, we use ecosystem-scale C flux data to illustrate how a normalized, standardized, and multidimensional stability framework offers a powerful complementary tool to approaches focused on absolute fluxes for interpreting, comparing, and synthesizing ecosystem functional responses to disturbance. We first show how a multidimensional stability framework developed for and largely applied to populations and communities can be modified to compare how different C fluxes respond to disturbance. Next, we apply this analytical framework to C flux time-series collected after insect or fire disturbance, illustrating how the approach may facilitate future syntheses of disturbance response. We demonstrate how the adoption of this type of framework by C cycling and other ecosystem ecologists could advance our ability to interpret, forecast, and manage for functional stability, particularly as advances in open data provide increasingly long-term, cross-scale C flux observations following disturbances.

A Multidimensional Stability Framework for Analysis of Carbon Flux Response to Disturbance

While several MDSFs have been proposed (Egli et al. 2019, Downing et al. 2020), we highlight that of Hillebrand et al. (2018) for three reasons. First, it is designed to enable analysis of compositional *and* functional responses to disturbance; this is appealing because compositional (e.g., taxonomic diversity) or structural (e.g., LAI) change may foreshadow or co-vary with C cycling responses to disturbance (Stuart-Haëntjens et al. 2015). Despite this knowledge, the study of compositional changes following disturbance is historically the domain of community ecologists and ecosystem-scale functional responses such as primary production the focus of ecosystem ecologists (Gough et al. 2021a). Second, while population and community properties such as species and richness more commonly decline after disturbance (Armesto and Pickett 1985, Murphy and Romanuk 2014), the analytical approach used here acknowledges that C fluxes may decrease or increase. For example, disturbance may initially increase soil respiration and organic mineralization as legacy detritus stimulates decomposition (Harmon et al. 2011), while intermediate levels of disturbance may prompt "overyielding" or increased primary production as suppressed vegetation is released from competition (Stuart-Haëntjens et al. 2015). Lastly, the MDSF is well suited to burgeoning time-series data generated from remote sensing platforms, meteorological flux towers, and on-the-ground inventories. Such open datasets are growing in number, duration, and spatial coverage with the deployment of satellite remote sensing platforms including NASA's Orbiting Carbon Observatory 2 (OCO-2) (Eldering et al. 2017), meteorological C flux tower networks including AmeriFlux and the National Ecological Observatory Network (NEON; Keller et al. 2008, Pastorello et al. 2020), and national inventories including the USDA Forest Inventory and Analysis (McRoberts et al. 2005).

An additional strength of the Hillebrand et al. (2018) framework is its standardization and normalization of stability dimensions, which allows for direct comparisons of disturbance response not readily made using absolute C fluxes. When control and treatment time-series data are paired or observations (without a control) span pre-disturbance through recovery, four stability dimensions can be calculated: *resistance, resilience, temporal stability,* and *recovery* (Fig. 1). Each dimension is calculated from the log response ratios of C fluxes (e.g., soil respiration) before and after disturbance or between a control and disturbance treatment; such log response ratios improve the normality of distributions and provide uniform contrasts between a treatment and reference value (Hedges et al. 1999). *Resistance* (r_s), a static variable, captures the initial magnitude and direction of disturbance response and is calculated from the log response ratio of pre–post or control-treatment C fluxes initially following disturbance. *Resilience* (r_l), a dynamic variable (i.e., changing over time), captures the rate and directionality of change over time following the initial disturbance response and is calculated as the slope of the log response C flux ratio. *Temporal stability* (s_t), also a dynamic



Dimension	Equation	Definition
resistance(r_t)	$r_t = \ln\left(\frac{F\ disturb.}{F\ control}\right)$	Magnitude of initial response
resilience(r_l)	$\ln\left(\frac{F\ disturb.}{F\ control}\right) = i + r_l * t$	Rate of return to pre-disturbance function
temporal stability(s_t)	$s_t = \left(\frac{1}{SE\ of\ resid}\right)$	Variation around resilience slope
recovery(r_v)	$r_v = \ln\left(\frac{F\ disturb.}{F\ control}\right)$	Degree of return to pre-disturbance

Fig. 1. A multidimensional stability framework (MDSF) with four distinct dimensions of stability adopted from Hillebrand et al. 2018 and revised to capture dynamic C cycling responses to disturbance. Conceptual figure shows two example C flux stability profiles following disturbance, one increasing (presented with positive stability dimension labels, e.g., r_{s+}) and one decreasing (presented with negative stability dimension labels, e.g., r_{s-}) immediately following disturbance. Illustration panels provide snapshots of the various stages of disturbance response corresponding with different stability dimensions. Table details mathematical and written definitions of each dimension. F represents the C flux rate from the y-axis, t represents time from the x-axis, and i represents the intercept of the resilience regression line.

variable, is calculated from the residuals of resilience (C flux vs. time) slopes and represents the interannual variability of C fluxes during this period. Finally, *recovery* (r_v) summarizes the degree to which the C fluxes return to or exceed pre-disturbance rates and is a static variable calculated from the log response ratio after the period of resilience. Because the timing of disturbance response may differ among disturbance sources and ecosystems, static variables such as resistance are ideally calculated when initial changes in log response ratios have peaked and recovery estimated once log response ratios no longer change over time (e.g., through change-point analysis, Gough et al. 2021b). All dimensions, aside from temporal stability, which can only be positive, can be positive, negative, or zero, representing an increase, decrease, or no change, respectively. A conceptual illustration of C flux time-series data and their relationship with multiple dimensions of stability along with the mathematical derivation of each stability variable is found in Fig. 1.

APPLYING A MULTIDIMENSIONAL STABILITY FRAMEWORK TO CARBON FLUX DATASETS

Application 1: Calculating carbon flux stability using experiments with controls

Motivated by the prevalence of ecosystem experiments with controls (Hanson and Walker 2020), our first example compares the multidimensional stability of C fluxes using a paired control-treatment disturbance manipulation. This approach could be applied to experiments with controls evaluating C flux responses to precipitation change (Rustad and Campbell 2012), temperature stress (Chivers et al. 2009), biomass removal and harvesting (Fakhraei et al. 2020), nutrient additions (Cusack et al. 2011), and elevated CO_2 (Selsted et al. 2012). We use data from the Forest Accelerated Succession Experiment (FASET; Gough et al. 2013), available through AmeriFlux (Pastorello et al. 2020) and COSORE (COntinuous SOil REspiration; Bond-Lamberty et al. 2020) open data repositories. The FASET study was implemented in 2008 via the stem girdling of >6700 trees within a 39 ha meteorological flux tower footprint to assess how a ~40% stem basal area reduction affects forest C cycling (Gough et al. 2013, Stuart-Haëntjens et al. 2015). We compare the multidimensional stability profiles of annual gross primary production (GPP), ecosystem respiration (R_e), and net ecosystem production (NEP), and instantaneous soil respiration (R_s), which, prior to normalization, spanned a range of absolute numeric values and possessed different units. Extensive descriptions of the study site, experimental design, and C flux methods are detailed in a series of research articles (Nave et al. 2011, Gough et al. 2013, 2021b).

We used regression analyses to assess absolute changes in C fluxes following implementation of the FASET treatment (Fig. 2). We found that 10-yr NEP in the treatment and control forests increased significantly by 1.4 and 0.36 Mg C $ha^{-1} \cdot yr^{-1}$, respectively, following disturbance ($P < 0.01$, $R^2 = 0.53$; $P = 0.02$, $R^2 = 0.36$). In contrast, GPP exhibited no significant decadal change in the treatment or control forest. R_e significantly declined in the treatment forest ($P = 0.01$, $R^2 = 0.45$) but did not change in the control forest. Treatment declines in R_e of 1.51 Mg C ha^{-1} over 10 yr suggest that lower C losses rather than higher C uptake drove increases in NEP. Similar comparisons of absolute C fluxes feature prominently in the literature and are critical for understanding how disturbances affect C sink–source dynamics (Seidl et al. 2014, Williams et al. 2014), C allocation within ecosystems (Litton et al. 2007), and for the parametrization and benchmarking of earth and ecosystem models (Shiklomanov et al. 2020).

Interpreting the same datasets using an MDSF elucidates three findings less obvious from our analysis of absolute fluxes. First, while GPP and R_e initially increased following disturbance, and therefore exhibited positive resistance values, NEP decreased, resulting in a negative resistance value (Table 1). This contrasting pattern indicates that the initial direction and magnitude of change by NEP and its component fluxes differed (Table 1). Second, correlations between some but not all stability dimensions suggest that early responses to disturbance may predict long-term responses or the degree of recovery. For example, resilience, the rate of C flux recovery following disturbance, was positively correlated with recovery, the extent to which fluxes returned to their pre-disturbance values (Fig. 3, $R^2 = 0.95$, $P = 0.015$). Comparable analyses of absolute fluxes, in the absence of standardized and normalized expressions of stability, may obscure such relationships because of differences among fluxes in units, scales, and timing of disturbance response. Lastly, our analysis indicates that the relative temporal stability of fluxes varies by an order of magnitude, a comparison that requires normalization (Table 1). This example illustrates how a MDSF powerfully complements absolute flux analyses; the latter is essential to predicting the quantitative changes in ecosystem

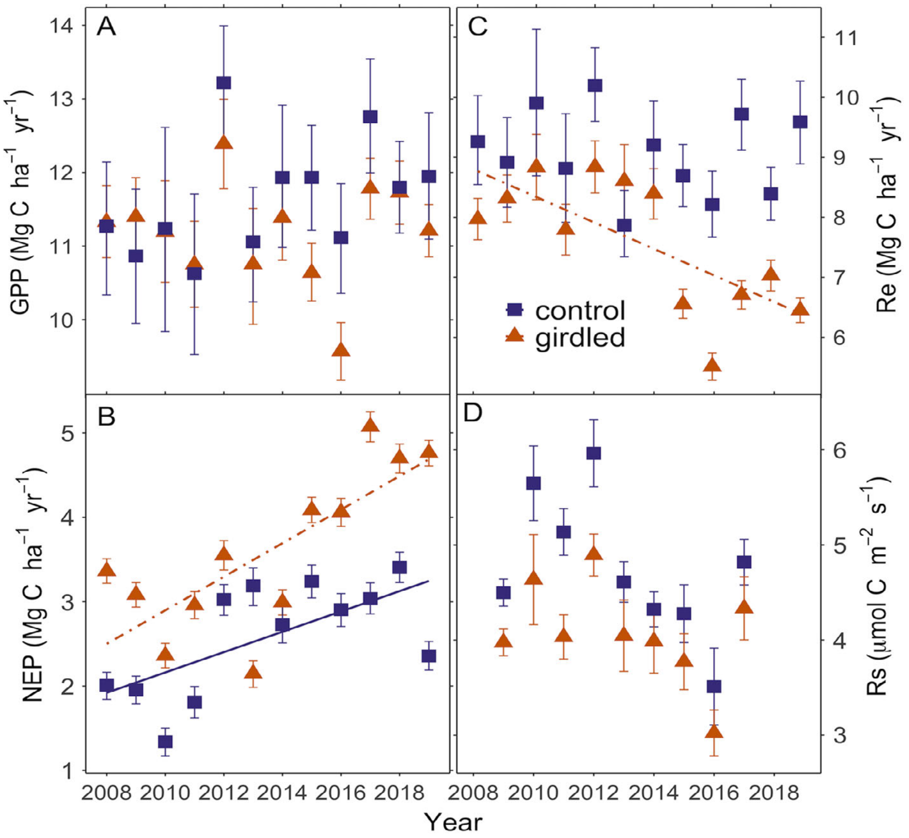


Fig. 2. Disturbance treatment via stem girdling (US-UMd) and control (US-UMB) forests time-series (2008–2019) analyzed with simple linear regression. (A) Annual gross primary production (GPP) ± uncertainty: Girdled (*P* value: n.s.), Control (*P* value: n.s). (B) Annual net ecosystem production (NEP) ± uncertainty: Girdled ($P < 0.01$, adjusted $R^2 = 0.53$), Control ($P = 0.02$, adjusted $R^2 = 0.36$). (C) Annual ecosystem respiration (R_e) ± uncertainty: Girdled ($P = 0.01$, adjusted $R^2 = 0.45$), Control (*P* value: n.s.). (D) Average growing season soil respiration (R_s) ± plot-level standard error, Girdled (*P* value: n.s.), Control (*P* value: n.s). The derivation of C fluxes and their uncertainty is detailed in Gough et al. 2021b.

and earth system properties, while the former provides new, potentially generalizable, information on the similarities, differences, and relationships among fluxes and features of stability.

Application 2: Deriving multidimensional stability values from carbon flux time-series

Our second example uses time-series data without controls to compare the resistance, resilience, and temporal stability of forests affected by two well-studied disturbance sources: fire and insect pests. This example highlights how an MDSF can be applied to long-term datasets that lack controls but include pre-disturbance observations as a reference. For example, multi-decadal open C flux datasets are available for forests disturbed by insects (Finzi et al. 2020) and fire (Kashian et al. 2013). To identify datasets for our example, we conducted a Web of Science search with the following keywords: "Net Ecosystem Product*" AND "insect" and "Net Ecosystem Product*" AND "fire." The criteria for inclusion were that annual NEP observations span at least one year before and four years after fire or insect disturbance. Our search yielded seven datasets, three documenting NEP after defoliating insect outbreaks and four after either prescribed burns or natural fire disturbances (Appendix S1: Table S1).

We focus first, again, on absolute NEP values. The time-series convey similar patterns of decline

Table 1. Multidimensional stability metrics for UMBS gross primary production (GPP), ecosystem respiration (R_e), soil respiration (R_s), and net ecosystem production (NEP) from the log response ratios of treatment and control estimates (Fig. 1).

Carbon flux	Resistance (r_s)	Resilience (r_l)	Temporal stability (s_t)	Recovery (r_v)
GPP	0.039 (±0.00002)	−0.011 (±0.002)	19.1 (±1.65)	−0.073 (±0.0025)
NEP	−0.128 (±0.01)	0.057 (±0.005)	2.3 (±0.25)	0.367 (±0.023)
R_e	0.073 (±0.001)	−0.027 (±0.003)	9.3 (±0.6)	−0.218 (±0.0065)
R_s	–	0.015 (±0.013)	8.1 (±1.0)	0.000 (±0.1)

R_s resistance could not be calculated because data were not available the year following disturbance. To account for pre-treatment site differences, the response ratios of control and treatment C fluxes were normalized to pre-disturbance values.

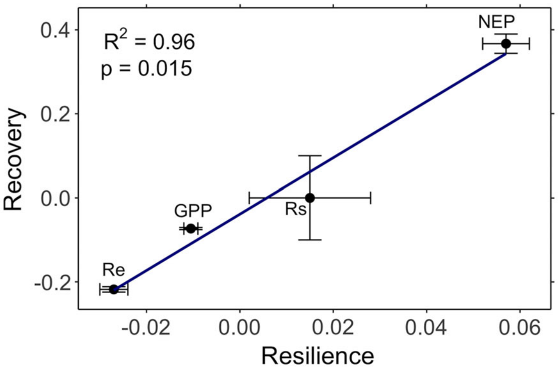


Fig. 3. Linear regression showing calculated gross primary production (GPP), net ecosystem production (NEP), ecosystem respiration (R_e), and soil respiration (R_s) recovery as a function of resilience from US-UMB and US-UMd flux tower sites.

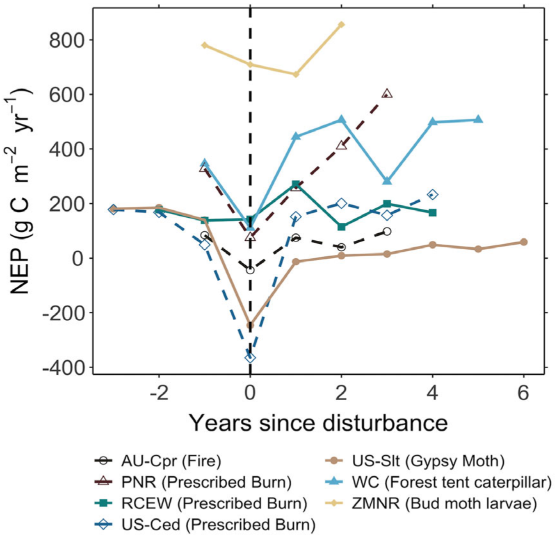


Fig. 4. Time-series of net ecosystem production (NEP) in years since disturbance (yr 0 = yr of disturbance, indicated with vertical dashed line) for seven forested sites that experienced either a fire (prescribed or natural) or defoliating insect disturbance. See Appendix S1: Table S1 for site information.

and rebound following fire and insect invasion, while illustrating a wide range in production among study sites (Fig. 4). For example, pre-disturbance NEP ranged from 49 to 780 g C·m^{-2}·yr^{-1} among sites, which was generally greater than within site-level temporal variability following disturbance. Insect and fire disturbances were followed by initial declines in NEP during the year of disturbance of up to 386 g C·m^{-2}·yr^{-1} and 141g C·m^{-2}·yr^{-1}, respectively (Fig. 4).

When an MDSF is applied, we find that, despite large site differences in absolute NEP values, forests responded similarly to insect and fire disturbances. Specifically, mean differences between insect and fire resistance, resilience, and temporal stability were not statistically significant (Fig. 5). In relative terms, both disturbances were followed by a similar initial drop in NEP or displayed a similar level of negative resistance, had overlapping rates of rebounding NEP or positive resilience, and exhibited comparable levels of interannual NEP variation during the period of resilience or temporal stability (Fig. 5). These similarities were not obvious from our unstandardized, non-normalized comparison of NEP. Although the NEP stability profiles were similar for the two disturbances, forests affected by fire displayed high variation within each stability dimension, while forests responded more uniformly to insect disturbance. We did not calculate recovery because, like many ecological

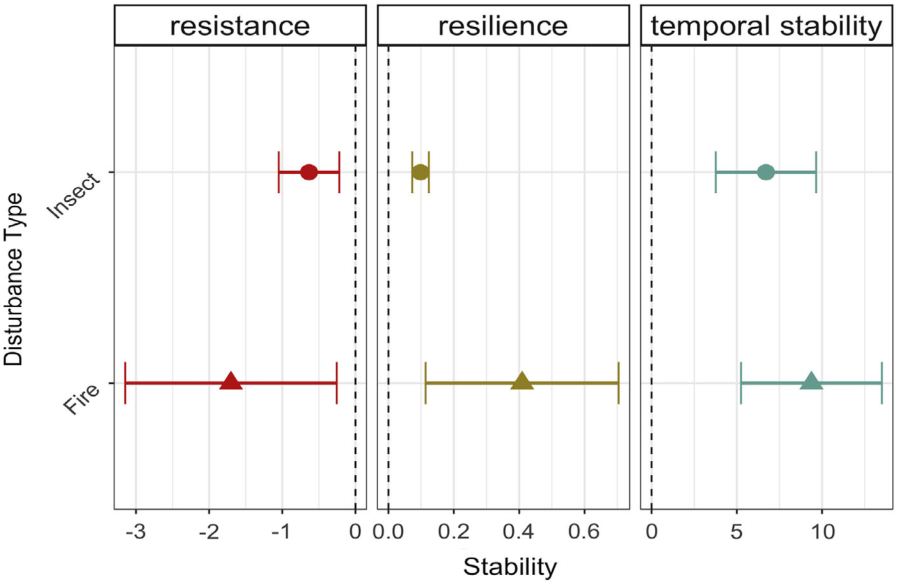


Fig. 5. Comparison of average net ecosystem production (NEP) stability (resistance, resilience, temporal stability) between fire (n = 4) and insect (n = 3) disturbances presented in Fig. 4.

studies of disturbance, observations did not extend to the period of recovery, when the ecosystems have attained a newly stable post-disturbance level of functioning.

Here, analysis of absolute NEP and relative responses viewed through the lens of an MDSF supplies complementary information, highlighting shared stability among disturbance types and sites, despite large differences in net C balance. While our sample size is small relative to meta-analyses summarizing mature areas of scientific investigation (Ainsworth et al. 2002, Nave et al. 2010), our example highlights the potential for syntheses of stability once a critical mass of C flux time-series overlapping with disturbance events becomes available through ecological networks. Similar analyses of absolute C fluxes have yielded important insights, demonstrating how quantitatively variable the net C balance of ecosystems is among sites and disturbances over time (Amiro et al. 2010, Hicke et al. 2012). However, given the wide range in magnitude of NEP values, duration of measurement, and temporal variation among sites, comparisons of stability between common disturbances, such as fire and insect pests, are challenging without a standardized and normalized analytical framework.

Conclusions and Recommendations

We conclude that the broader adoption of an agreed-upon multidimensional stability framework by C cycling scientists could greatly enhance understanding of disturbance responses by advancing standardized terminology, enabling new comparisons, supporting ecological forecasting, and providing a template for quantitative syntheses. Just as basins of attraction were conceived as a theoretical and analytical model with which to better conceptualize, assess, and compare state changes (Folke et al. 2004), the utilization of MDSFs by ecosystem ecologists will complement C flux and other ecosystem-scale functional analyses focused on absolute responses. Moreover, an MDSF that applies to multiple scales of biological organization—from organisms to ecosystems—will enable new discoveries only possible at the intersection of ecological disciplines (Table 2). Such interdisciplinary and integrative knowledge is essential for assessing coupled structural and functional mechanisms driving responses to disturbance at multiple scales and could provide fundamental insights relevant to ecosystem management focused on sustaining resources under changing disturbance regimes (Albrich et al. 2018). In

Table 2. Critical knowledge gaps in ecology that could benefit from a multidimensional stability analytical framework.

Knowledge gaps	Reference
Do plant community composition and structure correlate with functional stability?	Fraterrigo and Rusak (2008), Johnstone et al. (2016)
How does the stability of ecosystem functions, such as primary production and nitrogen cycling, feedback to alter compositional and structural stability?	Gough et al. (2021a), Nave et al. (2011)
Which dimensions of stability are correlated with one another and are therefore consistent trade-offs among stability dimensions?	Radchuk et al. (2019), Domínguez-García et al. (2019)
How can management cultivate ecosystems with more robust multidimensional stability profiles in an era of rapid global change?	Führer (2000), Albrich et al. (2018), Egli et al. (2019)
How does evolution shape functional stability across biomes?	Buma et al. (2013), Stuart-Haëntjens et al. (2018)

addition, greater understanding of how initial (i.e., *resistance*) and long-term (i.e., *recovery*) measures of stability relate to one another could constrain ecological forecasts of disturbance response and improve mechanistic representation of disturbance in ecosystem and Earth System Models (ESMs; Deser et al. 2020; Fisher and Koven 2020), which often fail to simulate observed disturbance responses (Bond-Lamberty et al. 2015).

Rather than our *Innovative Viewpoint* serving as a static commentary and tutorial on MDSFs, significant advances in stability research will require further consideration and contributions by multiple ecological disciplines along with the expertise and cooperation of data providers, modelers, managers, and technologists. For example, synthesizing stability across scales of biological organization is increasingly possible with data from open science networks such as FLUXNET, NEON, and Europe's Integrated Carbon Observation System (ICOS), which are accumulating years to decades of data through complete disturbance response cycles. However, such cross-scale syntheses necessitate broad analytical and ecological expertise. In addition, important questions for MDSF users and developers remain, including: What other dimensions of stability could or should be routinely characterized? What novel ecological and environmental questions will benefit from the broader, integrated application of MDSFs? How can MDSFs be revised to better accommodate temporal variability and the range of functional response to disturbance? Continuing to advance MDSFs to transform understanding of stability in an era of rapid global change necessitates greater integration of ecological disciplines and, moving forward, will require ecologists studying different levels of organization to intentionally intersect, drawing from equally rich, but often separate, areas of knowledge and theory.

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DATA AVAILABILITY

Data and code are available from Figshare: https://doi.org/10.6084/m9.figshare.14238008.v4. Data were analyzed using R version 4.0.1 (2020-06-06). Meteorological and carbon flux data for US-UMB (Gough et al. 1999) and US-UMd (Gough et al. 2016) are available through AmeriFlux: https://ameriflux.lbl.gov; soil respiration data are available through COntinuous SOil REspiration (COSORE) open data repository (Bond-Lamberty et al. 2020): https://doi.org/10.1111/gcb.15353

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3800/full