

1 **Running head:** Crowdsourcing to unify disturbance ecology
2 **Towards a unifying framework of disturbance ecology through crowdsourced science**
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- 44 **Key words:** perturbation, resistance, resilience, ecosystem stability, interacting disturbances,
- 45 compounding disturbances, spatial, temporal

46 **Abstract.** Disturbances fundamentally alter ecosystem functions; yet predicting the impacts of
47 disturbances remains a key scientific challenge. The study of disturbances is ubiquitous across
48 almost all ecological disciplines, yet varying terminology and methodologies have led to the lack
49 of an agreed upon, cross-disciplinary foundation for discussing and quantifying the complexity
50 of disturbances. This shortcoming presents an increasingly urgent challenge due to accelerating
51 global change and the threat of interacting disturbances that can further destabilize ecosystem
52 responses. By harvesting the ‘swarm intelligence’ of an interdisciplinary cohort of contributors
53 spanning 42 institutions across 15 countries, we propose a pathway towards a new conceptual
54 model of ecological disturbances. Together we identify an essential limitation in disturbance
55 ecology—that the word ‘disturbance’ is used interchangeably to refer to both the events that
56 cause and the consequences of ecological change, despite fundamental distinctions between the
57 two meanings. We develop a generalized framework of ecosystem disturbances to reconcile this
58 limitation and enable examination of the drivers and impacts of disturbances simultaneously. Our
59 proposed framework puts forth a well-defined lexicon for understanding disturbance across
60 perspectives and scales, thereby increasing the interoperability of research across scientific
61 domains. We also recommend minimum reporting standards that detail the magnitude, duration,
62 and rate of change of driver and response variables, regardless of scale. Importantly, while we
63 address some challenges of disturbance research here, developments in technology,
64 methodology, and cross-disciplinary approaches are necessary to close knowledge gaps. We
65 therefore propose four future directions to advance our interdisciplinary understanding of
66 disturbances and their social-ecological impacts: integrating across ecological scales,
67 understanding disturbance interactions, establishing baselines and trajectories, and developing
68 process-based models and ecological forecasting initiatives. Our experience through this process

- 69 motivates us to encourage the wider scientific community to continue to explore new approaches
- 70 for leveraging Open Science principles in generating creative and multidisciplinary ideas.

71 **Introduction.**

72

73 Disturbances, including those related to human activities and changing climate, are predicted to
74 continually increase in frequency and severity in the coming century. For instance, wildfires
75 have ravaged global landscapes over the last two decades, impacting human lives, crops, and
76 biodiversity — highlighted by recent outbreaks in Australia, Brazil, California, and British
77 Columbia (Cleetus & Mulik, 2014; Tedim et al., 2020). Twenty of the hottest years in history
78 have occurred in the past 22 years (WMO, 2018), and extreme events like marine heat waves are
79 projected to increase in frequency by more than an order of magnitude as climate change
80 continues (IPCC, 2019). Such disturbances can radically alter trajectories of ecosystem
81 processes, and importantly, they occur within a broader ecological context that can generate
82 disturbance interactions and lead to unpredictable ecosystem responses (Brando et al., 2019;
83 Calderón et al., 2018; Carlson, Sibold, Assal, & Negron, 2017; Knelman, Schmidt, Garayburu-
84 Caruso, Kumar, & Graham, 2019; Mehran et al., 2017; Pidgen & Mallik, 2013; Ryo, Aguilar-
85 Trigueros, Pinek, Muller, & Rillig, 2019; Zscheischler et al., 2018).

86

87 Despite increases in the frequency and severity of disturbance events, predicting their onset,
88 characteristics, and consequences remains difficult in part because of differences in conceptual
89 models, scales of investigation, and language used across scientific disciplines. Inconsistencies in
90 disturbance frameworks have long been noted by the ecological community (Pickett, Kolasa,
91 Armesto, & Collins, 1989; Poff, 1992; Rykiel Jr., 1985), and the struggle to derive a common
92 framework for understanding and predicting disturbances continues in modern literature (Borics,
93 Várбірó, & Padisák, 2013; Buma, 2015; Hobday et al., 2016; Jentsch & White, 2019; Smith,

94 2011b). Terms such as disturbance, pulse event, perturbation, threat, and stressor are often not
95 clearly defined or used interchangeably, but have subtle and meaningful differences in specific
96 fields of inquiry (Borics et al., 2013; Jentsch & White, 2019; Keeley & Pausas, 2019;
97 Kemppinen, Niittynen, Aalto, le Roux, & Luoto, 2019; Lake, 2000; Rykiel Jr., 1985). For
98 instance, Slette et al. (2019) revealed that the plethora of literature on drought is generally based
99 on loose descriptions rather than explicit definitions or quantitative metrics of drought, while
100 Hobday et al. (2018) noted that other disturbances lack even basic quantitative categorization or
101 naming schemes. Because of these inconsistencies, attempts to compare disturbances across
102 types and ecosystems have resulted in few outcomes that can be generalized across fields (Peters
103 et al., 2011). Collectively, these shortcomings point to the need for an interdisciplinary
104 understanding of disturbances.

105
106 Differences in how disturbances are studied are driven in part by their spatial and temporal
107 heterogeneity and by differences in typical scales of investigation across scientific disciplines.
108 Indeed, disturbances occur through space and time with different frequencies (number of
109 occurrences per unit time), intensities (magnitude of the disturbance), and extents
110 (spatiotemporal domain affected)(Grimm & Wissel, 1997; Miller, Roxburgh, & Shea, 2011;
111 Paine, Tegner, & Johnson, 1998). While some disturbance events have relatively discrete
112 temporal and spatial boundaries (e.g., wildfires, hurricanes, earthquakes), others are diffuse or
113 overlap in time and space (e.g., ocean acidification, overgrazing, nutrient loadings)(Godfrey &
114 Peterson, 2017). This makes it difficult to identify which events depart from ‘normal’ conditions,
115 especially within the broader context of ongoing environmental change (Duncan, McComb, &
116 Johnson, 2010; Mishra & Singh, 2010; Slette et al., 2019). Finally, because disturbances are

117 contingent on historical events and local social-economic conditions (Dietze et al., 2018; Duncan
118 et al., 2010; Seidl, Spies, Peterson, Stephens, & Hicke, 2016; Słowiński et al., 2019), a single
119 type of event can have many different outcomes. Dynamic hydrology, for example, is
120 fundamental to floodplain wetland systems, which are adapted and shaped by flooding events,
121 but flooding events are typically considered disturbances in upland contexts.

122

123 We therefore need generalizable theory to predict the frequency and significance of disturbance
124 events, and to more sustainably manage our planet's ecosystems in ethical and efficient ways.
125 Ideally, this framework would be able to manage the heterogeneity inherent in disturbances
126 while providing consistency in how disturbances are defined and studied. Such a foundation
127 would consist of shared goals and be built upon commonly agreed upon terms and metrics. To
128 address this challenge, we used an open call on social media to assemble a cross-disciplinary
129 team of 50 collaborators across 42 institutions in 15 countries with a diverse suite of scientific
130 specialties (Graham & Krause, 2020). We used our collective 'swarm intelligence' to propose a
131 pathway towards a new conceptual model of ecological disturbances that integrates contributions
132 across disparate disciplines. The project featured a flexible, collaborative, and iterative writing
133 process (using Google docs), freely open authorship opportunities advertised via Twitter, and
134 was coordinated by a small international leadership team. By proposing a unifying framework
135 for disturbances, we strive towards a common currency to compare ecological drivers and
136 responses under many conditions and in many systems.

137

138 We present this paper in five main sections. First, we provide an overview of the theoretical
139 ideas used across disciplines to study disturbances in 'System Stability as a Common

140 Foundation.’ Then, we highlight ‘Spatiotemporal Considerations’ as major challenges to and key
141 aspects of developing a unifying framework. The final three sections describe: i) a unifying
142 framework derived from crowdsourced scientific knowledge, ii) minimum reporting standards
143 for widely implementing this framework, and iii) cross-disciplinary approaches for addressing
144 areas of need. This emergent framework is intended to facilitate outcomes such as increased
145 potential for synthesis among historically disparate events and disciplines, more rigorous
146 tracking of events across space and time, and new ways of understanding disturbance impacts
147 between fields. In turn, resulting knowledge can influence the ways in which humans manage
148 ecosystems and their responses to disturbances by aiding managers in identifying slow-
149 developing disturbances as they occur, referencing disturbances against historical events by
150 comparing quantitative characteristics, and being able to better predict ecological impacts.

151

152 **System Stability as a Common Foundation.**

153

154 System stability has been a pillar of disturbance research across scientific domains (Duncan et
155 al., 2010; Hodgson, McDonald, & Hosken, 2015; Ives & Carpenter, 2007; Seidl et al., 2016;
156 Todman et al., 2016). Because many areas of research rely on stability concepts to describe a
157 system’s response to environmental change, it is integral for a cohesive understanding of
158 disturbances. For example, using this common theoretical foundation, biodiversity has been
159 repeatedly linked to the capacity of ecosystems to be resistant to biological invasions (Cardinale
160 et al., 2012; Cardinale & Palmer, 2002; Isbell, Polley, & Wilsey, 2009; Kardol, Fanin, & Wardle,
161 2018); and managed ecosystems rely on this theory to maintain a stable system with socially-
162 desirable flow of timber and food (Foley et al., 2005; Folke, 2002; Peterson, Collavo, Ovejero,

163 Shivrain, & Walsh, 2018; Rist et al., 2014). At the other end of the spectrum of biological
164 sciences, human geneticists have applied system stability theory to demonstrate that context-
165 specific gene expression buffers systems from changing ambient conditions (Ghavi-Helm et al.,
166 2019). Here, we review core and emerging system stability theory to form a conceptual basis for
167 an interdisciplinary approach to understanding disturbance discussed in later sections.

168

169 There are several aspects of system stability theory that are common throughout social-
170 ecological domains, including the concepts of resilience, resistance, and redundancy. Resilience
171 is commonly defined as the ability of a system to recover from disturbance, while resistance is
172 the ability of an ecosystem to remain unchanged when being subjected to disturbance (Griffiths
173 & Philippot, 2013; Gunderson, Holling, Pritchard, & Peterson, 2002; Crawford S Holling, 1973;
174 Crawford Stanley Holling, 1996; Lamentowicz et al., 2019; McCann, 2000; Seidl et al., 2016;
175 Westman, 1978). Resistance and resilience are quantified using various metrics, including the
176 time, slope/rate, and angle of recovery relative to a baseline state (J. H. Connell & Sousa, 1983;
177 Shade et al., 2012). Additionally, functional redundancy and the ‘insurance hypothesis’ (Yachi &
178 Loreau, 1999) are also used throughout ecology to describe the capacity of a system to resist and
179 recover from a disturbance whereby the presence of functionally redundant phenotypes enhances
180 ecosystem stability (Naeem & Li, 1997; Yachi & Loreau, 1999). Recent frameworks built on
181 these foundations have emerged to provide a more holistic and ecologically relevant concept of
182 system stability by employing multidimensional concepts of system stability (e.g., temporal
183 variability)(Hillebrand et al., 2018).

184

185 Another central paradigm in stability theory is that the intensity of disturbance response is often
186 non-linearly related to the intensity of the disturbance itself. There is a growing understanding of
187 the importance of tipping points that, when reached or exceeded, cause strongly non-linear
188 system responses and potential sudden shifts in system behavior (Dai, Vorselen, Korolev, &
189 Gore, 2012; Loecke et al., 2017). For instance, work by Scheffer et al. (2001) has shown that
190 ecosystems can deviate rapidly from their current state due to minor shifts in underlying biotic or
191 abiotic drivers. Similarly, slow and often undetectable changes can reduce ecosystem resilience,
192 leading to unpredictable system collapses (B. H. Walker, Carpenter, Rockstrom, Crépin, &
193 Peterson, 2012). When pressures exceed ecosystem tipping points, regime shifts can occur and
194 ecosystems are pushed into a different (alternative) state that is maintained by self-reinforcing
195 feedbacks (Pausas & Bond, 2020). While there is growing capacity to predict regime shifts (e.g.,
196 by rising variance in ecosystem properties or by slow recovery rates), several challenges remain
197 in their prediction, in part due to the challenge of measuring appropriate indicators for resilience
198 (Dai, Korolev, & Gore, 2013; Dai et al., 2012; Munson, Reed, Peñuelas, McDowell, & Sala,
199 2018; Scheffer, 2010; Scheffer et al., 2009; Van Nes & Scheffer, 2007). Collectively, historical
200 and emerging research on system stability provides a common foundation for understanding
201 disturbances across a broad suite of ecosystems and across lines of investigation with different
202 underlying objectives.

203

204 **Spatiotemporal Considerations.**

205

206 Though the specific nature of disturbance extent and duration can vary greatly, all disturbances
207 occur over space and time; any unifying framework must therefore consider the spatiotemporal

208 extent and variability of disturbance properties. This includes a critical need to define the
209 baseline conditions relative to which a disturbance is assessed in order to build a set of domain-
210 agnostic principles. These baselines may vary as a function of the spatiotemporal scale over
211 which an analysis is being performed, and the deviation a system undergoes from its baseline at a
212 given scale can be used to assess a disturbance's intensity and impact (e Silva, Semenov,
213 Schmitt, van Elsas, & Salles, 2013). However, as ecosystems change in response to climate,
214 land-use change, and other human impacts, conditions which were once considered disturbed
215 against a static baseline may now shift into a new normal range of variation (Figure 1). In this
216 section, we review key spatial and temporal perspectives that influence disturbances and that
217 should underlie an interdisciplinary understanding of disturbance.

218

219 *Spatial Perspectives on Disturbance Events*

220

221 The drivers and impacts of disturbance are dependent on the spatial features of their broader
222 landscapes and the spatial perspective of a given study's objectives. For example, pre-existing
223 ecosystem characteristics, such as habitat connectivity and topography, influence the spatial
224 structure of disturbance impacts by dictating its ability to spread as well as the ecosystem's
225 ability to be recolonized by surviving organisms in neighboring spaces (Buma, 2015; Drever,
226 Peterson, Messier, Bergeron, & Flannigan, 2006; Turner, Romme, & Gardner, 1994). Further,
227 the spatial perspective taken when studying a disturbance can also heavily influence conclusions
228 drawn about its effects. Spatial perspectives and extents can vary tremendously, and are defined
229 by the overarching research question as well as the ecosystems and/or organisms of interest.
230 Some disturbances, for instance fine-scale temperature shifts, may be apparent only at local

231 scales while others impact regional and coarser scales (Aalto, Riihimäki, Meineri, Hylander, &
232 Luoto, 2017; Lembrechts, Nijs, & Lenoir, 2019). In general, disturbances that directly affect
233 species interactions tend to be observable at local scales (Mod, le Roux, & Luoto, 2014), while
234 disturbances related to habitat alterations are detectable at coarser spatial resolution (Chase,
235 2014; Dumbrell et al., 2008; Hamer & Hill, 2000; Hill & Hamer, 2004).

236

237 Additionally, because separate factors control ecosystem dynamics at different spatial scales, the
238 impacts of, and ecosystem responses to, disturbances depend on how various disturbances
239 modify scale-specific controls on ecosystems (e.g. species interactions influence communities at
240 local scales vs. climate at larger scales)(Cohen et al., 2016; Dobson, Rodriguez, Roberts, &
241 Wilcove, 1997; Dumbrell et al., 2008; Wei & Zhang, 2010). For example, extant dispersal rates
242 and disturbance scale can regulate the recovery of disturbed ecological communities and the
243 spread of impacts across space to neighboring populations (Zelnik, Arnoldi, & Loreau, 2019).

244 Furthermore, spatial extent and patterning of disturbances can influence disturbance impacts.
245 Although disturbances that homogenize landscapes or reset successional trajectories such as
246 volcanic eruptions and glaciation events have been a core interest in ecological studies, less well-
247 studied moderate disturbances that do not decimate landscapes tend to increase system
248 heterogeneity, with entirely different functional consequences for ecosystems and resultant
249 landscape-scale spatial patterns (Curtis & Gough, 2018; Hardiman, Bohrer, Gough, Vogel, &
250 Curtis, 2011; Knelman, Graham, Trahan, Schmidt, & Nemergut, 2015; Lorimer, 1989; Luysaert
251 et al., 2008; Ruhi, Dong, McDaniel, Batzer, & Sabo, 2018; Turner, 2010; Turner et al., 1994).

252 Therefore, an interdisciplinary approach to understanding disturbance must consider both the

253 spatial properties of disturbances themselves as well as the spatial scale-dependence of their
254 effects.

255

256 *Temporal Perspectives on Disturbance Events*

257

258 For a common understanding of disturbances, we also need to acknowledge the central influence
259 of time without explicitly defining a single general time scale of disturbances; with the longest
260 potential timespan starting with the evolution of life and the shortest bounded by the finest
261 temporal grain at which any attribute of interest can be measured (Ladau & Eløe-Fadrosch, 2019).
262 Some disturbances impact ecosystem dynamics over short time scales (i.e., pulse events),
263 whereas other disturbances operate over long time periods (i.e., ramp and press events)(J.
264 Connell, 1997; J. H. Connell, Hughes, & Wallace, 1997; Jentsch & White, 2019). A single type
265 of event may constitute a disturbance at one timescale, but not at another. While a forest fire may
266 be a significant deviation from an environmental baseline considered on annual or decadal scale
267 (and therefore, a disturbance at this timescale), it may fall within the historical range of
268 environmental variation at a centennial timescale (and therefore, not a disturbance at this
269 timescale). Furthermore, the effects of slow increases in mean annual temperatures may be
270 insignificant over the course of a few years when considering the background variation in mean
271 annual temperatures (IPCC, 2018). However, at a centennial scale, the warming trend shifts the
272 mean as well as the extreme temperatures generating climates outside the range of historical
273 variation. Similar arguments can be made for nitrogen deposition, chronic fertilization, pesticide
274 applications, elevated CO₂, and many other global disturbances (Ferretti, Worm, Britten,
275 Heithaus, & Lotze, 2010; Jackson et al., 2001; Ripple et al., 2014).

276

277 This temporal perspective highlights that changing conditions through time ('non-stationarity'
278 (Wolkovich, Cook, McLauchlan, & Davies, 2014)) is also a central consideration for any
279 conceptualization of disturbances to be applicable in the future. Baseline conditions and driver-
280 response relationships are dynamically conditioned by the legacies of disturbance and ecological
281 memory (Johnstone et al., 2016; Nowicki et al., 2019). Ecological succession is a classic
282 example of ecosystem trajectories that interacts with more discrete events to yield an aggregate
283 disturbance impact. Disturbances can interrupt and potentially alter trajectories of succession
284 through impacts on community dynamics that dramatically alter ecosystem functions (Ghoul &
285 Mitri, 2016). For example, antibiotic administration and delivery mode can disrupt microbial
286 community assembly and succession in the human infant gut microbiome that in turn can drive
287 long-term impacts on host health (Koenig et al., 2011). Over longer timescales, the field of
288 paleoecology can describe pre-anthropogenic conditions to define the long-term baseline state
289 preceding a disturbance, but paleoecology is rarely integrated with other disciplines (Bartowitz,
290 Higuera, Shuman, McLauchlan, & Hudiburg, 2019; Lamentowicz et al., 2019; Ryo et al., 2019;
291 Słowiński et al., 2019).

292

293 *Rising Importance of Interacting Disturbances*

294

295 An obstacle to historical paradigms of disturbance theory is that changes in environmental
296 conditions will not only alter the frequency of disturbances, but also the potential for multiple
297 interacting disturbances to impact system stability (Seidl et al., 2017). Multiple interacting
298 disturbances can lead to novel ecosystem responses, compromising our abilities to understand

299 disturbances in unknown future environments (Brando et al., 2019; Calderón et al., 2018;
300 Carlson et al., 2017; Hobbs et al., 2014; Hobbs, Higgs, & Harris, 2009; Knelman et al., 2019;
301 Mehran et al., 2017; Pidgen & Mallik, 2013; Ryo et al., 2019; Zscheischler et al., 2018). Two or
302 more disturbances can have a multiplicative effect on an ecosystem, sometimes impacting an
303 ecosystem's resilience to the second disturbance (Buma, 2015; Darling & Côté, 2008; Folt,
304 Chen, Moore, & Burnaford, 1999). For instance, climate change-related disturbance can combine
305 with species interactions to alter the impact and outcomes of disturbances (Arora et al., 2019;
306 Mod & Luoto, 2016; Myers-Smith et al., 2011; Niittynen, Heikkinen, & Luoto, 2018; Zarnetske,
307 Skelly, & Urban, 2012). Additionally, impacts at multiple spatial scales can also interact. Local
308 disturbances can play an important role in maintaining regional biodiversity through patch
309 dynamics mediated by species traits (e.g., competition-colonization trade-offs)(He, Lamont, &
310 Pausas, 2019; le Roux, Virtanen, & Luoto, 2013; Tilman & Downing, 1994), which may reduce
311 vulnerability to larger scale disturbances. Local disturbances can also exacerbate impacts of
312 more widespread regional disturbances, placing ecosystems under increased threat of collapse
313 (Kendrick et al., 2019). If resilience is overcome because of multiple disturbances, then
314 compound disturbances may cause a state change or 'ecological surprise' that is largely
315 unpredictable (Paine et al., 1998).

316

317 Given the variation that occurs both in disturbed systems and in the goals of disturbance studies
318 and applications, we present a framework that describes a minimum foundation for best practices
319 for creating and sharing knowledge about disturbed systems in a novel and changing world.

320

321 **A unifying framework.**

322

323 Because of the spatial, temporal, and cross-disciplinary complexities in studying disturbances,
324 disturbance theory lacks a one-size-fits-all approach. A key challenge in the development of such
325 an approach is that individual disturbances operate within a broader context of historical events
326 that cumulatively alter disturbance magnitude and impact. For instance, Ryo et al. (2019)
327 describe the temporal dependency of interacting disturbances in terms of ‘nestedness’, wherein
328 the complexity of interactions is dependent on the relative closeness of the events. Within this
329 framework, a single event is a subset of multiple disturbances within a continuous trajectory.
330 Importantly, there are carryover effects within trajectories in which disturbance impacts can
331 accumulate and/or alter the internal mechanisms affecting responses through time, even for parts
332 of an ecosystem not affected by earlier disturbances (Nowicki et al., 2019). Therefore, driver-
333 response relations are dependent on both short- and long-term histories. While Ryo’s framework
334 only considers temporal aspects of disturbances (Ryo et al., 2019), it highlights the need for a
335 fluid framework to provide a common foundation for studying disturbances across scales and
336 lines of inquiry—one that can adjust for variation between systems and research goals.

337

338 One essential limitation in our understanding and managing of disturbances is that the word
339 ‘disturbance’ is used interchangeably to describe two distinct processes—events that cause
340 ecological change and consequences of extreme events—that are both termed disturbances
341 despite fundamental distinctions between the two types of processes. Some researchers define
342 disturbances by properties that describe an event (e.g., type, frequency, intensity)(Hobday et al.,
343 2016; Hobday et al., 2018), while others define disturbances by their impacts (e.g., ecological or
344 societal damages)(Smith, 2011a). Furthermore, many definitions of disturbances solely consider

345 short-term events that represent rapid deviations from a biotic or abiotic background state
346 without regard to historical processes (Jentsch & White, 2019). Finally, solely defining
347 disturbances by their impact size directly conflicts with the idea of ecological resistance and the
348 vast amount of theory developed for this phenomenon. If we were to define a disturbance based
349 only on its impact, highly resistant ecosystems would never be disturbed regardless of the
350 prevalence of extreme events.

351

352 By parsing disturbance theory between the causes and consequences of a disturbance, we
353 propose a robust and tangible framework of disturbance that is applicable regardless of the line
354 of inquiry and/or spatiotemporal scale of investigation (Figure 2). Specifically, we define a
355 *disturbance driver* as an event whereby a force, either biotic or abiotic, generates a deviation
356 from the local, prevailing background conditions. In the proposed framework, a driver is
357 characterized by its magnitude of deviation from an environmental baseline (low to high
358 deviation describes weak to strong drivers). In contrast, a *disturbance impact* represents the
359 social-ecological consequences of a driver relative to a scale-dependent baseline state. Impacts
360 can be positive or negative depending on the perspective of the study. Using relationships
361 between disturbance drivers and disturbance impacts, we generate *four universal definitions of*
362 *disturbances* with variation within each type due to the strength of the driver and the size of the
363 impact. We conceptualize disturbance drivers, either abiotic or biotic, on an x-axis and the
364 impact of disturbance impacts on a y-axis. This yields four quadrants: weak driver-positive
365 impact, strong driver-positive impact, weak driver-negative impact, and strong driver-negative
366 impact. The position of drivers and impacts across and within the quadrants slides with the line
367 of inquiry (Figure 2, examples in the following paragraph).

368

369 A single driver may yield a different impact depending on its impact relative to the scale and/or
370 scope of the investigation. For example, when viewed from the perspective of a drought-
371 sensitive microorganism, a 10-day drought is a severe disturbance whereas it could be
372 inconsequential for humans in urban environments (Figure 2). Two floods in rapid succession in
373 a single area may have disparate social-ecological outcomes dependent on the impacts of the first
374 event. Additionally, the disturbance impact for a single driver could be simultaneously positive
375 and negative, dependent on scale. For example, deforestation for agriculture could be positive
376 from an immediate human perspective (food production) but negative from an ecological
377 perspective (habitat loss). This allows for interacting and compounding disturbances to be
378 viewed within the same framework as single events and for events that cause tipping points to be
379 represented as weak driver-high impact events. Spatial and temporal scales are also implicitly
380 represented in the proposed framework, as historical exposures have direct effects on the impact
381 of a given driver and the scale of interest defines the magnitude of both the driver and impact.
382 Likewise, the ecological state of a system (e.g., its stability, resistance, resilience, and
383 successional stage) also influences the ‘impact’ axis of disturbances through escalating or
384 mediating the impact. Definitions and examples of each quadrant are presented in more detail in
385 Table 1 and Figure 2.

386

387 The advantage of conceptualizing and classifying disturbances into this inclusive framework is to
388 increase interoperability of disturbance research across scientific domains. While the current
389 framework is qualitative in nature and based upon discipline-specific expert knowledge of driver
390 and impact magnitudes, there are further opportunities to develop quantitative thresholds to

391 separate quadrants for particular lines of investigation. For example, a disturbance driver and
392 impact size falls within a range of historical variation that is specific to the event type.
393 Quantitative thresholds for event types can then be developed to separate events along driver and
394 impact axes based on the distribution of historical events along those axes. Towards this end, it
395 then becomes necessary to follow standardized reporting practices to characterize the historical
396 range of variation of disturbances and to classify individual events within a scale-flexible
397 framework. In the next section, we propose a set of minimum reporting standards to facilitate
398 comparability between distinct disturbance investigations.

399

400 **Minimum reporting standards.**

401

402 Because scales of investigation vary tremendously between disciplines, it is necessary to present
403 sufficient data in publications and community repositories that capture complexity for other
404 researchers to evaluate the placement within this framework. When possible, standardized
405 indices are suggested to explicitly describe disturbances (e.g., Palmer Drought Severity Index,
406 Standardized Precipitation Evapotranspiration Index)(Palmer, 1965; Slette et al., 2019). In
407 ecological research, indices are most well-described for plot-scale studies and anthropocentric
408 framings of scale that relate to our own human experiences rather than ecological processes (e.g.,
409 monetary losses from hurricanes), while they are more nascent for cross-scale disturbance work.
410 Therefore, in addition to indices, it is necessary to report variables that describe the magnitude,
411 duration, and rate of change of drivers and response variables in a consistent manner that is
412 applicable regardless of scale.

413

414 We suggest three categories of variables for minimum reporting standards: (1) ecosystem
415 properties, (2) driver descriptors, and (3) impact descriptors with suggested variables for each
416 listed in Table 2. An integral distinction of these standards compared to previous efforts is the
417 explicit recording of spatial and temporal scales needed for interoperable understanding of
418 disturbances (Peters et al., 2011). Ecosystem properties are foundational variables that provide
419 context for disturbance interpretation (e.g., ecosystem type, successional state, and system
420 stability). Driver and impact descriptors are each divided into three categories: reference, spatial,
421 and temporal variables. These variables capture system stability and spatiotemporal dynamics
422 that allow for multiscale comparisons including mild versus extreme intensity, acute versus
423 chronic timescales, and abrupt versus gradual change (Ryo et al., 2019). Collectively, they allow
424 for the placement of events on both the driver and impact axes of the proposed conceptual
425 framework as well as providing context that describes the scale and scope of the investigation.

426

427 **Promising Cross-Disciplinary Approaches to Address Areas of Need.**

428

429 While we address some challenges of disturbance research here, developments in technology,
430 methodology, and cross-disciplinary approaches are necessary to close knowledge gaps.

431 Questions such as “How do we define a disturbance in the context of a non-stationary baseline?”
432 and “When does a disturbance begin and end?” are difficult to address with current state-of-
433 science approaches. For the study of disturbance, there simply may not be a suitable universal
434 approach. Below, we propose areas of promise for advancing an interdisciplinary understanding
435 of disturbance.

436

437 In particular, we highlight the need to *integrate disturbance responses across scales of*
438 *ecological organization* from genes to ecosystems. We expect that future studies have the
439 opportunity to consider multiple scales of sampling and analysis that comprehensively evaluate
440 disturbances and their effects across spatial, temporal, and/or organismal scales. Ecological
441 hierarchies, in particular, underlie self-organized ecosystems and provide a structure for using
442 information theory and other advanced statistical techniques to predict whole ecosystem impacts
443 (Allen & Starr, 2017; Arora et al., 2019; Cumming, 2016). Social-ecological applications of
444 machine learning, graph theory, and information theory are exponentially increasing and can
445 decipher complex relationships in multidimensional data streams. These approaches are used to
446 collapse complex data types into tangible variables by deciphering classes of organisms and
447 relationships among these classes through space or time. They reveal the organizational structure
448 of a system through interaction networks that include both random and ordered processes (Ings et
449 al., 2009). Remote sensing can also aid in evaluating the spatial extent and spatial patterning of
450 disturbance, thereby defining the appropriate scale of sampling for these analyses (Shiklomanov
451 et al., 2019). However, empirical tests on the potential for disturbance impacts to propagate
452 through ecosystem hierarchies are lacking and is a major research need. One opportunity would
453 be the use of paired experimental and modeling approaches to elucidate networked changes in
454 ecological systems resulting from disturbance impacts. The use of experiments and clearly
455 outlined hypotheses is increasingly argued as a core need for generating predictive
456 understandings of ecosystem responses to disturbance (Currie, 2019; Spake et al., 2017).

457

458 Our second area of need also considers the broader issue of scale—understanding *how*
459 *disturbances interact with each other* and potentially compound through space and time. Recent

460 work has underscored interactions between extreme events occurring closely in space and time,
461 for example by elucidating discrete effects of flooding on biogeochemistry depending on prior
462 fire exposure (Knelman et al., 2019). Long-term processes such as environmental change also
463 have multifaceted impacts on ecosystems but are most frequently studied independently (Rillig et
464 al., 2019; Song et al., 2019). Such work raises new questions into ecosystem trajectories—as
465 disturbances increase through time, are there thresholds beyond which ecosystems are
466 irreversibly altered? The evolutionary consequences of living in an environment with recurrent
467 disturbances are also poorly understood (Pausas & Keeley, 2014; Pausas, Keeley, & Schwilk,
468 2017). Some species, for example, have evolved specific life-history adaptations that enable
469 them to not only survive and exploit disturbances, but even to require them for their persistence
470 (e.g., alpine vegetation, riparian cottonwoods)(le Roux et al., 2013; Lytle & Poff, 2004;
471 Mahoney & Rood, 1998). Similarly, disturbances have countervailing effects on population
472 dynamics in that they can cause immediate mortality of species, but also create new habitat,
473 thereby increasing growth rate or increasing population size post-disturbance (McMullen, De
474 Leenheer, Tonkin, & Lytle, 2017; Pausas & Keeley, 2014). For instance, if the consequences of
475 climate change related disturbances are studied separately, the results may be greatly biased as
476 compared to when the consequences are considered simultaneously (Niittynen et al., 2018).
477 Therefore, the interactions between disturbances that change eco-evolutionary dynamics provide
478 a relatively unexplored area for future research.

479
480 A third research need, *establishing appropriate baselines and trajectories* for different
481 ecosystems, disturbance, and organism types, is essential for evaluating disturbances that alter
482 ecosystem structure and function. Paleoecological data can provide historical reference baselines,

483 help evaluate sensitivity to disturbances across different windows of space and time, and unveil
484 past state changes that provide a foundation for understanding how ecological hierarchies will
485 respond to future environmental changes (Lamentowicz et al., 2019). Time series methods are
486 also well-equipped to separate disturbances from long-term trends and evaluate changes in
487 disturbance regimes through time (e.g. wavelet analysis)(Keitt, 2008; Tonkin, Bogan, Bonada,
488 Rios-Touma, & Lytle, 2017). For instance, Sabo and Post (2008) developed tools based on
489 Fourier analysis to disentangle the periodic (seasonal), stochastic (interannual), and catastrophic
490 components of river flow regimes. Space-for-time approaches, in which distances from an event
491 are used as a proxy for the time-since-event, can reveal long-term impacts without necessitating
492 decades of monitoring (Pickett et al., 1989; L. R. Walker, Wardle, Bardgett, & Clarkson, 2010).
493 Although space-for-time investigations require a correlation between the age of an ecosystem
494 attribute and spatial structuring that may not be applicable to highly disturbed landscapes,
495 chronosequences can be used to investigate plant and soil successional processes at decadal to
496 millennial scales (Laliberté et al., 2013; Sutherland, Bennett, & Gergel, 2016; L. R. Walker et al.,
497 2010; Zemunik, Turner, Lambers, & Laliberté, 2015).

498

499 Finally, we underline the need for enhancing predictive capabilities through *process-based*
500 *models and ecological forecasting initiatives* that represent the drivers of disturbance impacts on
501 ecosystem attributes, going beyond historical correlations that fail to represent causal
502 relationships (Dietze et al., 2018; Tonkin et al., 2019). Generating a model robust to disturbance
503 type, ecosystem, and scale that allows managers to detect disturbance drivers and predict
504 disturbance impact sizes is one of the ultimate goals of disturbance ecology. Mechanistic models
505 can further progress towards this goal by representing interactions among species through time

506 (Tonkin, Merritt, Olden, Reynolds, & Lytle, 2018). Microbial communities are useful empirical
507 tools for developing process-based models due to their short generation times and the ability to
508 rigorously test species-based interactions under controlled conditions (Friedman, Higgins, &
509 Gore, 2017; Gibbons et al., 2016; Hsu et al., 2019; Venturelli et al., 2018). Furthermore, thanks
510 to the availability of curated genome-scale metabolic models for hundreds of bacterial species,
511 detailed metabolic interaction networks can be simulated for entire communities (Diener,
512 Gibbons, & Resendis-Antonio, 2020; Magnúsdóttir & Thiele, 2018). Process-based and
513 forecasting models can be tailored to highly specific conditions and can provide managers with
514 both a predicted outcome and a range of uncertainty based on the underlying driver (Tonkin et
515 al., 2019). They are commonly used to guide management practices in fisheries and conservation
516 efforts (Tonkin et al., 2019). Collectively, process-based and forecasting models are potential
517 tools developing mitigation strategies and informing how humans might intervene at individual,
518 local, regional, and global scales to minimize social-ecological damages caused by disturbances
519 (Berkes, Colding, & Folke, 2000; D'Amato, Bradford, Fraver, & Palik, 2011; Dale, Lugo,
520 MacMahon, & Pickett, 1998; Folke, Hahn, Olsson, & Norberg, 2005).

521

522 **Conclusion.**

523

524 Using a completely open and crowdsourced scientific approach, we integrate the insights from
525 numerous scientific perspectives to present a conceptual foundation for cross-disciplinary
526 disturbance investigations. We highlight that the current lexicon used to discuss disturbances
527 generates confusion by conflating events that drive ecological change with the impacts of
528 extreme events. To overcome this challenge, we propose a unifying and tangible framework that

529 parses disturbance theory between disturbance drivers and disturbance impacts. Using drivers
530 and impacts as axes of variation, the framework generates four universal disturbance types that
531 are applicable regardless of the line of inquiry or its spatiotemporal scale (Figure 2). To provide
532 consistency in comparing disturbances within this framework, we suggest three categories of
533 variables for minimum reporting standards: i) ecosystem properties that provide context and ii)
534 disturbance driver and iii) disturbance impact descriptors that capture system stability and
535 spatiotemporal dynamics.

536

537 We also highlight promising lines of research to generate a more universal understanding of
538 disturbance events and their impacts, including integrating scales of ecological research,
539 understanding how disturbances interact with each other, establishing appropriate baselines and
540 trajectories, and developing process-based models and ecological forecasting initiatives that will
541 enable robust prediction capabilities and mitigation strategies.

542

543 Our work synthesizes knowledge across global institutions from Luxembourg to Singapore using
544 crowdsourced open science and demonstrates that novel approaches can generate emergent ideas
545 greater than the sum of their independent disciplinary parts. The integration of interdisciplinary
546 contributions of over 50 individuals, from 42 institutions - from academic, governmental, and
547 non-governmental organizations - in 15 countries, into the novel conceptual framework
548 presented here demonstrates the currently untapped potential for supporting collaborative co-
549 creation of research, facilitated by social media and collaborative writing platforms. Our
550 experiences through this process motivates us to encourage the wider scientific community to
551 continue to explore the suitability of similar approaches for facilitating collaborative research

552 that benefits from a large interdisciplinary knowledge base and allows to fully embrace Open
553 Science principles in collaborative interdisciplinary research.

554

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562

563 **References.**

- 564
- 565 Aalto, J., Riihimäki, H., Meineri, E., Hylander, K., & Luoto, M. (2017). Revealing topoclimatic
566 heterogeneity using meteorological station data. *International Journal of Climatology*,
567 37, 544-556.
- 568 Allen, T. F., & Starr, T. B. (2017). *Hierarchy: perspectives for ecological complexity*: University
569 of Chicago Press.
- 570 Arora, B., Wainwright, H. M., Dwivedi, D., Vaughn, L. J., Curtis, J. B., Torn, M. S., . . .
571 Hubbard, S. S. (2019). Evaluating temporal controls on greenhouse gas (GHG) fluxes in
572 an Arctic tundra environment: An entropy-based approach. *Science of the total*
573 *environment*, 649, 284-299.
- 574 Bartowitz, K. J., Higuera, P. E., Shuman, B. N., McLauchlan, K. K., & Hudiburg, T. W. (2019).
575 Post-Fire Carbon Dynamics in Subalpine Forests of the Rocky Mountains. *Fire*, 2(4), 58.
- 576 Berkes, F., Colding, J., & Folke, C. (2000). Rediscovery of traditional ecological knowledge as
577 adaptive management. *Ecological applications*, 10(5), 1251-1262.
- 578 Borics, G., Várbiro, G., & Padisák, J. (2013). Disturbance and stress: different meanings in
579 ecological dynamics? *Hydrobiologia*, 711(1), 1-7.
- 580 Brando, P. M., Silvério, D., Maracahipes-Santos, L., Oliveira-Santos, C., Levick, S. R., Coe, M.
581 T., . . . Nepstad, D. C. (2019). Prolonged tropical forest degradation due to compounding
582 disturbances: Implications for CO₂ and H₂O fluxes. *Global change biology*, 25(9), 2855-
583 2868.
- 584 Buma, B. (2015). Disturbance interactions: characterization, prediction, and the potential for
585 cascading effects. *Ecosphere*, 6(4), 1-15.
- 586 Calderón, K., Philippot, L., Bizouard, F., Breuil, M.-C., Bru, D., & Spor, A. (2018).
587 Compounded disturbance chronology modulates the resilience of soil microbial
588 communities and N-cycle related functions. *Frontiers in microbiology*, 9, 2721.
- 589 Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., . . . Wardle,
590 D. A. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59-67.
- 591 Cardinale, B. J., & Palmer, M. A. (2002). Disturbance moderates biodiversity–ecosystem
592 function relationships: experimental evidence from caddisflies in stream mesocosms.
593 *Ecology*, 83(7), 1915-1927.
- 594 Carlson, A. R., Sibold, J. S., Assal, T. J., & Negrón, J. F. (2017). Evidence of compounded
595 disturbance effects on vegetation recovery following high-severity wildfire and spruce
596 beetle outbreak. *PLoS One*, 12(8).
- 597 Chase, J. M. (2014). Spatial scale resolves the niche versus neutral theory debate. *Journal of*
598 *Vegetation Science*, 25(2), 319-322.
- 599 Cleetus, R., & Mulik, K. (2014). *Playing with fire: how climate change and development*
600 *patterns are contributing to the soaring costs of western wildfires*: Union of Concerned
601 Scientists.
- 602 Cohen, J. M., Civitello, D. J., Brace, A. J., Feichtinger, E. M., Ortega, C. N., Richardson, J. C., . . .
603 . Rohr, J. R. (2016). Spatial scale modulates the strength of ecological processes driving
604 disease distributions. *Proceedings of the National Academy of Sciences*, 113(24), E3359-
605 E3364.
- 606 Connell, J. (1997). Disturbance and recovery of coral assemblages. *Coral reefs*, 16(1), S101-
607 S113.

- 608 Connell, J. H., Hughes, T. P., & Wallace, C. C. (1997). A 30-year study of coral abundance,
609 recruitment, and disturbance at several scales in space and time. *Ecological Monographs*,
610 67(4), 461-488.
- 611 Connell, J. H., & Sousa, W. P. (1983). On the evidence needed to judge ecological stability or
612 persistence. *The American Naturalist*, 121(6), 789-824.
- 613 Cumming, G. S. (2016). Heterarchies: reconciling networks and hierarchies. *Trends in ecology &*
614 *evolution*, 31(8), 622-632.
- 615 Currie, D. J. (2019). Where Newton might have taken ecology. *Global ecology and*
616 *biogeography*, 28(1), 18-27.
- 617 Curtis, P. S., & Gough, C. M. (2018). Forest aging, disturbance and the carbon cycle. *New*
618 *Phytologist*, 219(4), 1188-1193.
- 619 D'Amato, A. W., Bradford, J. B., Fraver, S., & Palik, B. J. (2011). Forest management for
620 mitigation and adaptation to climate change: insights from long-term silviculture
621 experiments. *Forest Ecology and Management*, 262(5), 803-816.
- 622 Dai, L., Korolev, K. S., & Gore, J. (2013). Slower recovery in space before collapse of connected
623 populations. *Nature*, 496(7445), 355-358.
- 624 Dai, L., Vorselen, D., Korolev, K. S., & Gore, J. (2012). Generic indicators for loss of resilience
625 before a tipping point leading to population collapse. *science*, 336(6085), 1175-1177.
- 626 Dale, V. H., Lugo, A. E., MacMahon, J. A., & Pickett, S. T. (1998). Ecosystem management in
627 the context of large, infrequent disturbances. *Ecosystems*, 1(6), 546-557.
- 628 Darling, E. S., & Côté, I. M. (2008). Quantifying the evidence for ecological synergies. *Ecology*
629 *Letters*, 11(12), 1278-1286.
- 630 Diener, C., Gibbons, S. M., & Resendis-Antonio, O. (2020). MICOM: metagenome-scale
631 modeling to infer metabolic interactions in the gut microbiota. *mSystems*, 5(1).
- 632 Dietze, M. C., Fox, A., Beck-Johnson, L. M., Betancourt, J. L., Hooten, M. B., Jarnevich, C. S., .
633 . . Larsen, L. G. (2018). Iterative near-term ecological forecasting: Needs, opportunities,
634 and challenges. *Proceedings of the National Academy of Sciences*, 115(7), 1424-1432.
- 635 Dobson, A. P., Rodriguez, J. P., Roberts, W. M., & Wilcove, D. S. (1997). Geographic
636 distribution of endangered species in the United States. *science*, 275(5299), 550-553.
- 637 Drever, C. R., Peterson, G., Messier, C., Bergeron, Y., & Flannigan, M. (2006). Can forest
638 management based on natural disturbances maintain ecological resilience? *Canadian*
639 *Journal of Forest Research*, 36(9), 2285-2299.
- 640 Dumbrell, A. J., Clark, E. J., Frost, G. A., Randell, T. E., Pitchford, J. W., & Hill, J. K. (2008).
641 Changes in species diversity following habitat disturbance are dependent on spatial scale:
642 theoretical and empirical evidence. *Journal of applied ecology*, 45(5), 1531-1539.
- 643 Duncan, S. L., McComb, B. C., & Johnson, K. N. (2010). Integrating ecological and social
644 ranges of variability in conservation of biodiversity: past, present, and future. *Ecology*
645 *and Society*, 15(1).
- 646 e Silva, M. C. P., Semenov, A. V., Schmitt, H., van Elsas, J. D., & Salles, J. F. (2013). Microbe-
647 mediated processes as indicators to establish the normal operating range of soil
648 functioning. *Soil Biology and Biochemistry*, 57, 995-1002.
- 649 Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and
650 ecosystem consequences of shark declines in the ocean. *Ecology Letters*, 13(8), 1055-
651 1071.
- 652 Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., . . . Gibbs, H. K.
653 (2005). Global consequences of land use. *science*, 309(5734), 570-574.

- 654 Folke, C. (2002). *Social-ecological resilience and behavioural responses*: Beijer International
655 Institute of Ecological Economics.
- 656 Folke, C., Hahn, T., Olsson, P., & Norberg, J. (2005). Adaptive governance of social-ecological
657 systems. *Annu. Rev. Environ. Resour.*, 30, 441-473.
- 658 Folt, C., Chen, C., Moore, M., & Burnaford, J. (1999). Synergism and antagonism among
659 multiple stressors. *Limnology and oceanography*, 44(3part2), 864-877.
- 660 Friedman, J., Higgins, L. M., & Gore, J. (2017). Community structure follows simple assembly
661 rules in microbial microcosms. *Nature ecology & evolution*, 1(5), 1-7.
- 662 Ghavi-Helm, Y., Jankowski, A., Meiers, S., Viales, R. R., Korbel, J. O., & Furlong, E. E. (2019).
663 Highly rearranged chromosomes reveal uncoupling between genome topology and gene
664 expression. *Nature genetics*, 51(8), 1272-1282.
- 665 Ghoul, M., & Mitri, S. (2016). The ecology and evolution of microbial competition. *Trends in*
666 *microbiology*, 24(10), 833-845.
- 667 Gibbons, S. M., Scholz, M., Hutchison, A. L., Dinner, A. R., Gilbert, J. A., & Coleman, M. L.
668 (2016). Disturbance regimes predictably alter diversity in an ecologically complex
669 bacterial system. *Mbio*, 7(6), e01372-01316.
- 670 Godfrey, C. M., & Peterson, C. J. (2017). Estimating enhanced Fujita scale levels based on forest
671 damage severity. *Weather and Forecasting*, 32(1), 243-252.
- 672 Graham, E., & Krause, S. (2020). Social media sows consensus in disturbance ecology. *Nature*,
673 577(7789), 170.
- 674 Griffiths, B. S., & Philippot, L. (2013). Insights into the resistance and resilience of the soil
675 microbial community. *FEMS microbiology reviews*, 37(2), 112-129.
- 676 Grimm, V., & Wissel, C. (1997). Babel, or the ecological stability discussions: an inventory and
677 analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109(3), 323-334.
- 678 Gunderson, L. H., Holling, C., Pritchard, L., & Peterson, G. D. (2002). Resilience of large-scale
679 resource systems. *Scope-scientific committee on problems of the environment*
680 *international council of scientific unions*, 60, 3-20.
- 681 Hamer, K., & Hill, J. (2000). Scale-dependent consequences of habitat modification for species
682 diversity in tropical forests. *Conservation Biology*, 14(5), 1435-1440.
- 683 Hardiman, B. S., Bohrer, G., Gough, C. M., Vogel, C. S., & Curtis, P. S. (2011). The role of
684 canopy structural complexity in wood net primary production of a maturing northern
685 deciduous forest. *Ecology*, 92(9), 1818-1827.
- 686 He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity.
687 *Biological Reviews*, 94(6), 1983-2010.
- 688 Hill, J. K., & Hamer, K. C. (2004). Determining impacts of habitat modification on diversity of
689 tropical forest fauna: the importance of spatial scale. *Journal of applied ecology*, 41(4),
690 744-754.
- 691 Hillebrand, H., Langenheder, S., Lebet, K., Lindström, E., Östman, Ö., & Striebel, M. (2018).
692 Decomposing multiple dimensions of stability in global change experiments. *Ecology*
693 *Letters*, 21(1), 21-30.
- 694 Hobbs, R. J., Higgs, E., Hall, C. M., Bridgewater, P., Chapin III, F. S., Ellis, E. C., . . . Hulvey,
695 K. B. (2014). Managing the whole landscape: historical, hybrid, and novel ecosystems.
696 *Frontiers in Ecology and the Environment*, 12(10), 557-564.
- 697 Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: implications for conservation
698 and restoration. *Trends in ecology & evolution*, 24(11), 599-605.

- 699 Hobday, A. J., Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C., . . .
700 Feng, M. (2016). A hierarchical approach to defining marine heatwaves. *Progress in*
701 *Oceanography*, 141, 227-238.
- 702 Hobday, A. J., Oliver, E. C., Gupta, A. S., Benthuyssen, J. A., Burrows, M. T., Donat, M. G., . . .
703 Wernberg, T. (2018). Categorizing and naming marine heatwaves. *Oceanography*, 31(2),
704 162-173.
- 705 Hodgson, D., McDonald, J. L., & Hosken, D. J. (2015). What do you mean, 'resilient'? *Trends in*
706 *ecology & evolution*, 30(9), 503-506.
- 707 Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual review of ecology*
708 *and systematics*, 4(1), 1-23.
- 709 Holling, C. S. (1996). Engineering resilience versus ecological resilience. *Engineering within*
710 *ecological constraints*, 31(1996), 32.
- 711 Hsu, B. B., Gibson, T. E., Yeliseyev, V., Liu, Q., Lyon, L., Bry, L., . . . Gerber, G. K. (2019).
712 Dynamic modulation of the gut microbiota and metabolome by bacteriophages in a
713 mouse model. *Cell host & microbe*, 25(6), 803-814. e805.
- 714 Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., . . . Jones,
715 J. I. (2009). Ecological networks—beyond food webs. *Journal of Animal Ecology*, 78(1),
716 253-269.
- 717 IPCC. (2018). *Global Warming of 1.5° C: An IPCC Special Report on the Impacts of Global*
718 *Warming of 1.5° C Above Pre-industrial Levels and Related Global Greenhouse Gas*
719 *Emission Pathways, in the Context of Strengthening the Global Response to the Threat of*
720 *Climate Change, Sustainable Development, and Efforts to Eradicate Poverty:*
721 Intergovernmental Panel on Climate Change.
- 722 IPCC. (2019). *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.*
723 Retrieved from <https://www.ipcc.ch/srocc/>
- 724 Isbell, F. I., Polley, H. W., & Wilsey, B. J. (2009). Biodiversity, productivity and the temporal
725 stability of productivity: patterns and processes. *Ecology Letters*, 12(5), 443-451.
- 726 Ives, A. R., & Carpenter, S. R. (2007). Stability and diversity of ecosystems. *science*, 317(5834),
727 58-62.
- 728 Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., . . .
729 Estes, J. A. (2001). Historical overfishing and the recent collapse of coastal ecosystems.
730 *science*, 293(5530), 629-637.
- 731 Jentsch, A., & White, P. (2019). A theory of pulse dynamics and disturbance in ecology.
732 *Ecology*, 100(7), e02734.
- 733 Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., . . .
734 Perry, G. L. (2016). Changing disturbance regimes, ecological memory, and forest
735 resilience. *Frontiers in Ecology and the Environment*, 14(7), 369-378.
- 736 Kardol, P., Fanin, N., & Wardle, D. A. (2018). Long-term effects of species loss on community
737 properties across contrasting ecosystems. *Nature*, 557(7707), 710-713.
- 738 Keeley, J. E., & Pausas, J. G. (2019). Distinguishing disturbance from perturbations in fire-prone
739 ecosystems. *International Journal of Wildland Fire*, 28(4), 282-287.
- 740 Keitt, T. H. (2008). Coherent ecological dynamics induced by large-scale disturbance. *Nature*,
741 454(7202), 331-334.
- 742 Kempainen, J., Niittynen, P., Aalto, J., le Roux, P. C., & Luoto, M. (2019). Water as a resource,
743 stress and disturbance shaping tundra vegetation. *Oikos*, 128(6), 811-822.

- 744 Kendrick, G. A., Nowicki, R. J., Olsen, Y. S., Strydom, S., Fraser, M. W., Sinclair, E. A., . . .
 745 Burkholder, D. A. (2019). A systematic review of how multiple stressors from an
 746 extreme event drove ecosystem-wide loss of resilience in an iconic seagrass community.
- 747 Knelman, J. E., Graham, E. B., Trahan, N. A., Schmidt, S. K., & Nemergut, D. R. (2015). Fire
 748 severity shapes plant colonization effects on bacterial community structure, microbial
 749 biomass, and soil enzyme activity in secondary succession of a burned forest. *Soil*
 750 *Biology and Biochemistry*, *90*, 161-168.
- 751 Knelman, J. E., Schmidt, S. K., Garayburu-Caruso, V., Kumar, S., & Graham, E. B. (2019).
 752 Multiple, compounding disturbances in a forest ecosystem: fire increases susceptibility of
 753 soil edaphic properties, bacterial community structure, and function to change with
 754 extreme precipitation event. *Soil Systems*, *3*(2), 40.
- 755 Koenig, J. E., Spor, A., Scalfone, N., Fricker, A. D., Stombaugh, J., Knight, R., . . . Ley, R. E.
 756 (2011). Succession of microbial consortia in the developing infant gut microbiome.
 757 *Proceedings of the National Academy of Sciences*, *108*(Supplement 1), 4578-4585.
- 758 Ladau, J., & Elloe-Fadrosh, E. A. (2019). Spatial, temporal, and phylogenetic scales of microbial
 759 ecology. *Trends in microbiology*.
- 760 Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the north*
 761 *american Benthological society*, *19*(4), 573-592.
- 762 Laliberté, E., Grace, J. B., Huston, M. A., Lambers, H., Teste, F. P., Turner, B. L., & Wardle, D.
 763 A. (2013). How does pedogenesis drive plant diversity? *Trends in ecology & evolution*,
 764 *28*(6), 331-340.
- 765 Lamentowicz, M., Gałka, M., Marcisz, K., Słowiński, M., Kajukało-Drygalska, K., Dayras, M.
 766 D., & Jasey, V. E. (2019). Unveiling tipping points in long-term ecological records from
 767 Sphagnum-dominated peatlands. *Biology letters*, *15*(4), 20190043.
- 768 le Roux, P. C., Virtanen, R., & Luoto, M. (2013). Geomorphological disturbance is necessary for
 769 predicting fine-scale species distributions. *Ecography*, *36*(7), 800-808.
- 770 Lembrechts, J. J., Nijs, I., & Lenoir, J. (2019). Incorporating microclimate into species
 771 distribution models. *Ecography*, *42*(7), 1267-1279.
- 772 Loecke, T. D., Burgin, A. J., Riveros-Iregui, D. A., Ward, A. S., Thomas, S. A., Davis, C. A., &
 773 Clair, M. A. S. (2017). Weather whiplash in agricultural regions drives deterioration of
 774 water quality. *Biogeochemistry*, *133*(1), 7-15.
- 775 Lorimer, C. G. (1989). Relative effects of small and large disturbances on temperate hardwood
 776 forest structure. *Ecology*, *70*(3), 565-567.
- 777 Luysaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., . . . Grace, J.
 778 (2008). Old-growth forests as global carbon sinks. *Nature*, *455*(7210), 213-215.
- 779 Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in ecology &*
 780 *evolution*, *19*(2), 94-100.
- 781 Magnúsdóttir, S., & Thiele, I. (2018). Modeling metabolism of the human gut microbiome.
 782 *Current opinion in biotechnology*, *51*, 90-96.
- 783 Mahoney, J. M., & Rood, S. B. (1998). Streamflow requirements for cottonwood seedling
 784 recruitment—an integrative model. *Wetlands*, *18*(4), 634-645.
- 785 McCann, K. S. (2000). The diversity–stability debate. *Nature*, *405*(6783), 228-233.
- 786 McMullen, L. E., De Leenheer, P., Tonkin, J. D., & Lytle, D. A. (2017). High mortality and
 787 enhanced recovery: modelling the countervailing effects of disturbance on population
 788 dynamics. *Ecology Letters*, *20*(12), 1566-1575.

- 789 Mehran, A., AghaKouchak, A., Nakhjiri, N., Stewardson, M. J., Peel, M. C., Phillips, T. J., . . .
 790 Ravalico, J. K. (2017). Compounding impacts of human-induced water stress and climate
 791 change on water availability. *Scientific reports*, 7(1), 1-9.
- 792 Miller, A. D., Roxburgh, S. H., & Shea, K. (2011). How frequency and intensity shape diversity-
 793 disturbance relationships. *Proceedings of the National Academy of Sciences*, 108(14),
 794 5643-5648.
- 795 Mishra, A. K., & Singh, V. P. (2010). A review of drought concepts. *Journal of hydrology*,
 796 391(1-2), 202-216.
- 797 Mod, H. K., le Roux, P. C., & Luoto, M. (2014). Outcomes of biotic interactions are dependent
 798 on multiple environmental variables. *Journal of Vegetation Science*, 25(4), 1024-1032.
- 799 Mod, H. K., & Luoto, M. (2016). Arctic shrubification mediates the impacts of warming climate
 800 on changes to tundra vegetation. *Environmental Research Letters*, 11(12).
- 801 Munson, S. M., Reed, S. C., Peñuelas, J., McDowell, N. G., & Sala, O. E. (2018). Ecosystem
 802 thresholds, tipping points, and critical transitions. *New Phytologist*, 218.
- 803 Myers-Smith, I., Forbes, B., Wilmsking, M., Hallinger, M., Lantz, T., Blok, D., . . . Sass-
 804 Klaassen, U. (2011). Le vesque E. Boudreau S, Ropars P, Hermanutz L, Trant A, Collier
 805 LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen
 806 C, Me nard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker
 807 J, Grogan P, Epstein HE, Hik DS.
- 808 Naeem, S., & Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390(6659), 507-
 809 509.
- 810 Niittynen, P., Heikkinen, R. K., & Luoto, M. (2018). Snow cover is a neglected driver of Arctic
 811 biodiversity loss. *Nature Climate Change*, 8(11), 997-1001.
- 812 Nowicki, R., Heithaus, M., Thomson, J., Burkholder, D., Gastrich, K., & Wirsing, A. (2019).
 813 Indirect legacy effects of an extreme climatic event on a marine megafaunal community.
 814 *Ecological Monographs*, 89(3), e01365.
- 815 Paine, R. T., Tegner, M. J., & Johnson, E. A. (1998). Compounded perturbations yield ecological
 816 surprises. *Ecosystems*, 1(6), 535-545.
- 817 Palmer, W. C. (1965). Meteorological drought. Research Paper No. 45. Washington, DC: US
 818 Department of Commerce. *Weather Bureau*, 59.
- 819 Pausas, J. G., & Bond, W. J. (2020). Alternative Biome States in Terrestrial Ecosystems. *Trends*
 820 *in Plant Science*.
- 821 Pausas, J. G., & Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-
 822 prone ecosystems. *New Phytologist*, 204(1), 55-65.
- 823 Pausas, J. G., Keeley, J. E., & Schwilk, D. W. (2017). Flammability as an ecological and
 824 evolutionary driver. *Journal of Ecology*, 105(2), 289-297.
- 825 Peters, D. P., Lugo, A. E., Chapin III, F. S., Pickett, S. T., Duniway, M., Rocha, A. V., . . . Jones,
 826 J. (2011). Cross-system comparisons elucidate disturbance complexities and generalities.
 827 *Ecosphere*, 2(7), 1-26.
- 828 Peterson, M. A., Collavo, A., Ovejero, R., Shivrain, V., & Walsh, M. J. (2018). The challenge of
 829 herbicide resistance around the world: a current summary. *Pest management science*,
 830 74(10), 2246-2259.
- 831 Pickett, S., Kolasa, J., Armesto, J., & Collins, S. (1989). The ecological concept of disturbance
 832 and its expression at various hierarchical levels. *Oikos*, 129-136.
- 833 Pidgen, K., & Mallik, A. U. (2013). Ecology of compounding disturbances: The effects of
 834 prescribed burning after clearcutting. *Ecosystems*, 16(1), 170-181.

- 835 Poff, N. L. (1992). Why disturbances can be predictable: a perspective on the definition of
836 disturbance in streams. *Journal of the north american Benthological society*, 11(1), 86-
837 92.
- 838 Rillig, M. C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C. A., Buchert, S., Wulf, A., . . . Yang,
839 G. (2019). The role of multiple global change factors in driving soil functions and
840 microbial biodiversity. *science*, 366(6467), 886-890.
- 841 Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., . . .
842 Nelson, M. P. (2014). Status and ecological effects of the world's largest carnivores.
843 *science*, 343(6167), 1241484.
- 844 Rist, L., Felton, A., Nyström, M., Troell, M., Sponseller, R. A., Bengtsson, J., . . . Angeler, D.
845 (2014). Applying resilience thinking to production ecosystems. *Ecosphere*, 5(6), 1-11.
- 846 Ruhi, A., Dong, X., McDaniel, C. H., Batzer, D. P., & Sabo, J. L. (2018). Detrimental effects of
847 a novel flow regime on the functional trajectory of an aquatic invertebrate
848 metacommunity. *Global change biology*, 24(8), 3749-3765.
- 849 Rykiel Jr., E. J. (1985). Towards a definition of ecological disturbance. *Australian Journal of*
850 *Ecology*, 10(3), 361-365.
- 851 Ryo, M., Aguilar-Trigueros, C. A., Pinek, L., Muller, L. A., & Rillig, M. C. (2019). Basic
852 principles of temporal dynamics. *Trends in ecology & evolution*.
- 853 Sabo, J. L., & Post, D. M. (2008). Quantifying periodic, stochastic, and catastrophic
854 environmental variation. *Ecological Monographs*, 78(1), 19-40.
- 855 Scheffer, M. (2010). Foreseeing tipping points. *Nature*, 467(7314), 411-412.
- 856 Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., . . .
857 Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, 461(7260), 53-
858 59.
- 859 Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in
860 ecosystems. *Nature*, 413(6856), 591-596.
- 861 Seidl, R., Spies, T. A., Peterson, D. L., Stephens, S. L., & Hicke, J. A. (2016). Searching for
862 resilience: addressing the impacts of changing disturbance regimes on forest ecosystem
863 services. *Journal of applied ecology*, 53(1), 120-129.
- 864 Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., . . .
865 Honkaniemi, J. (2017). Forest disturbances under climate change. *Nature Climate*
866 *Change*, 7(6), 395-402.
- 867 Shade, A., Peter, H., Allison, S. D., Baho, D., Berga, M., Bürgmann, H., . . . Martiny, J. B.
868 (2012). Fundamentals of microbial community resistance and resilience. *Frontiers in*
869 *microbiology*, 3, 417.
- 870 Shiklomanov, A. N., Bradley, B. A., Dahlin, K. M., M Fox, A., Gough, C. M., Hoffman, F. M., .
871 . . Smith, W. K. (2019). Enhancing global change experiments through integration of
872 remote-sensing techniques. *Frontiers in Ecology and the Environment*, 17(4), 215-224.
- 873 Slette, I. J., Post, A. K., Awad, M., Even, T., Punzalan, A., Williams, S., . . . Knapp, A. K.
874 (2019). How ecologists define drought, and why we should do better. *Global change*
875 *biology*, 25(10), 3193-3200.
- 876 Słowiński, M., Lamentowicz, M., Łuców, D., Barabach, J., Brykała, D., Tyszkowski, S., . . .
877 Jażdżewski, K. (2019). Paleocological and historical data as an important tool in
878 ecosystem management. *Journal of environmental management*, 236, 755-768.
- 879 Smith, M. D. (2011a). An ecological perspective on extreme climatic events: a synthetic
880 definition and framework to guide future research. *Journal of Ecology*, 99(3), 656-663.

- 881 Smith, M. D. (2011b). The ecological role of climate extremes: current understanding and future
882 prospects. *Journal of Ecology*, *99*(3), 651-655.
- 883 Song, J., Wan, S., Piao, S., Knapp, A. K., Classen, A. T., Vicca, S., . . . Beier, C. (2019). A meta-
884 analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to
885 global change. *Nature ecology & evolution*, *3*(9), 1309-1320.
- 886 Spake, R., Lasseur, R., Crouzat, E., Bullock, J. M., Lavorel, S., Parks, K. E., . . . Mulligan, M.
887 (2017). Unpacking ecosystem service bundles: Towards predictive mapping of synergies
888 and trade-offs between ecosystem services. *Global Environmental Change*, *47*, 37-50.
- 889 Sutherland, I. J., Bennett, E. M., & Gergel, S. E. (2016). Recovery trends for multiple ecosystem
890 services reveal non-linear responses and long-term tradeoffs from temperate forest
891 harvesting. *Forest Ecology and Management*, *374*, 61-70.
- 892 Tedim, F., Leone, V., Coughlan, M., Bouillon, C., Xanthopoulos, G., Royé, D., . . . Ferreira, C.
893 (2020). Extreme wildfire events: The definition. In *Extreme Wildfire Events and*
894 *Disasters* (pp. 3-29): Elsevier.
- 895 Tilman, D., & Downing, J. A. (1994). Biodiversity and stability in grasslands. *Nature*,
896 *367*(6461), 363-365.
- 897 Todman, L., Fraser, F., Corstanje, R., Deeks, L., Harris, J. A., Pawlett, M., . . . Whitmore, A.
898 (2016). Defining and quantifying the resilience of responses to disturbance: a conceptual
899 and modelling approach from soil science. *Scientific reports*, *6*, 28426.
- 900 Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., & Lytle, D. A. (2017). Seasonality
901 and predictability shape temporal species diversity. *Ecology*, *98*(5), 1201-1216.
- 902 Tonkin, J. D., Merritt, D. M., Olden, J. D., Reynolds, L. V., & Lytle, D. A. (2018). Flow regime
903 alteration degrades ecological networks in riparian ecosystems. *Nature ecology &*
904 *evolution*, *2*(1), 86-93.
- 905 Tonkin, J. D., Poff, N. L., Bond, N. R., Horne, A., Merritt, D. M., Reynolds, L. V., . . . Lytle, D.
906 A. (2019). Prepare river ecosystems for an uncertain future. In: Nature Publishing Group.
- 907 Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*,
908 *91*(10), 2833-2849.
- 909 Turner, M. G., Romme, W. H., & Gardner, R. H. (1994). Landscape disturbance models and the
910 long-term dynamics of natural areas. *Natural Areas Journal*, *14*(1), 3-11.
- 911 Van Nes, E. H., & Scheffer, M. (2007). Slow recovery from perturbations as a generic indicator
912 of a nearby catastrophic shift. *The American Naturalist*, *169*(6), 738-747.
- 913 Venturelli, O. S., Carr, A. V., Fisher, G., Hsu, R. H., Lau, R., Bowen, B. P., . . . Arkin, A. P.
914 (2018). Deciphering microbial interactions in synthetic human gut microbiome
915 communities. *Molecular systems biology*, *14*(6).
- 916 Walker, B. H., Carpenter, S. R., Rockstrom, J., Crépin, A.-S., & Peterson, G. D. (2012).
917 Drivers, "slow" variables, "fast" variables, shocks, and resilience. *Ecology and Society*,
918 *17*(3).
- 919 Walker, L. R., Wardle, D. A., Bardgett, R. D., & Clarkson, B. D. (2010). The use of
920 chronosequences in studies of ecological succession and soil development. *Journal of*
921 *Ecology*, *98*(4), 725-736.
- 922 Wei, X., & Zhang, M. (2010). Quantifying streamflow change caused by forest disturbance at a
923 large spatial scale: A single watershed study. *Water Resources Research*, *46*(12).
- 924 Westman, W. E. (1978). Measuring the inertia and resilience of ecosystems. *BioScience*, *28*(11),
925 705-710.

- 926 WMO (2018). WMO climate statement. Retrieved from [https://public.wmo.int/en/media/press-](https://public.wmo.int/en/media/press-release/wmo-climate-statement-past-4-years-warmest-record)
927 [release/wmo-climate-statement-past-4-years-warmest-record](https://public.wmo.int/en/media/press-release/wmo-climate-statement-past-4-years-warmest-record)
- 928 Wolkovich, E., Cook, B., McLauchlan, K., & Davies, T. (2014). Temporal ecology in the
929 Anthropocene. *Ecology Letters*, *17*(11), 1365-1379.
- 930 Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating
931 environment: the insurance hypothesis. *Proceedings of the National Academy of*
932 *Sciences*, *96*(4), 1463-1468.
- 933 Zarnetske, P. L., Skelly, D. K., & Urban, M. C. (2012). Biotic multipliers of climate change.
934 *science*, *336*(6088), 1516-1518.
- 935 Zelnik, Y. R., Arnoldi, J. F., & Loreau, M. (2019). The three regimes of spatial recovery.
936 *Ecology*, *100*(2), e02586.
- 937 Zemunik, G., Turner, B. L., Lambers, H., & Laliberté, E. (2015). Diversity of plant nutrient-
938 acquisition strategies increases during long-term ecosystem development. *Nature plants*,
939 *1*(5), 15050.
- 940 Zscheischler, J., Westra, S., Van Den Hurk, B. J., Seneviratne, S. I., Ward, P. J., Pitman, A., . . .
941 Wahl, T. (2018). Future climate risk from compound events. *Nature Climate Change*,
942 *8*(6), 469-477.
- 943

Figures and Tables.

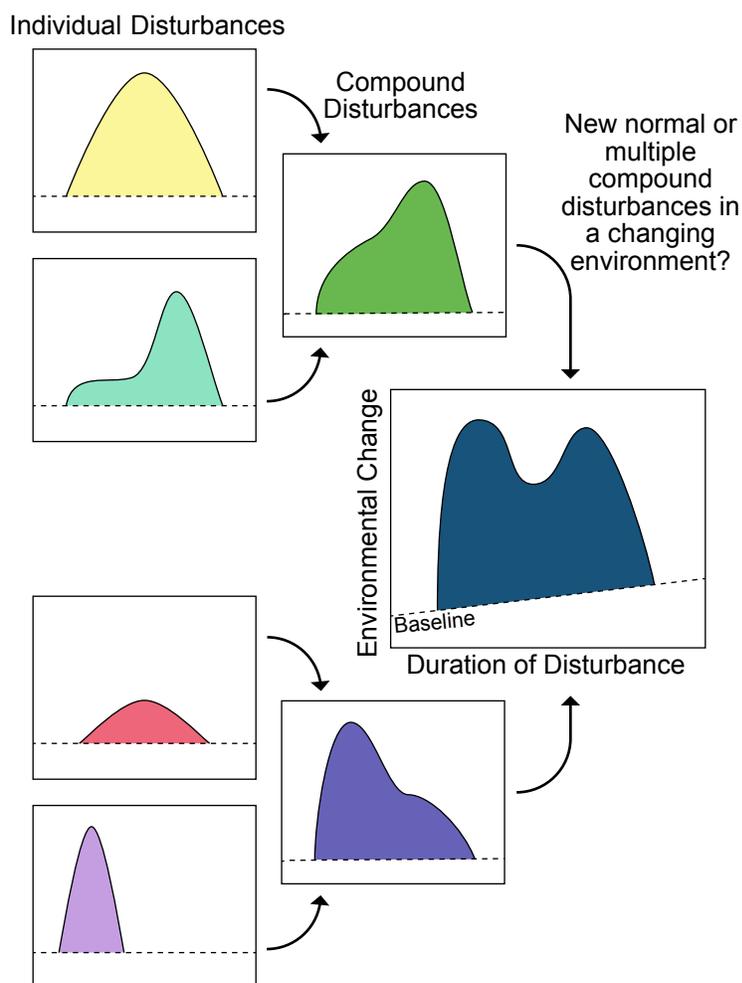


Figure 1. An obstacle to historical paradigms of disturbance theory is that changes in environmental conditions will not only alter the frequency of disturbances, but also the potential for multiple interacting disturbances. As multiple disturbances compound through time, a crucial question emerges: “When does a disturbed state become normal?” Compound disturbances can take many forms and result in both linear and non-linear ecosystem responses. As an example, Figure 1 shows an additive trajectory of disturbances and resultant environmental change. The leftmost panels represent single disturbance events that have long been the targets of scientific research. As disturbances aggregate through time, a new class of ‘compound’ disturbances have been a rising topic (middle panels). With the continuing increases in the frequency and intensity of disturbances, a key challenge remains to disentangle multiple compounding disturbances from normal variability in ecosystem functions (rightmost panel). Another challenge is that environmental baselines (dashed line) shift through time, adding a chronic component to the study of short-term disturbance events.

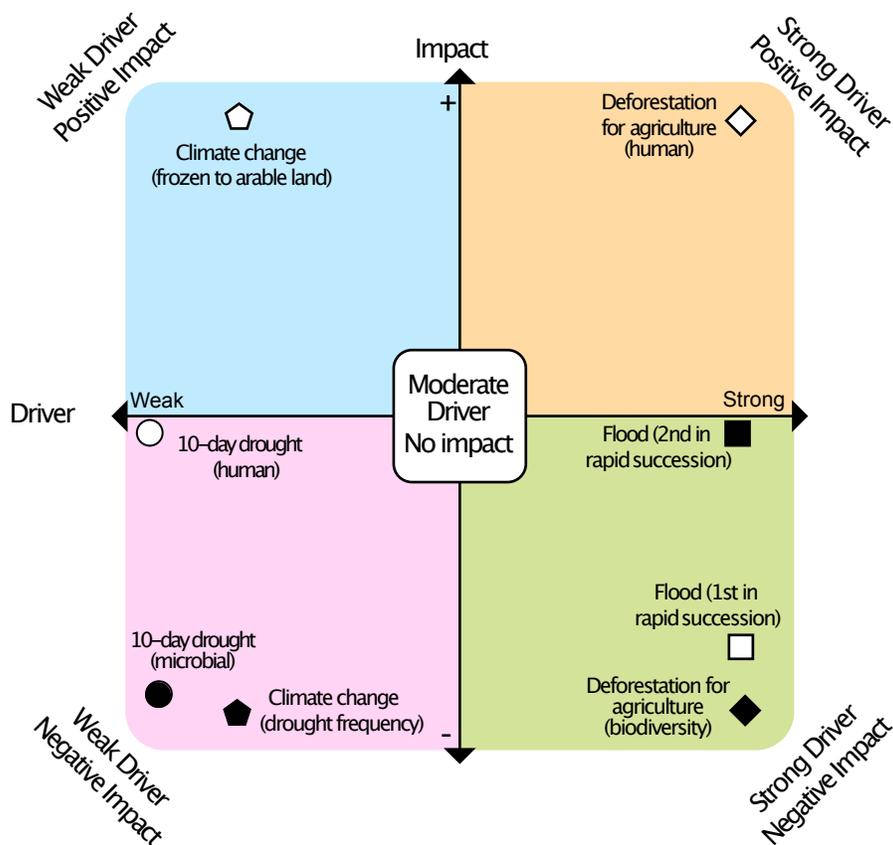


Figure 2. Current disturbance lexicon conflates two distinct processes—events that drive ecological change and impacts of extreme events—both interchangeably termed disturbances despite fundamental distinctions between the two types of processes. We disentangle these processes to derive four universal types of disturbances that are applicable regardless of the line of inquiry or its spatiotemporal scale. Drivers (x-axis) are defined as an event whereby a force, either biotic or abiotic, generates deviation from local, prevailing background conditions. A driver is characterized by its magnitude of deviation from an environmental baseline (low to high deviation denotes weak to strong driver). Impacts (y-axis) are defined as the impact of social-ecological consequences of a driver relative to a scale-dependent baseline state. Impacts can be positive or negative depending on the perspective of the study. Each quadrant is, therefore, a unique disturbance type defined in more detail in Table 1, and the position of drivers and impacts across and within the quadrants slides with the line of inquiry. Examples of disturbances across spatial and temporal scales are denoted within each quadrant.

Table 1. Description and examples of four universal disturbance types generated by proposed framework.

Quadrant	Description	Example
High Deviation-Negative Impact	Occur when large deviations from environmental baselines generate negative impacts on ecosystem functions.	Category 5 hurricane Mass wasting Oil spills Tornados Floods (human perspective) Wildfires (human perspective) Deforestation biodiversity impacts
High Deviation-Positive Impact	Occur when large deviations from environmental baselines generate positive impacts on ecosystem functions.	Deforestation for agriculture increasing crop production (human perspective) Floods (wetland ecosystems)
Low Deviation-Negative Impact	Occur when small deviations from environmental baselines generate negative impacts on ecosystem functions.	Short term drought-induced microorganism mortality Climate change-induced (i.e., temperature/CO ₂ driven) drought impacts
Low Deviation-Positive Impact	Occur when small deviations from environmental baselines generate positive impacts on ecosystem functions.	Climate change (human societies in very cold environments) Small wildfires that prevent catastrophic megafires

Table 2. Proposed minimum reporting standards for interoperability of disturbance investigations.

Ecosystem Properties	Reference Disturbance Properties (Reported for both Driver and Impact)	Temporal Disturbance Properties (Reported for both Driver and Impact)	Spatial Disturbance Properties (Reported for both Driver and Impact)
Ecotone	Reference Baseline State	Duration	Coordinates
Successional State	Method for determining baseline state	Rate of onset	Scale of study
Resistance	Intensity (deviation from mean or baseline)	Rate of decline	Scale of disturbance
Resilience		Variability through time	Area of extent
Recovery			Variability through space
Temporal Stability			
Method and input variables for determining resistance, resilience, recovery, and temporal stability (recommend Hillebrand et al 2018)			