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Manuscripts

1 **A unified framework for plant life history strategies shaped by fire and herbivory**

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Example using grasses	2876		
Discussion and conclusions	901		
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13

14

15 **Summary:**

16 Fire and herbivory both remove above-ground biomass. Environmental factors determine the type and
17 intensity of these consumers globally, but the traits of plants can also alter their propensity to burn and
18 the degree to which they are eaten. To understand plant life history strategies associated with fire and
19 herbivory we need to describe both response and effect functional traits, and how they sort within
20 communities, along resource gradients, and across evolutionary timescales. Fire and herbivore
21 functional traits are generally considered separately but there are advances made in understanding fire
22 which relate to herbivory, and vice versa. Moreover, fire and herbivory interact: the presence of one
23 consumer affects the type and intensity of the other. Here we present a unifying conceptual framework
24 to understand plant strategies that enable tolerance and persistence to fire and herbivory. Using grasses
25 as an example, we discuss how flammability and fire tolerance, palatability and grazing tolerance traits,
26 might organise themselves in ecosystems exposed to these consumers, and how these traits might have
27 evolved with reference to other strong selective processes like aridity. Our framework can be used to
28 predict both the diversity of life history strategies and plant species diversity under different consumer
29 regimes.

30 **Keywords:** flammability, grass, herbivory, palatability, plant defence, plant functional traits, tolerance,
31 trophic ecology

32

33 Introduction:

34 Globally, fire and large mammal herbivores are two major consumers of above-ground plant biomass,
35 particularly in tropical ecosystems where they are important drivers of plant evolution and vegetation
36 structure (Bond, 2005). Empirical evidence demonstrates that fire-adapted and herbivore-adapted plant
37 communities in the same abiotic environments differ in species composition, structure and plant
38 functional traits (Collins & Barber, 1986; Anderson *et al.*, 2007; Forrestel *et al.*, 2015; Kruger *et al.*,
39 2017). Indeed, fire and herbivory can be seen as ecological filters where organisms exposed to these
40 consumers must possess attributes enabling persistence and reproduction, or they will be lost from a
41 community (Belsky, 1992; Cingolani *et al.*, 2005). A substantial literature both in trophic and fire ecology
42 exists, but these bodies of research have developed independently with different theoretical
43 approaches. Fire is seen as a disturbance, whereas herbivory can be considered in terms of predator-
44 prey dynamics, but neither of these theoretical frameworks is entirely satisfactory – see McNaughton
45 (1983) for a discussion on this for herbivory, and Evans (1989) for fire. There are several reasons why it
46 would be beneficial to contrast these two ecological drivers as ‘consumers’ of vegetation (Bond &
47 Keeley, 2005) in a common framework. Firstly, individual plants are often exposed to both fire and
48 herbivory over their lifetime. Secondly, the intensity and frequency of fire and herbivory depend to
49 some extent on vegetation properties (Burkepile *et al.*, 2013; Platt *et al.*, 2016). Therefore, unlike a
50 disturbance such as drought, there can be feedbacks between community composition and these
51 consumers that can act either to promote or reduce their intensity. Finally, unlike most predator-prey
52 relationships, it is possible for individual plants to survive, or even benefit from a consumption event
53 (Strauss & Agrawal, 1999; Gagnon *et al.*, 2010).

54 Through the removal of above-ground biomass both fire and herbivory can alter competitive
55 interactions within communities by enabling tolerant plants to remain in environments where less-
56 tolerant plants – but better competitors – would otherwise dominate (Collins & Barber, 1986; Cingolani
57 *et al.*, 2005). Intense consumption can alter the architecture of plants, where less intense consumption
58 simply removes leaf material (Danell *et al.*, 1994). Fire is episodic and it is rare for an ecosystem to
59 sustain more than one fire per year (usually every 2-5 years in tropical grasslands and savannas, and
60 much less frequently elsewhere (Archibald *et al.*, 2013a)). Some insect herbivory is also episodic, but
61 many other herbivores are always present, and it is possible to be exposed to repeated, frequent
62 defoliation from herbivores within a day, week and year (McNaughton, 1983). With fire, plants need to
63 protect remaining, unconsumed living material from extreme heat, whereas with herbivory plants need

64 to be able to withstand the physical action of tugging and breaking of the plant. Moreover, as fire is a
65 physical process requiring energy, heat, and oxygen, and herbivory is a biological process requiring
66 energy, water and a range of other essential nutrients, these two consumers, while both consuming
67 above-ground biomass, are not necessarily attracted to the same plant parts or plant traits.

68 Here, we contrast the approaches of fire and trophic ecology integrating these parallel fields of research
69 to define a unified theoretical framework that enables predictions about community assembly and the
70 viability of plant ecological strategies with varying regimes of fire and herbivory. Using grasses as an
71 example, we identify plant functional traits associated with resistance and tolerance of fire and grazing,
72 versus attraction and avoidance of fire and grazing. We use our proposed framework to assess the
73 extent to which adaptations to fire and mammalian herbivory are compatible (i.e., result in the same
74 plant functional types), or antagonistic (select for different plant life histories) and how this might have
75 affected community assembly and therefore plant evolution. We discuss what this means for the
76 structure and dynamics of ecological communities exposed to these consumers, and how these
77 adaptations interact with other environmental drivers such as aridity and cold temperatures. Finally, we
78 consider whether and how the plant traits and life histories identified here relate to other theoretical
79 frameworks in the broader plant trait and plant economics literature.

80 **Why grasses?** Poaceae is a diverse family of over 11000 species that dominate the ground layer of ~40%
81 of the Earth's land surface, covering environments ranging from extreme heat and aridity to below
82 freezing (Linder *et al.*, 2017). In expanding to cover their current geographical range grass species
83 evolved functional characteristics that enabled survival under many combinations of fire, herbivory,
84 drought, light availability, water logging and low temperatures. Grasslands burn frequently and support
85 large numbers of livestock and/or indigenous animals (Lehmann & Parr, 2016). There are several
86 examples where removing herbivores from an ecosystem increases fire frequency, indicating
87 competitive interactions between fire and herbivory that are mediated by the composition and
88 functional traits of the grass community (Johnson *et al* 2018). Poaceae is therefore a useful model for
89 integrating understanding of how adaptations to fire and herbivory have emerged from and interact
90 with other dimensions of the environment.

91

92

93

94 **Contrasting current theoretical approaches in trophic vs fire ecology**

95 In the trophic ecology literature tolerance is generally defined as “the degree to which plant fitness is
96 affected by herbivore damage relative to fitness in the undamaged state” (Strauss & Agrawal, 1999).

97 Resistance is a separate concept: “any plant trait that reduces the preference or performance of
98 herbivores”. Other authors use different terms for the same concepts (Table 1), but it is generally
99 agreed that these represent alternative life history strategies – i.e. plants with traits that make them
100 unlikely to be eaten are not expected to have traits that confer tolerance (van der Meijden et al., 1988,
101 although see Núñez-Farfán et al. (2007) for further discussion).

102 Theory has been developed to predict when it would be beneficial for plants to invest resources in
103 avoiding herbivory (Feeny, 1976; Coley *et al.*, 1985; Herms & Mattson, 1992). The converse, that plants
104 might require herbivory in order to be fit, and that attracting herbivores could be advantageous, has
105 also been debated (McNaughton, 1983, 1986; Janzen, 1984; Belsky, 1986) but the focus has been on
106 consequences for productivity (overcompensation) rather than overall fitness (Belsky *et al.*, 1993). De
107 Mazancourt (2001) demonstrated that plant-herbivore mutualisms were possible, but only in very
108 restricted circumstances, and this has not been formulated in terms of individual-level selection for
109 palatability per se.

110 In the fire ecology literature, in contrast, there has been more focus on the mechanism by which species
111 persist in a fire-prone environment. Plants can resist fire (i.e. not be damaged by a fire event), they can
112 avoid fire (i.e. not be burned in a fire event), or they can be burned in a fire event, and regenerate either
113 from resprouting (individual level persistence) or from seed (population level persistence) (Whelan,
114 1995; Gignoux *et al.*, 1997; Pausas & Lavorel, 2003). In the fire literature there has also been discussion
115 on the degree to which flammability, or the lack thereof, interacts with fire tolerance strategies:
116 flammable plants have associated tolerance traits, and less flammable plants tend to show resistance
117 (Schwilk & Ackerly, 2001). Moreover, flammability has been proposed to increase individual fitness
118 through directing heat away from sensitive plant parts (Gagnon et al., 2010 - individual-level) or creating
119 a better environment for offspring by damaging other plants (Bond and Midgley, 1995 - population
120 level), and could therefore be selected for, although there are those that argue that flammability is
121 simply an emergent property of selection for other plant functions related to leaf economics (Midgley,
122 2013). See Pausas (2017) for an extensive review of this topic.

123 Some herbivore ecologists are more aligned in their terminology to fire ecologists. Briske (1996), for
124 example, defined “avoidance” as the ability to reduce the probability of being eaten (resistance in
125 Strauss and Agrawal’s (1999) formulation), and then defined resistance as a concept which integrates
126 both strategies to determine whether a plant can persist and reproduce in the face of a disturbance.
127 Moreover, defence has sometimes been used as an umbrella-term incorporating both tolerance and
128 resistance, and elsewhere used synonymously with resistance (Stowe *et al.*, 2000; Fornoni, 2011).

129 **An integrated framework**

130 We suggest that some of these confusions can be resolved by distinguishing between the ability to avoid
131 a defoliation event all together – i.e. be unpalatable or non-flammable, and the ability to “resist” a
132 defoliation event when it happens by protecting sensitive plant parts (Box 1). These two concepts are
133 usually conflated into ‘plant defence strategies’ (e.g. Agrawal, 2011), but are quite different ecologically.
134 The ability to “resist” defoliation is a subset of a range of plant tolerance strategies to defoliation, and
135 says nothing about an individual plant’s attractiveness to herbivores or fire (i.e. the probability of being
136 eaten/burned). For example Acacia species in African savannas with palatable leaves are also highly
137 defended by spines to prevent too much biomass being removed (Charles-Dominique *et al.*, 2017), i.e.
138 while they do not **avoid** herbivores, they **resist** them.

139 Once avoidance is clearly distinguished from resistance then it is easy to see plant life histories as
140 existing on an axis from “avoidance” to “attraction” of fire or herbivory, and that where a plant sits on
141 this axis affects the degree to which it is exposed to consumption, and therefore, the strategies that it
142 requires to persist in a community exposed to fire or herbivory.

143 We therefore propose that when considering fire/herbivory adaptations there are three distinct axes,
144 associated with three distinct functions which act over three distinct time periods that need to be
145 quantified for understanding plant life history strategies (Figure 1, Box 1). First is the “avoidance--
146 attraction continuum” which acts before a plant is defoliated and determines whether a defoliation
147 event is likely to occur. Second is the “resistance” continuum, which acts during the defoliation event,
148 and determines the amount and type of biomass that is damaged or lost by the event. Finally, the
149 “tolerance/persistence” continuum acts over the lifetime of the plant and beyond, integrating an
150 individual plant’s response to defoliation and whether a population and species can persist when
151 exposed to a particular level/type of consumer.

152 As discussed by Strauss and Agrawal (1999), a plant's location on the avoidance-attraction continuum
153 should strongly influence the type of plant resistance and tolerance traits that will be successful in a
154 given environment, i.e. not all portions of these three axes will be occupied, but by placing plants on
155 these axes it is possible to identify all possible strategies for surviving and persisting in consumer-prone
156 environments. This different approach (Figure 1) integrates ideas from both fire ecology and trophic
157 ecology, and should be able to be applied in both contexts. It both resolves confusion over avoidance vs
158 resistance herbivore defences, and incorporates the idea that **even the most tolerant plant needs to**
159 **resist at some level** – i.e. some part of its growth form needs to be protected from damage for recovery
160 to occur.

161 Moreover, once both fire and herbivore adaptations are viewed from this combined framework, it
162 should be possible to assess the degree to which adaptations for each consumer are aligned, or whether
163 they select for different types of organisms – for example, is it possible to evolve traits that allow a plant
164 to resist both fire and herbivory, or are there trade-offs such that fire-adapted species are more
165 susceptible to herbivory and vice versa?

166

167 **Contrasting avoidance-attraction traits for fire and herbivory in grasses**

168 The differences between fire and herbivory become very clear when one considers which traits are
169 associated with palatable vs flammable grasses. Fire burns more easily through dry grasses, with a high
170 energy content (high C:N ratio), because these are easier to ignite and sustain a fire (Simpson *et al.*,
171 2016). Moreover, thin leaves arranged in an aerated canopy increase ignitability and fire spread rate
172 (Schwilk, 2015). Low phosphorus content and the presence of volatile oils (Scarff & Westoby, 2008;
173 Ormeno *et al.*, 2009) have also been shown to increase flammability.

174 In contrast, leaves with a high moisture content are preferred by grazers, as this minimises dependence
175 on external water sources (Jarman, 1973), and is associated with actively growing leaf material with
176 higher crude protein levels (Murray & Brown, 1993). Indeed, grazers prefer forage with a low C:N ratio,
177 which is more digestible, and also high phosphorus content, as these nutritional components are
178 required as part of a balanced diet that optimally supports metabolic processes (Owen-Smith & Novellie,
179 1982). Large leaves, clustered together in the canopy provide high biomass per bite and reduce foraging
180 time, and are thus preferred (Stobbs, 1973).

181 Tannins, which deter herbivores (Cooper & Owen-Smith, 1985), also slow decomposition rates (Kraus *et*
182 *al.*, 2003), so will decrease palatability and increase flammability by making more dead fuel available for
183 longer (Grootemaat *et al.*, 2015). Sodium attracts grazers (McNaughton *et al.*, 1997), and silica is
184 thought to deter grazers (Massey *et al.*, 2009) but these elements have no known impact on fire spread.
185 Therefore, due to the differences between fire, a physical process, and herbivores, which are biologically
186 metabolising their food, the traits associated with flammability are exactly opposite to those associated
187 with palatability: plants that are very flammable are likely to be largely unpalatable and vice versa
188 (Figure 2, Table 2).

189

190 **Contrasting resistance and tolerance traits for fire and herbivory in grasses**

191 Key to understanding the response functional traits for resisting and tolerating disturbances is
192 assessment of what plant parts are being protected. Pausas and Lavorel (2003) suggest that a species
193 can persist in an environment exposed to disturbance at an individual, a population, a community, or a
194 landscape level, and propose that the expected traits for persisting at these levels would be very
195 different. An example in fire-prone environments is the distinction between reseeders which die in a fire
196 and reproduce again from seed (population level persistence) and resprouters which persist at an
197 individual level by resprouting from the base or stem after a fire (individual level persistence) (Bond &
198 Midgley, 2001; Pausas *et al.*, 2004).

199 We suggest that this distinction can be taken further to assess what part of an individual is being
200 protected. This can be leaf material, plant structure, aerial buds, flowering culms, basal buds or root
201 stocks. Resistance strategies thus range from preventing loss of photosynthesis to preventing death
202 (Figure 1), and traits associated with protecting leaf material and aerial meristems are likely to be
203 different from those that protect roots or basal meristems.

204 For grasses, resistance to fire requires protecting basal buds from heat, and this requires that they are
205 well hidden in dense layers of leaf material (Daubenmire, 1968). This is achieved through intravaginal
206 branching and retained leaf sheaths. Alternatively, erect culms and distal branching result in a
207 flammable aerial leaf material that carries flames away from the base of the plant, achieving high fire
208 resistance for basal buds (Gagnon *et al.*, 2010). (Figure 2 Table 2). In contrast, although resisting heavy
209 grazing also requires protecting basal buds the main risk is uprooting. We propose that a strong root

210 system (root crown below the soil surface), combined with leaves and culms that break easily (low leaf
211 tensile strength and weak nodes) can protect basal buds from grazing (Table 2).

212 All traits that allow plants to retain leaf material close to the soil surface (lateral (extravaginal)
213 branching, prostrate culms, rooting at the nodes, basal leaf material) could be considered leaf-level
214 resistance traits against grazing (Figure 2, Box 2). The lack of leaf abscission allows plants to retain dead
215 leaf material, and has been demonstrated to protect new leaves from grazing (Mingo & Oosterheld,
216 2009), and some grasses (e.g. *Pennisetum mezianum*, *Triodia basedowii*) retain hard spikey culms above-
217 ground as a defensive structure to prevent loss of aerial leaf material (O'Reagain & Mentis, 1989;
218 Drescher *et al.*, 2006). This physical defence would also be termed “resistance” in our framework as it
219 protects palatable leaf material from being eaten.

220 Large bud banks and high photosynthetic rates enable rapid recovery post-fire and promote fire-
221 tolerance. These would also promote grazing tolerance, but to prevent death under a patchy, chronic
222 disturbance like grazing, having large stored reserves is another key individual-level tolerance trait
223 (Table 2).

224 Population-level persistence in fire-prone environments requires preventing seeds from being burned,
225 and rapid germination and recruitment after fire. This is promoted by early seed-set and seed release,
226 smoke-stimulated germination, and seed dormancy (Pausas 2018). Tall culms with wind dispersed seeds
227 promote long-distance dispersal that would enable landscape-level persistence (Boucher 2017). In
228 grazed environments rapid clonal growth (through lateral spread and rooting at the nodes) promotes
229 population-level persistence. Ectozoochory, or edible inflorescences and endozoochory (Janzen, 1984)
230 would be strategies for persisting at a landscape level in a grazed environment.

231 Clearly resprouting and rapid growth after defoliation are shared individual-level tolerance traits for fire
232 and grazing, but the resistance traits are often incompatible (Table 2, Figure 2) – with lateral growth
233 being a good way to hide from grazer mouthparts, and vertical growth being a good way to reduce heat
234 at the soil surface.

235 Appendix 1 summarises available evidence linking each trait to the functions proposed here, and how to
236 measure it.

237

238 **Life history strategies in consumer-controlled environments**

239 The information presented above supports the idea that avoidance and tolerance should be alternative
 240 life-history strategies (van der Meijden *et al.*, 1988; Schwilk & Ackerly, 2001). It also aligns with recent
 241 evolutionary theory showing that ‘mixed strategies’ – involving particular combinations of traits
 242 associated with attraction vs resistance vs tolerance – could also be evolutionarily stable (Núñez-Farfán
 243 *et al.*, 2007; Carmona & Fornoni, 2013). However, considering fire and herbivory together adds a layer of
 244 complexity, as plants with traits that enable avoidance of grazing automatically become more
 245 flammable, and vice versa.

246 When one considers fire and herbivory traits together in the context of the three axes: attraction-
 247 avoidance, resistance, and tolerance (Figure 3) we expect that that:

- 248 • Traits that confer flammability and those that confer palatability are very different from each
 249 other. Therefore, a life history strategy that avoids defoliation by animals will make a plant more
 250 likely to be burned in fire.
- 251 • Protection from fire (aerial leaf material, keeping buds tightly inside culms) is not the same as
 252 protection from grazing (maintaining leaf material below graze height, using extravaginal
 253 branching to spread laterally). Therefore extremely fire-resistant grasses are likely to be less
 254 grazing-resistant, and vice-versa.
- 255 • Maintaining fitness after a defoliation event (tolerance) is most important for plants with
 256 intermediate levels of attraction and resistance, because these plants are likely to be exposed to
 257 highest levels of defoliation.

258 From this four grass life-history strategies emerge (Figure 3):

259 1: Fire resistor, grazer avoider – these plants are likely to be flammable both because avoiding grazing
 260 results in more flammable canopies, and because fire resistance traits can increase flammability
 261 (Gagnon *et al.*, 2010).

262 2: Grazer resistor, fire avoider – these plants are likely to be palatable both because avoiding fire results
 263 in more palatable canopies (Figure 2), and possibly because palatability itself can be advantageous as a
 264 mechanism to prevent over-shading by competitors (Belsky *et al.*, 1993), or to increase nutrient
 265 availability (de Mazancourt *et al.*, 2001).

266 3: Generalist tolerators – that are unlikely to withstand high levels of grazing or fire, but can tolerate
 267 both consumers to some degree. This is strategy is possible because the ability to resprout (stored

268 reserves and a substantial bud bank of basal meristems at ground level) is effective for both fire and
269 herbivory.

270 4: Generalist avoiders – these plants do not need to be fire or grazing tolerant as they are unlikely to be
271 exposed to these consumers. However, they are also unlikely to be competitive because avoiding both
272 fire and grazing requires extreme leaf traits and architectures that do not favour carbon gain.

273 Assessing the range of growth forms that exist in tropical grasslands indicates that examples of these
274 four life history strategies can be found, but that there are often multiple ways to achieve the same
275 functional outcome (Table 3). For example, there are at least three different growth forms of grazing
276 resistant grasses (Hempson *et al.*, 2015): mat-forming stoloniferous/rhizomatous grasses, cushion
277 forming grasses that have their culm bases below ground and are impossible to uproot, and cage-like,
278 stemmy architectures that protect leaf material in the same way spiny trees do. Moreover, grasses can
279 achieve fire resistance through spreading fire up and away from basal meristems (Gagnon *et al.*, 2010),
280 or by protecting meristems in dense basal tussocks (Trollope *et al.*, 2002). The generalist tolerance
281 strategy can be achieved through stored reserves and a physiology that enables continued regrowth
282 despite substantial loss of photosynthetic tissue (McNaughton, 1983; Tiffin, 2000). However, there are
283 many plants that tolerate both fire and herbivory through having flexible growth forms – growing
284 laterally when exposed to herbivory, and growing vertically when ungrazed and burned (Hempson *et al.*,
285 2015). This phenotypic plasticity represents a second generalist tolerator life history.

286 We have identified ~8 growth forms (Table 3) which could be effective in consumer controlled
287 ecosystems) which are by no means a complete set: the universality of these growth forms needs to be
288 tested with data from a wide range of grassy ecosystems. The growth form that dominates in a
289 particular environment will depend on the degree of grazing or fire, as well as other environmental
290 constraints plants are placed under (Coley *et al.*, 1985). For example, in very mesic environments carbon
291 is less limiting than nitrogen or phosphorus, so there could be selection for tall, stemmy, carbon-rich,
292 architectures that promote height gain. These growth forms are also more flammable, so the fire
293 resistor/grazer avoider strategy would be common. In arid environments light competition is less severe,
294 so the generalist avoider strategy might be able to persist, despite the reduced growth rates associated
295 with small, sparse canopies. Very cold environments might not be conducive to extravaginal branching
296 or distal tillering which exposes buds, but a dense tussock growth form could confer both fire and cold-
297 tolerance. The flexible growth-form switcher strategy is likely to be most effective in places where the
298 consumer shifts from fire to herbivory over time, whereas the generalist tolerator (compensator)

299 strategy is predicted to be effective when exposed to persistent but intermediate levels of either
300 consumer. Nutrient rich environments also probably enable the compensator strategy that requires high
301 rates of regrowth and productivity. Moreover, seasonal aridity determines how effective fire-avoidance
302 can be. Only in places without seasonal aridity can plants maintain a high leaf moisture content all year–
303 consequently in temperate places, we expect fire avoidance and grazing tolerance is the most common
304 strategy.

305 Many of these predictions fit with what has been observed by existing global analyses of grazing traits
306 (McIntyre *et al.*, 1999; Diaz *et al.*, 2007), however, here fire is explicitly integrated into the same
307 predictive framework.

308 Contrasting the strategies identified here with the classic “Increaser/Decreaser” strategy framework
309 (Foran *et al.*, 1978) often used in southern African grasslands demonstrates the value of our conceptual
310 model. “Increaser 2” species are defined by Foran *et al* (1978) as those that increase when landscapes
311 are heavily grazed. Ecologically this could occur because they are unpalatable and avoided by grazers
312 (*Aristida congesta*), or because they are palatable and resistant to grazing (*Pennisetum clandestinum*).
313 From a land management point of view it is essential to distinguish these two functional groups because
314 one is desirable to a cattle farmer, and the other not.

315

316 **Ecological and evolutionary implications**

317 When ordering grass communities across a ‘consumer’ gradient from frequent fire to intense grazing
318 one expects turnover in the functional types that persist and dominate (Figure 4). As the generalist
319 strategies are only effective at intermediate levels of fire and herbivory, the prediction would be that
320 there is higher functional diversity in these environments, and that fewer strategies should exist in
321 extreme fire and extreme grazing situations. For the same reason we would also expect generalist
322 species to have larger range sizes. Figure 4 predicts that high grazing can potentially result in two
323 distinct ecosystem states: grazing lawns (McNaughton, 1984) or systems where only generalist avoiders
324 can persist. There is ample field evidence for these two different grazing end-points (Mack & Thompson,
325 1982; Milchunas *et al.*, 1988), and understanding the conditions that result in each state is an important
326 management issue.

327 The axis from fire to grazing (Figure 4) can occur across regional gradients, where fire-prone mesic
328 ecosystems transition into to grazer-dominated ecosystems at lower rainfalls (Bond, 2005; Archibald &
329 Hempsen, 2016). However, it is also possible for feedbacks between grass communities and their
330 consumers to maintain either fire-adapted or grazer-adapted grasslands within a single landscape
331 (Hempsen et al. TREE in press). Here the genetic pool of grasses is similar, and differentiation occurs
332 through filtering of grass functional types, and through feedbacks to consumer regimes. Because grazing
333 promotes low-statured grasses with leaf traits that deter fire, and fire promotes tall-statured grasses
334 with leaf traits that deter herbivores (Figure 2, Table 2), these habitat types should be quite distinct in
335 terms of species composition. If the grasses in grazing lawns are also phylogenetically distinct from
336 those in surrounding tall grass landscapes, this would be strong evidence for different evolutionary
337 origins of fire vs herbivore-adapted ecological strategies. Alternatively, grasses from all lineages have
338 the capacity to evolve fire and herbivore-tolerance, in which case these communities would not show
339 strong phylogenetic patterns.

340 Field data indicate that geographically distant grasslands show similar functional and phylogenetic
341 responses to changes in fire regime, but divergent responses to changes in grazer regime (Forrestel *et*
342 *al.*, 2014, 2015). This implies that grazer adaptations vary more between regions than fire adaptations,
343 and are dispersed more widely in the phylogeny, a hypothesis that can now be tested using the traits
344 and life-history strategies identified here. Different suites of grazers, with different feeding ecologies,
345 evolved independently across the globe (Owen-Smith, 2013), whereas fire regimes are an outcome of
346 climate and fuel properties and will converge in conditions where these are similar (Archibald, 2013).
347 Demonstrated links between fire and grasses of just one lineage – the Andropogoneae - support this
348 (Ripley *et al.*, 2015; Simpson *et al.*, 2016).

349 Moreover, plant height is a key plant functional trait (Westoby, 1998; Díaz *et al.*, 2016) and selection for
350 a vertical (fire resistor) vs lateral (grazer resistor) growth, will have consequences for light competition
351 as well as other aspects of plant life history. For wind-pollinated plants like grasses height affects gene
352 flow and dispersal distance (Rodger *et al.*, 2018), with consequences for plant range size, and rates of
353 speciation (Boucher *et al.*, 2017). We would therefore expect that grazer adapted grasses should have
354 smaller ranges overall, although this would depend on dispersal mode.

355 It is important to recognise that fire is not actually a very strong filter for grasses: the absence of wood,
356 and concentration of meristems at/below the soil surface mean that most fires burn material that is
357 already dead and ready to be discarded (slow creeping back-fires (Trollope *et al.*, 2002) are the

358 exception here and might be the selective force behind leaf-sheath retention and dense basal tussocks).
 359 Individual-level resistance to fire therefore becomes less important than community-level processes
 360 after the fire (Pausas & Lavorel, 2003). Grass species with high growth rates and rapid height gain are
 361 effective competitors for space and light in the high-resource environment after a fire, and these tall
 362 grasses are more flammable (high rates of biomass accumulation and connected fuels). Thus, tall grasses
 363 competing for light reinforce a fire feedback to increase flammability (D'Antonio & Vitousek, 1992;
 364 Rossiter *et al.*, 2003). High-fire environments therefore exclude other herbaceous growth forms more
 365 through competition and shading than through the frequency of fire, whereas it is the fire itself that
 366 excludes many woody growth forms from these ecosystems.

367 We therefore expect:

- 368 1. Lower functional diversity in extreme fire/grazing situations, with highest functional diversity in
 369 systems with both consumers. This does not necessarily translate into higher species richness, as
 370 that will depend on evolutionary processes related to diversification rates and dispersal.
- 371 2. Turnover in life-forms and species across regional-scale gradients will be reflected at a
 372 landscape-scale between heavily grazed and frequently burned patches. These will emerge due
 373 to reinforcing feedbacks: palatable grasses are not flammable, and fire-resistant grasses are not
 374 necessarily grazing-resistant.
- 375 3. Grazer-adapted grasses are phylogenetically distinct from fire-adapted grasses, and likely more
 376 widely dispersed across the phylogeny. This is because of the wider diversity of grazers globally.
- 377 4. Laterally-spreading, grazer-adapted life histories will impose constraints on gene-flow and
 378 dispersal that will increase speciation rates and reduce species range sizes.
- 379 5. The annual "generalist avoider" life-history strategy is one outcome of intense heavy grazing,
 380 but not the only one. There is a wide range of grazer-adapted life histories within perennial
 381 grasses that has so far not been elaborated.

382

383 **Discussion**

384 We have demonstrated here that making sense of the ecological strategies found in consumer-
 385 controlled environments requires integrating understanding across disciplines. In particular, in
 386 grasslands it is only possible to develop clear predictions around community assembly and evolution
 387 when the drivers of fire and large mammalian herbivory are considered together, because adaptations

388 for one type of consumer can affect how susceptible plants are to other consumers. We therefore
389 advocate that datasets on fire and grazing traits be collated and the expected relationships tested.

390 Key to integrating fire ecology and trophic ecology was developing a theoretical framework related to
391 attraction/avoidance, resistance, and tolerance of consumption (Figure 1). This framework blends
392 aspects of previous conceptual models, but makes a strong distinction between resistance traits (that
393 act while a plant is being consumed), and attraction/avoidance traits (that determine whether plants are
394 likely to be consumed in the first place). Moreover, it also forces trophic ecologists to raise questions
395 about the degree to which palatability can be selected for – something fire ecologists have been
396 grappling with for years.

397 Once fire and herbivore adaptations can be placed on common axes (Figure 3), it is possible to assess
398 the degree to which they are correlated or antagonistic. In this example we show clearly that fire and
399 herbivore adaptations in grasses are often contradictory: that flammable grasses are not palatable, and
400 that grazing-resistant grasses are not necessarily fire-resistant (Figure 2, Table 2). This then results in
401 expectations about the dominance of different grass life history strategies across environmental
402 gradients, and also the degree to which fire and herbivory can shape ecosystems and act to re-inforce
403 particular consumer regimes through altering species composition.

404 It would be good to ask similar questions regarding fire and herbivory adaptations in trees and non-grass
405 herbaceous species, and to expand this thinking to other consumers such as insect herbivores. Testing
406 this framework in these different contexts will demonstrate its universality.

407 The tolerance strategies associated with different positions on the avoidance-attraction continuum have
408 already been identified for trees (Figure 3). For example in pines there is correlated evolution in traits
409 associated with attracting and tolerating vs avoiding and resisting fire (Schwilk & Ackerly, 2001; He *et al.*,
410 2012). Moreover, within savanna trees it has been shown that growth forms associated with resisting
411 herbivory can make trees less resistant to fire (Archibald & Bond, 2003), and that this can result in
412 sorting of savanna tree communities in space (Charles-Dominique *et al.*, 2015; Osborne *et al.*, 2018), and
413 over time (Staver *et al.*, 2007) as the consumer changes. Thus one of the major predictions of this
414 framework appears to hold true for woody species.

415 It has always been difficult to fit life history strategies associated with herbivory and fire into classic
416 ecological theory (Bond & Midgley, 2001; Pausas & Keeley, 2014). The ruderals in Grime's (1977) CSR
417 scheme are predicted to occur in highly disturbed environments, but this strategy represents only

418 population-level persistence and cannot encompass the full spectrum of strategies described here
419 (Figures 1,3). However, as discussed above, it should be possible to make predictions about what
420 combination of avoidance, resistance and tolerance traits are more likely for plants in different
421 environments, and these need to be reconciled with the strategies identified for carbon capture, water
422 and nutrient use efficiency, and reproduction in the same environments. For example, avoiders, which
423 have defensive chemicals in their leaves, have been shown to characterise Grimes's 'stress-tolerator'
424 strategy because protecting leaf and above-ground biomass is important when this biomass is hard-won
425 (Coley *et al.*, 1985).

426 Many of the traits we discuss here in the context of fire and herbivory are also considered important in
427 the broader trait and plant economics literature, such as C:N ratio and plant height (Westoby, 1998;
428 Wright *et al.*, 2004; Díaz *et al.*, 2016). However, classic leaf trait data are not sufficient to fully quantify
429 consumer-driven life histories, and there is a need for further quantification and empirical testing of
430 these consumer-related traits. To enable this in the supplementary material (SM) we describe sampling
431 protocols for the fire and grazer traits mentioned in Table 2, and contrast them with similar traits in
432 woody plants. We include traits associated with population and landscape-level persistence although we
433 were not able to elaborate on these here.

434

435 **Conclusions:**

436 We have developed a framework for thinking about consumer-driven ecological strategies in terms of
437 three components - avoidance/attraction, resistance, and tolerance. We predicted that successful
438 ecological strategies in consumer-driven environments require unique combinations of traits, i.e. not all
439 parts of this strategy space are occupied, but there are combinations of avoidance, resistance and
440 tolerance traits that will be successful for a particular consumer.

441 We then described grass traits associated with avoidance/attraction, resistance and tolerance of fire and
442 mammalian herbivory, and demonstrated that these are not aligned: i.e. fire-adaptations affect a plant's
443 avoidance, resistance, and tolerance of herbivory and vice versa. We used this information to develop
444 expectations on what types of grass ecological strategies will be successful in environments exposed to
445 both fire and herbivory, and discuss the environmental conditions that are most likely to favour
446 particular strategies; i.e. we expand on Coley's (1985) Resource Availability Hypothesis.

447 This represents a first step towards reconciling two disparate fields of ecology (fire and trophic ecology)
448 that have a lot to offer each other. It provides tools for predicting both the diversity of life history
449 strategies and the plant species diversity under different consumer regimes.

450

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458

459 **Author Contributions:** SA, GPH and CL jointly conceived the manuscript and developed the ideas. SA
460 wrote the manuscript with contributions from GPH and CL. GPH perfected the figures.

461

462 Table 1: Summarising the different ways that terms associated with fire and herbivore adaptations have
 463 been used in key texts and how we define them here.

464

	Crawley 1983 and Belsky <i>et al.</i> 1993	Rosenthal & Kotanen 1994	Stowe <i>et al.</i>, 2000	Briske 1996	Strauss & Agrawal 1999	Pausas & Lavorel 2003	In this manuscript
Degree to which a plant is palatable or flammable	Resistance (Avoidance)	Avoidance	Resistance	Avoidance (biochemical)	Resistance	Resistance	Avoidance
Protecting plant parts during a defoliation event	Resistance (Avoidance)	Avoidance/ Tolerance	Resistance	Avoidance (morphological)	N/A	Avoidance/ tolerance	Resistance
Ability to regrow lost biomass/recover fitness following a consumption event	Resistance (Tolerance)	Tolerance	Tolerance	Tolerance	Compensation/ Tolerance	Resprouting capacity	Tolerance (individual-level persistence)
Ability to recover from seed following a consumption event	N/A	N/A	N/A	N/A	N/A	Population level persistence	Population level persistence
Ability to take advantage of space/resources following a consumption event)	N/A	N/A	N/A	N/A	N/A	Community level persistence	Tolerance
Ability to recolonize via dispersal following a defoliation event.	N/A	N/A	N/A	N/A	N/A	Landscape level persistence	Landscape level persistence

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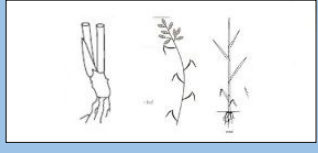



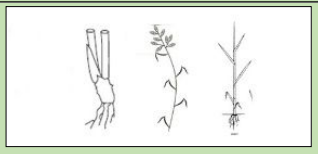

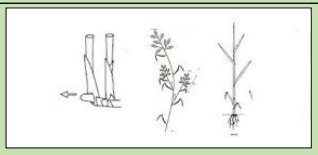
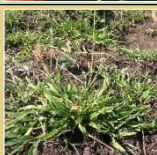
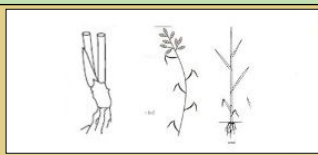
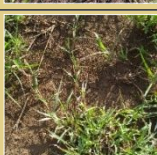
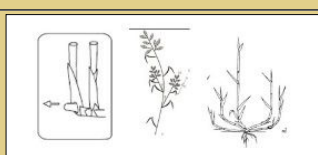

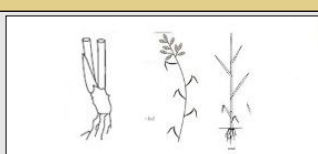
467 Table 2: Key grass traits associated with attraction/avoidance, resistance, and tolerance of grazing vs
 468 fire. Items coloured blue represent traits that are compatible (i.e. are shared for grazing and fire), and
 469 red traits that are antagonistic (i.e. are opposed for grazing and fire). Traits listed in the
 470 attraction/avoidance section are those that maximise the attractiveness of grasses to either grazers or
 471 fire. Generalist strategies that work for both consumers are possible in terms of tolerance, but less so
 472 for resistance and avoidance.

	Grazing	Fire
Attraction/avoidance traits (palatability/flammability)	Low C:N ratio High bulk density High leaf moisture content Low tannin content High phosphorus content Large leaves High salt content Low silica content	High C:N ratio Low bulk density Low leaf moisture content High tannin content Low phosphorus content Thin leaves High biomass
Resistance traits	Meristems at/below the soil surface Lateral growth (extravaginal branching, prostrate culms, stoloniferous/rhizomatous) Strong root system which prevents uprooting Leaves and culms with low tensile strength (alternatively) Spikey hard culms/spines that protect aerial leaf material.	Meristems at/below the soil surface Vertical growth (intravaginal branching, erect culms, short rhizomes) Distal tillering to move flames away from the basal meristems Retain leaf sheaths to protect buds
Tolerance traits (individual level persistence)	Rapid resprouting/large bud bank Substantial stored reserves	Rapid resprouting/large bud bank
Population-level persistence traits	Geniculate growth form (flowers not eaten) Clonal growth (rooting at nodes)	Early seed set and release (before fire season) Smoke stimulated germination Seed dormancy
Landscape-level persistence traits	Good dispersal ability (especially ecto- and endozoochory) Rapid germination and establishment Short generation times	Good dispersal ability (especially wind dispersal) Rapid germination and establishment Short generation times

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175 Table 3: There are theoretically four distinct life-history strategies associated with fire and grazing. These are exemplified in ~8 different growth forms that are
 176 common in tropical grassland flora, each associated with particular combinations of plant traits (Box 2) that result in unique architectures.

Life history strategy	Potential growth forms	Examples	Image	Key traits
1: Fire resistor, grazer avoider.	Aerial flammable tussocks - with vertical growth, and distal tillering that maintains flames above the soil surface (fire-resistance largely achieved through being flammable).	<i>Hyparrhenia filipendula</i> , <i>Schizachyrium sanguineum</i>		
	Basal resistor tussocks - with vertical growth and dense intravaginally branched culms that protect buds from fire (fire resistance largely achieved through protecting basal meristems).	<i>Panicum natalense</i> , <i>Alloteropsis semialata</i> , <i>Aristida junciformis</i>		
2: Grazer resistor, fire avoider	Mat-forming lawn grasses - with extravaginal branching, laterally-growing stems, and palatable high-density leaves (require grazing to avoid self-shading and prevent being out-competed).	<i>Stenotaphrum secundatum</i> , <i>Cynodon dactylon</i>		
	Cushion-forming grasses - maintain culms and leaf bases below the soil surface, leaving palatable leaf blades within graze height (require grazing to avoid self-shading and prevent being out-competed).	<i>Sporobolus nitens</i> , <i>Microchloa kunthii</i>		
	Stemmy, cage-like architecture that protects green leaves from being eaten.	<i>Pennisetum mezianum</i> , <i>Triodia basedowii</i>		
3: Generalist tolerators	Compensators: tussock grasses that can resist uprooting and have stored reserves, and thus persist when lightly/briefly defoliated.	<i>Themeda triandra</i> , <i>Heteropogon contortus</i> , <i>Digitaria eriantha</i>		
	Growth-form switchers - that can grow laterally with stolons when grazed, but grow vertically in tall, fire-prone communities.	<i>Urochloa mosambicensis</i> , <i>Panicum coloratum</i>		
4: Generalist avoiders	Sparsely branched tussocks with thin leaves, low productivity, and low bulk density.	<i>Aristida congesta</i> , <i>Eragrostis rigidior</i>		

478

479 **Box 1: Resolving terminology**

480 There is no consistent terminology for discussing fire and herbivory functional traits. Here we set up the
 481 definitions we will use for this paper and discuss how these contrast with those used by other
 482 researchers.

483 BEFORE DEFOLIATION OCCURS:

484 **Palatability: Having leaf material that is preferred by grazers**485 **Flammability: Having leaf material that is easily ignited and carries a fire**

486 **Avoidance: Having leaf material that is not preferred or easily ignited.** We take a constrained
 487 definition here where avoidance refers to a mechanism for avoiding the probability of being exposed to
 488 a stress via low palatability or low flammability. Traits that reduce the impact of a stress when it occurs
 489 (e.g. mechanical plant defence strategies such as spines or thick bark) confer resistance and are
 490 considered elsewhere. In this we differ from other key references such as Briske (1996), but the reasons
 491 for this break from tradition will become evident.

492 Plants therefore exist on a continuum of **avoidance vs attraction** of defoliation. Plants that are
 493 “attractive” to grazers are termed palatable, and plants that are “attractive” to fire are termed
 494 flammable. The traits associated with this continuum could be considered *effect traits* sensu Lavorel and
 495 Garnier (2002).

496 DURING DEFOLIATION:

497 **Resistance: the ability to protect certain plant parts from being lost.** Depending on the ecological
 498 strategy of the plant this could be leaf material, structural material (stems/branches), or basal
 499 buds/roots, and the resistance strategy defines the degree to which the plant will need to recover
 500 from/compensate for a defoliation event. In this we diverge from Strauss and Agrawal (1999) who use
 501 the term resistance in the same way we use avoidance.

502 AFTER DEFOLIATION/DURING THE LIFETIME OF THE PLANT:

503 **Tolerance: the ability to survive defoliation and to reproduce/spread while exposed to defoliation.** In
 504 this we are aligned with Strauss and Agrawal (1999) who define it as “the degree to which plant fitness is
 505 affected by herbivore damage relative to fitness in the undamaged state”. Highly tolerant plants survive
 506 and spread under higher levels of consumption. We also consider competitive ability (i.e. the ability to
 507 capture space/resources and benefit from a defoliation event) to be a component of this (Pausas &
 508 Lavorel, 2003).

509 OVER EVOLUTIONARY TIMESCALES:

510 **Persistence: whether or not a species is found in a system exposed to fire/herbivory.** This can occur at
 511 an individual, population, or landscape (species) level (Pausas and Lavorel 2003). At an individual level it
 512 is a synonym for tolerance.

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Box 2: Traits associated with fire/grazing adaptations

517 **Bud position:** Grasses have a hemicryptophyte life form with perennating organs at or close to the soil
518 surface, but there is variability in where the buds form. When buds are maintained below the soil
519 surface they are more resistant to uprooting by grazers and protected from fire.

520 **Culm orientation:** Vertical growth increases height gain and light capture and moves flammable material
521 away from the sensitive buds, horizontal growth enables lateral spread and keeps palatable material out
522 of reach of grazers. This trait is very flexible within species (Kellogg, 2015) and over the lifetime of an
523 individual.

524 **Distal tillering (also called aerial branching):** Distal tillering enables space-filling by initiating new shoots
525 from the nodes of existing culms: it increases light capture and aerial biomass for vertically-growing
526 grasses, and is necessary for the branched growth form of mat-forming grasses (Kellogg, 2015).

527 **Stemminess:** Thick, woody culms enable height gain, and when associated with distal tillering can create
528 a cage-like architecture. Moreover some grass species also have spines which achieve the same effect
529 (Clayton *et al.*, 2014). Like spines on trees these stems increase resistance of certain grass species to
530 grazing (O'Reagain & Mentis, 1989).

531 **Extra vs intravaginal branching:** Tillers produced from intravaginal branching result in a caespitose
532 architecture that enables height gain and protects basal buds within layers of leaf sheaths in a dense
533 basal tussock. Tillers produced through extravaginal branching enable space-filling and lateral growth,
534 but expose buds: the stolons of mat-forming grasses form from extravaginal tillers.

535 **Storage:** Some grasses, mostly pooids, have below-ground storage organs of modified leaves or stems
536 (Kellogg, 2015). Rhizomes, stolons, and roots store sufficient reserves for rapid resprouting after once-
537 off defoliation in most species, but a truly tolerant plant that can persist in the face of repeat defoliation
538 would need to maintain a positive carbon balance, and could not depend on stored reserves (Belsky,
539 1986).

540 **Photosynthetic pathway:** The high C:N ratio that strongly correlates with flammability is to some degree
541 a consequence of C4 photosynthesis but this is an over simplification: flammable C3 species with high
542 C:N ratios, and palatable C4 species with low C:N ratios exist.

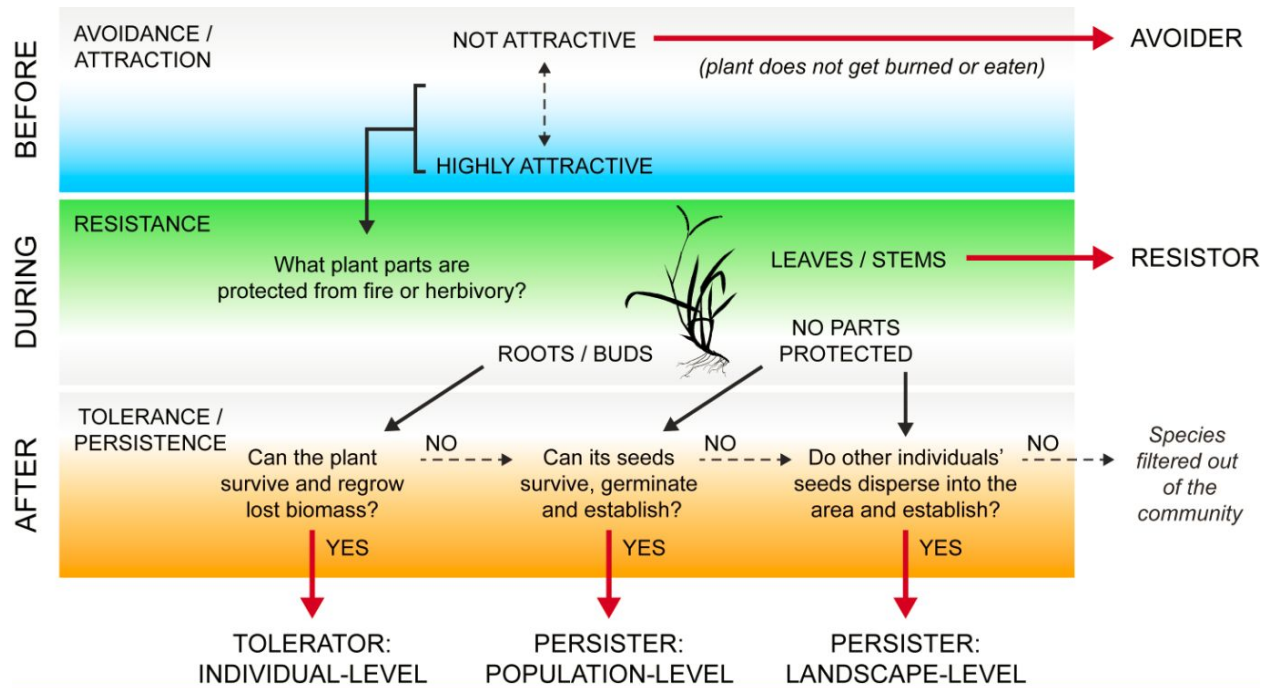
543 There is much phylogenetic sorting of the key traits mentioned above: Distal tillering is unknown in all
544 pooideae grasses, but is common in Panicoids and particularly common in Andropogonoids (Kellogg,
545 2015). Buds below the soil surface and rhizomes are ancestral to Poaceae. Moreover, extravaginal
546 branching is also the ancestral trait (Linder *et al.* 2017), although the tussock, intravaginally branched
547 growth form is far more common currently across Poaceae (Kellogg, 2015).

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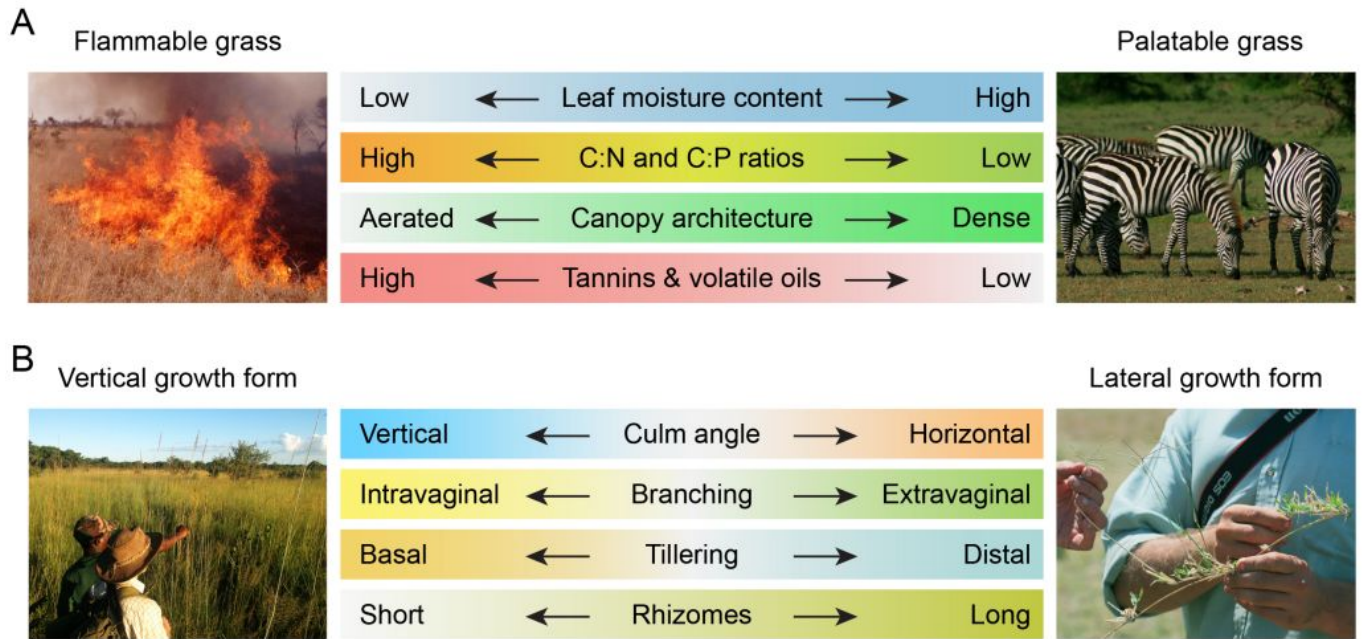
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554 Figure 1: Describing how traits associated with avoidance, resistance, and tolerance act across time
 555 periods and scales (plant part, individual, population or landscape) to filter plant communities. Different
 556 axes, associated with different plant traits, operate before, during, and after defoliation. If a plant has
 557 the right combination of avoidance, resistance, and tolerance traits then it can persist in a community,
 558 otherwise it is filtered out. In this formulation resistance is a prerequisite for tolerance but the degree of
 559 resistance determines the level of tolerance required (i.e. this doesn't contradict trophic ecology
 560 theory). See Figure 3 for an example of how this scheme can be applied to predict grass life history
 561 strategies for fire and grazing.

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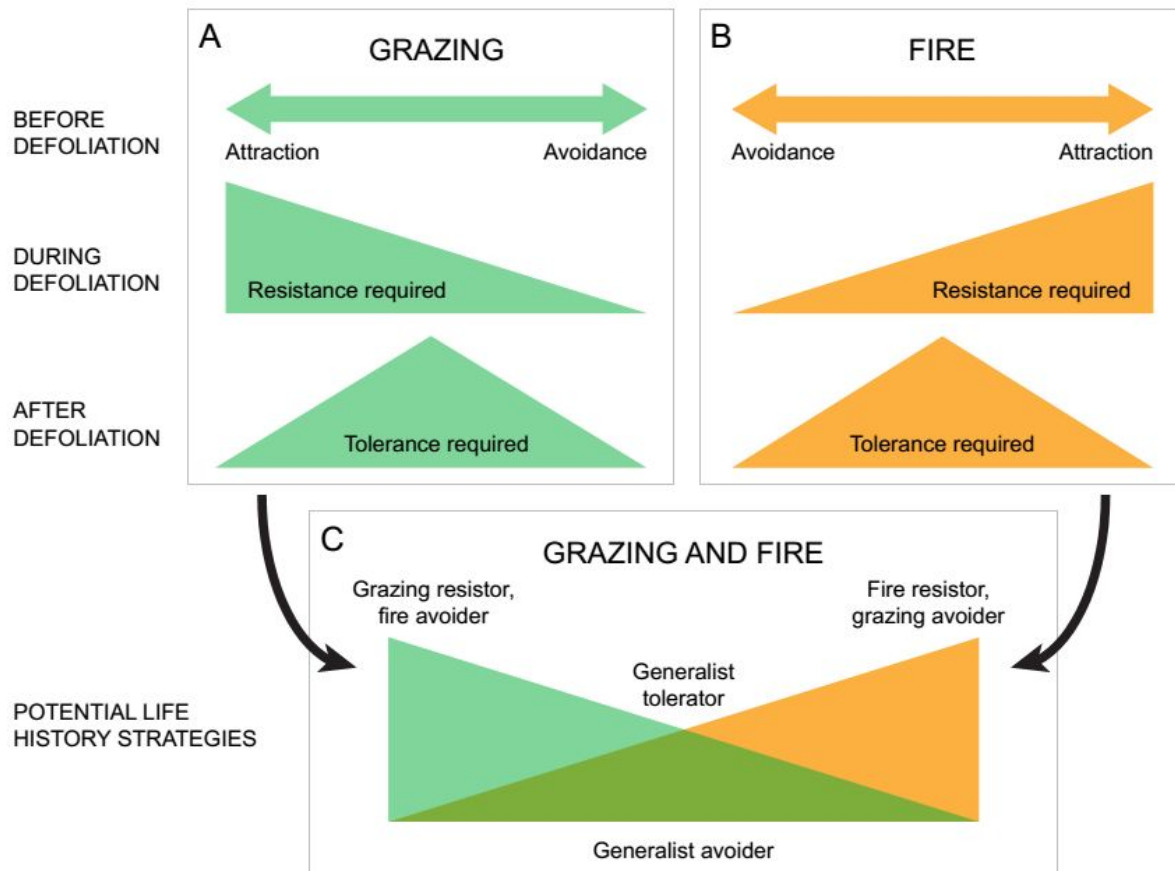
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566 Figure 2. A: Contrasting flammable and palatable grass traits. Due to the differences between fire, a
 567 physical process, and mammalian herbivores, that biologically metabolise their food, the traits
 568 associated with palatability are opposite to those associated with flammability, and plants that are very
 569 flammable are likely to be largely unpalatable. B: Contrasting the traits associated with vertical and
 570 lateral growth in grasses: due to differences in the traits required to resist herbivore mouthparts vs hot
 571 flames grazer adapted grasses tend to grow laterally whereas fire-adapted grasses tend to grow
 572 vertically.

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577 Figure 3: Four potential life history strategies emerge when fire and grazing traits are compared on axes
 578 associated with avoiding, resisting, and tolerating fire and herbivory. Key to this model is the fact that
 579 traits associated with flammability are different from those associated with palatability. Likewise,
 580 because fire resistance traits are different from grazing resistance traits, there is no generalist resistor
 581 strategy, but there can be a generalist tolerator strategy.

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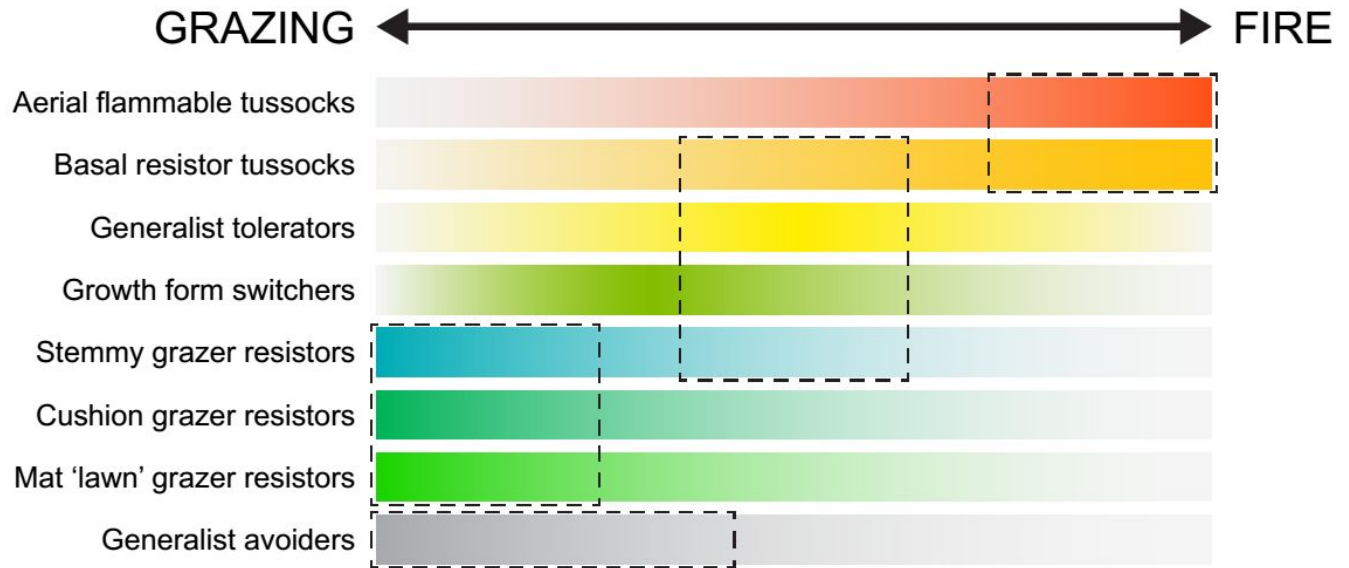
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595 Figure 4: Showing how functional composition is expected to change across a 'consumer' gradient from
 596 frequent fire to intense grazing. Higher functional diversity is expected in environments with both
 597 consumers present. These different communities could be found within a single landscape (e.g. Arnold
 598 *et al.* 2014), or across the regional tropics – where fire-prone mesic ecosystems give way to grazer-
 599 dominated ecosystems at lower rainfalls (Archibald & Hempson, 2016). High grazing can potentially
 600 result in two ecosystem states: grazing lawns, or systems dominated by generalist avoiders. Generalist
 601 avoiders are unlikely to dominate in high fire environments as they are inferior competitors.

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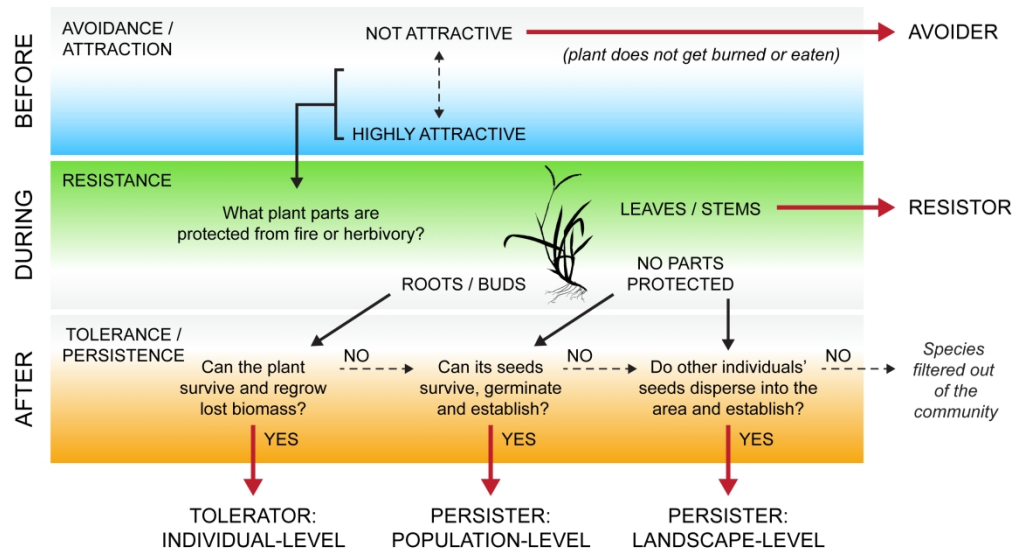


Figure 1: Describing how traits associated with avoidance, resistance, and tolerance act across time periods and scales (plant part, individual, population or landscape) to filter plant communities. Different axes, associated with different plant traits, operate before, during, and after defoliation. If a plant has the right combination of avoidance, resistance, and tolerance traits then it can persist in a community, otherwise it is filtered out. In this formulation resistance is a prerequisite for tolerance but the degree of resistance determines the level of tolerance required (i.e. this doesn't contradict trophic ecology theory). See Figure 3 for an example of how this scheme can be applied to predict grass life history strategies for fire and grazing.

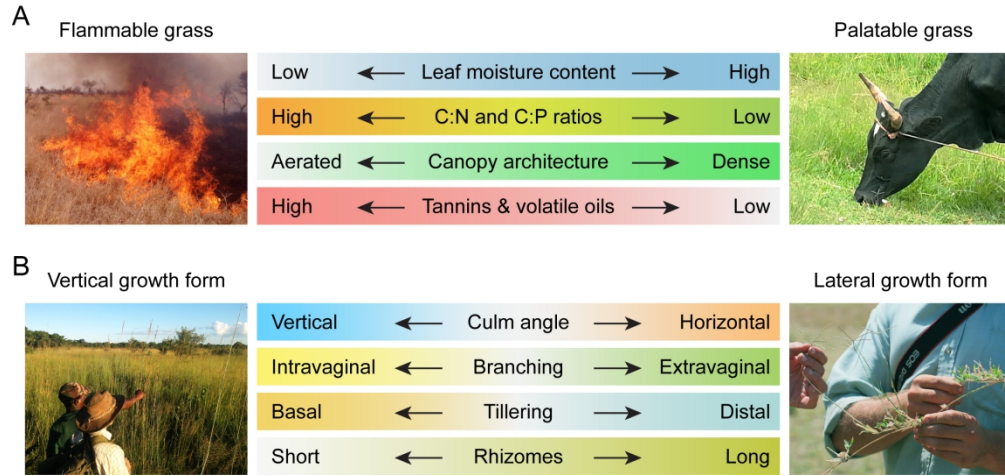


Figure 2. A: Contrasting flammable and palatable grass traits. Due to the differences between fire, a physical process, and mammalian herbivores, that biologically metabolise their food, the traits associated with palatability are opposite to those associated with flammability, and plants that are very flammable are likely to be largely unpalatable. B: Contrasting the traits associated with vertical and lateral growth in grasses: due to differences in the traits required to resist herbivore mouthparts vs hot flames grazer adapted grasses tend to grow laterally whereas fire-adapted grasses tend to grow vertically.

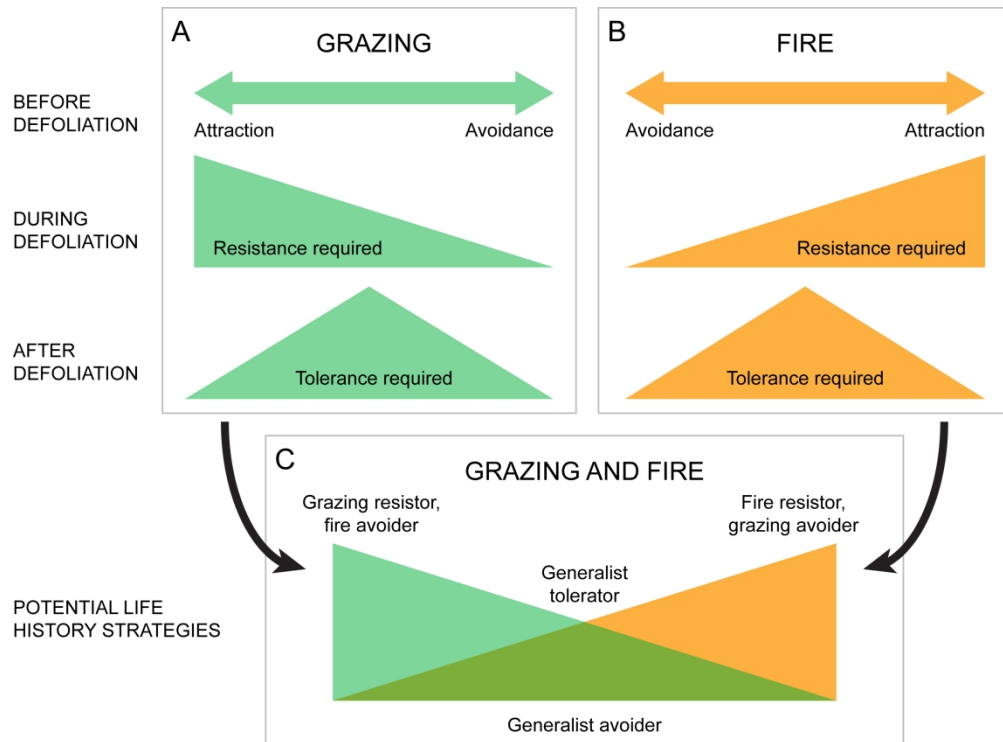


Figure 3: Four potential life history strategies emerge when fire and grazing traits are compared on axes associated with avoiding, resisting, and tolerating fire and herbivory. Key to this model is the fact that traits associated with flammability are different from those associated with palatability. Likewise, because fire resistance traits are different from grazing resistance traits, there is no generalist resistor strategy, but there can be a generalist tolerator strategy.

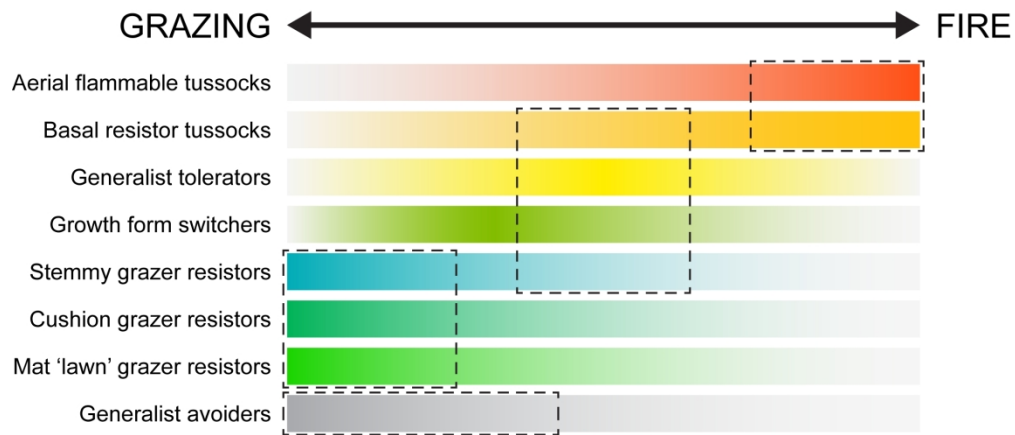


Figure 4: Showing how functional composition is expected to change across a 'consumer' gradient from frequent fire to intense grazing. Higher functional diversity is expected in environments with both consumers present. These different communities could be found within a single landscape (e.g. Arnold et al. 2014), or across the regional tropics – where fire-prone mesic ecosystems give way to grazer-dominated ecosystems at lower rainfalls (Archibald & Hempson, 2016). High grazing can potentially result in two ecosystem states: grazing lawns, or systems dominated by generalist avoiders. Generalist avoiders are unlikely to dominate in high fire environments as they are inferior competitors.