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Mechanisms of forest resilience.

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Abstract:	<p>Ecosystems are dynamic systems with complex responses to environmental variation. In response to pervasive stressors of changing climate and disturbance regimes, many ecosystems are realigning rapidly across spatial scales, in many cases moving outside of their observed historical range of variation into alternative ecological states. In some cases, these new states are transitory and represent successional stages that may ultimately revert to the pre-disturbance condition; in other cases, alternative states are persistent and potentially self-reinforcing, especially under conditions of altered climate, disturbance regimes, and influences of non-native species. These reorganized states may appear novel, but reorganization is a characteristic ecosystem response to environmental variation that has been expressed and documented throughout the paleoecological record. Resilience, the ability of an ecosystem to recover or adapt following disturbance, is an emergent property that results from the expression of multiple mechanisms operating across levels of organism, population, and community. We outline a unifying framework of ecological resilience based on ecological mechanisms that lead to outcomes of persistence, recovery, and reorganization. Persistence is the ability of individuals to tolerate exposure to environmental stress, disturbance, or competitive interactions. As a direct expression of life history evolution and adaptation to environmental variation and stress, persistence is manifested most directly in survivorship and continued growth and reproduction of established individuals. When persistence has been overcome (e.g., following mortality from stress, disturbance, or both), populations must recover by reproduction. Recovery requires the establishment of new individuals from seed or other propagules following dispersal from the parent plant. When recovery fails to re-establish the pre-disturbance community, the ecosystem will assemble into a new state. Reorganization occurs along a gradient of magnitude, from changes in the relative dominance of species present in a community, to individual species replacements within an essentially intact community, to complete species turnover and shift to dominance by plants of different functional types, e.g. transition from forest to shrub or grass dominance. When this latter outcome is persistent and involves reinforcing mechanisms, the resulting state represents a vegetation type conversion (VTC), which in this framework represents an end member of reorganization processes. We explore reorganization in greater detail as this phase is increasingly observed but the least understood of the resilience responses. This resilience framework provides a direct and actionable basis for</p>

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Highlights

- Resilience is an emergent outcome of persistence, recovery, and reorganization processes, reflecting mechanisms specific to each type of response
- Persistence and recovery are most closely associated with return to pre-disturbance conditions
- Reorganization is a natural process of ecosystem adaptation to changing conditions
- Projected environmental changes make ecosystem reorganization increasingly likely
- Managers can use understanding of resilience to guide ecosystem transitions

1 **Abstract**

2 Ecosystems are dynamic systems with complex responses to environmental variation. In
3 response to pervasive stressors of changing climate and disturbance regimes, many ecosystems
4 are realigning rapidly across spatial scales, in many cases moving outside of their observed
5 historical range of variation into alternative ecological states. In some cases, these new states are
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25 replacements within an essentially intact community, to complete species turnover and shift to
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27 dominance. When this latter outcome is persistent and involves reinforcing mechanisms, the
28 resulting state represents a vegetation type conversion (VTC), which in this framework
29 represents an end member of reorganization processes. We explore reorganization in greater
30 detail as this phase is increasingly observed but the least understood of the resilience responses.
31 This resilience framework provides a direct and actionable basis for ecosystem management in a
32 rapidly changing world, by targeting specific components of ecological response and managing
33 for sustainable change.

1 **Mechanisms of forest resilience**

2 **1. Introduction**

3 Ecological communities, and the species that comprise them, are always in a state of flux
4 in response to environmental variation. Nonetheless, the pace and magnitude of observed
5 ecosystem change in recent decades appears to exceed recorded rates of change over recent
6 centuries and even millennia (Barnosky et al. 2011, Scheffers et al. 2016, IPCC 2018, Nolan et
7 al. 2018, Turner et al. 2020). Observed and projected changes for forest ecosystems include
8 accelerated mortality among long-lived organisms such as trees (Bennett et al. 2015, McDowell
9 et al. 2016), tree recruitment and forest regeneration failure in established populations (Stevens-
10 Rumann et al. 2018, Davis et al. 2019), and rapid changes in species distributions (Chen et al.
11 2011, Burrows et al. 2014, Talluto et al. 2017). Because of the broad spatial scale of climatic
12 impacts, and the increasing cumulative extent of ecosystem disturbances and non-native species
13 invasions (including pests and pathogens), projected changes in ecological communities
14 represent a massive upheaval and reorganization of ecological communities over broad regions
15 of the globe (McDowell et al. 2020).

16 One consequence of increasing acute and chronic stress from these profound
17 environmental changes is that forest ecosystems are being pushed outside of their recent
18 observed ranges of variation into alternative ecological states, such as conversion of forest or
19 shrub-steppe to self-reinforcing flammable grasslands (Balch et al. 2013, Syphard et al. 2019,
20 Batllori et al. 2020, O'Connor et al. 2020, Landesmann et al. 2021). In some instances, these new
21 states are transitory and represent successional stages that may ultimately lead back toward the
22 pre-disturbance condition; elsewhere, alternative states are persistent and potentially self-
23 reinforcing, especially under prevailing conditions of altered climate, disturbance regimes, and
24 presence of non-native species.

25 Community-level change in forest vegetation is driven largely by individual species
26 responses and interspecific interactions across spatial scales (Gleason 1926). In some cases,
27 communities change as certain species are excluded by disturbance, competitive interactions,
28 loss of key symbionts or mutualists, or persistent changes in key soil or hydrological resources.
29 Community-level change can also occur when species reach a limit of tolerance in key niche
30 parameters driven by shifting climatic zones (Notaro et al. 2012, Shirk et al. 2018), ultimately

31 altering demographic balances of local extirpation and colonization (Comte et al. 2014, Talluto
32 et al. 2017). This filtering process of change and adaptation, abundantly evident in the
33 paleoecological record, includes adaptation to variable and novel environments and novel
34 disturbances (Jackson et al. 2009, Crausbay et al. 2017). In the current era of rapid climatic
35 change, the pace of change over the landscape (climate velocity) may exceed the capacity of
36 species to adapt through either geographic movement or evolutionary change (Davis et al. 2005,
37 Colwell and Rangel 2009, Loarie et al. 2009, Brito-Morales et al. 2018). The result is an
38 increasing occurrence of potentially irreversible change and reorganizing of ecological
39 communities.

40 *1.1 A framework for ecological resilience*

41 Ecological resilience can be decomposed into three distinct components operating at different
42 levels of biological organization: persistence, recovery, and reorganization, each with a distinct
43 set of underlying mechanisms (Millar et al. 2007, Falk 2017, Falk et al. 2019). *Persistence* is the
44 ability of individuals to tolerate exposure to environmental stress, disturbance, or competitive
45 interactions. Persistence is the most direct expression of life history evolution and adaptation to
46 environmental variation and stress, and is manifested in survivorship and continued growth and
47 reproduction of established individuals. Persistence also provides the highest degree of
48 continuity with the pre-disturbance community, maintaining a wide range of ecological legacies
49 (Higgs et al. 2014, Johnstone et al. 2016).

50 When persistence has been overcome (e.g., following widespread mortality events), populations
51 must *recover* by reproduction. Recovery requires the establishment of new individuals from seed
52 or other propagules following dispersal from the parent plant. Population recovery is particularly
53 sensitive to the environmental conditions required for germination, establishment, and growth of
54 young individuals, as well as inter- and intra-specific interactions. Both persistence and recovery
55 tend to result in a community with a high degree of similarity to the pre-disturbance state.

56 When recovery fails to re-establish the pre-disturbance community, the ecosystem will
57 *reorganize* into a new state (Beisner et al. 2003). Community reorganization occurs along a
58 gradient of magnitude, from changes in the relative dominance of species already present in a
59 community, to individual species replacements within an essentially intact community, to
60 complete species turnover and a shift to dominance by plants of different functional types, e.g.

61 transition from forest to shrub or grass dominance (Fletcher et al. 2014, Guiterman et al. 2018,
62 Miller et al. 2019). These reorganized states can be persistent or transient depending on ongoing
63 disturbance, climatic suitability, and competitive relationships. When reorganization is persistent
64 and involves reinforcing mechanisms, the resulting state is termed a *vegetation type conversion*
65 (VTC), which in this framework represents an end member of reorganization processes
66 (Kitzberger et al. 2016, Syphard et al. 2019, O'Connor et al. 2020).

67 Resilience, the ability of a vegetation community to recover or adapt following disturbance, is
68 thus an emergent outcome that results from the expression of multiple mechanisms operating at
69 levels of organism, population, and community interaction (Figure 1). Each primary element of
70 resilience (persistence, recovery, reorganization) reflects a set of mechanistic processes that must
71 be understood in order to interpret and predict ecosystem responses.

72 In this paper, we summarize existing observations of forest vegetation persistence, recovery, and
73 reorganization across levels of biological organization, and explore the primary mechanisms that
74 regulate these processes (Table 1). Our objective is to provide a detailed, mechanistic framework
75 for the science of ecological resilience in forests and its application to ecosystem management
76 (Millar et al. 2007, Falk 2017, Coop et al. 2020, Stevens et al. 2021, Guiterman et al. *in rev.*). We
77 provide examples of these processes in the literature, focusing on forests of western North
78 America but with additional cases from other regions.

79

80 **2. Mechanisms of Persistence**

81 Persistence is the ability of individuals to survive disturbance, be it stressful droughts or
82 biophysical destruction such as fire. This section deals with mechanisms of how individuals in a
83 population survive these disturbances. We illustrate the mechanistic basis of persistence using
84 two widespread stressors: wildfire and drought.

85 *2.1 Individual tree persistence: Fire*

86 Fire is one of the more ubiquitous forms of disturbance in forest ecosystems, and a significant
87 influence on species evolution (Gagnon et al. 2010, Pausas et al. 2017). However, even plant
88 communities dominated by fire-adapted species encounter perturbations that are outside the fire

89 regime to which they are adapted, which can result in mortality and loss of reproductive
90 capacity, coupled with community reorganization (Keeley and Pausas 2019). During wildfire,
91 heat is transferred to all parts of the plant by various energy transfer mechanisms, requiring
92 specific anatomical and physiological adaptations (Michaletz and Johnson 2007).

93 The evolutionary response to fire generally follows one of two pathways: through niche selection
94 for environments that avoid fire, or by developing morphological characteristics that allow the
95 plant to survive fire (Rowe 1983, Clarke et al. 2015). In relatively productive environments,
96 especially those with strong seasonality that provide a dry period sufficient to convert biomass to
97 flammable fuel, fire is a predictable feature of the environment, and traits that confer resistance
98 to fire are selected. These traits include thick insulating bark, self-pruning of dead branches, or
99 resprouting from protected buds (Keeley and Zedler 1998, Pausas 2015).

100 The temporal scale of predictability of fire varies with climate and biome. For example,
101 Mediterranean climate ecosystems experience conditions that potentially allow fire every
102 summer and fall; dry temperate forests generally carry fire during dry spring or early summer
103 weather (Arizpe 2016), whereas mesic and boreal forests are fire-prone primarily during multi-
104 annual to decadal scale climate events (Gedalof et al. 2005). These regimes represent very
105 different evolutionary environments: trees in the former areas have higher levels of persistence
106 following fire (at least when fire burns within its historical range of variation in fire behavior),
107 whereas in the latter areas, individuals are generally killed by fire, and populations rely primarily
108 on post-mortality reproduction.

109 *2.1.1 Surface fire regimes*

110 Western North American mixed conifer forests are moderately productive ecosystems where
111 growth rates are sufficient for the canopy to outgrow surface fuels. This creates a spatial gap
112 between surface and canopy fuels, increasing the likelihood of tree survival. This persistence
113 strategy is globally widespread in seasonal environments where natural lightning ignitions are
114 predictable during the dry season (Williams et al. 1999, Hoffmann et al. 2003). Discontinuity
115 between surface and canopy fuels is a common feature of both coniferous forests and oak
116 woodlands in the northern hemisphere, as well as in tropical savanna trees (Hoffmann et al.
117 2003) and the drivers of persistence are tied to multiple morphological and ecological parameters
118 (Hood et al. 2018, Furniss et al. 2019, van Mantgem et al. 2020b).

119 Frequent fire regimes select for traits that enhance survival. The abscission of lower branches is a
120 critically important adaptation that increases the spatial gap between surface fuels and the tree
121 canopy, placing live branches above characteristic flame length and plume of combustion gases,
122 as well as protecting the lower stem cambium (Figure 2.a) (Keeley and Zedler 1998, Schwilk and
123 Ackerly 2001). This trait is well developed in many trees adapted to frequent surface fire
124 regimes, but is largely absent in those species found in high intensity crown fire regimes (Keeley
125 2012). The exposure of aboveground plant parts (stems, branches, foliage) to aboveground
126 flaming combustion may be relatively short (minutes), but residence time of belowground
127 smoldering combustion can extend to hours or days, exposing fine roots to extensive mortality
128 (Michaletz and Johnson 2007).

129 Since the lower stems of trees cannot escape direct exposure to surface fires, a critical potential
130 stress is heat penetration, which can be lethal to the underlying cambium cells at temperatures
131 above 60° C (Bauer et al. 2010). Many fire-adapted pines have developed heat-resistant bark that
132 protects the critical growth layers of the cambium (Figure 2.b). The insulative capacity of bark is
133 affected most strongly by bark thickness, although other characteristics such as surface structure
134 and density play a role (Michaletz and Johnson 2007, Wei et al. 2020). Thick bark is more
135 common in fire-prone ecosystems (Rosell et al. 2017) and is associated with higher survival
136 (Ryan and Reinhardt 1988), although this depends largely on the fire regime. The importance of
137 bark thickness increases with age, as survivorship of young trees is favored more by height
138 growth (Kidd and Varner 2019). For example, arborescent oaks subject to frequent surface fires
139 have relatively thick bark (Pellegrini et al. 2017), distinctly unlike the thin bark of scrub oaks in
140 infrequent-fire regimes (Zedler 1995); this is also true of pines (Keeley and Zedler 1998) and a
141 variety of other tree species (Pausas 2015).

142 Bark thickness evolves in response to other environmental drivers, such as protection from heat,
143 cold, and insects; however, in pines it is associated strongly with species in surface fire regimes
144 and is not found in species adapted to arid or alpine conditions (Keeley and Zedler 1998). Across
145 a wide spectrum of tree clades, thick bark is not markedly associated with climate (Rosell 2016,
146 Schubert et al. 2016, Rosell et al. 2017). Complicating our understanding of the role of bark in
147 affecting persistence is the marked changes in bark characteristics with growth form and tree
148 size. Allometric relationships of tree size and bark thickness produce divergent patterns in

149 different climates, further complicating interpretations (Jackson et al. 1999, Schwilk et al. 2013).
150 Despite its importance to persisting through fire disturbances, bark characteristics are just one set
151 of traits that characterize species in surface fire regimes, along with physiological properties such
152 as rapid wound response (Smith et al. 2016, Varner et al. 2016).

153 Although there are clear species-specific differences in capacity to persist in the face of recurrent
154 surface fires, there is finer scale variation both spatially and temporally. Within a forest there are
155 microsites with anomalous fuel accumulation that can be lethal to even the most fire-resistant
156 species, especially as a result of recent forest management practices (Jeronimo et al. 2020).
157 Conversely, topography and spatial variation in fuels can create refugia that allow the persistence
158 even of fire-sensitive species. Persistence of individual trees following fire is also affected by
159 environmental conditions (such as drought), biotic interactions, and topographic patterns
160 (Schwilk and Keeley 2006, van Mantgem et al. 2018a, Furniss et al. 2021). Thus, while
161 persistence traits vary with different fire regimes, those regimes are not static and vary both
162 spatially and temporally.

163 This effect is further complicated by changes in climate, which in some regions have led to
164 longer fire seasons and increasingly severe fire weather, resulting in higher fire intensities, larger
165 areas burned, and larger high-severity patch sizes (Kitzberger et al. 2017, Williams et al. 2019).
166 However, the complexity of wildland fire across spatial scales makes it difficult to separate the
167 relative importance of a more than century of fire exclusion from climate change (Collins et al.
168 2019). Nor is it clear how climate change will affect tree persistence through changing fire
169 regimes; some research predicts that increasing temperatures will produce more intense fires
170 with greater tree mortality (Halofsky et al. 2020), whereas other models forecast changes in
171 vegetation structure that will decrease fuel mass and availability and thus decrease fire intensity
172 (Pausas and Paula 2012, Batllori et al. 2013, Hurteau et al. 2019).

173 *2.1.2 Crown fire adaptations*

174 Crown fires by definition involve exposure of apical meristems and foliage to radiant and
175 convective heat and potential tissue necrosis (Michaletz and Johnson 2007). Resprouting is a
176 mechanism that allows individual regrowth from buds following major biomass loss (Clarke et
177 al. 2015). Many woody angiosperm genera (e.g., *Eucalyptus* L'Her., *Quercus* L., *Populus* L.)
178 have the capacity to resprout, but this trait is far less common in gymnosperms (McDonald and

179 Tappeiner 1996, Bond and Van Wilgen 2012). Resprouting is often viewed as an adaptation to
180 high-severity fire (Clarke et al. 2013b, Pausas et al. 2016), although resprouting can occur
181 following other disturbances such as drought or grazing (Zeppel et al. 2015). Because
182 resprouting allows plants to take advantage of surviving tissues (e.g., roots, lignotubers),
183 recovery of the individual may be relatively rapid and less uncertain compared to regeneration
184 from seed. Recovery times may also be influenced by the position of the resprouting buds
185 (below-ground, basal, or aerial); species that maintain epicormic buds on the existing skeleton of
186 the main stem may recover forest structure and function more rapidly compared to basally
187 resprouting species (Pausas and Keeley 2017), assuming the buds are not damaged by the
188 disturbance. Large, high-severity disturbance can thus shift species composition toward
189 dominance of sprouting species if these species are present prior to disturbance (§3.4, Recovery:
190 *Competitive effects and community interactions*).

191 In crown-fire ecosystems there are many examples of persistence through resprouting. Basal
192 resprouting is widespread in fire-prone shrublands throughout the world (Keeley et al. 2011a) as
193 well as shrubs and small trees that form forest understories (Figure 3a), whereas epicormic
194 resprouting along the stems of burned trees is less widely distributed (Pausas and Keeley 2017).
195 Epicormic resprouting arises from latent buds along tree stems that are typically protected by
196 thick bark, although in some *Eucalyptus* they are embedded in the woody tissues beneath
197 relatively thin bark. The primary distinction between these two modes is that basal resprouting
198 allows for persistence of the genet, whereas epicormic resprouting ensures persistence of
199 individual ramets. The latter facilitates retention of the arborescent skeleton, thus allowing for
200 rapid recovery under recurrent high intensity fires (Collins 2020). Indeed, certain *Eucalyptus*
201 species exhibit over 99% epicormic resprouting, such that the forest recovers relatively rapidly to
202 its original composition and structure (Figure 3b). In most temperate forests, we generally think
203 of crown fires as stand-replacing events where recovery is primarily from reproduction, but in
204 certain Australian forest types, as well as North American and European forests dominated by
205 *Quercus* and other resprouting broadleaved trees, even crown fires are not stand-replacing;
206 rather, the individual trees persist. This is in contrast to *Pinus* in the Northern Hemisphere, where
207 the resprouting strategy is almost unknown (although there are notable exceptions, e.g., *Pinus*
208 *canariensis* C. Sm. Ex. D.C. (Pausas and Keeley 2017)).

209 Counterintuitively, many woody plants subject to crown-fires lack resprouting traits for
210 persistence. In those species commonly associated with crown-fire regimes, such as lodgepole
211 pine (*Pinus contorta* Douglas), this is perhaps not unexpected since resprouting is a rare trait in
212 the genus. However, within Mediterranean-climates, most shrublands that are dominated by
213 angiosperm shrubs include entire clades that lack the capacity for persistence through
214 resprouting, and there is evidence that this is a derived trait (Keeley et al. 2011a). This is
215 surprising since basal resprouting is nearly ubiquitous in woody angiosperms (Wells 1969).
216 Hypotheses for this loss of persistence center on the capacity to adapt to new climates through
217 increased number of sexual generations, and on ecological effects, e.g., resprouts may also
218 increase competition with new seedlings (Keeley 2012). Considering the widespread distribution
219 of resprouting capacity, it likely represents a persistence strategy in response to multiple forms of
220 disturbance, including intense browsing or extreme climatic events including freezing and
221 drought (Keeley et al. 2011a).

222 *2.2 Individual tree persistence: Drought*

223 Drought is a common ecosystem disturbance, and most climate change models suggest a future
224 of increasingly severe droughts worldwide (Trenberth et al. 2014). The ecological impacts of
225 drought (an extended period of unusually low rainfall, leading to shortage in soil moisture) are
226 exacerbated by elevated temperatures, leading to the “warm drought” syndrome that is becoming
227 increasingly pervasive (Lloret and Batllori 2021). Extreme droughts can alter community
228 composition through differential survival, which is well documented worldwide for both
229 angiosperms and gymnosperms (McDowell et al. 2008), especially in arid and semi-arid
230 ecosystems. During the 1950s a severe drought in the semi-arid southwest U.S. resulted in a 2
231 km shift in the distribution of ponderosa pine, which was replaced by more drought tolerant
232 piñon-juniper woodland (Allen and Breshears 1998). Such rapid climate-driven shifts occur
233 mostly by differences in persistence; during this episode, the ecotone shift was driven largely by
234 mortality of ponderosa pine compared to persistence of piñon and juniper. On a similar
235 landscape during a 15-month drought between 2002-2003, the piñon-juniper community was
236 altered dramatically by mortality of more than 90% of the dominant tree, *Pinus edulis* Engelm.,
237 whereas 75% of the associated *Juniperus monosperma* (Engelm.) Sarg. survived (Breshears et al.
238 2005).

239 Persistence during severe droughts is highly dependent on characteristics of the plant hydraulic
240 system (Choat et al. 2018). Within the same plant community, coexisting woody species
241 commonly have diverse hydraulic strategies, and as a consequence may express different
242 patterns of persistence during severe droughts (Johnson et al. 2018). The ecological and
243 physiological effects of drought *per se* (precipitation anomalies) also interact strongly with
244 changes in temperature regimes; warmer droughts are more likely to induce widespread mortality
245 than droughts that occur under normal temperatures (Adams et al. 2009, McDowell 2011),
246 although mechanisms remain a matter of debate (Sala et al. 2010, Anderegg et al. 2012).

247 Woody plants prevent desiccation injury by xylem transport of water from the roots, but xylem
248 fluid under tension is vulnerable to sudden shifts from water to gas; these air bubbles block water
249 transport in the xylem, a process known as *cavitation* (Davis et al. 2002, Maherali et al. 2004).
250 Adaptations to drought revolve around avoiding embolism by anatomical features of the xylem
251 cell and porosity of cell walls. Resistance to cavitation is a key determinant of persistence in the
252 face of severe drought (Vilagrosa et al. 2012). Stomatal conductance, rooting depth and cellular
253 osmotic conditions are also key plant functions that determine drought persistence (Markesteyn
254 et al. 2011).

255 Understanding mechanisms of tolerance to drought is complicated by the range of plant
256 hydraulic strategies for dealing with this stress. Even in the absence of catastrophic failure in
257 water transport, persistence can be threatened by changes in carbohydrate reserves necessary for
258 respiratory function and osmotic regulation (Hammond et al. 2019, Sapes et al. 2021). Many
259 plants regulate water loss by stomatal closure, which reduces water loss but also limits carbon
260 uptake necessary for photosynthesis and Calvin cycle processes that convert CO₂ to glucose via
261 carbon fixation and reduction reactions. Reduced xylem flow also reduces a key tree defense
262 against insects, leading to increased vulnerability to these mortality agents (Bentz et al. 2010,
263 Huang et al. 2020).

264 Plant functional traits play a key role in determining persistence through severe drought, which
265 can confer different advantages dependent on the pattern of drought (Trugman et al. 2020).
266 McDowell et al. (2008) proposed a model explaining persistence patterns in the context of
267 different water use strategies in ways that affect carbon balance and pathogen resistance.
268 Although water use strategies comprise a continuum within and among species, their model

269 suggests different outcomes for isohydric vs. anisohydric strategies in the face of different
270 patterns of drought. Isohydric strategies maintain constant leaf water potentials by regulating
271 stomatal conductance, whereas anisohydric plants maintain high stomatal conductance in the
272 face of diminished leaf water potentials (Sade et al. 2012). Associated with these strategies are
273 differences in water availability due to rooting depth, and cellular tolerance to desiccation
274 through osmotic adjustments.

275 There is circumstantial evidence that global warming is changing persistence traits resulting in
276 coordinated shifts toward communities with more drought-tolerant traits driven by selective
277 mortality (Trugman et al. 2020, Roos and Guiterman 2021). Global warming is altering fire
278 regimes in the North American boreal forest (Kelly et al. 2013), resulting in increased drought
279 impacts that are changing plant assemblages, moving conifer forests to broadleaf deciduous
280 forests (Keeley and Pausas 2019). However, drought is a broad term that is quantified by over
281 100 different indices to describe its properties and impact (Zargar et al. 2011). With respect to
282 plant communities, there are species-specific differences dependent on the pattern of drought,
283 and traits favorable for persisting in the face of short-term extreme droughts may differ from
284 traits favoring persistence in the face of long-term droughts. The primary mechanisms of
285 drought-induced tree mortality, carbon starvation (resulting from stomatal closure) and hydraulic
286 failure, vary widely across taxa (Adams et al. 2017). Loss of xylem hydraulic conductivity is the
287 most prevalent cause of mortality, although simultaneous loss of carbon reserves is widespread,
288 particularly in gymnosperms (McDowell and Sevanto 2010). Selection may increasingly favor
289 traits that confer the capacity to maintain plant hydraulic function, photosynthesis, and non-
290 structural carbohydrate reserves during periods of low productivity, and mechanisms to maintain
291 resistance biotic stressors such as insects and pathogens (McDowell et al. 2008).

292

293 **3. Mechanisms of Recovery**

294 If persistence mechanisms are overcome, vegetation *recovery* is the next potential pathway of
295 ecological resilience. Recovery represents the replacement of the pre-disturbance population
296 through recruitment or colonization; thus, recovery processes occur at the level of populations
297 (Figure 1). The post-disturbance period is a critical stage in community development, during
298 which the persistence and coexistence of multiple species is determined in part by life history

299 adaptations to the unique properties of such environments (the ‘regeneration niche’, *sensu* Grubb
300 (1977)). Recovery processes determine the initial density, establishment success, and
301 survivorship of recruits. For example, how propagules or recruits arrive at sites following
302 disturbance is of critical importance for recovery processes, whether from a persistent seed bank,
303 or via seed dispersal (Bond and Van Wilgen 2012, Pausas and Keeley 2014, 2017).
304 Understanding the mechanisms that underly recovery strategies is essential to assessing the
305 potential for resilience following major disturbances.

306 *3.1 Seed banks, serotiny, and advance regeneration*

307 Populations may not be solely dependent on the survivorship of reproductive individuals, but
308 may rely instead on the survivorship of seeds or propagules. Seeds that are developed and stored
309 in the soil or other protected structures (e.g., closed arboreal cones) prior to disturbance represent
310 an *in situ* seed bank, allowing for recovery of populations without the need for dispersal from
311 surviving individuals elsewhere. A large literature has been developed around the dynamics of
312 soil seedbanks (Leck 2012, Saatkamp et al. 2014). Although few conifer species have persistent
313 (longevity > 1 yr) soil seedbanks, soil seed banking is common in many other taxa, especially
314 among angiosperm shrub, grass, and forb species (Knapp et al. 2012, USDA-USFS 2021). The
315 availability of soil-stored seed following disturbance can allow a variety of plant functional types
316 to dominate previously forested post-fire landscapes rapidly, at least initially. Some shrub and
317 herbaceous species exhibit seedbank-mediated adaptation to disturbance, such as smoke- (Keeley
318 1997, Abella 2009) and heat-induced germination (Keeley and Keeley 1987) of seeds that
319 otherwise remain dormant in soil.

320 As an alternative to soil seed banking, some conifer species possess aerial seedbanks (Figure 4).
321 A common mode of aerial seed banking is serotiny, in which trees store viable seeds in closed
322 cones for one to many years and release them following disturbance, even when that disturbance
323 kills the adult trees (Schwilk and Ackerly 2001). Serotiny in response to fire appears across
324 many unrelated taxa (Bond and Van Wilgen 2012). Some conifer species that are not generally
325 serotinous may display facultative serotiny if a fire burns in the late summer or fall, when cones
326 have matured, and kills the tree but does not destroy its seeds (Larson and Franklin 2005,
327 Pouden et al. 2014). Relative to species that rely on residual live reproductive individuals to
328 disperse seeds into a disturbed site (§3.2: *Dispersal*), serotinous species are well adapted to

329 recruit following large disturbances with extensive high-severity patches (Turner et al. 1997).
330 Large high-severity wildfires can thus shift composition in favor of serotinous species (Donato et
331 al. 2009, Hansen et al. 2018).

332 Under some circumstances, large, mature individuals may be killed by disturbance while small,
333 immature individuals survive. The surviving juvenile cohort functions as advance regeneration
334 and may allow for relatively rapid recovery (Greene et al. 1999). Advance regeneration may be
335 particularly important following drought, windstorms, or pest outbreaks where mortality may be
336 concentrated in large individuals (Kayes and Tinker 2012, Redmond et al. 2018). Because
337 advance regeneration becomes established in the forest understory prior to disturbance, it is often
338 enriched in shade-tolerant species, which may lead recovering communities to be similarly
339 enriched in such species (Veblen et al. 1991, Kayes and Tinker 2012, Young et al. 2019b).

340 *3.2 Dispersal*

341 Seed dispersal is of critical importance for obligate seeding species that do not create persistent
342 seed banks. Recovery in ecosystems dominated by these species in disturbed sites generally
343 depends on wind or animal dispersal of seeds into the site from nearby surviving reproductive
344 trees (McCaughey et al. 1986)(Figure 5).

345 The influence of seed source proximity on seed input has been confirmed by numerous empirical
346 studies of post-fire seedling recruitment patterns, which, for non-serotinous species, consistently
347 find a strong negative relationship between tree seedling density and distance to the nearest
348 surviving reproductive tree(s) or low-severity/unburned patch (Donato et al. 2009, Welch et al.
349 2016, Owen et al. 2017, Stevens-Rumann and Morgan 2019, Stewart et al. 2021). Most conifer
350 seeds are initially wind-dispersed and exhibit relatively limited dispersal distances; the majority
351 of species studied disperse seeds < 50-75 m (Burns and Honkala 1990, Greene et al. 2004,
352 Bonnet et al. 2005, Rother and Veblen 2016, Halpern and Antos 2021) (Figure S-1), although
353 longer-distance dispersal does occur, often aided by secondary dispersal by rodents or birds
354 (Vander Wall 1992, 2008).

355 Short dispersal distances may be beneficial in the context of historic high-frequency, low-
356 severity disturbance regimes that produce spatially heterogeneous mortality patterns, such that
357 few high-mortality areas are far from residual reproductive trees (Safford and Stevens 2017). In

358 contrast, the increasingly common large patches of high-severity area lie beyond the reliable
359 dispersal range of the nearest surviving reproductive trees (Tautenhahn et al. 2016, Stevens et al.
360 2017a, Steel et al. 2018, Falk et al. 2019). However, fires that burn large areas of forest at high
361 severity do not necessarily create completely dispersal-limited patches. Many large fires are
362 spatially heterogeneous, leaving a patchy distribution of surviving trees that can serve as seed-
363 source islands in post-fire landscapes (Figure 6). Patches of surviving trees (*fire refugia*) may
364 play an important role in determining recovery in many coniferous forests (Turner et al. 1998,
365 Coop et al. 2019).

366 Infrequent long-distance dispersal may be an important mechanism behind tree population
367 expansion (Allen 1987, Clark 1998, Clark et al. 1998). Birds may play a keystone role in long-
368 distance seed dispersal of certain conifer species, such as dispersal of *Pinus albicaulis* Engelm.
369 seeds by Clark's nutcrackers (*Nucifraga columbiana* Wilson) (Williams et al. 2020). While
370 substantial long-distance (e.g., > 200 m) dispersal is relatively rare for western U.S. dry forest
371 tree species, it is sometimes recorded. For example, Kemp et al. (2016) estimated the probability
372 of observing at least one non-serotinous conifer seedling in a 600 m² area 300 m from the nearest
373 seed source more than 10 years following fire to be approximately 20%. However, even a 300-m
374 dispersal range is short relative to the scale of contiguous high-severity patches spanning more
375 than 2 km in the shortest dimension in many recent large wildfires (Eidenshink et al.
376 2007)(Figure 6). Shade-tolerant conifer species (e.g., true firs, *Abies* Mill spp.) tend to have
377 smaller seeds and longer dispersal ranges than shade-intolerant species such as pines
378 (McCaughey et al. 1986, Burns and Honkala 1990), so sites far from residual forest may receive
379 seed rain more heavily dominated by shade-tolerant species. Within conifers, seed size tends to
380 be larger for species with animal-dispersed seeds compared to those with seeds dispersed
381 primarily by wind (Leslie et al. 2017), but animal dispersed species may be able to more easily
382 colonize large, high severity patches in post-fire landscapes. In the case of *Pinus albicaulis*,
383 animal dispersal of seeds into post-fire landscapes may be key to its ability to persist under
384 historical fire regimes (Keane et al. 2012).

385 Conceptually, seed input should depend on not only the proximity of seed sources but also their
386 density and spatial pattern (Greene and Johnson 1996, Clark et al. 1999, Peeler and Smithwick
387 2020). Empirical approaches that incorporate seed source density and/or spatial arrangement into

388 seed availability metrics also detect the expected relationship between seed source density and
389 seedling recruitment (Shive et al. 2018, Stewart et al. 2021), further supporting the idea that
390 recovery from more spatially heterogeneous disturbances may be more likely and/or rapid (Haire
391 and McGarigal 2010, Tepley et al. 2017) The generally high spatial heterogeneity associated
392 with drought-related mortality may also help to explain the high densities of seedlings sometimes
393 found following drought-related mortality events (Young et al. 2019b, Fettig et al. 2019), as
394 could instances where seed production is unaffected during drought (Wright et al. 2021);
395 alternatively, these seedlings may largely represent advance regeneration. Other spatially
396 heterogeneous drought-related mortality events in areas with presumably little advance
397 regeneration have not exhibited substantial post-drought seedling recruitment (Allen and
398 Breshears 1998).

399 When disturbed areas are beyond the scale of long-distance dispersal, large disturbed patches
400 may be re-colonized over time by multiple successive generations of trees, each reaching
401 maturity before dispersing seeds further into the patch (Falk et al. 2019). In a severely burned
402 patch approximately 500 m wide, Nagel and Taylor (2005) observed trees that recruited in the
403 center of the patch were on average 22 years younger than trees recruited near the edge of the
404 patch; similarly, Schwilk and Keeley (2006) observed a decrease in mean age of *Pinus sabiniana*
405 Douglas ex D. Don recruits with distance from a fire refugium. Similar recruitment patterns have
406 been observed in conifer invasions of grasslands and alpine meadows (Coop and Givnish 2007,
407 Halpern et al. 2010). In these ecosystems conifer invasions may subsequently change
408 microenvironments and fuel composition, discouraging fire and promoting further invasions
409 (Engber et al. 2011). These observations are consistent with progressive multi-generational
410 recruitment into burned areas, although they are also consistent with initial tree reestablishment,
411 and exclusion of later recruits, where seed rain is strongest.

412 *3.3 Germination, seedling survivorship, and growth*

413 After seeds arrive at a site, they must germinate, and seedlings must establish and grow, for
414 forest recovery to proceed (Harper 1977, Dobrowski et al. 2015). Many conifer species—
415 especially, but not exclusively, shade-intolerant pines—establish more successfully on bare
416 mineral soil than on litter-covered soil (McDonald 1976, Gray and Spies 1997, Safford and
417 Stevens 2017). Therefore, the potential for seed rain to translate into forest recovery will depend

418 partially on the type of disturbance: for example, fire may consume litter and duff layers, leaving
419 mineral soil exposed (although also vulnerable to surface erosion), while drought-related
420 overstory mortality is often associated with additional litter deposition.

421 Following successful germination (or resprouting) after disturbance, survivorship and growth of
422 juvenile plants are particularly sensitive to environmental conditions. Seedling establishment
423 following disturbance tends to be more limited closer to the arid extremes of forest and/or tree
424 species distributions (Rodman et al. 2020, Stewart et al. 2021), although fine-scale climatic and
425 topographic refugia such as those afforded by woody debris can ameliorate otherwise harsh
426 conditions and promote seedling recruitment (Dobrowski et al. 2015, Owen et al. 2020, Marsh et
427 al. 2022). Weather in the years immediately following disturbance can also strongly influence
428 forest recovery (Littlefield et al. 2020). The effects of short-term post-disturbance climatic stress
429 are corroborated by numerous studies that find reduced post-fire conifer recruitment under
430 unusually hot and/or dry post-fire conditions (Harvey et al. 2016, Urza and Sibold 2017,
431 Stevens-Rumann et al. 2018, Davis et al. 2019, Hansen and Turner 2019, Young et al. 2019b,
432 Stewart et al. 2021) Low-elevation forests in the western U.S. are increasingly experiencing
433 years in which weather conditions do not meet minimum thresholds for successful forest
434 regeneration (Figure 7) (Stevens-Rumann et al. 2018, Davis et al. 2019). Tree species recovery in
435 the context of weather and climate variation is constrained by the dependence of tree
436 regeneration on seed rain from the residual reproductive trees (Young et al. 2019a). When post-
437 fire weather and climate do not match the requirements of the available seed, the system may be
438 vulnerable to reorganization.

439 *3.4 Competitive effects and community interactions*

440 Successful recovery is determined partially by the capacity of recruits to compete for resources
441 within the post-disturbance community. In ecosystems with strong post-disturbance shrub
442 growth and poor initial conifer regeneration, sites often become dominated by shrubs and remain
443 so for decades (Russell et al. 1998, Lauvaux et al. 2016). Comparable self-reinforcing dynamics
444 have been observed in shrublands that have been invaded by exotic grasses (Keeley and Brennan
445 2012). Nonetheless, continued seed dispersal and seedling recruitment over time may allow for
446 delayed recovery. Tree seedling establishment is often observed over at least a 10-year period
447 following fire (Harvey et al. 2016, Stevens-Rumann et al. 2017, Davis et al. 2019) and

448 sometimes over multiple decades (Russell et al. 1998, Nagel and Taylor 2005, Savage and Mast
449 2005, Haire and McGarigal 2010, Lauvaux et al. 2016), even when little recruitment was
450 observed in the first 10 or more years (although other studies have found regeneration pulses
451 limited to the first 3-10 years post-fire (Tepley et al. 2017, Urza and Sibold 2017, Davis et al.
452 2019). Long-term recruitment may be particularly important for recovery in sites far from seed
453 sources, as multiple years of low-density, long-distance seed rain may accumulate to support
454 meaningful tree establishment that lags behind sites closer to seed sources (Turner et al. 1998,
455 Haire and McGarigal 2010). Delayed (e.g., > 10-year post-disturbance) tree recruitment appears
456 more often in shade-tolerant species (Nagel and Taylor 2005, Lauvaux et al. 2016), likely due to
457 the need for establishing trees to tolerate competition from other vegetation that establishes in the
458 intervening years (Tepley et al. 2017, Werner et al. 2019, Tubbesing et al. 2021).

459 Despite the potential for delayed forest establishment far from seed sources, regeneration is
460 likely to become increasingly difficult as competing vegetation (often shrubs) becomes
461 established over time (Figure 8). This may explain why some studies find the strongest pulse of
462 recruitment relatively soon after disturbance (Harvey et al. 2016, Tepley et al. 2017, Urza and
463 Sibold 2017, Davis et al. 2019). For example, following fire in dry coniferous forests of the
464 southwestern U.S., vigorously resprouting Gambel oak (*Quercus gambelii* Nutt.) shrubs may
465 outcompete *P. ponderosa* Douglas ex D. Lawson seedlings for light and water, limiting their
466 capacity for recovery (Guiterman et al. 2018). In areas where trembling aspen (*Populus*
467 *tremuloides* Michx.) co-occurs with conifer species, aspen often initially dominates the
468 recovering tree community, likely a consequence of its resprouting ability, but over subsequent
469 decades composition generally shifts toward conifer dominance due to their relative juvenile
470 shade tolerance and greater adult height and longevity; this constitutes a *transient reorganization*
471 (Figure 9) (Smith and Smith 2005). A wide range of other perennial early successional species
472 have been observed to dominate landscapes in the years initially following fire, including
473 bracken fern (*Pteridium aquilinum* (L.) Kuhn); whitethorn, deerbrush, and buckbrush
474 (*Ceanothus* L. spp.); New Mexico locust (*Robinia neomexicana* A. Gray); bigleaf maple (*Acer*
475 *macrophyllum* Pursh.) and others. High-severity fire may facilitate invasions of native and exotic
476 ruderal species, which may lead to self-reinforcing changes in community composition and fire
477 hazards (Keeley and Brennan 2012, Coop et al. 2016). However, in some cases topoclimate (e.g.,
478 aspect, elevation) may be more important than cover of competing vegetation for predicting

479 regeneration success following fire (Rother and Veblen 2016). Transient vegetation communities
480 may also alter fire regimes, encouraging further vegetation change (e.g., Engber et al. 2011).

481 The preceding sections highlight the capacity of species to recover from disturbance. However,
482 recent literature suggests that recovery is becoming more difficult under current conditions in
483 many ecosystems regardless of species adaptations to disturbance regimes (Fairman et al. 2019,
484 Davis et al. 2019, Turner et al. 2019). If a population's capacity to recover from disturbance is
485 overwhelmed, the next phase of resilience is community reorganization.

486

487 **4. Reorganization**

488 When mechanisms of persistence have been overcome, and recovery processes fail or are
489 compromised, an ecological system will reorganize. Ecological reorganization can take a wide
490 variety of forms, from temporary shuffling of species dominance relationships, to persistent type
491 conversion involving major changes in plant functional types (Figure 1) (Falk et al. 2019, Keeley
492 et al. 2019, Steel et al. 2021). Individual disturbance events, or interactions between two or more
493 disturbances, may act as triggers for abrupt change; however, the ecosystem is unlikely to persist
494 in the alternative state unless subsequent disturbances, climate, or plant–disturbance interactions
495 function as an equilibrating force to promote stability of the new state, while limiting the
496 potential to return to the previous condition or transition to another state.

497 *Observations and definition:* Reorganization (referred to variously as realignment, ecosystem
498 transition, transformation and conversion (van Mantgem et al. 2020a)) is expressed in changes at
499 the community level along a spectrum of magnitude. In some cases, reorganization consists
500 primarily of changes in relative abundance of existing species in the community; these changes
501 can be transient, or they can represent a persistent vegetation shift (Barton and Poulos 2018).

502 More extensive reorganization can involve turnover in community composition, structure, and
503 physiognomy, as when new species enter the community, and other formerly present species are
504 eliminated (Figure 10). More fundamental forms of reorganization are expressed by a change in
505 dominant plant functional types, such as forest-shrub, forest-grass, or shrub-grass conversions
506 (Guiterman et al. 2018, Batllori et al. 2020, Armenteras et al. 2021). Vegetation type conversion
507 (VTC) is notable as a special case of reorganization in which the change in community type and

508 dominant plant functional types are extensive, and the alternative state is persistent and
509 reinforced by novel interactions among climate, vegetation, and disturbances.

510 *Time scales:* There is no single time threshold at which reorganization is delineated; indeed, the
511 multiple expressions of reorganization can progress at different rates (Falk et al. 2019). On
512 centennial to millennial and longer time scales, reorganization occurs in response to changing
513 climate; in this context it is understood as an inherently adaptive Earth system process expressed
514 over the history of life (Jackson and Overpeck 2000, Pausas and Keeley 2009, Keeley 2012). On
515 shorter ecological time scales (years to centuries), reorganization is more likely to be driven by
516 disturbance events, episodes of extreme climate (droughts or heat waves), or other triggering
517 events (Ruthrof et al. 2018).

518 To understand the mechanisms that drive ecological reorganization, we examine the following
519 questions: (1) What ecological changes constitute reorganization, and which factors drive these
520 changes across time scales? (2) What are the mechanisms and ecological dynamics of
521 reorganization? (3) What factors (external drivers and internal feedbacks) reinforce these
522 changes, causing them to persist as alternative metastable states instead of transient successional
523 change?

524 *4.1 Observations: where is ecosystem reorganization being observed and documented?*

525 Ecosystems are inherently dynamic, so the observation of change over space and time does not
526 necessarily indicate that a system is reorganizing permanently or uncharacteristically. The study
527 of seral ecology was foundational to the development of modern ecological theory, including
528 species interactions and community assembly rules (Whittaker 1960, Chase 2003). One of the
529 earliest debates in ecology concerned mechanisms and temporal patterns of post-disturbance
530 succession: Clements (1936) argued that plant communities are holistic and essentially integrated
531 entities in which succession is an orderly and well-regulated process analogous to an organism
532 healing to return to its canonical state, while Henry Gleason (1926) contended that communities
533 are transient associations among species acting individualistically. These arguments are
534 surprisingly relevant today as we consider the emergent patterns and mechanisms of ecosystem
535 reorganization.

536 *Gradual reorganization in response to changes in mean conditions.* Evidence of ecosystem
537 reorganization is a salient feature in the paleoecological record (Iglesias and Whitlock 2020),
538 reflecting recombination and reorganization of ecological communities as species ranges shift
539 due to changes in climate (Colwell and Rangel 2009, Jackson and Blois 2015, Crausbay et al.
540 2017, Fernandez et al. 2021). Processes of ecosystem transformation driven by climatic variation
541 continue into the present, and are likely to accelerate under projected future climate change
542 scenarios (Parmesan 2006, Nolan et al. 2018). Superimposed on background processes of
543 climate-driven ecosystem reorganization, we may expect anthropogenic activity to promote or
544 alter trajectories and rates of reorganization through anthropogenic climate change and other
545 global change pressures including landscape fragmentation, human alteration of disturbance
546 regimes, altered global biogeochemical cycles, and proliferation of non-native species that alter
547 disturbance–feedback dynamics (Dale et al. 2001, Jackson et al. 2009, McWethy et al. 2010,
548 Falk 2017).

549 While community change in the paleoecological record may seem less relevant to understanding
550 ecological resilience today, there is no clear line that divides the processes or mechanisms at
551 work. Reorganization can (and does) occur over decadal and longer time scales, through
552 demographic processes and turnover in species composition, even without abrupt episodes of
553 mortality, reflecting the inherent inertia of plant communities (Westman 1978, Eriksson 1996,
554 Lloret et al. 2012). Expressed changes in species distributions reflect changes in the ratio of
555 colonization to extinction at the leading and trailing margins of a species range (Loarie et al.
556 2009). When the rate of climate change exceeds species dispersal rates, lags or disequilibria may
557 occur in species ranges (e.g., where long-lived adults persist after the climate has become
558 unsuitable for new seedling establishment of the same species). This ecological inertia creates
559 lags in local extinction and colonization that over time determine the trajectory of species
560 turnover and community change on the landscape (Webb 1986, Jackson and Sax 2010, Talluto et
561 al. 2017). Extinction debt represents local persistence with population vital rates below
562 replacement, resulting ultimately in recruitment failure and local extirpation. In contrast,
563 colonization credits occur in unoccupied locations fitting existing niche requirements, as well as
564 areas open for some species in the regional pool potentially better adapted to emerging climate.
565 Ultimately, changes in fundamental demographic parameters (birth, immigration, death, and
566 emigration) underlie all shifts in species distributions. There is abundant evidence of climate-

567 driven species range shifts leading to community reorganization (Chen et al. 2011), reflecting the
568 species-individualistic nature of community organization. Contemporary observations are largely
569 associated with accelerated shifting of climatic zones in relation to species niche space (Colwell
570 and Rangel 2009, Thomas 2010, Hannah et al. 2014, Shirk et al. 2018). It is likely that similar
571 processes have been at work for millions of years as species have adapted to changing climate.

572 *Reorganization in response to the loss of formerly frequent disturbance.* Reorganization can
573 proceed along different time scales beyond gradual reorganization in response to changing
574 climate. Ecosystems can reorganize rapidly in response to the elimination or a reduced frequency
575 of an ecosystem's characteristic disturbances. In some regions, wildfire area burned has been
576 decreasing due to human fire suppression and landscape fragmentation (Andela et al. 2017).
577 Such changes would be most consequential for communities in which characteristic wildfire
578 plays a stabilizing role in community structure and composition (Parsons and DeBenedetti 1979,
579 Binkley 2021). For example, reduction in the frequency of burning in dry oak and oak–pine
580 forests of eastern North America led to increases in the abundance of mesophytic species (e.g.,
581 maples, beech, ashes, and basswood); increasing abundance of these species in turn altered forest
582 microclimate and fuel characteristics, producing a self-perpetuating feedback that made the
583 forests less conducive to fire and more favorable to the persistence of these species at the
584 expense of oaks and pines (Nowacki and Abrams 2008, Kreye et al. 2013, McDaniel et al. 2021).

585 In drier western North American conifer forests, exclusion of fire has led similarly to changes in
586 community composition, *viz.* increased abundance of shade-tolerant species such as white fir,
587 *Abies concolor* [Gordon & Glend.] Lindl. ex Hildebr. (Dolanc et al. 2014). These changes have
588 made forests more prone to high-severity fire, and increasingly vulnerable to drought-induced
589 mortality (Earles et al. 2014, Restaino et al. 2019). Because these shade-tolerant conifers
590 typically have longer seed dispersal distances than their shade-intolerant counterparts, they may
591 be better suited to re-establish and become dominant in large patches of high-severity fire. For
592 example, shade-tolerant conifers or drought-tolerant oaks have become more abundant in many
593 formerly ponderosa pine and dry mixed-conifer forests. In a southwestern Sky Island forest,
594 O'Connor et al. (2017) found a shift from disturbance-adapted species to competition- and
595 productivity-mediated recruitment as fire intervals increased beyond the historical mean.

596 Reduction in fire frequency can also lead to type conversion of savannahs and grasslands to
597 shrubland or closed forest (Bond 2019). The high flammability and rapid post-fire recovery of
598 grasses puts them at an evolutionary advantage over woody vegetation in systems that are
599 exposed frequently to fire (annually to every few years); human-driven reductions in burning
600 have led to woody plant encroachment in many of these systems globally (Luger and Moll 1993,
601 Ratajczak et al. 2012, Stevens et al. 2017b). Restoring fire regimes can thus play a key role in
602 maintaining the spatial extent and ecological functions of grass-dominated and savannah
603 ecosystems (Smit et al. 2010).

604 *Rapid reorganization in response to novel disturbance.* Unlike decadal range shifts driven by
605 climate, many observations of ecosystem reorganization represent *abrupt change*, especially
606 when triggered by disturbance episodes that are larger, more severe, or occur more frequently
607 than background temporal variability (Ratajczak et al. 2018, Jentsch and White 2019, Turner et
608 al. 2020). Among the most common triggers of abrupt change in terrestrial systems are wildfires
609 (Holz et al. 2015, Hansen et al. 2021), heat waves and episodes of extreme drought (Batllori et
610 al. 2020, Senf et al. 2020), and insect outbreaks (Weed et al. 2013, Kautz et al. 2017). In some
611 cases, combinations of two or more stress or disturbance types, or a sequence of successive
612 disturbances, may drive more substantial change with greater potential to persist compared to
613 that expected from individual disturbances (Batllori et al. 2019). Abrupt ecological change may
614 also reflect the cumulative effect of other factors that have been at work for much longer periods,
615 such as decades of invasion by non-native species that create the conditions for a tipping point
616 event.

617 Conversions from forest to shrubland or grassland, or from shrubland to grassland, are among the
618 most widely observed type conversions on contemporary landscapes following severe wildfire
619 and drought (Walker et al. 2018). Globally, approximately one-quarter of forest loss is
620 attributable to wildfire (Curtis et al. 2018), a trend that is likely to increase as fire severities (van
621 Mantgem et al. 2018b, Singleton et al. 2019, Parks and Abatzoglou 2020), sizes (Westerling
622 2016), and area burned (Abatzoglou and Kolden 2013, Kitzberger et al. 2017) increase under the
623 influence of changing climate and fuel accumulation. As climate simultaneously becomes less
624 favorable to tree establishment (Savage et al. 2013, Rother and Veblen 2016, Tepley et al. 2017),
625 wildfires are likely to trigger widespread ecosystem conversion.

626 Reorganization also may occur in response to introductions of non-native plants, insects, or
627 pathogens. In deciduous forests of eastern North America, where tree species diversity tends to
628 be higher than western conifer forests, several former canopy dominants have been lost or
629 converted to short-lived, smaller trees by invasive insects and pathogens introduced over the last
630 century (e.g., American chestnut due to the chestnut blight, American elm due to Dutch elm
631 disease, ash species due to emerald ash borer). In the late 20th to early 21st century, the hemlock
632 woolly adelgid (*Adelgis tsugae* Annand) drove extensive mortality of eastern hemlock trees
633 throughout much of its range. By 2007 in Shenandoah National Park, Virginia USA, adelgids
634 had eliminated hemlock from all permanent plots where it was present in 1991 (Anderson-
635 Teixeira et al. 2021). Invasive insects and pathogens have also caused extensive mortality of
636 some of the dominant tree species in swamp forests (e.g., American elm and ashes) (Barnes
637 1976, Abella et al. 2019). In many cases, however, the loss of these canopy dominants was
638 compensated by increases in other tree species already present in the forests, leading to less
639 substantial changes in ecosystem processes (e.g., carbon sequestration, litter decomposition, and
640 water and nutrient cycling) than would be expected following persistent physiognomic change
641 (Ellison et al. 2005).

642 *4.2 Mechanisms: what are the drivers and dynamics of reorganization?*

643 Observations can provide valuable insights into the expression of ecosystem reorganization.
644 However, reorganization is an emergent outcome of numerous mechanistic processes.
645 Understanding the mechanisms that underly reorganization is key to predicting when and where
646 such outcomes may occur (Figure 11).

647 *4.2.1 Trigger events*

648 Abrupt reorganization is triggered most commonly by severe disturbance, particularly wildfire
649 and climatic episodes that cause locally extensive mortality of dominant vegetation.
650 Uncharacteristic disturbances can also serve as triggers, such as fire driven by the proliferation of
651 flammable invasive species, or an unusual sequence of disturbances, e.g., severe, multi-year
652 drought after fire, or reburns before obligate seeder species can grow old enough to produce new
653 seeds (Coop et al. 2016, Batllori et al. 2019, Whitman et al. 2019). Large, high-severity
654 disturbances can accelerate the pace of landscape transformation from decades to days, affecting
655 not only overstory vegetation, but also ground cover, soils, and hydrology (Figure 12). The

656 energy output during extreme wildfire behavior can exceed the adaptive capacity of even fire-
657 adapted species, overcoming their resistance to thermal stress and leading to extensive individual
658 mortality through loss of photosynthetic apparatus, destruction of meristems, cambial and xylem
659 damage, and damage to root systems.

660 Changes to the fire regime (i.e., changes in the distribution of fire intervals, severities, sizes,
661 seasonality, etc.) can also trigger ecosystem reorganization (Hagmann et al. 2021). Vandewater
662 and Safford (2011, 2014) documented fire intervals in coastal and montane ecosystems in
663 southern California 50-100% shorter than the historical reference. Bowman and colleagues
664 (2014) documented rapid population collapse of alpine ash (*Eucalyptus delegatensis* R. T.
665 Baker), an obligate seeder, in the Australian Alps after extensive wildfires burned more than $\frac{3}{4}$
666 of the species range in Victoria and southeast Australia in the early 2000s. Despite abundant
667 post-fire seedling establishment, large portions of these fires reburned within a decade, killing
668 nearly all of the regenerating seedlings and driving conversion to grasses and shrubs. Short-
669 interval fires, i.e. less than the characteristic fire interval, have also been documented to
670 overwhelm the resprouting capacity of moderate sized (22 to 36 cm diameter) fire-tolerant
671 *Eucalyptus* (Fairman et al. 2019). Even in forest types with a high representation of serotinous
672 species such as *Pinus contorta* var. *latifolia* (interior lodgepole pine), high frequency fire may
673 reduce post-fire recruitment dramatically if fire return intervals are significantly shorter than
674 mean time to first reproduction (Turner et al. 2019). Similar effects of short return intervals on
675 recruitment have been observed in Mediterranean-climate shrublands in southwestern Australia
676 (Enright et al. 2014) and boreal *Picea mariana* [Mill] BSP in Yukon Territory (Brown and
677 Johnstone 2012). As climate warms and becomes increasingly conducive to widespread burning,
678 the intervals between successive high-severity fire could become shorter; at the same time, a
679 harsh post-fire climate could lengthen the time needed for forests to recover after severe fire,
680 creating the “interval squeeze”, when fire re-occurs before the juvenile cohort reaches
681 reproductive maturity (Enright et al. 2015). Modifying Baker’s (2006) equation, post-disturbance
682 reproduction could be constrained if:

$$683 \frac{FRI_p}{R_a} \ll 1,$$

684 where FRI_p is the point (tree-scale) fire return interval and R_a is mean time to first reproduction.

685 Reorganization and resulting large-scale type conversion can be triggered directly by widespread
686 die-off driven by extended severe drought and associated hotter temperatures (Adams et al. 2009,
687 Adams et al. 2010, Allen et al. 2010, Sankaran 2019), often covering wide geographic areas
688 (Fettig et al. 2019, Senf et al. 2020), and sometimes triggered by extreme climate episodes such
689 as heat waves (Lloret and Batllori 2021). Drought can cause tree mortality directly (via
690 physiological stress, cavitation, and/or carbon starvation), or by weakening tree defenses to
691 biotic agents such as bark beetles, defoliators, and plant pathogens (DeSoto et al. 2020); these
692 mortality episodes can then have persistent cascading demographic effects (Law et al. 2019).
693 Like wildfire, biotic disturbance agents are natural and essential components of forest ecosystem
694 dynamics. However, changes in climate may affect insect and disease activity, as well as tree
695 defenses and susceptibility (Weed et al. 2013, Anderegg et al. 2015, Hicke et al. 2016, Kautz et
696 al. 2017). Drought and temperature stress can interact with wildfire exposure, resulting in
697 elevated mortality rates for a given level of fire behavior (van Mantgem et al. 2020b).

698 *4.2.2 Mortality creates open resource space*

699 Once widespread mortality has occurred, resources (space, light, water, nutrients) become
700 available for multiple species, not only the prior dominants. Species that are able to resprout
701 from belowground structures after being top-killed may have an advantage in the ability to
702 recapture growing space, both above- and below-ground (§1, *Persistence*) (Lawes and Clarke
703 2011, Clarke et al. 2013a) provided that fire return intervals allow replenishment of non-
704 structural carbohydrates used for tissue growth (Nolan et al. 2021). In a study of community
705 assembly after a large high-severity landscape fire in southern Colorado, USA, Abella and
706 Fornwalt (2015) found that species that either persisted or recolonized quickly constituted 62-
707 83% of species present in the post-fire community. Similarly, 71-82% of pre-existing understory
708 species persisted following clearcutting and broadcast burning in western Oregon, USA, whereas
709 a smaller number of species ($n = 14$) were lost temporarily before eventually re-colonizing, and
710 colonization by new species ($n = 11-19$ species/yr) occurred primarily within the first two years
711 (Halpern 1988, 1989). In addition to the capacity for some species to resprout following fire-
712 driven mortality of their above-ground parts, some species have seeds that can persist in the soil
713 long after the adult plants that produced those seeds have been lost (Knapp et al. 2012).

714 Persistent dormant seedbanks likely contribute to the large increases in shrub species following
715 wildfire and prescribed burning in many mixed-conifer forests (Webster and Halpern 2010).

716 *4.2.3 Recolonization failure*

717 Initially, pre-disturbance dominants may have an inherent advantage during the recolonization
718 phase (Abella and Fornwalt 2015). They tend to be well adapted to local environmental
719 conditions and typically provide local seed sources, depending on the extent and severity of
720 disturbance. In some cases, however, population-level recovery of prior dominant species can
721 fail or be severely limited due to soil moisture deficit and excessive evaporative demand, or
722 disturbance-altered soil properties including the loss of soil organic matter, key limiting nutrients
723 (Adkins et al. 2019), or essential symbionts such as mycorrhizae (Remke et al. 2020) (§3,
724 *Recovery*). The primary mechanisms that may limit or inhibit post-fire tree seedling
725 establishment following mortality include (1) post-disturbance landscape structure, which may
726 limit propagule availability, especially in the case of large contiguous high-severity or treeless
727 patches, limiting the spatial distribution of surviving mature trees and species-specific seed
728 production and seed-dispersal capacity (Stevens et al. 2021); (2) limitations to germination,
729 influenced by soil condition and microclimate (Chambers et al. 2016, Law et al. 2019, Burrell et
730 al. 2021); (3) severe soil and hydrological effects following wildfire, which may prevent
731 successful recolonization even where seed sources are available (Sidman et al. 2016, Niemeyer
732 et al. 2020), including soil hydrophobicity, loss of soil organic matter and key limiting nutrients
733 (Adkins et al. 2019), or essential symbionts such as mycorrhizae (Remke et al. 2020); and (4)
734 failure of seedling establishment, driven by soil microorganisms, plant functional traits,
735 competitive environment, and species capacity to cope with competition and climatic stress
736 (Tercero-Bucardo et al. 2007, Enright et al. 2014, Rother and Veblen 2016, Davis et al. 2018,
737 Simeone et al. 2019).

738 Flammability of the vegetation that develops after severe burning can either amplify or buffer the
739 effects of a climate that is warming and becoming more conducive to fire (Tepley et al. 2018).

740 Where the post-fire vegetation has low flammability, as in many boreal landscapes, resistance to
741 reburning may limit the degree to which climate change drives increases in annual area burned,
742 thereby extending the time available for forests to recover after severe fire (Héon et al. 2014). By
743 contrast, where highly flammable vegetation develops after severe fire, relatively small increases

744 in climatic potential for fire could drive extensive increases in high-severity reburns at intervals
745 too short for forests to recover (Pausas et al. 2017). Landscapes colonized aggressively by
746 pyrophilic and flammable shrubs after severe fire can become particularly vulnerable to
747 extensive and persistent conversion from forest to non-forest cover (Odion et al. 2010,
748 Kitzberger et al. 2016, Tepley et al. 2017, Batllori et al. 2019, Miller et al. 2019).

749 *4.2.4 Landscape species pool*

750 Individual species life history and functional traits shape their responses in the post-fire
751 environment, and ultimately drive community reorganization (Gleason 1926, Diamond 1975).
752 Following disturbance, communities reassemble reflecting functional trait-based species
753 responses, including intraspecific variation (Laughlin et al. 2012). Both stochastic and
754 deterministic assembly processes guide the particular trajectory of reorganization, and new
755 competitive hierarchies become established based on multiple species interactions that shape the
756 new community (Temperton et al. 2004).

757 In the absence of significant persistence by resprouting or protected local seedbanks, community
758 reassembly is largely dependent on species dispersing into the site, creating competitive
759 advantages for different life history traits (e.g., dispersal ability, tolerance of poor site quality or
760 high light levels) than those that are favored under more stable conditions (Mittelbach and
761 Schemske 2015). Nearby undisturbed refugia and other ecological legacies can play a key role as
762 a source of propagules into the reorganizing community (Johnstone et al. 2016). The relative
763 increase in available space and physical resources following a large mortality event creates
764 opportunities for species within the regional pool to establish new populations that may alter the
765 environment for species that arrive subsequently (“priority effect”) (Fukami 2015, Helsen et al.
766 2016).

767 Reorganization is dependent on the presence of species that are available to colonize and adapted
768 to the disturbance-modified environment (Belyea and Lancaster 1999, Fukami 2015). In
769 demographic terms, the failure of persistence and recovery of pre-disturbance dominants
770 (Crotteau et al. 2013, Davis et al. 2020) create colonization opportunities for species better
771 adapted to emerging climate space, e.g., drought or temperature tolerance, in the unique
772 characteristics of post-disturbance environments (Butaye et al. 2002, Jain et al. 2012, Burrell et
773 al. 2021). For example, Barton and Poulos (2018) found that the conversion of Madrean pine-oak

774 forest to oak shrubland after high-severity wildfire in Arizona, USA was triggered initially by
775 uncharacteristically high-severity fires, but oak species increased because they are better adapted
776 to emerging conditions of drought and increasing incidence of fire. Species such as *Robinia*
777 *neomexicana* (New Mexico locust), *Populus tremuloides* (aspen), *Quercus gambelii* Liebm.
778 (Gambel oak) and shrubs in the genus *Ceanothus* are all present in pre-fire landscapes, but
779 increase opportunistically in fire modified environments, whereas prior dominant species that
780 depend on persistence or seed dispersal from surviving adults may experience mortality and
781 recruitment failure (Guiterman et al. 2018).

782 4.2.5 Community assembly processes

783 During the post-disturbance period, the community re-assembles from species that either are able
784 to persist through disturbance, or others in the landscape species pool that are able to disperse
785 and establish successfully. Community assembly epitomizes a stochastic process: some
786 processes, such as dispersal, are highly variable depending on dispersal mode and the landscape
787 availability of propagules, whereas other processes (such as the environmental template or
788 pairwise interspecific interactions) are more predictable or systematic, typically viewed as a set
789 of successive filters (Davis et al. 2018). The net result is that community assembly is historically
790 contingent and can be influenced strongly by priority effects, leading to niche pre-emption and
791 niche modification by early arrivals, as well as the presence of metapopulations across the
792 landscape (Belyea and Lancaster 1999, Fukami 2015, Mittelbach and Schemske 2015).
793 Outcomes of community assembly processes may be better predicted by plant functional types
794 than by species *per se* (Laughlin et al. 2012) (Figures 10, 13).

795 The net result of these post-disturbance assembly processes may create multiple reorganization
796 pathways leading to *alternative metastable states* (AMS) (Elmqvist et al. 2003, Falk 2013). Two
797 or more community types (e.g., forest and shrubland) may co-exist in the same landscape (e.g.,
798 in a shifting mosaic that varies in response to changing disturbance frequency and patterns);
799 alternatively, one type may become dominant under the prevailing climate and disturbance
800 regime. Climate or an unusual disturbance event (either an uncharacteristically large or severe
801 disturbance, or an unusual disturbance sequence) can push the landscape toward one community
802 type, which may then persist even after the climate or disturbance regime shifts back to the
803 conditions where both communities previously persisted. Such persistence would depend in part

804 on stabilizing feedbacks between the community type and the climate or disturbance regime that
805 perpetuate the existing community at the expense of the other (Miller et al. 2019). Evidence of
806 alternative states has been demonstrated in tropical prairie-savannah-grassland mosaics in
807 regions climatically and edaphically conducive to forest (Hoffmann et al. 2002, Staver et al.
808 2011, Hoffmann et al. 2012); there is increasing evidence that similar mechanisms are operating
809 in temperate and boreal regions, or could soon operate in response to climate change (Kitzberger
810 et al. 2016, Keyser et al. 2020, Hansen et al. 2021).

811 Alternative states may themselves not persist indefinitely, but there is no inherent time scale to
812 community reorganization (Falk et al. 2019, Pausas and Bond 2020). Following type conversion,
813 return pathways may differ from the pathway of degradation; due to altered community
814 interactions, recovery pathways are not simply reverse travel of degradation pathways, creating
815 the emergent property of *hysteresis* (Suding and Hobbs 2009, Litzow and Hunsicker 2016,
816 Ratajczak et al. 2018). For example, an increase in the frequency of high-severity fire could drive
817 extensive conversion from forest to shrubland, but a reduction in burning does not necessarily
818 lead to a similarly abrupt return to forest cover (Tepley et al. 2018) (Figure 13). In addition to the
819 decades typically required for trees to grow large enough to become resistant to fire (e.g., by
820 developing thick bark or elevated crown bases), fire–vegetation feedbacks may alter substantially
821 the rate of return to forest cover. Where post-fire shrublands are dominated by highly flammable
822 species, once this vegetation occupies a large portion of the landscape, much less fire may be
823 required to maintain its dominance than was needed to initially drive the conversion from forest
824 to shrubland. In such cases, the transition from one community type to the other may be
825 asymmetrical: the magnitude of change in the environment or disturbance regime needed to drive
826 the shift in one direction may be greater than that needed to drive the shift in the other direction.
827 From an evolutionary perspective, the very fact that many species are adapted to the
828 opportunities presented by disturbed ecosystems is a reminder that these states represent space in
829 the evolutionary environment of species (Keeley et al. 2011b, Keeley 2012).

830 *4.2.6 Reinforcing feedbacks*

831 Some of the factors that initially trigger reorganization (§4.2.1) can also reinforce alternative
832 states, effectively locking in reorganization and making it more likely to persist for extended

833 time (Figure 11). Here we examine two factors that can create strong self-reinforcing feedbacks
834 in reorganized systems.

835 *Disturbance.* Disturbances, such as wildfire, can be particularly effective in reinforcing an
836 altered community state through selection for different flammability and tolerance strategies
837 (Dantas et al. 2016, Pausas et al. 2017). In cases in which the species dominating the reorganized
838 community are more fire-tolerant (i.e., more flammable and better able to survive or re-colonize
839 after fire) than the pre-disturbance dominants, altered fire cycles can effectively preclude return
840 to the prior community (Newberry et al. 2020). This dynamic is observed widely in cases of
841 conversion from woody (tree or shrub) to grass dominance. Most grasses are highly flammable at
842 some stage in their life cycle and have evolutionary adaptations to surviving, and even
843 promoting, frequent fire (Gagnon et al. 2010, Pausas et al. 2017). By altering fuel types, mass,
844 continuity, and seasonality, non-native grasses cause persistent change in the dominant fire
845 regime type to a grass-fire cycle, creating an invasive fire regime that excludes woody plant
846 recruitment (Brooks et al. 2004, Gaertner et al. 2014). This reinforcing feedback makes the
847 reorganized community highly resilient in its altered state, and resistant to return to the pre-
848 disturbance community (Brooks and Chambers 2011). Notable examples of fire-reinforced
849 alternative states include conversion of Great Basin sage steppe to annual cheatgrass (*Bromus*
850 *Scop.*) grassland (Balch et al. 2013), invasion of Sonoran upland by cool season non-native
851 grasses (Stevens and Falk 2009, McDonald and McPherson 2011, Chambers et al. 2014),
852 chaparral-grassland conversion in southern CA (Syphard et al. 2018, 2019) (Figure S-2), and
853 conversions in southwestern ponderosa pine forests (Coop et al. 2020). Fire can thus play a dual
854 role in reorganization, acting first as a trigger for initial destabilization (by causing extensive
855 mortality and modifying the post-disturbance environment), and then as a positive feedback
856 factor reinforcing the AMS, especially where life history adaption to fire (including flammability
857 and the capacity to survive or re-colonize after fire) differs among species and plant functional
858 types.

859 *Climate.* Like disturbance, climate can play a dual role as both a trigger and subsequent
860 reinforcing mechanism for community reorganization (Figure 11). Shorter (annual to
861 multiannual) climate episodes can cause extensive mortality, creating open niche space and
862 allowing new species to enter the community (Ruthrof et al. 2018). If the climate episode is

863 brief, and conditions return to the normal range of variation, these effects may be transient if
864 conditions are suitable for recovery. However, extreme climate episodes superimposed on
865 rapidly changing mean conditions can effectively prevent prior dominants from re-establishing,
866 even for species with long-lived individuals (Matusick et al. 2018).

867 Abundant evidence is accumulating of persistent species realignments and geographic shifts in
868 response to changing climate (Chen et al. 2011, Iverson and McKenzie 2013, Burrows et al.
869 2014, Shirk et al. 2018). Altered climate conditions can favor different species once
870 reorganization begins, if they are better adapted in terms of climate tolerance to persistent
871 emerging conditions. For instance, field experiments evaluating seedling survival and growth
872 under experimental warming indicate that many tree species could soon lose the capacity to
873 regenerate in areas currently occupied by conspecific adults (Tercero-Bucardo et al. 2007, Rother
874 et al. 2015, Hansen and Turner 2019). The degree to which these differences are projected to
875 increase with increasing climatic warming becomes more pronounced with reduction of the
876 buffering effect of the forest canopy, which may be expected under increasing rates of forest
877 disturbance (Dobrowski et al. 2015, Wolf et al. 2021). Even in the absence of triggering events,
878 changes in mean, variance, and seasonality of climate parameters can drive widespread type
879 conversion (Williams et al. 2007, Nolan et al. 2018).

880

881 **5. Management Implications**

882 In this synthesis, we have outlined a range of ecological resilience processes and associated
883 mechanisms leading to persistence, recovery, and reorganization. These phases are dynamic and
884 can occur at the scale of individuals, populations, and communities, occurring synchronously or
885 asynchronously within and among stands. Land managers are tasked to maintain the integrity of
886 ecosystems as dynamic entities, but there is currently no clear roadmap for how to manage these
887 trajectories, nor what the objectives should be in a rapidly changing world. Managers are
888 challenged to recognize the history of an area, including how it was managed by Indigenous
889 peoples, what were its historical keystone processes, when and how these may have been
890 interrupted, and what has transpired since then to promote or erode resilience, including logging,
891 development, wildfire, and post-fire management. Understanding these influences on present
892 ecosystem conditions, and how they direct a range of potential trajectories in composition and

893 structure, is vital to devising strategies that steer ecosystem trajectories toward a desired
894 condition (Chazdon et al. 2021). Management actions can be undertaken at any point along this
895 sequence of resilience, and can be targeted toward a single species, groups of species (e.g., a
896 particular plant functional group), or the community as a whole.

897 Forest management has long emphasized managing for persistence through restoration efforts
898 aimed toward historical conditions (Stoddard et al. 2021). As large and severe disturbances such
899 as droughts and fire have become more common and extensive, greater emphasis has been
900 placed on post-disturbance recovery efforts to reverse these changes. However, in many cases
901 recovery efforts are challenged by increasingly stressful environmental conditions and/or
902 economic restraints and agency mandates (Guiterman et al. *in rev.*), or long-term changes to
903 ecosystem function and disturbance regimes, such as mesophication of forests in eastern North
904 America (Nowacki and Abrams 2008). Past fire management practices in many forests have
905 distorted historical fire regimes through fire exclusion, such that fuel accumulation now makes it
906 less likely that even fire-adapted trees will be able to regenerate and persist over large areas of
907 high-severity fire (Keeley 2009, Stephens et al. 2018, Hagemann et al. 2021, Hagemann et al.
908 2022). In many areas where non-native grasses have established (Balch et al. 2013), changes can
909 be so difficult to reverse that accepting alternative states may be the only viable pathway (Hobbs
910 et al. 2006, Kerns et al. 2020, Lynch et al. 2021). These factors are already driving managers to
911 consider alternative states as potential management objectives. In the sections that follow, we
912 outline some modes of management that align with the primary resilience processes, explored
913 further in a companion article by Guiterman et al. (*in rev.*) as well as other recent work
914 (Schuurman et al. 2020, Lynch et al. 2021).

915 *5.1 Managing for persistence*

916 Managing for persistence takes advantage of the adaptation of species capacity to tolerate
917 disturbance without major change. Persistence is often assumed to be the preferred means of
918 maintaining ecosystem services, is usually the most socially acceptable, and may be mandated by
919 land-management agencies (Lynch et al. 2021). Fuel treatments can reduce the risk of mortality
920 due to fire (Stephens and Moghaddas 2005, Prichard and Kennedy 2012) and/or drought (van
921 Mantgem et al. 2016, Restaino et al. 2019), and help post-disturbance communities to align more
922 closely with the historical range of variation (Young et al. 2019a, Prichard et al. 2021). Stand

923 density or basal area reduction may also assist areas adapting to the drier and warmer climate
924 projected for coming decades (Young et al. 2019b, Tepley et al. 2020). These areas should also
925 be able to support recurrent low- to moderate-severity fire, thus enabling persistence of keystone
926 disturbance processes (Huffman et al. 2020). Especially at the warm/dry ecotone (Parks et al.
927 2019), greater moisture stress among dominant conifers (Allen and Breshears 1998, van
928 Mantgem et al. 2009) could leave fewer large, old trees to maintain desired stand structure and
929 composition.

930 Traditionally, persistence measures have focused on restoring historical conditions or dynamics
931 (Falk 1990, Reynolds et al. 2013). Recent emphasis has included resisting changes in highly
932 valued, culturally important areas and/or landscape refugia, and developing greater landscape
933 heterogeneity through a mix of management practices. Refugia provide multiple benefits to
934 sustaining biodiversity and promoting long-term recovery; often a stochastic result of
935 heterogeneity in landform, hydrology, forest structure and composition, and recurrent fire,
936 refugia can be created strategically ahead of disturbance through localized management actions
937 to enhance persistence (Michalak et al. 2018, Krawchuk et al. 2020, Doxa et al. 2022). Another
938 important strategy to generate a diverse mosaic across many landscapes is to reinstate or emulate
939 indigenous fire use (Kimmerer and Lake 2001). Small-scale, frequent burning that was common
940 historically among many indigenous communities in North America (and has been returned to
941 some areas) limits the intensity and spread of wildfires through fuel reduction, aiding in the
942 persistence of overstory structure and composition (Lake et al. 2017, Roos et al. 2021).
943 Managing at large spatial scales, taking advantage of resilience mechanisms among species and
944 communities, integrating indigenous styles of management through collaborations with
945 knowledge-keepers, and utilizing the refugia of past disturbances can help to promote persistence
946 in the face of extreme events and changing baseline climate conditions (Stevens et al. 2021).

947 *5.2 Managing for recovery*

948 As more forested area is affected by large and severe disturbance, management is turning
949 increasingly toward recovery efforts to recoup potential losses to resources and values.
950 Optimizing recovery following major disturbance draws on the deep knowledge of land
951 managers to initiate and facilitate recruitment and colonization of desired pre-disturbance
952 dominant species through various species- and site-level strategies. Natural regeneration of seed-

953 obligate species can occur relatively quickly on some sites when conditions are favorable
954 (Figures 5, 6, S-1) (Harvey et al. 2016, Tepley et al. 2017, Urza and Sibold 2017). Forest
955 managers can often anticipate the trajectory of a stand based on initial post-disturbance
956 vegetation. For example, initial dominance of shrubs with little tree regeneration may indicate
957 that a site may remain shrub-dominated for decades or longer (Airey Lauvaux et al. 2016,
958 Guiterman et al. 2018). One of the primary indicators of likely recovery failure following
959 disturbance is the absence of a nearby seed source for the previously dominant species (§4.3
960 *Recolonization failure*). New tools allow managers to predict conifer re-establishment (or lack
961 thereof) following fire (Stewart et al. 2021, Tubbesing et al. 2021), and the success of post-fire
962 tree planting relative to natural tree establishment based on residual tree seed source maps and
963 other environmental variables.

964 The spatial scale of the recovery site is critical, because smaller sites may have adequate parent
965 trees nearby (within ~60-100 m), alleviating the need for planting (Ouzts et al. 2015, Owen et al.
966 2017, Stevens-Rumann and Morgan 2019). Site conditions following high-severity fire, in
967 particular, can be challenging for regeneration (Feddemma et al. 2013), especially in large patches
968 ($10^3 - 10^4$ ha) or following salvage operations (Lindenmayer et al. 2012). Analysis of the spatial
969 arrangement of refugia as a seed source and other environmental conditions can highlight areas
970 that may require planting in order for pre-disturbance species to recover rapidly (Stevens-
971 Rumann and Morgan 2019, Stevens et al. 2021, Stewart et al. 2021). North et al. (2019)
972 introduced a zonal framework for post-disturbance reforestation efforts that includes utilizing
973 selective planting locations to establish “founder stands.” This may be effective because it (i)
974 capitalizes on advantageous conditions for seedlings from variability in soil moisture and
975 topography (Rother and Veblen 2016), and (ii) does not require the extensive resources needed
976 for continuous planting of a large area. Residual or newly accumulated fuel loads following
977 high-severity fire or other disturbances may be high, which can both facilitate regeneration by
978 providing moisture retention while also posing a threat to recovery if the site should burn again
979 (Keyser et al. 2020). Seeds for focal reforestation species can be obtained from non-local
980 ecotypes believed to be better adapted to the new conditions at the planting site (Aitken and
981 Bemmels 2016, Young et al. 2020).

982 *5.3 Managing reorganization*

983 The capacity of a system to reorganize is an expression of ecological resilience in the face of
984 changing conditions. In some cases, reorganization may benefit both the ecosystem and society.
985 For example, pushing a site toward a non-forest state could be an act of restoration, as in the case
986 of montane meadows encroached upon by conifers (Matonis and Binkley 2018). However, in
987 other cases sites may reorganize into less desirable conditions, such as shrublands in formerly
988 forested areas, which could persist for centuries (Guiterman et al. 2018). At broader spatial
989 scales, diverse landscape mosaics appear to have been characteristic of resilient ecosystems
990 under historical conditions, creating a complex balance among the forces of soils, climate, and
991 disturbance (Hessburg et al. 1999, Cansler et al. 2018). In recent years, uncharacteristically large
992 and/or severe wildfire events have affected landscape forest structure, triggering transitions
993 across large areas; it remains unclear whether these events will enhance landscape diversity and
994 resilience, or erode it. Anticipating major transitions could help increase chances of success,
995 enhance the resilience of refugia areas, and protect ecosystem services (Millar and Stephenson
996 2015). Promoting a diverse landscape-scale mosaic of forest, shrubland, and grassland ahead of
997 major disturbance events including wildfire can moderate changes associated with widespread
998 vegetation type conversion (Lynch et al. 2021, Stevens et al. 2021).

999 In many areas of western North America, extensive transitions are already underway, including
1000 chaparral, sagebrush, and desert systems converting to non-native grasses, and many forests
1001 converting to shrublands (Guiterman et al. *in rev.*). Type conversions are now a common
1002 consequence of anthropogenic stressors on ecological communities (Stevens-Rumann et al. 2018,
1003 Batllori et al. 2020, Coop et al. 2020). Managing these areas is challenging due to the frequency
1004 and spatial scale of change, with limited funding or social support to attempt large-scale
1005 recovery. Moreover, managers can be overwhelmed by uncertainties regarding the trajectory of
1006 natural recovery, efficacy of recovery efforts (many of which may fail or are experimental), or
1007 whether there is social license to introduce species that could be more tolerant of emerging
1008 conditions. In many areas, these hurdles have slowed or stalled management actions in type-
1009 converted areas, with the result that active management may occur on only a relatively small
1010 fraction of affected areas (Guiterman et al. *in rev.*). In cases where persistence and recovery are
1011 unlikely and reorganization is inevitable, managers could view this as an opportunity to direct
1012 reorganization toward a more desirable future state, instead of as a strictly negative outcome.

1013 Given the frequency and scale of type conversions across western North America, further
1014 research is needed to resolve uncertainties by documenting successes and failures. Experiments
1015 and trials present key opportunities for co-production between scientists and managers
1016 (Krawchuk et al. 2020), and avenues to apply indigenous knowledge of long-term ecosystem
1017 resilience. Resilience frameworks described here and elsewhere (Schuurman et al. 2020, Lynch
1018 et al. 2021) can offer crucial guidelines and for planning and decision making in an era of
1019 widespread and rapid ecological change.

1020

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1920

Falk et al., Mechanisms of forest resilience

Figure captions

Figure 1. A unified framework for ecological resilience. Individuals persist through levels of disturbance to which they are adapted, but mortality occurs when these thresholds are exceeded. Recovery is a population-level process that requires establishment of new individuals from seed or other propagules following dispersal from a parent plant, eventually creating a new replacement population. When recovery fails or is impaired, community-level reorganization occurs, involving different species or functional groups. Reorganization can be transient, leading to eventual re-establishment of the pre-disturbance community, or leading to alternative metastable states that are reinforced by disturbance and/or climate.

Figure 2. Anatomical adaptations to resisting effects of fire include (a) lifted crowns (*Pinus ponderosa* Douglas ex D. Lawson, Valles Caldera National Preserve, New Mexico, USA, and (b) thick heat-resistant bark in *P. sylvestris* L., Mongolia). Photos: PM Brown, Rocky Mountain Tree-Ring Research.

Figure 3. A. Silverleaf oak (*Quercus hypoleucoides* A. Camus) basal resprouting one year after 2020 Bighorn Fire, Coronado NF, Arizona, USA. Photo JR Malusa, University of Arizona. B. Epicormic resprouting in *Eucalyptus* L'Her. 11 months after the 2009 Victoria fires. Photo: JE Keeley.

Figure 4. Post-fire reproduction of serotinous species. Left: knobcone pine (*P. attenuata* Lemmon), Mendocino National Forest, California USA. Photo: DJN Young. Right: interior Lodgepole pine (*P. contorta* var. *latifolia* Engelm.), following 2016 Cold Springs Fire, Arapaho-Roosevelt NF, Colorado, USA. Photo: C Rhoades, Rocky Mountain Research Station, US Forest Service.

Figure 5. Dense post-disturbance *P. ponderosa* seedling recruitment. Monument Canyon Research Natural Area, Santa Fe National Forest, NM. Photo: DA Falk.

Figure 6. Severity map of the 2007 Moonlight Fire, Plumas National Forest, California, USA. Severity is indicated by colors: red indicates high severity (75-100 % overstory mortality); yellow, light and dark green indicate moderate, low, and unburned areas respectively within the fire perimeter. The five pairs of concentric circles show dispersal radii of 60 m and 300 m around 5 hypothetical residual trees. The inset map shows the location of the severity map within the state of California. Severity map from MTBS (www.mtbs.org).

Figure 7. Climate space for the persistence and recruitment niches, in axes of minimum growing season soil water potential and maximum growing season temperature. The climate space for established trees (E_0) is broader than the recruitment niche (R), which is limited to the cooler, more mesic conditions within E_0 . Projections of future climate (E_1) are moving toward warmer, drier conditions, potentially problematic for seedling and sapling growth stages.

Figure 8. Intense competition may inhibit successful establishment of prior dominant species. Dense post-fire *Quercus gambellii* Liebm. thicket, Sandia Mountains, Cibola National Forest, NM, USA. Photo: DA Falk.

Figure 9. Shade-tolerant conifer recruitment in the understory a century after stand-replacing fire, indicating transient reorganization. The overstory is currently dominated by aspen (*Populus tremuloides* Michx.) that initiated post-fire from basal sprouts. San Francisco Peaks, Coconino NF, Arizona, USA. Photo: DA Falk.

Figure 10. Observations of post-fire ecological reorganization with varying degrees of persistence involving plants of four different functional groups: (upper left) dense post-fire growth of bracken fern (*Pteridium aquilinum* (L.) Kuhn) nine years post-fire in a previous mixed-conifer stand, Chiricahua Mountains, Coronado NF, Arizona, USA. Photo: DA Falk; (upper right) bunchgrass post-fire dominance of previous dry conifer stand nine years post-fire, Chiricahua Mountains, Coronado NF, Arizona, USA. Photo: DA Falk; (lower left) *Ceanothus velutinus* Douglas dominance of former mixed-conifer forest 11 years after the 2007 Moonlight Fire, Plumas NF, California, USA. Photo: DJN Young; (lower right) conversion of conifer (Douglas-fir, white fir) forest to mixed species hardwood-shrub dominated forest, Klamath NF, California, USA 14 years after the 2001 Happy Camp Complex. Photo: AJ Tepley.

Figure 11. Mechanisms of ecological reorganization. Abrupt reorganization typically follows a triggering climatic or disturbance event leading to extensive mortality. If climate and subsequent disturbance constrain recovery, community reassembly processes may result in an alternative metastable state, which is reinforced by the new climate and disturbance regime. See text for details.

Figure 12. “Suspended succession” 20 years post-fire at Devil’s Postpile National Monument, California, USA. Photo: Sequoia-Kings Canyon National Park Fire Effects Program, National Park Service.

Figure 13. Forest-shrubland conversion 28 years after the 1989 Layman Fire, Plumas NF, California, USA. *Ceanothus velutinus* dominance of former Jeffrey pine-white fir forest. Photo: DJN Young.

Figure S1. Density of post-fire recruiting tree seedlings (trees m⁻², all species) as a function of distance to the nearest surviving reproductive tree in plots surveyed 4-5 years following fires in yellow pine and mixed-conifer forests across California (Welch et al. 2016, Young et al. 2019).

Figure S2. Chaparral-grassland conversion, southern CA. Photo A Jacobsen, courtesy A Syphard, Conservation Biology Institute.

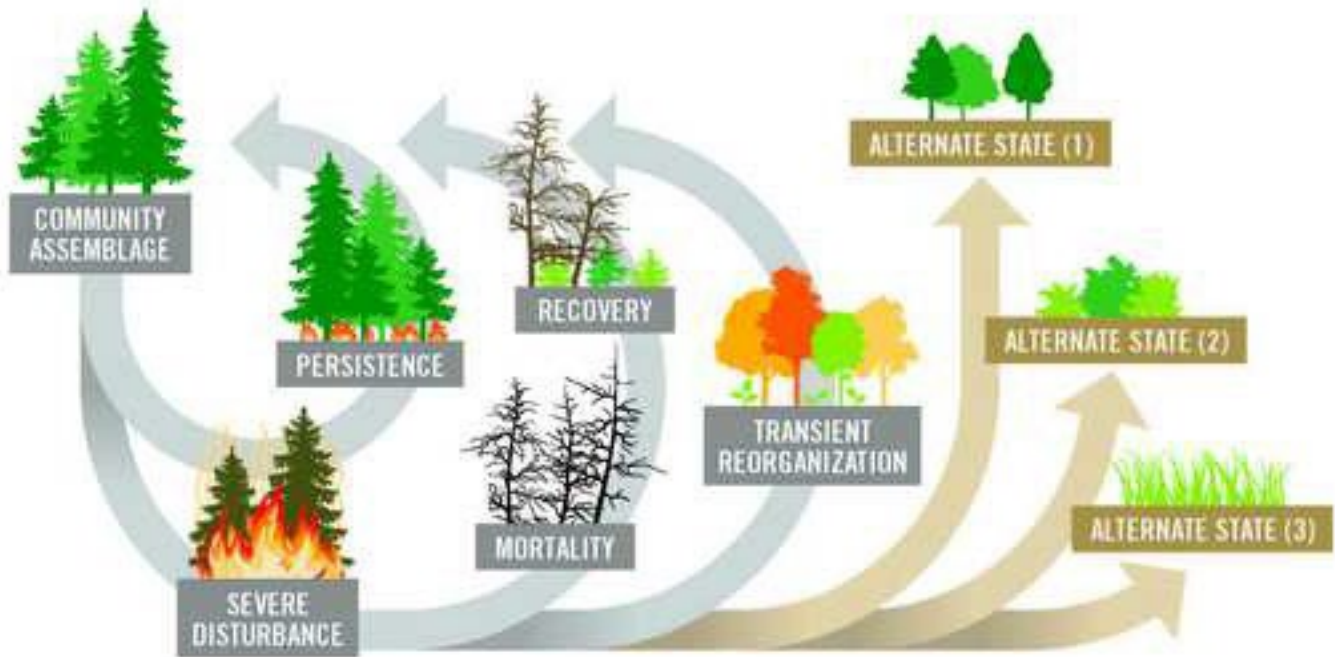


Figure 2.a, b



Figure 3.



Figure 4.



Figure 5.



Figure 6

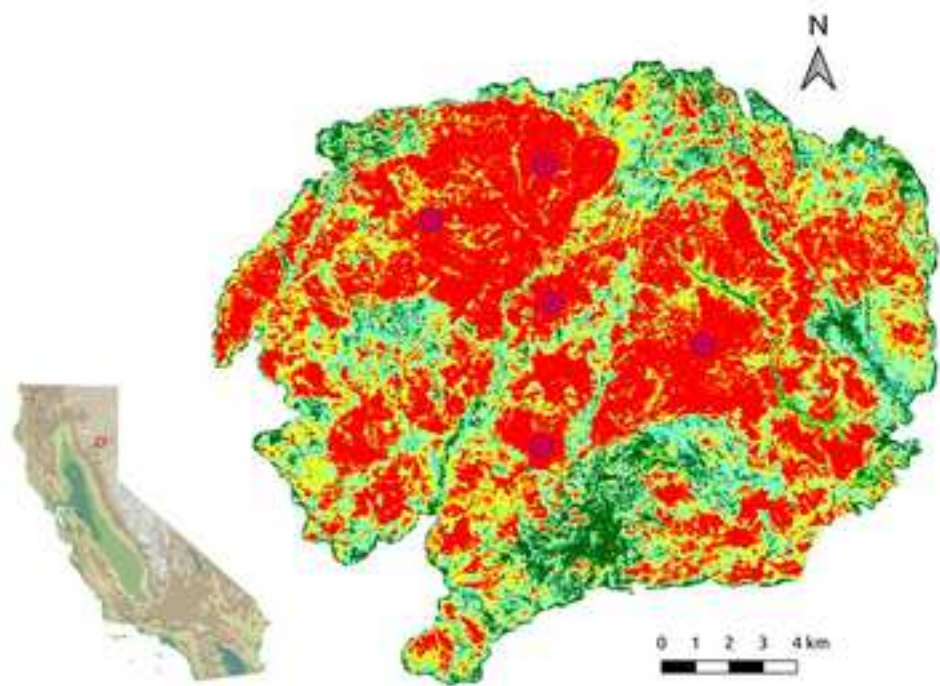


Figure 7.

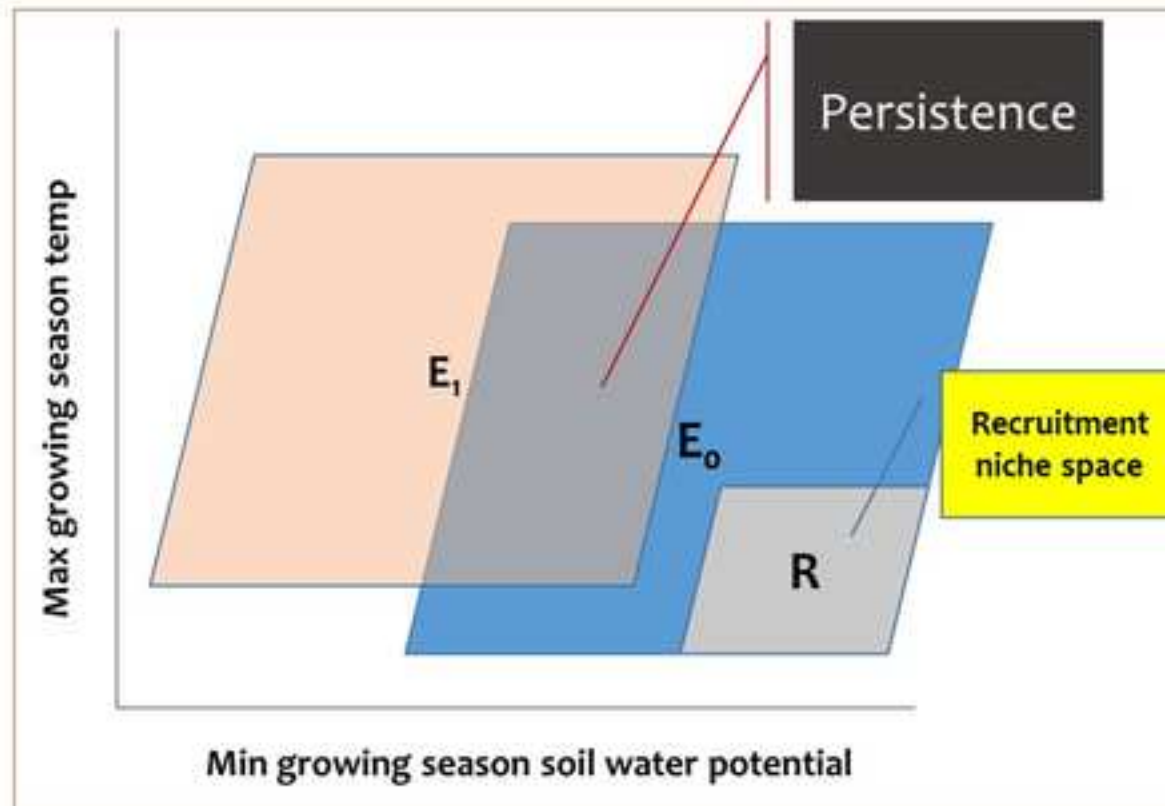


Figure 8.



Figure 9.



Figure 10.





Figure 12



Figure 13.



Figure S1.

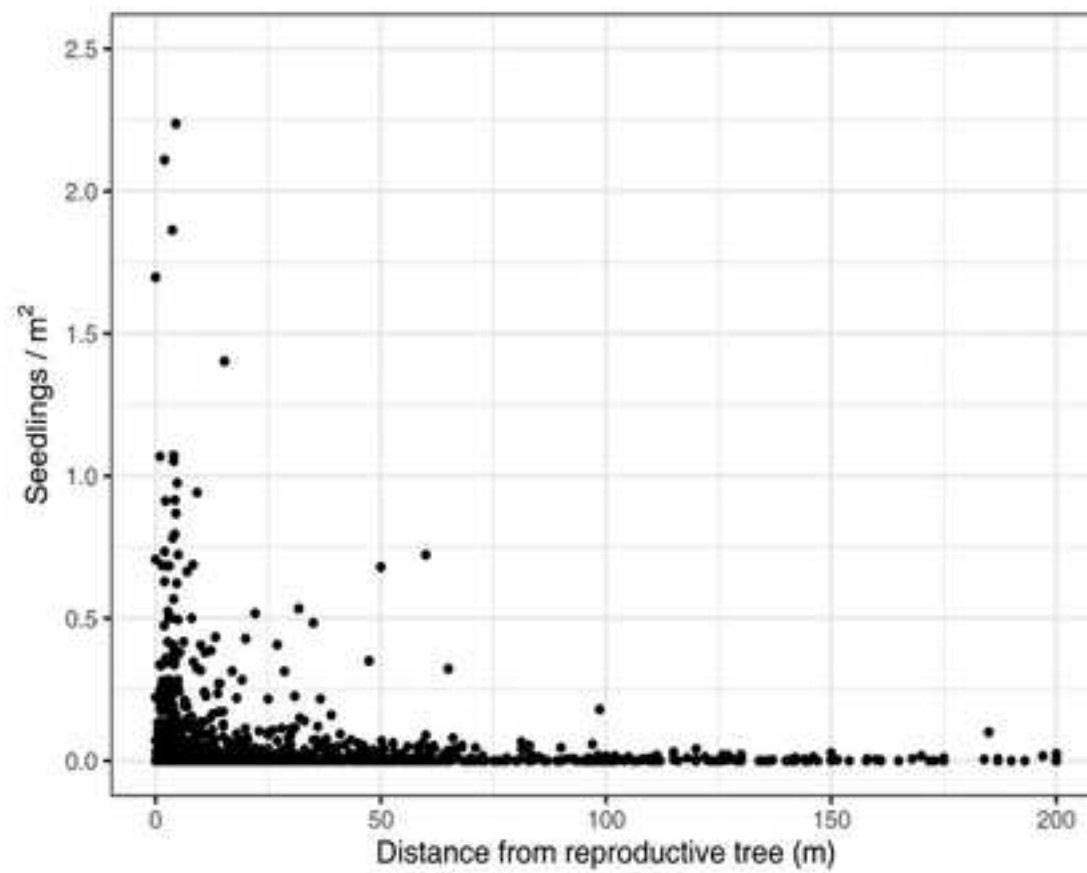




Figure S2.

Outcome (level of organization)	Process	Mechanisms
Persistence (individual)	Anatomical and physiological resistance to heat exposure from fire	Thick bark insulates cambium cells from heat flux, preventing necrosis; abscission of lower branches prevents spreading combustion into canopy
	Wound responses to fire damage	Wound compartmentalization prevents infection of lesions and damaged tissue; growth closure repairs cambial continuity
	Vegetative regrowth capabilities	Basal and epicormic resprouting capacity; non-structural carbohydrate storage and mobilization
	Drought survival, maintenance of essential functions	Plant hydraulic traits prevent xylem cavitation and embolisms; isohydric and anisohydric stomatal regulation
Recovery (population)	Post-fire propagules from <i>in situ</i> sources	Recruitment from soil and canopy seed banks, advance regeneration. Heat- and smoke-cued germination.
	Post-fire dispersing propagules	Wind-, gravity-, and animal-mediated seed dispersal from nearby unburned areas or refugia; continued seed rain
	Germination, seedling survivorship, and growth	Species-specific seed and seedling climate envelopes and microhabitat; post-disturbance weather; rooting access to mineral soil
	Interspecific and community interactions	Interspecific interactions may facilitate (e.g. amelioration of microclimate) or inhibit (resource competition) seedling and sapling survivorship and growth; interactions may be temporally variable
Reorganization (community)	Gradual reorganization in response to changes in mean conditions	Shifting species geographic ranges during periods of rapid climate change
	Reorganization in response to the loss of formerly frequent disturbance	Increased relative abundance of mesophytic species in deciduous forests, increased forest density in dry conifer forests following fire exclusion; conversion of grasslands and savannahs to closed-canopy woodlands
	Rapid reorganization in response to novel disturbance	Forest loss from extensive tree mortality, followed by recruitment failure
	Trigger events	Mortality over large contiguous areas from uncharacteristically high-severity wildfire in ecosystems adapted to frequent low-severity fire regimes. Widespread forest die-off from extended drought and episodic heat waves and associated insect outbreaks.
		Recruitment failure in fire-tolerant and serotinous forests and chaparral due to uncharacteristically short fire return intervals
	Open resource space following extensive mortality	Shuffling of species relative dominance based on plant functional capacity (resprouting, obligate seed recruitment) and disturbance-cued germination Dispersal limitations in large high-severity patches beyond seed dispersal distance; germination failure of dispersed seed in severely altered post-fire environments (soil, microclimate, microbial symbionts); short fire return intervals
	Recolonization failure	
	Landscape species pool	Pre-disturbance species depend on dispersal from limited remaining refugia; rapid dispersing and early successional species able to establish in post-fire environment
	Community reassembly, hysteresis	Interactions among species colonizing the post-disturbance environment through biotic and abiotic filters, leading to novel community assemblages and potential alternative metastable state
Reinforcing feedbacks	Invasion of non-native annual grasses into woody communities when fire regimes are perturbed, leading to conversion to persistent novel grass-fire cycle. Soil and hydrological alteration prevents recolonization	
	Climate trends (temperature, precipitation, VPD) and episodes (e.g. heat waves) prevent recruitment of prior dominant species and favor better adapted species, creating novel community assemblages	

Table 1. Main components of resilience operating at varying levels of biological organization, primary processes, and key mechanisms of ecological resilience. Literature references provided in main text.

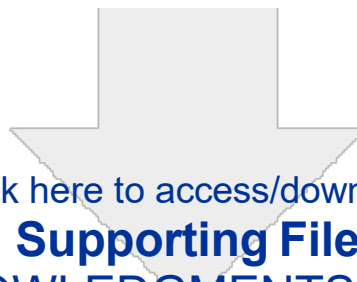
Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Falk et al, Tamm Review: Draft author contributions

PVM, DAF and JEK secured funding for the project. DAF, PVM, JEK, and RMG conceived the paper. All authors contributed to writing, review, and editing. DAF supervised final editing of the manuscript.



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