

1 Title: **Drought legacies and ecosystem responses to subsequent drought**

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3 **Running head:** Drought legacy review

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11 **Abstract**

12 Climate change is expected to increase the frequency and severity of droughts. These events, which
13 can cause significant perturbations of terrestrial ecosystems and potentially long-term impacts on
14 ecosystem structure and functioning after the drought has subsided are often called ‘drought legacies’.
15 While the immediate effects of drought on ecosystems have been comparatively well characterized,
16 our broader understanding of drought legacies is just emerging. Drought legacies can relate to all
17 aspects of ecosystem structure and functioning, involving changes at the species and the community
18 scale as well as alterations of soil properties. This has consequences for ecosystem responses to
19 subsequent drought. Here, we synthesize current knowledge on drought legacies and the underlying
20 mechanisms. We highlight the relevance of legacy duration to different ecosystem processes using
21 examples of carbon cycling and community composition. We present hypotheses characterizing how
22 intrinsic (i.e. biotic and abiotic properties and processes) and extrinsic (i.e. drought timing, severity,
23 and frequency) factors could alter resilience trajectories under scenarios of recurrent drought events.
24 We propose ways for improving our understanding of drought legacies and their implications for
25 subsequent drought events, needed to assess the longer-term consequences of droughts on
26 ecosystem structure and functioning.

27

28 **Key words:** drought legacy, drought recovery, drought response, lagged effects, legacy duration, post-

29 drought state, recurrent drought, resilience

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30 1. Introduction

31 Climate change has been and will likely be causing a significant increase in the severity and frequency
32 of drought events (Trenberth *et al.* 2014; Spinoni *et al.* 2018; IPCC 2021) with strong repercussions on
33 ecosystem processes and services (Ciais *et al.* 2005; Reichstein *et al.* 2013; Thonicke *et al.* 2020;
34 Vicente-Serrano *et al.* 2020; Bastos *et al.* 2020; Feeley *et al.* 2020). In addition to the concurrent effects
35 of drought events on ecosystems, manifold changes can persist after the drought has subsided (Frank
36 *et al.* 2015). These post-drought effects are commonly referred to as “drought legacies” (Vilonen *et al.*
37 2022) and have been demonstrated for various aspects of ecosystem structure and functioning.
38 Drought legacy effects have been associated with altered carbon (C) cycling (Scott *et al.* 2010; Craine
39 *et al.* 2013; Xie *et al.* 2020; Kannenberg *et al.* 2020; Wei *et al.* 2022; Liu *et al.* 2022), nitrogen (N) cycling
40 (DeVries *et al.* 2012; Legay *et al.* 2018; DeLong *et al.* 2019), growth (Anderegg *et al.* 2015b; Wu *et al.*
41 2018; Zhao *et al.* 2020; Gazol *et al.* 2020), phenology (Kang *et al.* 2018; Sippel *et al.* 2018; Peng *et al.*
42 2019; Berwaers *et al.* 2019; Zeng *et al.* 2021; Hoover *et al.* 2021), species composition (Stampfli *et al.*
43 2018; DeBoeck *et al.* 2018; Griffin-Nolan *et al.* 2019; Winkler *et al.* 2019; Stampfli & Zeiter 2020),
44 herbivory (Gutbrodt *et al.* 2011) as well as soil physicochemical properties (Goebel *et al.* 2011;
45 Sánchez-García *et al.* 2019). Drought legacies have also been associated with increased plant mortality
46 (Bigler *et al.* 2007; Trugman *et al.* 2018; Hartmann *et al.* 2018; Sippel *et al.* 2018; Zhou *et al.* 2019;
47 Hammond 2020), and with reduced plant defence against pests and pathogens (Jactel *et al.* 2012;
48 Wiley *et al.* 2016; Trugman *et al.* 2021).

49 All these biotic and abiotic legacies from species to ecosystem scale are summarized below and
50 referred to as legacies in intrinsic factors. In addition to these intrinsic factors a range of extrinsic
51 factors, including drought *timing*, drought *severity* (intensity and duration), and drought *frequency* can
52 affect drought legacies.

53 Although the relevance of drought legacies for a longer-term perspective on ecosystem resilience (the
54 resistance to and recovery from subsequent drought events (Lloret *et al.* 2011; Ingrisich & Bahn 2018)
55 has been increasingly acknowledged in recent years (Anderegg *et al.* 2020; DeSoto *et al.* 2020; Canarini

56 *et al.* 2021; Hahn *et al.* 2021), our understanding of drought legacies and the underlying processes is
57 still restricted to a few case studies or specific aspects of plant and ecosystem functioning, such as
58 radial tree growth (see Fig. S1) (Kannenberg *et al.* 2019b; Kannenberg *et al.* 2020; Gazol *et al.* 2020).
59 Hence, we still lack a clear understanding of how drought legacies alter the resilience of ecosystems to
60 subsequent drought events. This is of particular relevance given that drought frequency is likely to
61 increase in the coming decades (Wang *et al.* 2021b; IPCC 2021).
62 This review aims to i) synthesize our current understanding of drought legacies and the underlying
63 mechanisms from species and communities to ecosystem (biotic and abiotic) scale and ii) summarize
64 the legacy duration of previously documented drought legacy responses. Furthermore, we iii) develop
65 hypotheses as to how drought legacies could influence the resilience trajectories of ecosystem
66 responses to subsequent drought events.

67

68 **2. Defining and characterizing drought legacies**

69 Drought legacies are commonly defined as any alterations of an ecosystem state or processes that
70 occur after a drought has subsided (Sala *et al.* 2012; Rousk *et al.* 2013; Walter *et al.* 2013; DeBoeck *et*
71 *al.* 2018; Griffin-Nolan *et al.* 2018; Buttlar *et al.* 2018; Delgado-Balbuena *et al.* 2019; Vilonen *et al.*
72 2022). They refer to changes of intrinsic factors after a disturbance event (see material legacies
73 (Johnstone *et al.* 2016)) compared to evolutionary adaptations to historical disturbance regimes (see
74 information legacies (Johnstone *et al.* 2016)). Drought legacies can involve both reductions and
75 enhancements in response parameters (Sala *et al.* 2012; Frank *et al.* 2015; Griffin-Nolan *et al.* 2018).
76 Next to the term 'drought legacy' several other terms have been used in the literature, including
77 'lagged effects' (Zhao *et al.* 2018), 'stress imprint' (Bruce *et al.* 2007), 'stress memory' (Walter *et al.*
78 2013; Fleta-Soriano & Munné-Bosch 2016) or 'drought memory' (Walter *et al.* 2011; Ogle *et al.* 2015;
79 Canarini *et al.* 2021) (for a broader discussion see also (Vilonen *et al.* 2022)).

80 In this paper we use the term drought legacy to describe any shift in ecosystem properties or processes
81 after a drought has subsided (Fig. 1). Thus, drought legacies include both the recovery phase after the

82 drought has ended and the post-recovery phase, in the case of incomplete recovery (Fig.1). The
83 recovery phase is characterized by the rate of recovery (arrow 2) following the maximum impact of the
84 drought event (arrow 1). The post-recovery phase starts when the rate of recovery levels off (arrow
85 3), and the recovery is complete (yellow trajectory, no legacy) or incomplete, i.e. the baseline has been
86 shifted (red and blue trajectories, legacy). These shifts can occur on all organizational scales, including
87 species-, community- and / or ecosystem (Fig. 2).

88 Given that the ecosystem state changes dynamically during the recovery phase, the most coherent
89 approach to quantifying and comparing drought legacies would be to compare the ecosystem post-
90 recovery state with the baseline state (see below) (Fig. 1). However, this may be difficult to achieve in
91 cases when recovery rates are difficult to quantify, e.g. due to insufficient time resolution for assessing
92 recovery dynamics or to intrinsic factors which recover very slowly, e.g. community properties which
93 can take years or decades to recover fully (Albertson & Weaver 1944; Stampfli & Zeiter 2004).

94 To date, different baselines of an ecosystem state, such as pre-disturbance level (Gazol *et al.* 2020),
95 control (Yahdjian & Sala 2006; Arredondo *et al.* 2016; DeBoeck *et al.* 2018; Mackie *et al.* 2019), or
96 predicted level (Anderegg *et al.* 2015b; Peltier *et al.* 2016; Wu *et al.* 2018; Delgado-Balbuena *et al.*
97 2019) have been used to characterize drought legacies. We suggest a characterization of drought
98 legacies post-drought or, if possible, post-recovery via the legacy duration (arrow 5) and the legacy
99 size (deviation from the pre-drought, control, or the predicted baseline (arrow 4)). While we
100 acknowledge that pre- and post-drought baselines can fluctuate strongly over time (Bahn & Ingrisch
101 2018), we suggest that such a characterization can enhance comparability of drought legacies across
102 ecosystems and response parameters in future studies, especially when combined with a consistent
103 design of drought studies (Slette *et al.* 2019; Munson *et al.* 2020).

104 Given that drought legacies may have strong repercussions on ecosystem responses to subsequent
105 droughts, we argue that a drought legacy should consider the whole timespan during which the
106 ecosystem state and its responses to environmental conditions, including a subsequent drought, are
107 altered by a drought event (see also section 5).

108

109 3. Drought legacies and the underlying mechanisms at species-, community- and ecosystem 110 scale

111 Drought can have long lasting effects on intrinsic factors from species-, community-, to ecosystem scale
112 (see Fig. 2 and below). The legacy size and duration of these intrinsic factors can be affected by a range
113 of extrinsic factors, including drought timing, drought severity (intensity and duration), and drought
114 frequency. For example, drought *timing* can alter growth legacies in forests, such that the legacy size
115 is higher in the later (Kannenber *et al.* 2019a) or drier part of the growing season (Huang *et al.* 2018).
116 In grasslands, the effects of drought *timing* on the size of growth legacies increase the later the drought
117 occurs in the season (Hahn *et al.* 2021). Also drought *intensity* impacts the legacy size, which increases
118 with increasing drought intensity (Yahdjian & Sala 2006; Kannenberg *et al.* 2019a). Furthermore, a
119 longer drought *duration* was observed to also enhance legacy duration (Jiao *et al.* 2021). Moreover,
120 there is increasing evidence that ecosystem responses to drought *intensity* and *duration* are nonlinear
121 during drought (Dannenberg *et al.* 2019; Zhang *et al.* 2021; Wang *et al.* 2021a; Felton *et al.* 2021), with
122 potential consequences for drought legacies, though these remain to be explored.

123 In the following, we provide an overview of post-drought legacies and the underlying mechanisms from
124 species- to community- and ecosystem scale (broadly summarized in Fig. 2).

125

126 Species scale

127 Drought can lead to a range of **structural** changes on the species scale. For example, in grasslands
128 drought can decrease the tiller and stolon density, with consequences for ecosystem productivity
129 (Reichmann *et al.* 2013; Reichmann & Sala 2014; Delgado-Balbuena *et al.* 2019). Moreover, drought
130 can reduce belowground bud density (Qian *et al.* 2022) as well as reproductive output with
131 consequences for grassland community composition (Zeiter *et al.* 2016). Furthermore, drought can
132 increase the number of seeds and decrease the number of leaves (Metz *et al.* 2020). Moreover,
133 drought can induce a shift towards resource-conservative root traits such as lower specific root length

134 (DeVries *et al.* 2016) and can increase community-weighted plant traits such as specific leaf area and
135 leaf N content, which reflects a shift towards communities with drought avoidance and escape
136 strategies (Griffin-Nolan *et al.* 2019). After recovery from drought, increased shoot, root, and tissue N
137 concentrations of herbaceous species have often been observed, which is probably due to higher post-
138 drought N availability (see also ecosystem section below) (Roy *et al.* 2016; Ingrisch *et al.* 2018; DeLong
139 *et al.* 2019). In forests, drought can lead to structural changes such as a decrease in active xylem area,
140 as well as needle shedding or canopy loss (Peltier & Ogle 2019).

141 On a **physiological** level, drought can alter the growth rate of species across plant functional types,
142 and as a result, legacy effects can be positive or negative (DeVries *et al.* 2012; Darenova *et al.* 2017;
143 Itter *et al.* 2019; Peltier & Ogle 2019; Kannenberg *et al.* 2019b; Kannenberg *et al.* 2020; Li *et al.* 2020;
144 Zhao *et al.* 2020). Drought legacies of tree ring studies predominantly suggest negative effects on
145 growth (Anderegg *et al.* 2015b; Kannenberg *et al.* 2020). In trees, post-drought reductions of root
146 functioning (Peltier & Ogle 2019) and an altered stomatal sensitivity to soil and plant water status
147 (Grossiord *et al.* 2018) have been observed. Furthermore, drought can alter molecular mechanisms
148 such as pathways of signalling metabolites, transcription factors, or epigenetics involving modifications
149 in DNA, histone, or chromatin organization (Bruce *et al.* 2007; Ding *et al.* 2012; Sahu *et al.* 2013;
150 Kinoshita & Seki 2014; Crisp *et al.* 2016; Alves *et al.* 2020), with consequent structural changes,
151 including short-term changes such as the pigment composition of leaves (Fleta-Soriano & Munné-
152 Bosch 2016).

153 Drought legacies have also been associated with altered **phenology** both of herbaceous and woody
154 species, e.g. earlier end-of-season senescence leading to a shortened growing season (Kang *et al.* 2018;
155 Peng *et al.* 2019; Berwaers *et al.* 2019; Hoover *et al.* 2021). These effects are especially pronounced in
156 regions with generally low water availability (Peng *et al.* 2019). Prior-season drought (Zeng *et al.* 2021)
157 and spring drought (Kang *et al.* 2018) can lead to a delay in the onset of spring growth and hence the
158 start of the growing season, with negative impacts on summer growth rates (Zeng *et al.* 2021). Finally,
159 drought can advance the flowering date and increase the flowering duration. The phenological

160 response can vary depending on the species and the diversity of a stand with potential long-term
161 effects on reproductive fitness (Jentsch *et al.* 2009).

162 **Plant mortality** is a widespread drought legacy with significant consequences for the community and
163 the ecosystem scale. Mortality can occur both during (Choat *et al.* 2018; Jung *et al.* 2020) and after a
164 severe drought event (Bigler *et al.* 2007; Anderegg *et al.* 2013; Frank *et al.* 2015; Anderegg *et al.* 2015a;
165 Schlesinger *et al.* 2016; Trugman *et al.* 2018; Stampfli *et al.* 2018; Sippel *et al.* 2018; Harrison *et al.*
166 2018; Brodribb *et al.* 2020; Trugman *et al.* 2020; Senf *et al.* 2020). Tree mortality has frequently been
167 associated with hydraulic failure, but also C limitation has been discussed as a possible cause in some
168 cases (Gessler *et al.* 2017; Adams *et al.* 2017; Choat *et al.* 2018; McDowell *et al.* 2020; McDowell *et al.*
169 2022). Additionally, lags in soil water replenishment following drought (van der Molen *et al.* 2011) can
170 enhance species mortality (Goulden & Bales 2019). Furthermore, drought often leads to reduced **plant**
171 **defence** against herbivory, pests, and pathogens, which increases the risk of plant mortality in trees
172 and herbaceous species (Gutbrodt *et al.* 2011; Jactel *et al.* 2012; Gaylord *et al.* 2013; Anderegg *et al.*
173 2015a; Kolb *et al.* 2016; Wiley *et al.* 2016; Schlesinger *et al.* 2016; Trugman *et al.* 2021).

174

175 Community scale

176 Drought can exert legacy effects on **plant communities** by reducing species richness (Stampfli *et al.*
177 2018), abundance of specific species (Jung *et al.* 2014; Hoover *et al.* 2014), and diversity (Xu *et al.*
178 2017), but drought has also been shown to increase functional diversity (Griffin-Nolan *et al.* 2019). In
179 grassland exposed to drought, plant composition shifted towards more stress-resistant slower growing
180 species (Wilcox *et al.* 2021). Results of single case studies performed in prairie (Hoover *et al.* 2014) or
181 with alpine grassland mesocosms (DeBoeck *et al.* 2018) suggest that grasses are probably more
182 drought resistant than forbs. In addition to different resistance to drought, community reorganization
183 towards grass domination can also be driven by altered plant-plant interactions, such as competition,
184 with resource-acquisitive grasses dominating at the expense of resource-conservative forbs (Stampfli
185 *et al.* 2018). In contrast, droughts may favour an increase of forbs, which have been suggested to

186 outperform grasses in their capacity to recruit from seed (Stampfli & Zeiter 2004). In grasslands where
187 shrubs are present, they can replace perennial grasses as a response to drought due to their more
188 extensive root systems permitting access to deeper water (Winkler *et al.* 2019).

189 In forests, community reorganization following drought can lead to shifts in dominant tree species and
190 their associated above- and belowground communities, involving a.o. shifts towards more drought
191 tolerant and xeric communities and related traits, and in savannas shifts towards non-woody
192 vegetation (Suarez & Kitzberger 2008; Anderegg *et al.* 2013; Clark *et al.* 2016; Trugman *et al.* 2020;
193 Batllori *et al.* 2020; Brodribb *et al.* 2020). Community shifts can also be species-unspecific, as e.g.
194 mortality is often related to tree density and tree size, irrespective of the species involved (McDowell
195 *et al.* 2020; Brodribb *et al.* 2020; Trugman *et al.* 2020; Cui *et al.* 2022).

196 Drought and rewetting have strong impacts on **soil communities**. Drought can alter species
197 composition and generally tends to decrease the abundance and the richness of **soil fauna** (Lindberg
198 *et al.* 2002; Lindberg & Bengtsson 2006; DeVries *et al.* 2012; Coyle *et al.* 2017). It has recently been
199 shown to also cause legacies in the **microbial community** composition (Kaisermann *et al.* 2017;
200 Meisner *et al.* 2018; Meisner *et al.* 2021; Canarini *et al.* 2021; Liu *et al.* 2022; Evans *et al.* 2022; Xi *et al.*
201 2022). Drought was observed to promote fungi and to reduce bacteria (Fuchslueger *et al.* 2014; Preece
202 *et al.* 2019) and bacterial networks (DeVries *et al.* 2018). Drought can also alter microbial community-
203 level traits, but the magnitude and persistence of such drought legacies is under debate (Wang &
204 Allison 2021). Drought effects on plant-soil feedbacks, which can strongly alter above- and
205 belowground communities, will be discussed in the ecosystem section.

206 Drought-induced changes on the community scale can also be driven by **invasive species**. Generally,
207 when invasive species are already established, they tend to negatively affect plant communities
208 through a loss in plant diversity, shifted community composition, and a dampened recovery capacity
209 of natives from drought (Fahey *et al.* 2018; Vetter *et al.* 2020; Xu *et al.* 2022). In invaded grassland
210 plant communities, drought was observed to impact growth of invasive species less (Meisner *et al.*
211 2013) or more (Valliere *et al.* 2019) compared to native species. When negatively affecting plant

212 growth of invasives, drought can lead to a long lasting reduction in the presence of invasive plants post
213 drought (Kelso *et al.* 2020). The effects of growth and reproduction can be weakened by higher
214 germination rates of seeds of invasive compared to natives species (Valliere *et al.* 2019).

215

216 Ecosystem scale

217 Drought can lead to a range of legacies on the ecosystem scale, which can be driven by changes on
218 species or community scale and can feed back to these scales.

219 Drought can induce pronounced legacy effects on **ecosystem carbon (C) cycling**, e.g. through legacy
220 effects on plant biomass (Yang *et al.* 2018; Wigneron *et al.* 2020) and biomass production. Drought
221 legacy effects on aboveground net primary production (ANPP) can be positive (Griffin-Nolan *et al.*
222 2018) or negative (Sala *et al.* 2012; Petrie *et al.* 2018). Enhanced post-drought growth can compensate
223 for the growth reductions during drought and stabilize overall biomass production (Stampfli *et al.*
224 2018; Mackie *et al.* 2019; Hahn *et al.* 2021). In grasslands, drought legacy effects on ANPP have been
225 associated with tiller recruitment (Reichmann *et al.* 2013; Reichmann & Sala 2014), changes in the
226 composition of species and functional groups (Hoover *et al.* 2014; DeBoeck *et al.* 2018; Gao *et al.* 2021),
227 as well as changes in nutrient availability (DeLong *et al.* 2019; Mackie *et al.* 2019). Drought can also
228 lead to increased (Berwaers *et al.* 2019) or decreased carbon uptake and respiration (Delgado-
229 Balbuena *et al.* 2019), and affect soil respiration (Dong *et al.* 2021; Liu *et al.* 2022). Post-drought
230 changes in microbial biomass or in microbial community-level traits can alter soil C cycling such as soil
231 respiration (Dong *et al.* 2021; Evans *et al.* 2022; Liu *et al.* 2022) and soil organic matter decomposition
232 (Wang & Allison 2021). Furthermore, drought can have a positive or negative legacy effect on water
233 use efficiency (WUE), that is the amount of C taken up relative to the amount of water lost (Yang *et al.*
234 2016; Huang *et al.* 2017; Ji *et al.* 2021). Generally, post-drought changes in WUE last longer for forests
235 (up to one year) than for shrubland and sparse vegetation (up to four months) (Ji *et al.* 2021). In the
236 longer term, changes in plant species composition after a drought event towards drought-tolerant
237 species has been suggested to increase C and water cycling (Craine *et al.* 2013).

238 Drought and rewetting can alter N cycling and the short-term dynamics of **soil N availability**. Upon
239 rewetting, large pulses in nutrient release and N mineralization can occur (Birch 1958; Manzoni *et al.*
240 2012; Leitner *et al.* 2017; Schimel 2018; van Sundert *et al.* 2020). This higher availability of N post-
241 drought was observed to enhance recovery of plant growth in grasslands (Schrama & Bardgett 2016;
242 Roy *et al.* 2016; Ingrisch *et al.* 2018; Karlowisky *et al.* 2018), thereby reducing potential subsequent
243 plant growth legacies. Indeed, an increase in soil N following drought was found to be accompanied in
244 grasslands by higher plant growth and in consequence biomass (DeVries *et al.* 2012; Legay *et al.* 2018;
245 Mackie *et al.* 2019; DeLong *et al.* 2019). In forests, the higher nutrient supply post drought can enhance
246 tree recovery, which strongly depends on the re-establishment of root functions as well as root
247 damage and mortality (Gessler *et al.* 2017). Furthermore, drought-induced effects on roots as well as
248 leaf senescence can affect nutrient status and nutrient demand post-drought (Schlesinger *et al.* 2016).
249 For example, N uptake under drought can be reduced (Joseph *et al.* 2021) and detrimental impacts of
250 drought on K availability can reduce tree resistance to subsequent drought (Touche *et al.* 2022).
251 Post-drought N availability can also be altered by changes in microbial communities (Meisner *et al.*
252 2018). For example, drought can select for microbial communities with a lower capacity to immobilize
253 N which leads, together with lower root N uptake, to higher soil N concentration (DeVries *et al.* 2016).
254 Also drought-related changes in fungi / bacteria ratios can result in altered ecosystem N and C cycling
255 (DeVries *et al.* 2018) and induce possible feedback to plants and alter plant-plant interactions
256 (Kaisermann *et al.* 2017). Furthermore, drought legacy effects on N cycling in grasslands can be induced
257 by a decrease in soil microbial activity post-drought, as microbial enzymatic activities are highly
258 sensitive to drought (Acosta-Martinez *et al.* 2014; Legay *et al.* 2018).
259 A major driver of drought legacies in grasslands is related to drought-induced changes in **plant-soil**
260 **feedbacks** (PSFs), that is the interactions between plants, soil organisms, and abiotic soil factors, which
261 lead to altered plant composition and performance and have cascading effects on ecosystem
262 properties (van der Putten *et al.* 2013; Preece & Peñuelas 2016; van der Putten *et al.* 2016; Peguero *et*
263 *al.* 2019; DeVries *et al.* 2019; Pugnaire *et al.* 2019; Williams & DeVries 2020; Crawford & Hawkes 2020;

264 Buchenau *et al.* 2022). Drought can influence PSFs e.g. via drought-driven changes in the composition
265 of plant species, whose roots interact with the respective symbionts, decomposers, and pathogens
266 (van der Putten *et al.* 2016; Pugnaire *et al.* 2019). Similarly, drought can influence PSFs via changes in
267 belowground community composition (van der Putten *et al.* 2016; Pugnaire *et al.* 2019). Thereby,
268 drought-induced changes in microbial communities can alter the direction and intensity of PSFs with
269 consequences for ecosystem properties, e.g. by positively or negatively affecting plant growth
270 (Kaisermann *et al.* 2017). Drought effects on PSFs can be mediated both in terms of quantity and
271 quality by altered plant inputs in soil, such as litter and rhizodeposition (Kuzyakov 2002; Sánchez-
272 Cañizares *et al.* 2017; Karlowsky *et al.* 2018; Sasse *et al.* 2018; DeVries *et al.* 2019; Williams & DeVries
273 2020). Drought-induced changes of rhizodeposition strongly depend on species identity and drought
274 intensity (Preece & Peñuelas 2016) and can alter nutrient availability through shifts in fungi / bacteria
275 ratios, causing shifts in plant composition (Preece & Peñuelas 2016; Peguero *et al.* 2019). Drought also
276 reduces litter quality and thereby leads to lower mineralization rates. The resulting deceleration of
277 nutrient cycling and the enhancement of fungal dominance in the microbial community in turn can
278 alter plant community composition and favour more drought adapted species (Pugnaire *et al.* 2019).
279 Finally, drought legacies not only affect PSFs between species but also within species, by favoring
280 genotypes within plant species that develop less negative feedback and thereby decreasing
281 intraspecific diversity (Crawford & Hawkes 2020).

282 Drought legacies have been shown to lead to reduced leaf area index in grasslands and forest
283 (Kannenbergh *et al.* 2019b; Jiao *et al.* 2021) and to affect the **canopy structure** (Beloïu *et al.* 2022),
284 driven by changes in species abundance and composition, e.g. in forests subjected to wide-spread
285 mortality (Saatchi *et al.* 2013; Senf *et al.* 2021). Changes in canopy structure can alter **abiotic**
286 ecosystem properties such as light availability and **microclimate**, with consequences for the
287 composition and biodiversity of the understory as well as nutrient and C cycling (Kane *et al.* 2011;
288 Royer *et al.* 2011; Anderegg *et al.* 2012; Anderegg *et al.* 2013). Drought can have a positive or negative
289 legacy effect on soil moisture in grasslands, lasting up to a half year post-drought (Robinson *et al.* 2016;

290 Reinthaler *et al.* 2021; Hoover *et al.* 2021). Positive soil moisture legacies can be driven by a post-
291 drought decrease of species with low drought resistance, which can reduce community-level water
292 demand (Hoover *et al.* 2021). Drought can also cause legacy effects on **soil properties**, by altering the
293 chemical and physical soil structure. Drought has been shown to increase the soil water repellency
294 (Goebel *et al.* 2011; Sánchez-García *et al.* 2019), decrease soil moisture retention and soil moisture
295 storage capacity (Robinson *et al.* 2016). It can also change aggregate stability (Goebel *et al.* 2005) with
296 cascading effects on ecosystem functioning. For example, an increase in soil water repellency caused
297 by drought can reduce the mineralization of soil organic matter by microbes with potential
298 consequences for plant productivity and plant community structure (Goebel *et al.* 2011).

299

300 **4. Drought legacy durations**

301 To date few studies have explicitly looked into drought legacy duration, which has been best
302 documented for C cycle processes. Here, we synthesize drought legacy duration post-drought for a
303 range of C cycle parameters and for community properties, which both strongly depend on the plant
304 functional types and the specific response parameter studied (Fig. 3).

305 In grasslands, most C-cycle related legacies return to pre-disturbance level roughly within the first year
306 after the drought and can last several years for forests (Fig. 3a). This is in line with the suggestion by
307 Wu *et al.* (2018), and Zhang *et al.* (2022) that drought legacies tend to be longer for forest and woody
308 species compared to grasslands and non-woody/herbaceous species.

309 Overall, flux parameters return to pre-disturbance levels within the first year (Fig. 3a, see also
310 (Schwalm *et al.* 2017; Zhao *et al.* 2020)), while biomass- and growth-related legacies tend to persist
311 long afterwards (Fig. 3a). This supports the emerging notion of a post-drought decoupling of temporal
312 dimensions of response parameters in forests such as C uptake, tree rings, and NDVI (Kannenber *et al.*
313 *et al.* 2019b; Gessler *et al.* 2020; Gazol *et al.* 2020; Kannenberg *et al.* 2020), showing that the legacy
314 duration of different C cycle response parameters is highly variable.

315 Furthermore, we observed that legacies in community properties, such as species abundance,
316 composition, and richness tend to last longer in woody species and understory compared to grasslands
317 (see Fig. 3b). Moreover, the drought legacy effects on community properties tend to last longer than
318 those related to C cycle parameters (Fig. 3). For example, while biomass recovered after drought in a
319 grassland experiment (Fig 3a), species composition still remained affected after one (Hoover *et al.*
320 2014) and two years (DeBoeck *et al.* 2018; Xu *et al.* 2021) (Fig. 3b). Following severe drought events,
321 community properties often do not return to pre-disturbance levels (Fig. 3) (Hillebrand & Kunze 2020).
322 Overall, the temporal aspect of drought legacies and their dependencies are still poorly understood
323 across response parameters and plant functional types. This is especially relevant for long-term
324 legacies that are related to community properties (Hillebrand & Kunze 2020) (see Fig. 3b). By
325 conducting continuous measurements long after the drought has subsided and thereby revealing when
326 deviations of response parameters return to the baseline, studies could provide insight into the
327 duration and cumulative magnitude of drought legacies. Based on the scarce available evidence we
328 suggest that to fully quantify drought legacies, observations of up to five and fifteen years may be
329 required for grasslands and forests, respectively.

330

331 **5. Effects of drought legacies on responses to subsequent drought events**

332 While legacies after a drought event have been increasingly studied in recent years, we still lack a
333 profound understanding of how these drought legacies alter the resilience (i.e. resistance and recovery
334 (*sensu* Ingrisch & Bahn 2018) of ecosystems to subsequent droughts (or other extreme events, see e.g.
335 Zscheischler *et al.* 2018). Drought legacy effects on ecosystem responses of a subsequent drought can
336 relate to all ecosystem properties and processes (intrinsic factors, IFs) outlined above. In the following,
337 we develop hypotheses about the main determinants of the resilience trajectories of an IF to
338 subsequent drought events.

339 First, we hypothesise that the resilience of an IF to a subsequent drought depends on its *post-recovery*
340 *state* following the antecedent drought event. Relations can be manifold and depend on the particular

341 IF, hence for simplicity we only present one option here, showing the highest resilience when the IF
342 reveals no legacy from the previous drought (Fig. 4).

343 Second, we suggest that the resilience of an IF to a subsequent drought depends on the *adaptation*
344 and *degradation* of all further IFs of the ecosystem (Fig. 2, Fig. 4). We hypothesize that post-drought
345 legacy adaptation/ degradation of all further IFs of an ecosystem can shift the response of an IF to a
346 subsequent drought towards higher/ lower resilience, respectively (Fig. 4, 5). Importantly, different IFs
347 can be affected by adaptations and degradations to different degrees (Fig. 5).

348 On the species scale, **adaptations** imply that species become more adjusted to drought, which can
349 moderate the impact of a subsequent drought event. For example, a reduced xylem conduit size in
350 trees can reduce the risk of hydraulic failure and thereby increase resistance to a subsequent drought
351 (Gessler *et al.* 2020). Proline, a water retaining compound that can regulate osmotic adjustments, was
352 found to be adaptively enriched in grassland species under recurrent drought conditions (Li *et al.*
353 2022). The observed higher water retention and concurrent higher stomatal conductance can maintain
354 plant functioning during subsequent droughts (Li *et al.* 2022). Furthermore, an adaptation towards
355 higher photosynthetic rate was observed under recurrent drought and during its recovery (Alves *et al.*
356 2020). Moreover, a higher root biomass as a legacy from a previous drought can increase resistance
357 and recovery to a new drought (Legay *et al.* 2018). It is known that molecular mechanisms such as
358 accumulation of proteins and transcription factors, as well as epigenetic changes can change plant
359 responses to subsequent stress (Bruce *et al.* 2007; Jacques *et al.* 2021). For example, drought was
360 suggested to result in epigenetic changes leading to structural changes (Fleta-Soriano & Munné-Bosch
361 2016) or enhanced transcription of stress-response genes (Ding *et al.* 2012), thereby increasing plant
362 resistance to a subsequent drought. These mechanisms of 'drought memory' (Walter *et al.* 2013) were
363 hypothesized to be an underlying cause for increased resistance of plant biomass during subsequent
364 drought (Walter *et al.* 2011; Backhaus *et al.* 2014).

365 Long-term adaptations on the community scale have been documented for all plant functional types.
366 Such adaptations frequently involve increased dominance of drought adapted species (Hoover *et al.*

2014; DeBoeck *et al.* 2018; Xu *et al.* 2021; Wilcox *et al.* 2021) and lead to corresponding shifts in the community-level plant traits (Trugman *et al.* 2020; Evans *et al.* 2022). They have also been shown to involve increases in functional diversity (Griffin-Nolan *et al.* 2019). Such community-level adaptations can moderate the impact of a subsequent drought (Coleman & Wernberg 2020) (see Fig. 5). For example, an increase of trees with drought-tolerant hydraulic traits can buffer forest productivity during subsequent droughts (Trugman *et al.* 2020). Moreover, an adaptation of soil biota and processes can dampen the negative effect of a subsequent drought on native plant species while reducing the success of invasive species (Meisner *et al.* 2013). It has recently also been shown that multiple recurrent droughts can alter soil microbial community composition and enhance soil multifunctionality during subsequent drought events (Canarini *et al.* 2021).

On the ecosystem scale, increased N availability upon rewetting can favour resistance to and recovery from subsequent drought (Legay *et al.* 2018). Recurrent drought events have been shown to enhance such rewetting-induced N release both in the lab (Miller *et al.* 2005; Lu *et al.* 2019) and in the field (DeVries *et al.* 2012). However, several studies also suggest that under recurrent droughts this rewetting effect can be dampened (Borken & Matzner 2009; Yu *et al.* 2014; Kaisermann *et al.* 2017; Sánchez-García *et al.* 2019), which might lead to an overall reduction of N availability in the ecosystem, as rewetting can fail to balance the decreased N mineralization rates during drought events (Borken & Matzner 2009) or lead to enhanced N leaching (Sardans *et al.* 2020; Krüger *et al.* 2021).

In addition to drought-induced adaptations, **degradations** of intrinsic factors can have an important influence on ecosystem responses to subsequent droughts. In fact, it has been suggested that an increasing amount of land area globally may be degraded by aridity in the long-term due to shifts in precipitation regimes (Berdugo *et al.* 2020). Increased aridity can hamper the recovery after a drought event and lead to more extreme responses to recurrent drought events. Degradation can involve both plant- and soil-related parameters such as plant cover and soil aggregate stability (Berdugo *et al.* 2020). Furthermore, legacies in fungi/ bacteria ratio can decrease the ability of soil microbial communities to maintain the same functions under recurrent drought (Preece *et al.* 2019). Degradation can also imply

393 reduced biodiversity (Jung *et al.* 2014; Hoover *et al.* 2014; Xu *et al.* 2017; Stampfli *et al.* 2018), which
394 is an important stabilizing factor for ecosystem productivity and both increases the resistance to (Isbell
395 *et al.* 2015) and recovery from drought (van Ruijven & Berendse 2010; Kreyling *et al.* 2017; Craven *et*
396 *al.* 2018). Moreover, negative effects on seedbanks can affect plant communities and could reveal
397 themselves after a long time, as they are often not reflected in the aboveground vegetation (Basto *et*
398 *al.* 2018).

399 Finally, we hypothesize that the resilience trajectories of an IF to a subsequent drought event are
400 strongly influenced by extrinsic factors, including drought timing, frequency, and severity (Fig. 4). Next
401 to seasonality effects, timing matters for the degree of the recovery from the previous drought (Fig.
402 4). Overall we expect that resilience is lower when the species, community, or ecosystem property or
403 process has not yet recovered from the previous drought (Fig. 1, S1 and S2) and higher when it is fully
404 recovered (Fig. 1, S3) (Mitchell *et al.* 2016; Schwalm *et al.* 2017; Peltier & Ogle 2019; Szejner *et al.*
405 2020; Hoover *et al.* 2021). Furthermore, resilience to a subsequent drought is probably decreased by
406 drought frequency, i.e. the number of consecutive drought events. Several studies in fact support the
407 notion that a higher drought frequency decreases both resistance (Bose *et al.* 2020; Xu *et al.* 2021) and
408 recovery (Gao *et al.* 2018; Peltier & Ogle 2019; Szejner *et al.* 2020; Jiao *et al.* 2021; Serra-Maluquer *et*
409 *al.* 2021). However, the opposite, i.e. a higher drought frequency leading to a higher resilience, has
410 also been shown (Yao *et al.* 2022) (see also the above section on adaptations shaping the resilience to
411 a subsequent drought event). Also, increasing drought severity is expected to decrease resistance to
412 and recovery from a subsequent drought (Fig. 4). This hypothesis is based on studies of single drought
413 events, where longer duration hampered resistance (Buttler *et al.* 2018; Reynaert *et al.* 2020), and
414 higher intensity reduced resistance (Xu *et al.* 2019) and recovery (Schwalm *et al.* 2017). Given the
415 broad lack of evidence on the interactive effects of intrinsic and extrinsic factors, experimental and
416 observational studies are urgently needed to improve our understanding of ecosystem responses to
417 recurrent drought events.

418

419 **6. Conclusion and Outlook**

420 In times of increasing severity and frequency of drought events in many parts of the world, it is
421 essential to not only assess the concurrent effects of droughts, but to understand the lasting
422 consequences such extreme events may have on ecosystems. In our review we have provided a broad
423 overview of drought legacies and the underpinning mechanisms from species to community and
424 ecosystem scale. To date, quantitative analyses of drought legacy responses have mainly focused on
425 aboveground growth-related parameters and some community attributes, suggesting that the legacy
426 duration can differ vastly for different parameters and different plant functional types. For a more in-
427 depth understanding of drought legacies on ecosystems it will be important for future studies to
428 extend the observational timescale and explicitly consider a range of interrelated biotic and abiotic
429 factors, including above-belowground interactions. To advance the field, it will be essential to
430 illuminate the particular role of adaptation and degradation of properties and processes across scales
431 in determining ecosystem resilience to subsequent drought events. Furthermore, future studies should
432 consider potential interactions of drought legacies with other global change factors such as warming,
433 elevated CO₂, N deposition and land-use changes, as well as interactions with other climate extremes,
434 such as heatwaves and heavy precipitation events. Accounting for these potential interactions and the
435 implications of drought legacies for subsequent drought events is essential for understanding and
436 projecting the long-term consequences of a changing climate for ecosystems.

437

438

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444

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1030

1031 **Fig.1:** Post-drought trajectories of the recovery and post-recovery phase after a drought event. The
1032 recovery phase is characterized by the rate of recovery (arrow 2) following the maximum impact of the
1033 drought event (arrow 1). The post-recovery phase starts when the rate of recovery is zero (arrow 3),
1034 irrespective of whether the recovery has been complete (yellow trajectory) or has resulted in a shifted
1035 baseline, the latter reflecting an immediate drought legacy (red and blue trajectories). In the post-
1036 recovery phase drought legacies can be characterized by the deviation from the pre-drought baseline
1037 (arrow 4) and the legacy duration (arrow 5). Starting timepoints (S1-S3) of a potential subsequent
1038 drought event (see Fig. 5) are indicated as dotted grey arrows.

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1041 **Fig. 2:** Drought legacies on species, community and ecosystem scale. Colours refer to autotrophic
1042 (green), heterotrophic (brown) and abiotic (blue) ecosystem components, respectively. White arrows
1043 indicate interactions of legacies across properties within a given scale (cross-scale interactions not
1044 shown for simplicity). See Fig. S1 for the number of papers published on the respective topics.

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1067 **Fig.3:** Drought legacies durations of a) carbon-cycle parameters and b) community properties (species
1068 abundance, composition, and richness) for different plant functional types and ecosystems,
1069 respectively. Abbreviations for 3a: Asat = light saturated photosynthetic exchange rate, growth = in
1070 forest/woody species this refers to radial growth/tree ring width, ANPP = aboveground net primary
1071 production, GPP = gross primary productivity, AGC = aboveground carbon stocks
1072 *References for Fig. 3a are indicated as follows: 1. Xu et al. 2021, 2. Hahn et al. 2021, 3. Xie et al. 2020, 4. Mackie*
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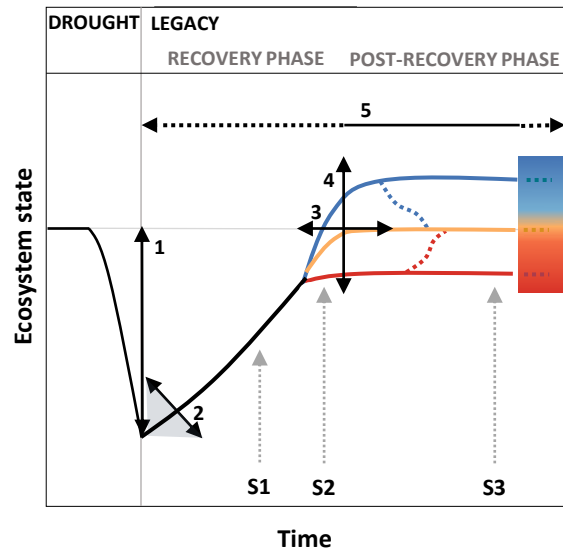
1082 **Fig. 4:** Hypothesized changes in ecosystem resilience of an ecosystem property or process (intrinsic
1083 factor, IF) to a subsequent drought in relation to i) its post-recovery state following the antecedent
1084 drought event, ii) the adaptation versus degradation of other ecosystem properties and processes (IFs)
1085 as well as iii) characteristics of the subsequent drought. The colour code of post-recovery state refers
1086 to Fig. 1, blue and red indicating an increase or decrease in ecosystem state, respectively. Next to the
1087 post-recovery state, adaptation and degradation of IFs (for a summary of IFs see Fig. 2, for examples
1088 on adaptations and degradations of IF see Fig. 5) can alter resilience to subsequent drought. Extrinsic
1089 factors, including timing (S1-S3, see Fig. 1), the severity, and the frequency of the subsequent
1090 drought(s) can affect resilience (defined here as the combined resistance to and recovery from a
1091 drought event).

1092

1093

1094 **Fig. 5:** Post-drought adaptation / degradation of selected processes and properties on species,
1095 community, ecosystem scale (intrinsic factors) associated with higher/lower resilience (i.e. capacity to
1096 resist and recover) towards a subsequent drought event. An adaptation, e.g. through increases in fine
1097 root mass, mycorrhizae or water use efficiency (CO₂ uptake relative to H₂O loss), will lead to higher
1098 resilience, while a degradation, e.g. of plant cover, species diversity or soil texture, will typically lead
1099 to a lower resilience. For further explanations see text.

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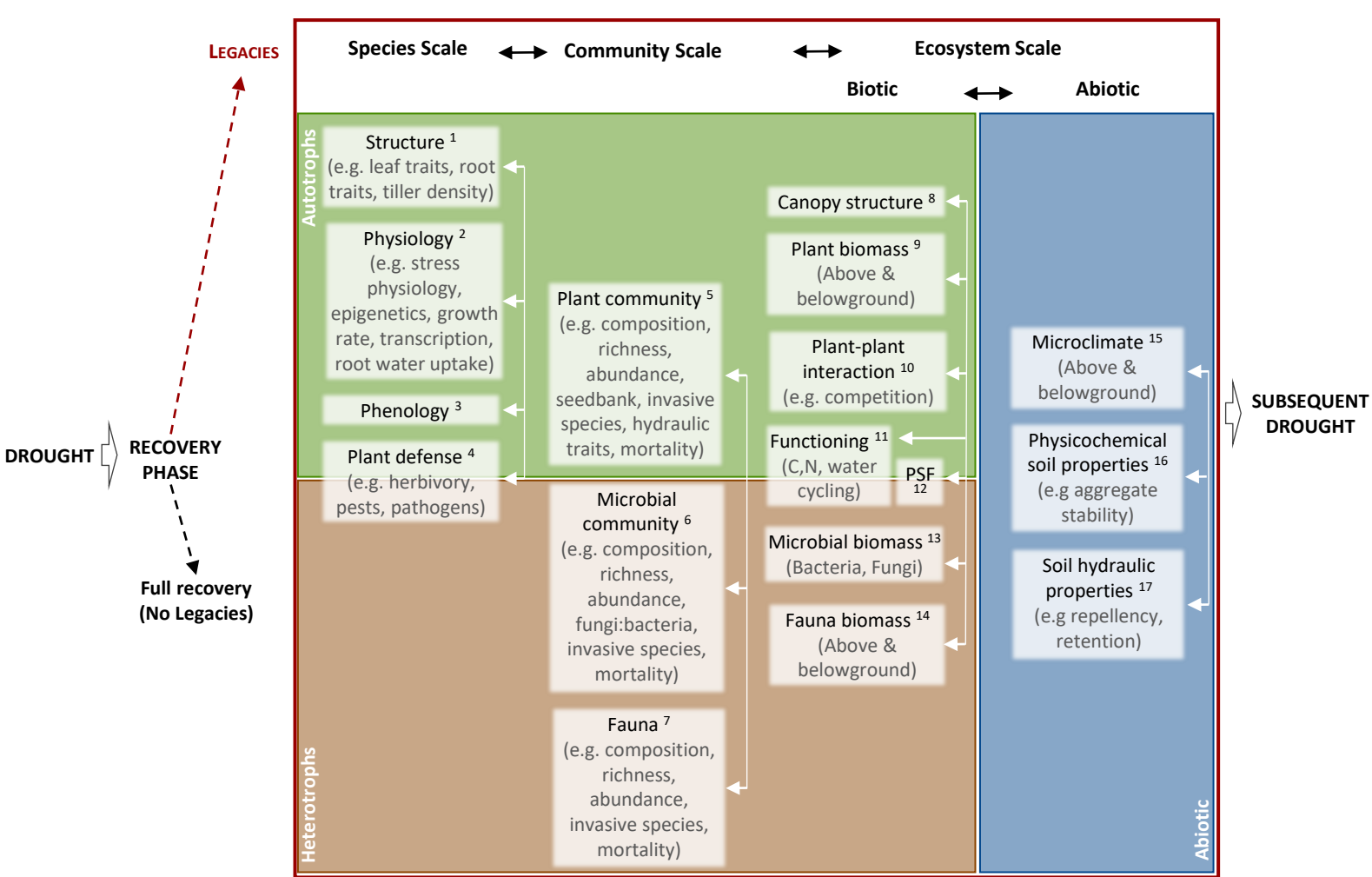


Fig. 3 (a)

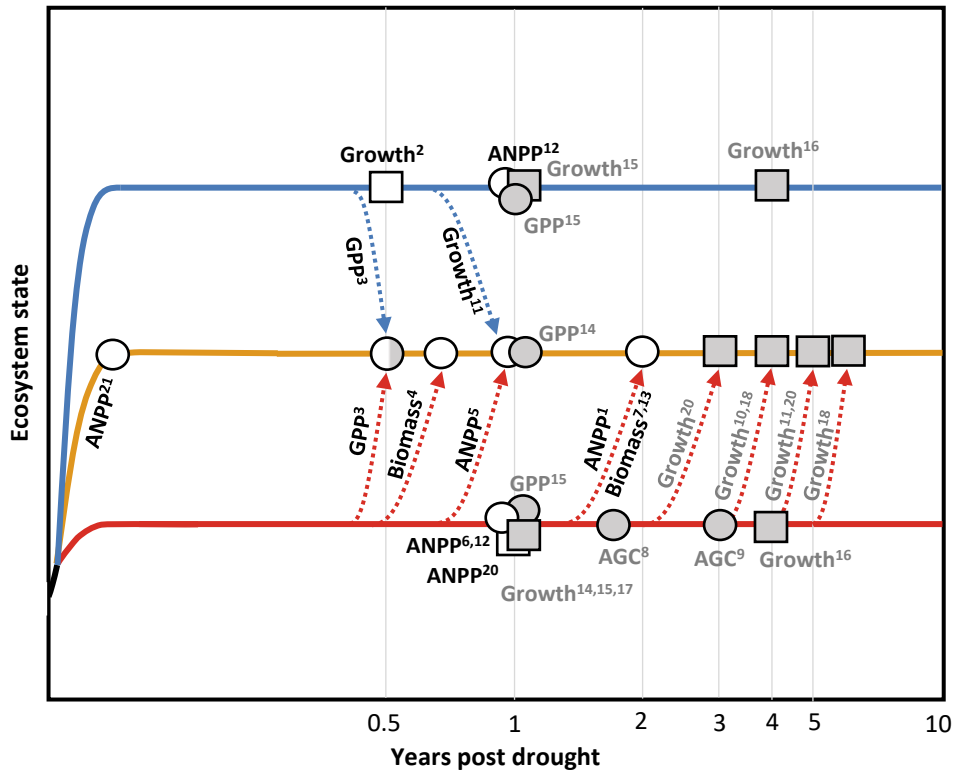
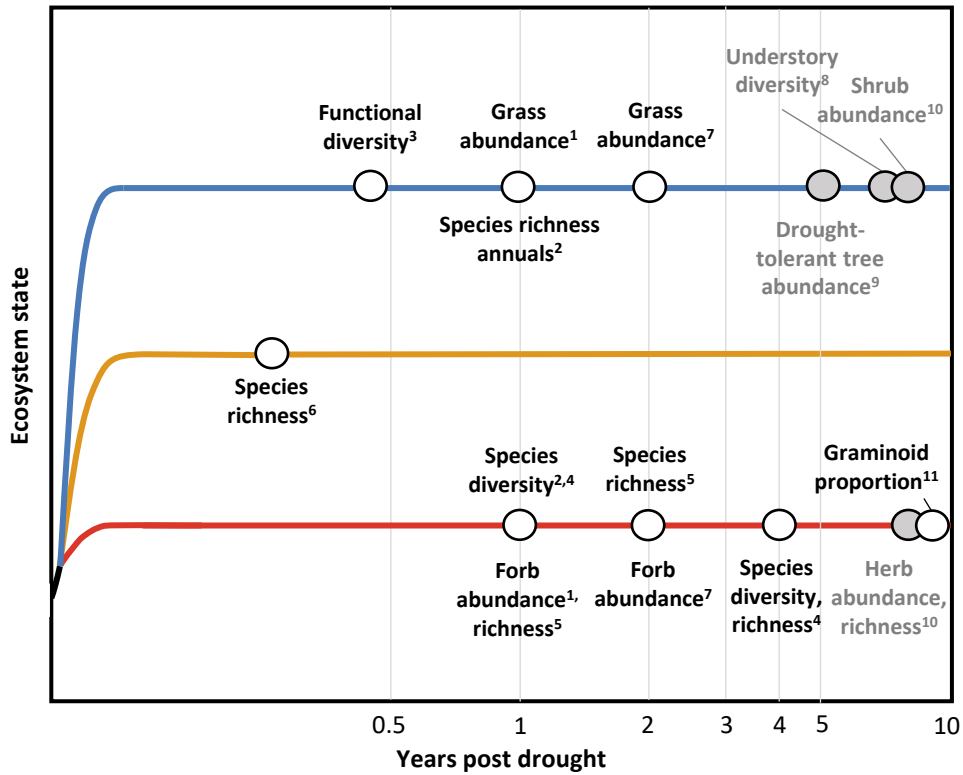


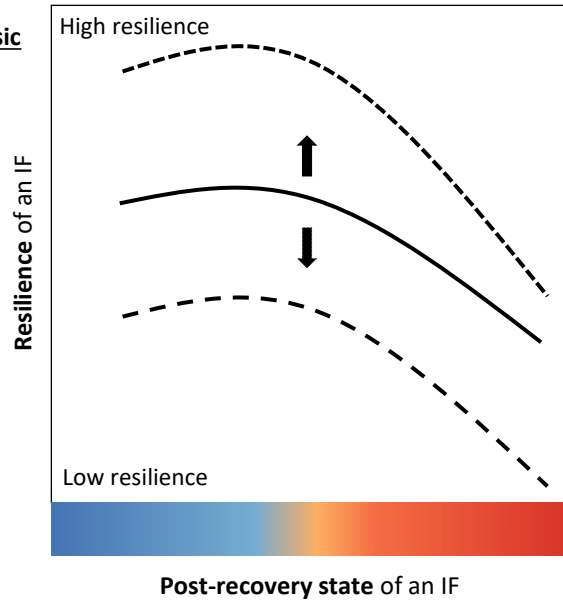
Fig. 3 (b)



- Grassland
- Forest, understory
- Higher ecosystem state
- Full recovery = pre-drought state
- Lower ecosystem state
- Non-woody / herbaceous species
- Woody species

Characteristics of an ecosystem (intrinsic factors, IF) affecting resilience

- ↑ Adaptation of IFs
- ↓ Degradation of IFs

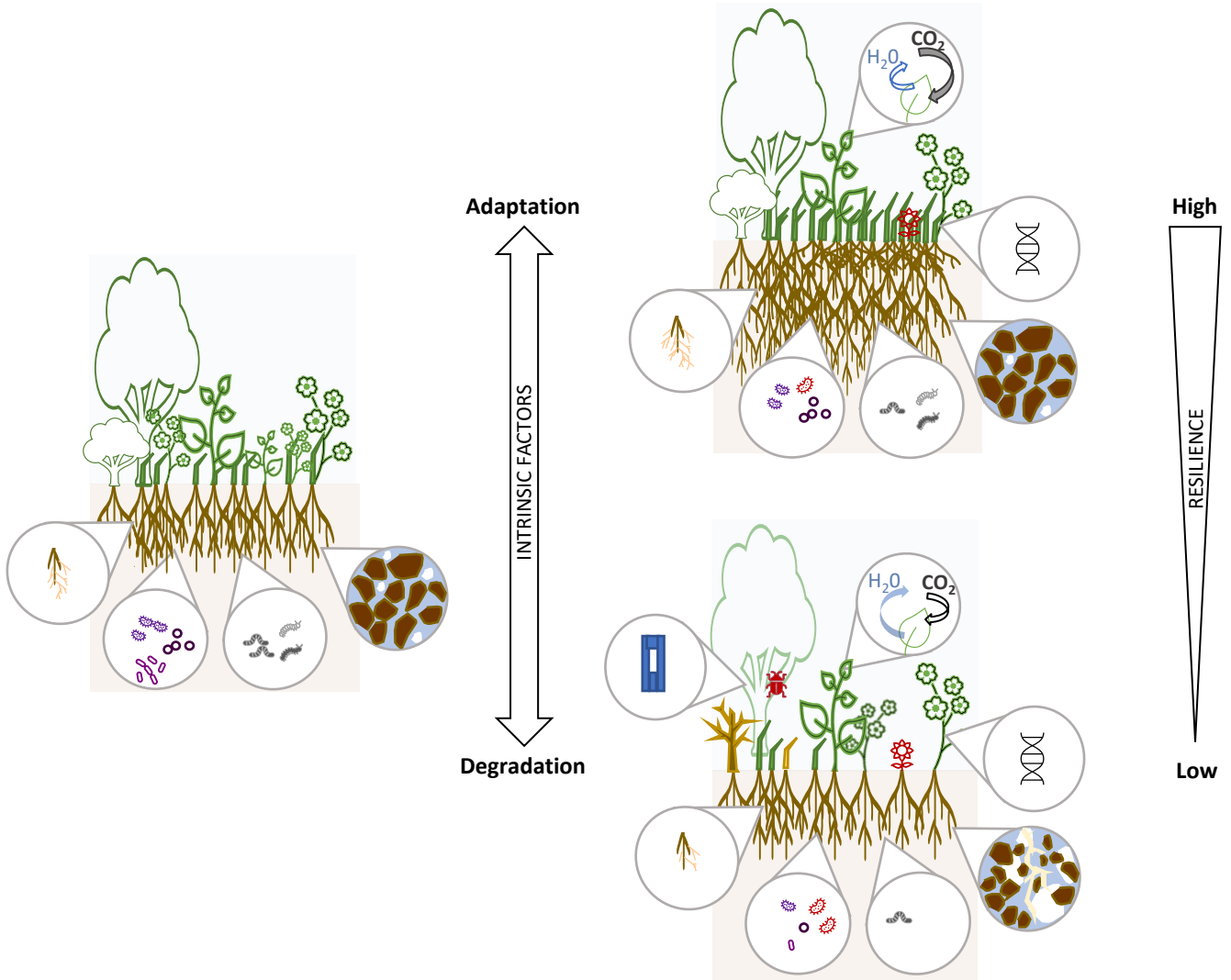


Characteristics of the subsequent drought (extrinsic factors) affecting resilience

- | Severity, frequency of subsequent drought | Timepoint of the subsequent drought |
|---|-------------------------------------|
| ↑ Low | S3 ↑ |
| ↓ High | S2 ↓ |
| | S1 ↓ |

Pre-drought

Post-drought



	Water-use efficiency		Mortality		Soil fauna
	Hydraulic failure		Bacteria		Pests, pathogens, invasive plants
	Epigenetics		Mycorrhiza		Soil texture