Title: Quantifying disturbance effects on ecosystem services in a changing climate

Authors:
[†]Laura Dee[1*], [†]Steve Miller[2], Kate J. Helmstedt[3], Kate S. Boersma[4], Steve Polasky[5,6], & Peter B. Reich[7,8,9]

Affiliations:
[1]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA.
[2] Environmental Studies Program, University of Colorado, Boulder, Colorado 80309 USA.
[3] School of Mathematical Sciences, Queensland University of Technology, Brisbane, Australia
[4] Department of Biology, University of San Diego, San Diego, CA, 92110, USA
[5] Department of Applied Economics, University of Minnesota, St. Paul, MN, 55108, USA
[6] Department of Ecology, Evolution & Behavior, University of Minnesota, St. Paul, MN, 55108, US
[7] Department of Forest Resources, University of Minnesota, St. Paul, MN, 55108, USA
[8] Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, 2753, Australia
[9]Institute for Global Change Biology, and School for the Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109, United States

[†]***These authors contributed equally to this work.***
***Corresponding author**: laura.dee@colorado.edu

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Summary Statement –191 words

Disturbances, such as hurricanes, fires, droughts, and pest outbreaks, can cause major changes in ecosystem conditions that threaten nature's contributions to people (ecosystem services). However, approaches to assess these impacts on diverse services under climate change are rare. To advance such efforts, we build on the accelerating research on disturbance ecology and ecosystem services to develop a functional trait-based approach to quantify ecological, ecosystem service, and economic outcomes under risk and climate change. We demonstrate this general approach by quantifying impacts to ecosystem services—timber and recreational enjoyment—from extreme windstorms in a mid-latitude forest. We find that expected ecosystem service losses from these windstorm disturbances are large and likely to increase with climate change. Yet, we show that common ecological metrics of compositional and biomass stability are inadequate for predicting these impacts to ecosystem service, necessitating more direct measures of services with disturbance. We then illustrate our approach for other applications spanning different ecosystems, services, and disturbances, including crop pollination, flood hazard mitigation, and cultural values. These examples highlight the pressing need to consider disturbances in future ecosystem service assessments, given the increase in mega-disturbances occurring globally with climate change.

Main Text

Ecosystems are subject to disturbances – transient, often rapid, changes in conditions. Disturbances modify ecosystems[1,2] and in turn can disrupt the flow of ecosystem services[3–6], also referred to as nature's contributions to people[7]. For instance, disease outbreaks reduce pollinator populations and the services they provide to farmers[8], and dry spells can decrease forage quality and production by impacting plant communities in grasslands [9]. Anticipating when, where, and how disturbances will impact ecosystems and their services is increasingly urgent under climate change, but climate change also makes this task more difficult. Under climate change, ecosystems are facing novel, variable, and more extreme disturbance regimes,[10] including more extreme storms and heat waves[11], increasing fire severity and extent[12], and unprecedented insect outbreaks[13]. Even in communities adapted to disturbances, like boreal forests[14,15] and arid-land streams, increased disturbance intensity and frequency under climate change[14,16,17] can increase mortality, change species composition, and alter ecosystem functioning[14,18]. Given significant predicted changes to disturbance regimes in the near- and medium-term[19,20], and mounting evidence for disturbance impacts to ecosystem services in particular systems (e.g. [5,6,21–24]), a broadly applicable approach to predicting ecosystem service impacts is needed.

Anticipating the consequences of disturbances for ecosystem services under climate change is a demanding task that requires integrating models of several processes (Figure 1). The impact of disturbances on ecosystem services (Fig. 1) depends on the disturbance regime and its intensity (Fig. 1*i*), how disturbances affect ecological communities (Fig. 1*ii*), how changes in ecological communities modify ecosystem services (Fig. 1*iii*), and how people value or benefit from services (Fig. 1*iv*). Several complexities challenge our understanding of how these parts combine to translate disturbance regimes to service impacts. For instance, the timing and intensities of disturbances are uncertain, and responses of individuals and species differ based on their distinct characteristics (e.g., traits like body size and thermal tolerance)[25,26]. Further, not all community changes will affect services in the same way, because a species' contribution to one or more services depends on its identity (e.g., pollinator of crops or not) and traits (e.g., size for harvestable biomass)[26,27], and the way a service is valued by people can be altered by disturbances too[5,28]. Some recent studies of disturbance impacts to ecosystem services seek to integrate some, if not all, of these components and complexities[21,22], particularly for market-valued services. Yet, the vast majority of studies involve ecosystem assessments that are static, and do not allow for these nuances in disturbance impacts. For instance, ecological studies measuring community response to disturbance stop short of tracing impacts to ecosystem services and human well-being; analogously, assessments quantifying, mapping, or valuing services do not always consider how climate change will impact disturbance regimes and thus the communities underpinning ecosystem services. Herein we attempt to bridge ecological and ecosystem service approaches, building on and extending trail-blazing work[6,22].

We study how disturbances can alter ecosystem services through two questions: **(1)** How do current and future disturbance regimes affect the levels and stability of ecosystem services, and how well do static ecosystem service assessments predict these outcomes? And, **(2)** How well do metrics of ecological stability, particularly compositional and biomass resistance, predict the resistance of ecosystem services to disturbances? Because assessing disturbance impacts on ecosystem services can be both complex and data-intensive to determine, our questions assess the viability or risk of methods that omit either disturbance or service production. The first question addresses the *risk of ignoring disturbances* when assessing ecosystem services under historical versus future disturbance regimes. The second question assesses the extent to which commonly used stability metrics from ecology [29] can be used to predict ecosystem service resistance as *short-cuts* for anticipating impacts. If measures describing how ecological communities respond to disturbances also predict changes in ecosystem services, a large body of ecological research could be extended for rapid insights into how disturbance regimes impact ecosystem services. This association, however, remains underexplored, because many ecological studies measure changes in terms of number, abundance, or biomass of species within an ecological community[1,30–32], rather than of a process or service itself (*reviewed in*[33], *but see*[34]). On one hand, ecosystem services clearly depend on ecological communities and their functions[27,35,36], implying that services could be altered as communities change. On the other hand, ecosystem services may remain stable even when communities change, if the species or individuals impacted by disturbances are not the ones contributing most to services[26] or if replacement or remaining species compensate for lost species. Further, the benefits from services to people depend on societal values[37], so a shift in people's preferences can alter how a service is valued without any change to an underlying ecological community.

To address these questions, we provide a flexible, trait-based mathematical framework that formalizes the ideas in (Fig. 1), considers probabilistic disturbance regimes, and integrates approaches linking global change to ecosystem functions using species' functional traits[25,26], with ecosystem service production functions[38]. We demonstrate our approach with an application quantifying how extreme windstorms impact forests, and the timber production and recreational enjoyment that forests provide, in Minnesota, U.S.A (Fig. 1B; see *Methods* and Fig. S1 for more detail). The application serves as a vehicle for gaining insights into the consequence of omitting key components of service production under disturbance rather than a detailed investigation of the context. We use the application to highlight substantial impacts of disturbances on ecosystem services that common ecological stability measures fail to adequately and precisely capture. This illustration underscores the perils of ignoring socioeconomic components of ecosystem services[39] and ecological changes in studies of economic or ecosystem service valuation[40]. We then outline how our approach could serve for a broad range of applications spanning different kinds of disturbances and ecosystems, ranging from agricultural to riparian to marine, and a variety of relevant services. Overall, our approach (Figure 1 and Fig. S1) provides a quantitative, broadly applicable way to incorporate scenarios of disturbances which could be used in future assessments of biodiversity and ecosystem services (e.g., the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, IPBES) that explicitly consider climate change.

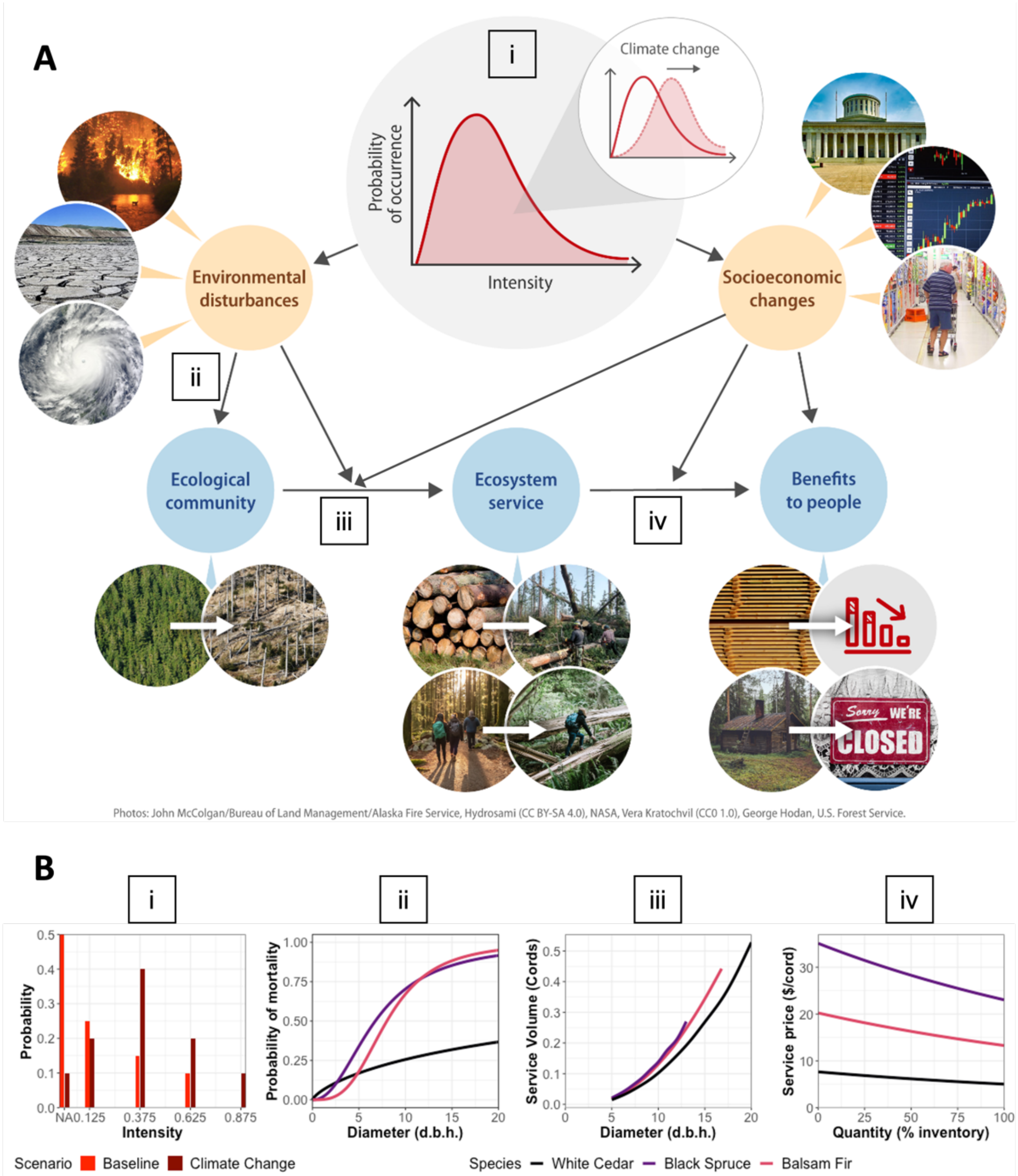

Figure 1. Framework for linking environmental disturbance regimes to ecosystem service outcomes. This framework allows evaluation of ecosystem service benefits under changing probabilistic disturbance regimes. **(A)** Illustrates our approach, which integrates and formalizes four concepts mathematically: **(i)** Imperfect knowledge of whether a disturbance will occur and how intense it will be, with disturbance regimes becoming more extreme with climate change. **(ii)** Disturbance alters ecological communities, mediated by the composition of species and "response traits" in the community. **(iii)** Ecological communities produce ecosystem services, mediated by traits of organisms and socioeconomic factors (e.g., management). **(iv)** Ecosystem services provide diverse values and contributions to people, mediated by management practices and societal values. **(B)** Example relationships underlying the four key components of our framework as applied to forests facing windstorms in Minnesota, USA. We model (i) a disturbance regime characteristic of historical conditions ('lower severity') and a hypothetical future regime ('climate change') where high intensity disturbances are more likely under climate change. To parameterize the "response function" in Aii, we use known relationships between the size of a tree and its probability of mortality which varies by species (see Bii) and the disturbance intensity (not shown here, see Fig. S1). To translate community and trait composition to services, we use the ecosystem service production function in (Biii) to determine the biophysical amount and then the value based on timber market data and the inverse

Approach to quantify disturbance impacts on ecosystem services

We ground our investigation in a mathematical framework that traces the effects of disturbances through ecological communities to ecosystem services and human well-being (Fig. 1, see Methods for details). Our framework traces a pathway from (i) the probability of disturbances of different intensities occurring; (ii) how each potential disturbance alters ecological communities, (iii) how an ecological community produces ecosystem services, through to (iv) how those services contribute to human well-being based on how people value them in monetary and non-monetary ways. Our general approach nests both highly complex, process-based models parameterized for specific systems (e.g.[6,21,22,24]) as well as approaches intended to capture ecosystem responses to disturbance (e.g.[41,42]; steps i-ii) or static ecosystem service values (e.g.[43,44] ; steps iii-iv). Combining these components shows how a distribution of potential disturbances could affect the distribution of future ecosystem services and their contributions to human well-being.

In the context of our framework, our research questions ask whether we can omit any of these components (i-iv, above) without fundamentally changing the predictions about the provision of ecosystem services. We evaluate these predictions using three key metrics for evaluating benefits in the presence of risk (see *Methods*). First, we measure service levels as the expected present value. Second, we measure risk as the variance of the present value under the distribution of future communities, environmental conditions, and socioeconomic responses to the disturbance regime (see *Methods*). Finally, we measure ecosystem service stability by introducing a metric, “ecosystem service resistance,” defined as the ratio of the mean present value under disturbance to the present value in the absence of disturbance (see *Methods*, equation [5]).

Application

We demonstrate this framework by examining the potential impacts of windstorms on timber production (e.g., sawtimber and pulpwood from red pine *Pinus resinosa* and white spruce *Picea glauca*) and recreational enjoyment in a 13-county region of northern Minnesota (MN), USA. Our application is based on data from 777 forest inventory plots with tree communities representative of southern boreal forests (Figure 1B; *Methods*). Windstorms are a useful illustration because, like many disturbances, they impact tree species differently depending on species' traits and identity[45] (Fig. 1B), change forest community composition[46,47], cause significant damages[47,48] and [15]are highly variable in space and time[49]. Many analyses suggest that wind disturbance is predicted to increase in frequency and intensity in many forested regions in the future, driven largely by cyclones in maritime regions and straight-line winds elsewhere[50–54] (see Methods). We focus on the impacts of potentially higher wind disturbance to timber revenue because of its importance to local economies and because traits influence trees' contributions to timber products and value, as well as their responses to wind (Fig. 1B). Then, we show how our approach can be extended to consider both non-market values and more complex relationships between forest structural complexity, species diversity, and recreational value (based on [55]).

We present this application to demonstrate how these processes can be integrated in a disturbance-to-services framework that could be applied in diverse contexts, including those in which data constraints preclude the use of precise and sophisticated—but data-hungry—process-based models (e.g., iLand and LANDIS-II[56–58]). As models become more detailed with complex processes and dynamics, more data is needed to parameterize them confidently; therefore, we opt for a compromise here, acknowledging that this application misses dynamics available in some mechanistic, process-oriented models.

Comparison to current approaches

We compare output from a model implementing all parts of the framework to that from *status quo* approaches in two sub-fields: (1) widely-used ecosystem service models based on land cover classes and average conditions that omit disturbances (e.g. InVEST [43] *but see* [21]) and (2) ecological studies that measure the stability of the responses to disturbances in terms of the ecological community[33] or biomass[32] -- but not services. First, we first quantify the importance of considering disturbances for services by comparing the expected value, variance, and resistance of the ecosystem services under the *status quo* of assuming no disturbance versus under scenarios with probabilistic disturbance regimes. Second, we quantify how well several common measures of ecological community resistance[33] – the dimension of stability most often used to compare community changes before and after disturbances [29] -- predict changes in ecosystem services. In particular, we measure ecological community resistance using three

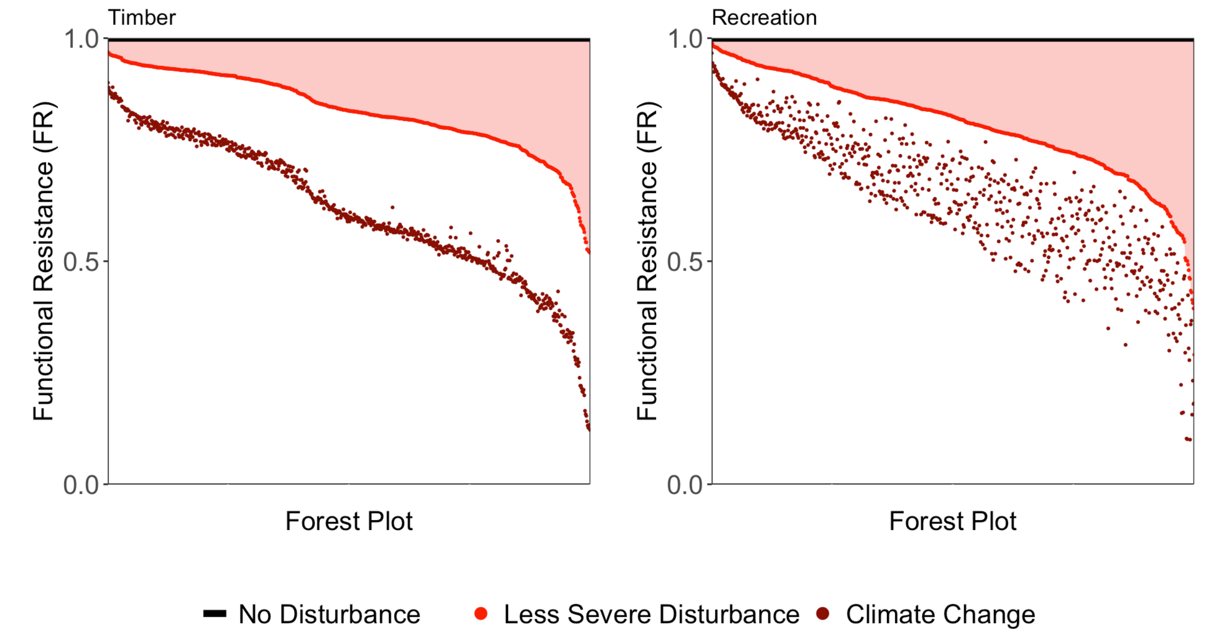

Figure 2: Ecosystem service resistance (y-axis) per forest plot (x-axis) for two ecosystem services (timber, recreation) under a simulated lower severity disturbance regime (red) and a climate change disturbance regime (dark red), with forest plots ordered from least (left) to most (right) impacted by the simulated disturbance regime. Resistance is, by definition, 1 in the absence of disturbance (black line) representing *status*

measures of compositional stability (aggregate similarity between the abundances of species before and after disturbance, *see Methods*) and with a metric proposed before in ecology[17]: resistance calculated using biomass that is expected to serve as a proxy for productivity-based services [32] (see *Methods*).

Results and Discussion

Importance of disturbances in ecosystem service assessments

Our application illustrates that the impacts of disturbance on ecosystems can alter the amount, variance, and expected value of ecosystem services in profound ways. Simulated estimates for Minnesota, USA, include losses in expected total economic timber value of 23.0% under a less severe disturbance regime and 50.7% under a stylized, more severe disturbance regime (Figure S4), representative of what could occur under climate change (Figure 2, left panel). The magnitude of these losses varies substantially across the region (Figure S4). Moreover, even if timber prices rise when trees are lost to disturbance (if downed trees cannot be salvaged)[59], expected loss in service value remains high (39.5%; Figure S4). Recreational enjoyment, valued non-monetarily, shows a similar pattern of impacts, but with substantially more variability in service resistance between disturbance regimes (Figure 2, *right panel*). Together, these results suggest that ecosystem service analyses that ignore disturbance could thus miss economically and societally important losses, particularly as disturbances intensify under climate change. Whether disturbance impacts would routinely cause large losses in ecosystem services, and even larger ones under climate change, remains an open question. These large potential losses under our two stylized disturbance regimes also point to the importance of improving our understanding of both current and future disturbance probabilities, which are often poorly resolved.

For our illustrative application, losses in ecosystem services caused by disturbance are not only predicted to be large on average, but also variable across space. Places where an ecosystem service is most resistant, on average, may still see large losses under some possible futures (Figures S3 & S6). In fact, we observe a strong, positive relationship between expected ecosystem service value and the standard deviation in that value across locations (Fig. S6 shows $r = 0.932$), which suggests a risk-return tradeoff resulting from the disturbance (see *Supplemental Discussion*). Such trade-offs prompt important questions for managers, including *whether to manage or select sites for high returns or for consistent returns.* While most ecosystem service assessments either ignore disturbance, treat responses to disturbance as deterministic, or evaluate services under average conditions, recent work from ecological economics has assessed risk-return tradeoffs, primarily for forest ecosystem services[60]. These

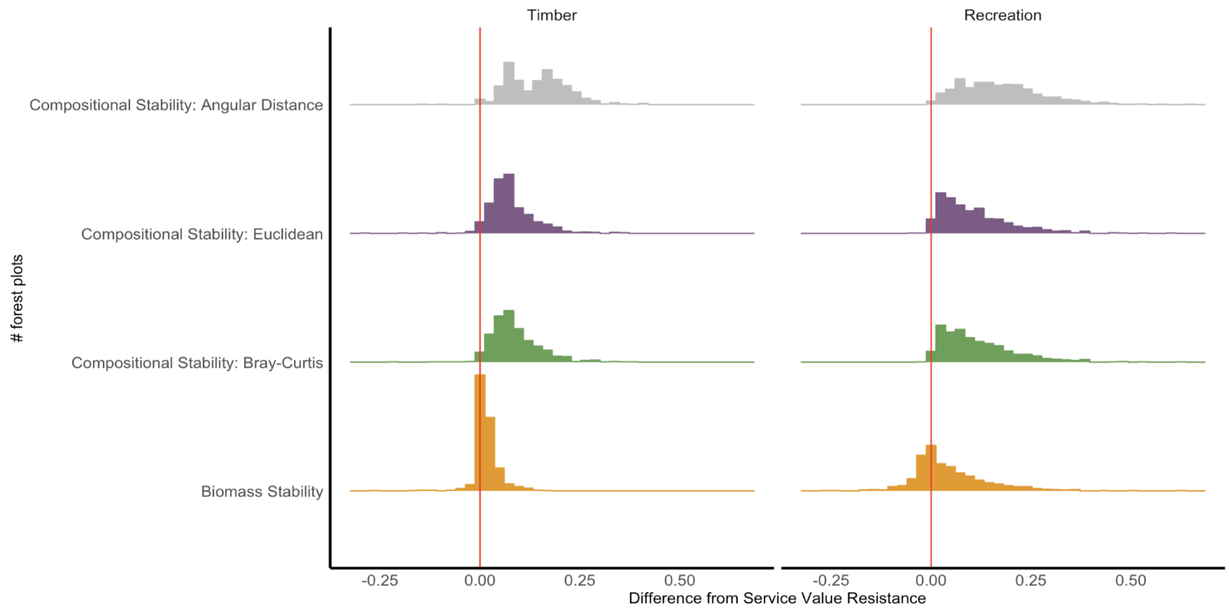

Figure 3: Differences between measures of stability and Ecosystem Service Resistance. The distribution of plot level differences (horizontal axis) between a measure of ecosystem stability (rows; one minus angular distance, inverse Euclidean distance, Bray-Curtis similarity, and biomass resistance) and ecosystem service resistance for two ecosystem services (timber and recreation) under the simulated, lower severity disturbance regime. Distributions indicate that, for the simulated, lower severity disturbance regime and services, ecosystem measures of stability tend to overestimate service resistance, with greater spread for the recreation service. Supplemental Figure S6 shows these comparisons under the simulated climate change disturbance regime.

studies provide a path forward to balance these potential trade-offs for the broader field. Moving forward, our approach can be integrated with these and other tools (e.g., from Modern Portfolio Theory[61]) for selecting management strategies under quantifiable risk-return tradeoffs which could reveal different management priorities for ecosystem services.

Value of direct measures of service stability

Our results also suggest that stability metrics commonly used in ecology to assess resistance to disturbance can be inadequate proxies for understanding ecosystem service production under disturbance (Figure 3). In our application, three measures of compositional stability based on abundance vectors and a biomass-based resistance measure consistently overestimate plot-level service resistance for the lower severity disturbance regime. All compositional measures fall short, likely by missing the details of how species produce services

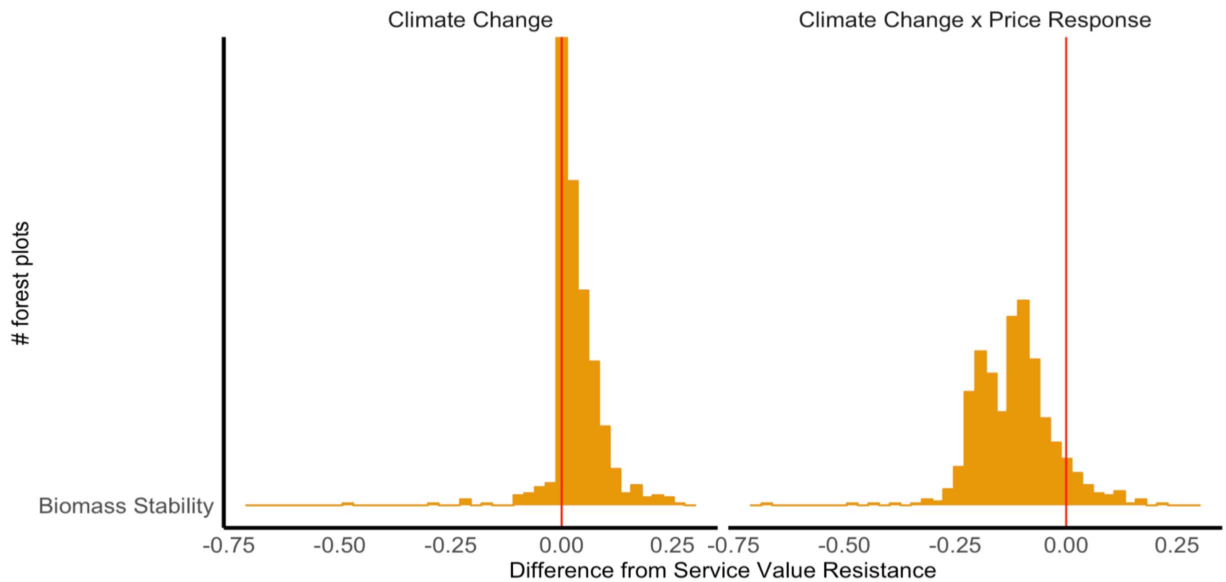

Figure 4: Influence of service valuation on the relevance of ecosystem stability measures for predicting service resistance under disturbance. The distribution of plot level differences (horizontal axis) between biomass-based resistance and ecosystem service resistance (red line) for timber services under the assumptions of no price response (left) and an endogenous price response to a disturbance-induced timber shortfall (right), simulated for the climate change disturbance regime.

and how people value these contributions (e.g., timber prices differ by species, recreators value diversity in tree structure). Of the compositional stability measures, one minus angular distance between pre- and post-disturbance abundance vectors is least informative for service resistance; after all, it is also insensitive to absolute abundance changes as well as species' specific contributions to services. Biomass-based resistance comes closest to capturing service-based resistance for both services, yet differential contributions of species to services (for timber) or a preference for variety (for recreation) lead to biomass-based resistance still exhibiting systematic biases in our application (Figure 3, bottom panel). Given that timber production depends on biomass, we would expect that this setting is one where ecological metrics would be better predictors of service responses than may be typical. For recreation, which is less tightly linked to biomass, plot-level bias of ecological metrics for recreation are larger and more variable than for timber (Figure 3), which unfortunately may be more typical for other services that do not depend linearly or as directly on aboveground biomass (e.g., water quality, soil carbon sequestration, inspiration and other cultural values).

The utility of ecological stability metrics for predicting service resistance is challenged further by socioeconomic responses to disturbance. To illustrate this point, we focused on the market-valued timber service and calculated the bias in the best-performing ecological stability metric (biomass-based resistance) under our climate change disturbance regime with and without allowing prices to adjust after a disturbance occurs (Figure 4). If prices do not adjust after a disturbance, biomass-based resistance *overstates* service resistance in our application because the lost biomass tends to come from higher value species (Figure 4, left panel). By contrast, if the disturbance creates a timber shortfall and prices rise, biomass-based resistance *underestimates* service resistance in our application because loss of the service makes remaining trees more valuable (Figure 4, right panel). Under different assumptions about how timber prices respond to the downing of trees (e.g., if salvage is possible, the flood of downed trees could drive prices down, exacerbating overprediction of resistance; alternatively, foresters in other areas could adapt to changing prices, dampening price responses) the bias of biomass-based metrics could be quite different, but still present. No matter the direction of price changes, metrics focused on ecological impacts diverge from the predictions from our service-focused framework in important ways, even in an application focus on timber where the ecosystem service closely depends on biomass.

The reasons why metrics of community stability may poorly predict responses of ecosystem services to disturbances include uneven contributions to services across species (Figure 1Biii) and the varying values people attach to those services (Figure 1Biv). Our example illustrates these issues: for our recreation service, value partly derives from a community-level property (diversity), such that individuals' contributions to services are uneven and community-dependent. For timber, not all species considered are harvested, smaller trees have biomass but may not yet be large enough for use, and timber products differ in value by species and location. These same considerations are likely to apply in other settings; for example, subsets of the species within a community provide the bulk of services for pollination[62] and carbon sequestration[63]. In sum, when species have unequal contributions to the amount and value of services, there is a wedge between community responses to disturbances and ecosystem services. As such, the predictions from our approach provide quantitative evidence in support of recent calls to better integrate ecological models and socioeconomic components of ecosystem services[39].

Understanding disturbance impacts across contexts

While our application focuses on two services and one type of disturbance, the limitations of ignoring disturbances in ecosystem service assessments or ignoring ecosystem service production and valuation in ecological studies apply in many more contexts. Potential applications include dry spells and forage production; storm surges, coastal vegetation, and flood mitigation; fire and/or pest outbreaks and carbon storage in forests; marine heat waves and fish production; drought, urban trees and human heat stress; and water filtration and water quality from filter feeders. Future work could quantify the nuanced impacts of disturbance on services in a diverse array of systems and push beyond the simplifying assumptions made in our application. To illustrate potential extensions raised by broader applications, we highlight three disturbances and corresponding ecosystem services in Figure 5 that are very different than the forest application. The first outlines how extreme heat waves could influence pollinator communities

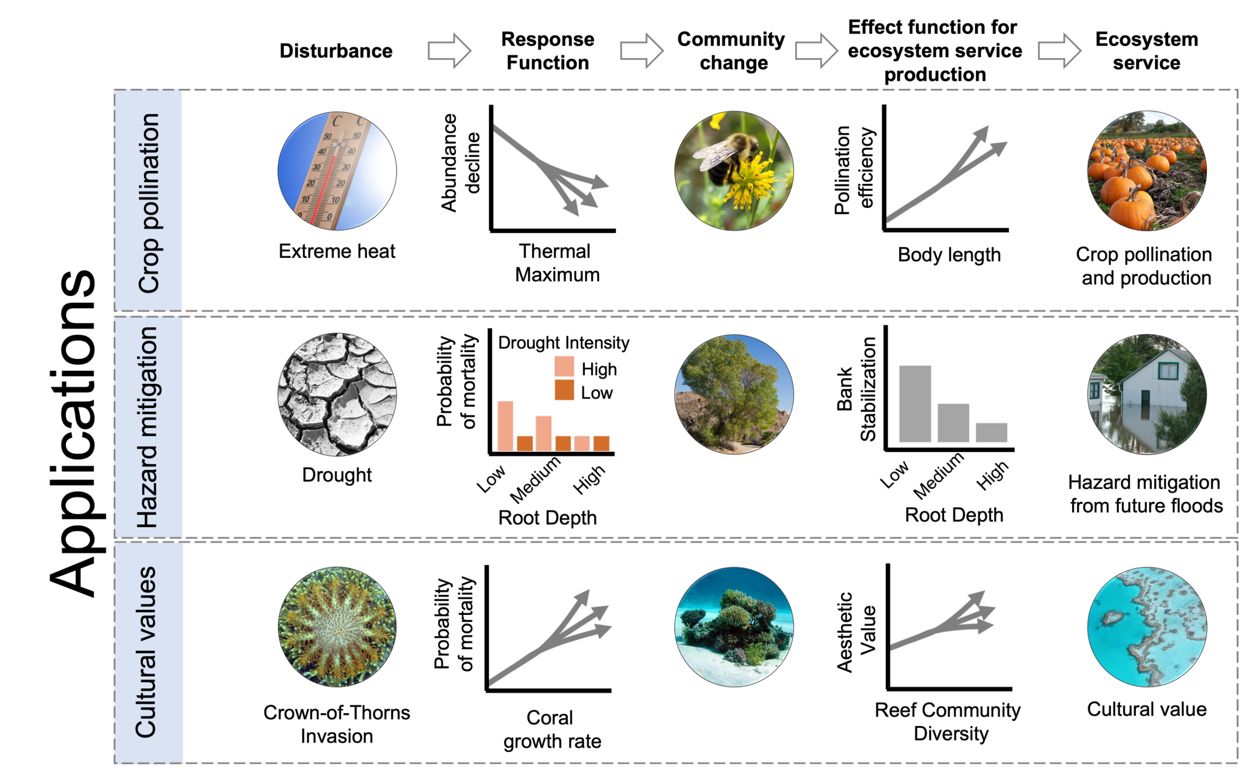

Figure 5. Applying our framework to quantifying the consequences of other disturbances for ecosystem services using response and effect functions. Our framework is broadly applicable to any ecosystem providing a service which is subject to disturbances. Conceptually, we show applications to (a) crop pollination, (b) hazard mitigation, and (c) cultural values, in response to abiotic (extreme heat, drought) and biotic disturbances (invasion).

and thus crop production (Figure 5, top panel), a second involves the way drought could affect riparian tree communities and their capacity to mitigate flood impacts (Figure 5, middle panel), and the third reflects how biotic invasion can adversely affect ecosystem services provided by coral reefs, including cultural ones (Figure 5, bottom panel).

First, the impacts of a heat wave on pollination services illustrate how effects of a disturbance on services depend on whether a species' susceptibility to a disturbance and that species' contribution to service provision are directly or inversely related. For example (Figure 5), in some crop systems and climate zones, larger-bodied bees tend to better tolerate higher temperatures during heat waves and more efficiently pollinate crops (e.g., bumble bees, *Bombus spp*., that pollinate oilseed rape[64] and pumpkins[65]). In this case, impacts of disturbances on services may hypothetically be smaller than their impact on ecological communities, although this would require larger-bodied bees compensating for losses of smaller pollinators (Fig. 3). This contrasts with our timber application, in which individuals contributing more to services were also more susceptible to disturbance.

Second, a riparian-drought-flood context shows how community responses to one disturbance could also make a system differentially susceptible to another disturbance. For instance, riparian trees with relatively shallow roots protect nearby property by stabilizing riverbanks but are more susceptible to drought[66] (Figure 4). Drought shifts these communities to deep-rooted shrubby trees that provide less bank stabilization due to an ecological trade-off between deep versus wide roots[67] – making these places more susceptible to future flooding events. Such impacts of one disturbance on susceptibility to another are likely common[19].

Third, coral reefs under biotic invasion and climate change illuminate how multiple types of disturbance may be present, and services could depend on a suite of traits or even community-level properties and aspects of diversity. For example, the Great Barrier Reef is threatened by both bleaching and invasions, and beyond its value for seafood production, provides value through both tourism and cultural value, which may depend on community-level properties (e.g., morphological diversity). An analogous approach to the recreational enjoyment of disturbed forests could be changes in appreciation of impacted coral reefs, which similarly depends on coral structural complexity, as determined by coral morphological traits *and* species diversity[28].

Implementing an integrated approach

Given the importance of considering disturbances and ecosystem service production jointly, we suggest that researchers and managers adopt an integrated, interdisciplinary modeling approach. The mathematical framework we outlined and illustrated in Fig. 1 requires context-specific choices about disturbance regimes, community responses ("*response functions"*), ecosystem service production ("*effect functions*"), and how people value those services ("*utility functions*"). To implement this end-to-end approach, one option is to use detailed process-oriented models, such as those recently developed for forests in the ecological economics literature[22]. However, in many ecosystems, researchers do not have the resources so support for such data-hungry modeling approaches. Alternately, Diaz et al.[68] ranked service vulnerability of communities based on linear correlations between species' responses to environmental drivers and their contributions to services. In our application, we opted for a middle ground using empirically-derived functions that describe disturbance response, service production, and service value relationships rather than the more detailed process models available for forests, in order to demonstrate the framework and address our research questions.

There are benefits and drawbacks to each approach. Diaz et al.'s correlation-based approach [68] in requires the least data, but it yields very different rankings of vulnerabilities across communities in our example application (see *Supplemental Note*). These differences are partly driven by the within-species trait variation captured in our framework, which allows us to account for both abundance and intraspecific variation in contributions to services and non-linear responses to disturbance. In contrast, when detailed process-oriented models are available for certain systems, disturbances, and services, we acknowledge they may be preferable for their ability to capture transient dynamics and trends in time, to generate more specific and precise predictions (e.g., [56–58]). However, they require additional assumptions and often far more data and parameterization that may not be possible in many contexts. Along with data availability, the relevant scales in space and time for the research question, the extent of ecosystem service delivery[69], or management context could help determine which technique to use to implement this general end-to-end approach.

The function-based but phenomenological approach we employed in our example application seeks to balance complexity with accessibility and generalizability, so it can be applied in a diverse set of cases, including those with additional complexity like coral reefs as described above and with different levels of data availability. Uncertainty will increase with complexity and data limitations under a changing climate; quantifiable components of that uncertainty could be incorporated in each step in Figure 1. For instance, even in a data limited context, a range of response and effect functions as shown in Figure 5 could be elicited from experts. Embedding different plausible functions in the framework can then provide a range of potential consequences of disturbance for service provision. Other limitations are more difficult to overcome; quantitative frameworks like ours are not suitable for handling qualitative service values without more fundamental modifications.

Using an integrated, quantitative approach to study the effects of disturbance on ecosystem services enables several promising avenues for future research. First, it provides an explicit and quantitative way to account for multiple disturbances and potential interactions among risks. For example, simultaneous threats of fire and windstorms in forests pose tradeoffs for managers. Increases in tree diameter may reduce flammability[70] but raise susceptibility to wind damage in non-linear ways[45] (Figure 1B), while changes in crown fire, groundfire, and windstorm occurrence could change the spatial arrangement of ladder fuels, either decreasing or increasing potential fire contagion, depending on specifics of disturbances and the system in question. Second, this approach allows for compensatory responses. We demonstrate a socioeconomic version of a compensatory response, i.e. a price response, but ecological compensatory responses (e.g., competitive release) are also plausible and potentially important.[68] Third, this approach also facilitates exploration of socioeconomic "disturbances" (Fig. 1), such as new policies or sudden changes in demand (e.g., due to COVID-19), and could be used to investigate whether the impacts to services from disturbances are distributed inequitably across diverse demographic and stakeholder and rights-holder groups. Finally, this approach can be embedded within frameworks for decision-making under risk and easily modified to suit other management objectives (e.g., maxi-min) or settings in which uncertainties are not quantifiable ("deep uncertainty") (e.g. [71]).

Conclusions

Disturbances can be important determinants of ecosystem services, with long-lasting effects, and are likely to become more important in the future as climate change increases disturbance frequency and intensity[23,49,72]. Our results suggest that accounting for how ecosystem services respond to disturbances (as proposed in Fig. 1) is crucial. We find that ecological predictions alone are insufficient to predict disturbance impacts if ecosystem service outcomes are of interest[37] while socioeconomic valuation studies could similarly miss important climate-driven impacts that occur through changes in ecological communities based on how people value them. To that end, we provide a general framework for understanding impacts of changing probabilistic disturbance regimes on ecosystem services using functional traits. As shown here, incorporating disturbances can alter predictions about the amount and variance of nature's contributions to people, with important implications for management of ecosystems in the face of global change. We show that incorporating ecological community structure into production functions can help understand the consequences of disturbances for ecosystem services in ways missed by current assessments, but – on their own – measures of changes in ecological communities do not necessarily predict changes in ecosystem services. Together, our results highlight the pressing need to consider disturbances in future ecosystem service assessments**,** given the increase in mega-disturbances occurring around the world with climate change, and for greater integration across research communities. This research is an important step towards anticipating impacts to ecosystem services, adapting management strategies accordingly, and informing future science-policy efforts that simultaneously assess biodiversity and climate change.

Methods

Mathematical framework

Our framework combines components (i)-(iv) as in Figure 1 to yield the present value (*V*) of ecosystem services produced by a community C_t subjected to random disturbances D_t:

$$V = \sum_t \beta(t) U(F(C_t, E_t, H_t), H_t), \quad [1]$$

where

$$C_t = G(C_{t-1},, H_{t-1}, D_{t-1}). \quad [2]$$

The present value *V* is the sum across time *t* of utility U, discounted (by $\beta(t)$), which is derived from service levels F produced by community C_t under environmental conditions E_t and socioeconomic factors H_t. The community changes through time according to a function *G* that depends on the previous community C_{t-1}, socioeconomic factors (e.g., management actions) H_{t-1}, and a stochastic disturbance D_{t-1} drawn each period from a distribution of disturbance types and intensities that may be altered by climate change. We assume that the set of possible disturbances $\mathbb{D}$ contains at least one individual disturbance, with each disturbance $d \in \mathbb{D}$ defined by attributes: type (e.g., fires, floods, pest outbreaks, windstorms, and drought), intensity, and duration. The possibility of no disturbance can be included through $d^0 \in \mathbb{D}$ that has no effect (see *How each potential disturbance alters ecological communities* below). With this notation in place, we next describe each component at the core of the framework.

Ecological communities and traits

We begin by describing how we represent ecological communities. Communities are composed of groups of individuals, with groups defined such that all individuals in a group are assumed to have the same values across all disturbance- and service-relevant traits. For example, a group may represent an entire species and use trait averages, or may be further divided beyond species, including intraspecific variation in traits. We represent a community $C_t = \{A_t, \boldsymbol{T_t}\}$ at time t by a vector of group abundances (A_t) and a matrix of trait values ($\boldsymbol{T_t}$). Elements of A_t and rows of $\boldsymbol{T_t}$ correspond to groups, while columns of $\boldsymbol{T}_t$ correspond to different traits. For example, in our application, columns of $\boldsymbol{T_t}$ include species, diameter at breast height, and bole height; groups are defined by unique combinations of values of those traits. In that case, for each site, C_t represents size-distributions of individuals from each species.

Because functional traits can mediate how disturbances alter communities[25], as well as how ecological communities produce services[35,73], our approach incorporates traits in F and G. Traits may include, for example, physiological traits that determine the response to disturbance (e.g., thermal optimum) or morphological traits that determine a species' contribution to a function or service (e.g., body size, leaf structure)[74]. Unlike in most ecological frameworks[25,26,73], both the level of services and value derived from them may also be influenced by socioeconomic factors H_t. Including socioeconomic factors is important, for instance, because demand determines which species or traits provide a service (e.g., appreciated for its aesthetics, harvested for food or products), and management rules can determine which range of trait values contributes to the production of a service (e.g., rules about size limits for harvesting fish or timber). Further, socioeconomic factors may make the service contributions of individuals or species interdependent (e.g., when the timber value of one tree may increase because other trees are lost to a disturbance).

How each potential disturbance alters ecological communities

We define a '*disturbance-response function'* $G(\cdot)$, representing how disturbance drives a community change from its current state C_t to a future state $C_{t+1} = G(C_t, D_t)$. Disturbances can have group-specific impacts that also depend on traits (e.g., *as in* Figure 2B) or on abundances. Exactly how $G(\cdot)$ affects each group in the community depends on the traits and abundances within that group (e.g., following group-specific functional forms). $G(\cdot)$ can be determined based on mathematical models or existing empirical studies quantifying the impacts of a particular disturbance on species survival or mortality (e.g., drought impacts on survival). $G(\cdot)$ can also capture feedbacks between how the groups respond (e.g., competitive release when one species is more impacted than another[75]). Species loss or invasion can be accounted for by changes to relevant entries in the abundance vector because we assume that corresponding elements of C_t and C_{t+1} are the same dimension. The possibility of no disturbance can be included as $C = G(C, d^0)$.

How likely different disturbances are

A disturbance regime consists of a set of disturbances $\mathbb{D}$ and a conditional probability distribution $P(D_t = d|E_t)$ detailing the likelihood of a particular disturbance $d \in \mathbb{D}$ occurring. The probability of a particular disturbance can shift through time because of climate change or other gradual shifts in conditions E_t (Figure 1). Therefore, gradual or press disturbances, such as warming from climate change, can enter in the framework by modifying the distribution of D_t, and by altering the probability and intensity of punctuated disturbances. A null regime in which no disturbance occurs, as is often implicitly assumed in studies mapping current distributions of ecosystem services, can be represented by the regime with $P(D_t = d^0|E_t) = 1$.

How an ecological community produces ecosystem services

We calculate the services an ecosystem provides by defining an *ecological production function,* $F(C_t, E_t, H_t)$, depending on the community composition (and thus trait composition) C_t, environmental conditions E_t, and socioeconomic factors H_t [38,76,77]). The exact form of $F(\cdot)$ will depend on the services of interest and should be based on knowledge of the system. For instance, $F(\cdot)$ could include non-linear effects of having multiple species (i.e., biodiversity effects, e.g., ref. 56[56]). Further, inclusion of H_t incorporates socioeconomic factors (e.g., management rules, labor for provisioning services such as timber) to influence how ecosystem functions translate to services. For instance, demand determines which species or traits provide a service (e.g., appreciated for its aesthetics, harvested for food or products), and management rules can determine which range of trait values contributes to the production of a service (e.g., rules about size limits for harvesting fish or timber).

How ecosystem services provide benefits

People benefit from ecosystem services according to the function $U(F(C_t, E_t, H_t), H_t)$. This *benefit function* $U(\cdot)$ represents how people or society values different combinations of services provided at different levels (e.g., $F(\cdot)$), and inputs needed to obtain those services defined by H_t (e.g., land maintenance or opportunity costs). For example, in our timber application, the benefit function, $U(\cdot)$, considers information from timber markets, particularly stumpage prices, which differ across products, species, and counties.

How to evaluate those benefits under risk

To analyze the outputs of our modeling framework, we define several candidate statistics that summarize the provision of ecosystem services across a range of potential futures. First, the expected present value of benefits of ecosystem services over time given the disturbance regime is as follows:

$$EV_P \equiv E_P[V]. \qquad [3]$$

Here $E[\cdot]$ is the expectation operator and V is the present value of ecosystem services as defined in [1] in the main text. Expectations are taken with respect to probabilities (or current beliefs) over disturbance occurrence, broader environmental conditions, and socioeconomic factors. These current beliefs embed our subjective predictions about how future beliefs may shift through time due to climate change or our understanding of it, or other social or environmental factors. The subscript P indicates the probability distribution with respect to which expectations are taken.

Second, we consider the variance in ecosystem service benefits, defined as follows:

$$VV \equiv E[(PV - EV)^2]. \qquad [4]$$

Measures of variability such as VV may prove important for managers or communities interested in the risk associated with ecosystem services.

Finally, we define a new metric "Ecosystem Service Resistance (ESR)" as the ratio of expected ecosystem services value under a disturbance regime defined by P to the service value if no disturbance occurs:

$$ESR \equiv \frac{EV_P}{EV_0}. \quad [5]$$

Here EV_0 denotes the expected value under the null disturbance regime described earlier, with $P(D_t = d^0|E_t) = 1$. Thus, ESR is the average fraction of service value retained under disturbance and accounts for pre-disturbance differences in service provision across communities to help isolate the effects of disturbance.

Application to windstorm events in forests

We analyze the impact of windstorms on both the provision of timber and recreation in Minnesota (MN), USA using Monte Carlo simulations. Initial tree communities are based on plot-level survey data for 777 plots from the USDA Forest Inventory database (http://apps.fs.fed.us/fiadb-downloads/datamart.html) from 2014. We focus on 11 focal boreal forest tree species (Table S1), because they have known response and effect functions and comprise the vast majority of trees in these communities (77%). Moreover, those same species make up 91.5% of the total timber revenue in these 13 counties. Below we detail how we parameterize our general framework for this application. The SI provides additional details and parameter values and code for this analysis. To simplify our comparison with existing approaches, the application focuses on a single time period in which one disturbance can occur and no discounting occurs ($\beta(t) = 1$).

Likelihood of different disturbances

We simulate three potential windstorm disturbance regimes: 1) no disturbance ("*Status quo approach for ecosystem services*"), 2) a disturbance regime representative of current conditions and the recent past ("*Lower severity regime"*), and 3) a stylized, representative future regime in which high intensity windstorms are more probable (the "*Climate change regime*"), detailed in Table S2. In Northern Minnesota, extreme windstorms are anticipated to increase in frequency in the future as conditions become wetter, yet the actual intensity and frequency of future windstorms, and where they will occur in the landscape, remain highly uncertain.[15] Records for St. Louis County (the largest of the 13 Minnesota counties in our application) show a significant increase ($P<0.001$) in reported thunderstorm wind events from 1974 to 2023 (see SI, Figure S2). More broadly, thunderstorm energy levels conducive to strong downdrafts and straight-line winds have grown consistently since 1980[52,79] and when such systems develop in a future warmer climate, they may affect much larger areas[80]. As a result, the distribution of windspeeds across a landscape should shift to higher values in a warmer future, consistent with our simulation. While little data is currently available for projecting future windstorms for this specific region, forecasts (e.g., of projected droughts) can be incorporated into the framework to determine the probability and intensity of potential disturbances in the future when available.

Disturbance response function

We parameterize how each potential disturbance alters ecological communities based on ref. [45]. For these species, individual tree size (measured as diameter at breast height [dbh]), species identity, and disturbance intensity predict the probability of mortality[45]. For each tree in a plot, we compute its probability of mortality, given a windstorm of a particular intensity, using parameters from ref. [45] (see Extended Data: Table S2). For each disturbance intensity, we repeatedly sample a community after disturbance using Monte Carlo simulations and the probability of mortality for each tree for a particular disturbance intensity. Thus, the community response depends on the range of sizes and the species in the community, as well as the windstorm intensity. For each disturbed community, we then compute community change metrics for the disturbed ecological community (Figs. S1 and S2).

Ecological Production Function

We model how *an ecological community produces ecosystem services* based on known empirical relationships and established methods.[81] We do this separately for timber production and recreation. We calculate ecosystem services from timber products as amount in volume for sawtimber, fuelwood, pulpwood, and pulp & bolts products, considering pulpwood and pulp & bolts together (as recommended by the MN Department of Natural Resources [MN DNR]). We compute merchantable volume based on dbh and bole height for each tree, using methods from USDA Forest Inventory Analysis[81](see SI). Thus, we consider not only ecological traits (dbh and bole height) and species identity but also the type of timber product each species provides, county, and management rules (e.g., harvest rules about tree size) as inputs to $F(\cdot)$ in equation [**1**] (see SI for details). We assume that, if a tree is blown down and dies, it is not harvested due to damages (e.g., for sawtimber) and extremely high costs for salvage, especially in remote areas that are hard to access after a large wind blow-down event.

For recreation, we model the production of ecosystem services as a function of both the fraction of trees that remain alive and the diversity of species in a site after disturbance.

Specifically, we compute the product of the fraction of trees that remain alive and a power function of the Simpson diversity of trees at a site. That production function reflects a recreational preference both for live trees over dead wood[82] and for diversity[55] .

Measuring ecosystem services value

For timber, we measure value as the potential revenue in USD$ from a stand of trees in each plot based on the three-year average stumpage prices per county, timber product, and species and the merchantable volume in cords and board feet (mbf; see SI). For products, we consider sawtimber, fuelwood, pulpwood, and pulp & bolts products, considering pulpwood and pulp & bolts together. Stumpage prices for each product differ by county and species; not all species in these communities are harvested for timber products, and the species present differ in their stumpage prices and the timber products for which they are harvested (MN DNR 2015). In computing timber value, we assume each tree would be put to its highest value use if harvested. We then define utility from a risk-neutral forest owner's perspective, with utility equal to potential revenue. For recreation, a service without direct market value, we equate the value of the service to the output of the ecological production function just described.

Evaluating benefits under risk

We use a Monte Carlo approach to simulate a distribution of present values of ecosystem services at each site under each disturbance regime (Extended Data: Fig. S3). For each regime, a single Monte Carlo run samples a disturbance intensity and applies that disturbance across the landscape (Fig. S3). For the resulting post-disturbance community, we compute physical properties and the ecosystem service value. We repeat this process for 5000 Monte Carlo samples —each time sampling a new disturbance intensity—then use the resulting distribution of service values across simulation runs to calculate ecosystem service resistance, expected value, and variance in value (Fig. S4).

Price responses to supply shocks

In our final scenario ("*Climate Change x Price Response*"), we also allow stumpage prices to respond to supply shocks caused by the disturbance[59]. In our illustration, following ref. [59], prices rise in response to supply shortfalls for a given product while retaining spatial heterogeneity in prices observed in real market data. We use a constant-elasticity inverse demand function, where price is a function of quantity, and price elasticities from ref. [59] (see SI for details).

Comparison to static ecosystem service assessments

To quantify the importance of considering disturbances for services in assessments, we calculate the expected value, variance, and resistance of the ecosystem services under disturbances for each disturbance regime. Instead, static assessments of ecosystem services often assume the probability of disturbances is 0 and thus that disturbance impacts are 0.

Comparison to ecological measures

We also compute three measures of ecological community similarity[33] and a biomass-based measure of resistance[32] using the simulation results. Ecological community similarity is quantified as (1) one minus normalized Euclidean distance, (2) Bray-Curtis similarity, or (3) one minus angular distance, all based on abundance vectors (number of individuals) in a community before and after a disturbance. In all cases, we compute the expected compositional stability (for different metrics of community similarity) under a disturbance regime (see Figure S5). The relatively few ecological studies that do consider the resistance of *functions* (as opposed to community composition) consider biomass, summed across all species[32,33]. Thus, we compute biomass-based resistance as the ratio of expected above-ground biomass after disturbance to above-ground biomass prior to disturbance, a measure closely related to prior work[32], and compare it our measure of ecosystem service resistance (Figure 3 and 4).

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Code availability Statement

We provide R code used to conduct this analysis at our GitHub project page (https://github.com/LauraDee/DisturbanceAndES).

Data availability statement

We use publicly available data and provide references to relevant data sources.

Author Contributions Statement

LED led and conceived of the paper, developed the model with SJM and KH, did the parameterization for the application, contributed to the code with SJM, wrote and revised the paper, developed additional applications, and made the figures with SJM. SJM co-conceived the paper and model development with LED, led the coding with contributions and input from LED, co-wrote and edited the paper and made the figures with LED. KH contributed to model formulation, writing, editing, and conception of broader applications. KB co-conceived of early conceptual versions of the framework, assisted with writing and revision, provided feedback on drafts and figures, and the conception of broader applications. PBR co-conceived the framework and application with LED and SJM, contribute to writing and conception of broader applications, contributed to the framework conceptional contributed to project formulation, feedback on figures, and editing. SP contributed feedback on project formulation, figures, and to the economic model and relevance to ecosystem service research.

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