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***A functional ecology framework for understanding and predicting animal responses to plant invasion***

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1 **Abstract**

2 Plant invasions can alter food resources and habitat conditions that structure animal  
3 communities. These effects are negative for many native animals, but neutral or even positive  
4 for others. Understanding why we see this variation in responses is critical for mitigating  
5 invasion outcomes, yet we lack a synthetic framework to explain and potentially predict effects  
6 of invasive plants on native animals. We propose a trait-based framework for understanding  
7 how invasive plants affect native fauna, which draws on community assembly, niche, and trait  
8 theories to define the mechanisms by which invasive plants alter ecological conditions relevant  
9 to native animals. This approach moves beyond prior frameworks by explicitly accounting for  
10 the context dependency that defines most ecological interactions and invasion outcomes.  
11 Namely, by characterizing the plant community in terms of functional effect traits (e.g., seed  
12 size) relevant to consumers and quantifying those traits along a consumer resource axis, we can  
13 map the functional relationship between plant resources and animals. We can then delineate how  
14 plant invaders alter the plant community and associated resource axes to restructure consumer  
15 communities. We apply this framework to case studies of rodents, spiders, and birds to  
16 demonstrate the process and explore its utility. For example, we show that by focusing on how a  
17 nonnative grass altered seed sizes (relative to the native plant community), we can better  
18 understand declines in abundance of granivorous rodents and increases in opportunists. This  
19 approach can elucidate which native animals will be most likely affected by plant invasion, as  
20 well as how and why they might respond. Moreover, these mechanistic explanations provide  
21 working hypotheses for how invasive plants impact native animals more generally, with potential  
22 for predicting impacts of future invaders.

23 **Keywords** community assembly · conceptual framework · functional effect traits · niche theory  
24 · plant invasion · wildlife

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## 34 **Introduction**

35 Human activities have altered nearly all ecosystems on the planet, disrupting ecological  
36 functions and threatening biological diversity in myriad ways (Vitousek et al. 1997). However,  
37 not all of these changes have resulted in population declines or extinctions of native species;  
38 some species benefit and even thrive under conditions created by human-induced change (see  
39 Sih et al. 2010, 2011). A key challenge for conservation, and ecology in general, is to  
40 understand how variation in species' responses to shifting conditions can predict which  
41 organisms will be winners and which will be losers in the face of anthropogenic change (Colles  
42 et al. 2006; Sih et al. 2010; 2011).

43 One ubiquitous and powerful source of human-induced global change is exotic plant  
44 invasions. Because plants provide the base for primary productivity, food-web interactions, and  
45 habitat structure, invasive plants can alter biotic and even abiotic conditions in ways that can  
46 strongly influence native fauna (Crooks 2002; Levine et al. 2003). As with other forms of  
47 anthropogenic change, invasive plants can affect many native species negatively and even cause  
48 local extinctions, but effects on other species can be neutral or even positive (e.g., Murray et al.  
49 2007; Litt and Steidl 2011; Pyšek et al. 2012; Smith et al. 2016; Nelson et al. 2017).  
50 Understanding why some native fauna respond negatively to invasive plants and others  
51 positively is critical for predicting and mitigating invasion outcomes. Several researchers have  
52 highlighted important concepts (Sax et al. 2005; Martin and Murray 2011) and identified key  
53 mechanisms that help to explain native faunal responses to invading plants, particularly  
54 evolutionary responses (e.g., Strauss et al. 2006; Ghalambor et al. 2007; Sih et al. 2011; Berthon  
55 2015); we describe these contributions below. However, we still lack a synthetic framework that  
56 can integrate these and other factors to fully explain and potentially predict effects of invasive  
57 plants on native animals. Here, we propose a new framework to address key knowledge gaps.

58 Most frameworks for predicting invader impacts on native species recognize that  
59 alignment between the traits of native and invading species is central to understanding native  
60 species responses to invaders (e.g., Ricciardi et al. 2013; Sih et al. 2010, 2011). However,

61 existing frameworks do not sufficiently address the importance of ecological context (see McGill  
62 et al. 2007, Catford et al. 2021), referred to here as context dependence or conditionality. This  
63 context dependence establishes the specific conditions that determine how well the native species  
64 is aligned with invader traits and invader-induced changes within a given system. Some  
65 frameworks ignore context entirely, proposing that the degree of specialization of native species  
66 can predict their response to invaders across systems, under the premise that generalist species  
67 will have a greater likelihood of aligning with or rapidly adapting to new conditions than  
68 specialists (Colles et al. 2009). However, while generalists are more likely to fit invader-driven  
69 change on average, specialists can benefit far more than generalists when invaders happen to  
70 alter conditions in ways that align with their specific niche requirements (Colles et al. 2009;  
71 Hansen et al. 2009; Smith et al. 2016). Other frameworks have attempted to incorporate basic  
72 aspects of conditionality without explicitly addressing context. For example, Martin and Murray  
73 (2011) introduced a framework that incorporates general understandings of wildlife-habitat  
74 relationships to predict responses of native fauna to plant invasions. Although this approach  
75 incorporates some degree of context dependence, resulting predictions were not widely  
76 supported because they were too generic. For example, when they applied their framework to  
77 specific case studies that explicitly incorporated community context, it seemed to predict  
78 outcomes reasonably well, but when applied across many species and conditions without  
79 accounting for community-specific context, general predictions were not borne out.

80 In sum, the context dependence of invasions remains an enigma to understanding  
81 invasion outcomes. Overcoming this conceptual gap requires first defining the niche of the  
82 native fauna of interest, then determining how plant invaders have or will change aspects of that  
83 niche space, to finally interpret how those changes might alter the native species' abundance.  
84 Below, we draw from community assembly, trait, and niche theories to construct a framework  
85 for explicitly delineating the alignment between native species' traits and invader-driven changes  
86 in a community context.

## 87 **A Framework for Understanding Invader-Driven Change: Incorporating Ecological** 88 **Context**

89 Community assembly theory (Keddy 1992; Weiher and Keddy 1999) offers a framework  
90 for delineating the niches of native species prior to invasion in a given system. This context

91 establishes the baseline for understanding how plant invasion reassembles the plant community  
92 to alter niche dimensions relevant to native consumers. In community assembly theory, species  
93 occurrence and relative abundance are determined by the interactions between species'  
94 functional traits and local filters (Keddy 1992; Weiher and Keddy 1999). The abiotic conditions  
95 present in a system provide one set of filters that exclude species in the regional pool whose  
96 traits and fundamental niche requirements do not match local conditions (Fig. 1a). Biotic  
97 interactions with other organisms in the community (including food items, competitors,  
98 predators, pathogens) create another set of filters that exclude additional species and constrain  
99 the fundamental niches of remaining species (Fig. 1a, Hutchinson 1957). In hierarchical and  
100 interactive ways, these abiotic and biotic filters determine the composition, structure, and  
101 function of local communities (Fig. 1a, Keddy 1992; Weiher and Keddy 1999) and define the  
102 realized niches of individual species (Hutchinson 1957).

103 From this starting point, community assembly theory also provides the means for  
104 understanding how “community reassembly” (*sensu* Smith et al. 2016; see also “response rules”  
105 of Keddy 1992) driven by invading plants alters conditions that affect the niche space of native  
106 animals and hence their success under the newly defined conditions. Because key functional  
107 traits and their interaction with the environmental context define the native niche space (herein  
108 we refer to the Hutchinsonian niche, Hutchinson 1957; *sensu* Leibold 1995) as described above,  
109 understanding that niche space and how plant invasions change it is key to delineating the  
110 alignment between the invader and native traits to understand and predict invasion outcomes.

111 Historically, the niche concept evolved separately in the plant and consumer realms, but  
112 merging these perspectives is necessary to understand how changes induced by invasive plants  
113 may affect the niche space and success of native animals. Theoretically, niches of consumers  
114 relative to their food and habitat dimensions are depicted as resource utilization curves  
115 (MacArthur and Levins 1967), with the breadth of these curves delineating the relative  
116 specialization of different consumers and the peak of each curve identifying the resource optima  
117 for each species (Fig. 1c). Hence, narrower utilization curves reflect greater specialization (see  
118 species x and z in Fig. 1c) and broader curves reflect greater generalization (species y in Fig. 1c).  
119 These niche dimensions translate to relative success of different species as measured by relative  
120 abundance or species-level fitness (*sensu* Chesson 2000, see also HilleRisLambers et al. 2012)

121 (Fig. 1d). Here, we assume that bottom-up processes provide the basis for understanding food  
122 webs (*sensu* Odum and Odum 1953) and later address other biotic drivers (e.g. competition,  
123 predation, see Conclusions). For plants, niche dimensions have commonly been expressed as  
124 curves quantifying fitness/abundance relative to abiotic axes (Whittaker 1965; Whittaker et al.  
125 1973). However, because we are interested in how plants provide the resources to consumers  
126 that structure consumer niches, we must translate the abundance distribution of plant species into  
127 plant-derived resources relevant to the consumers by focusing on important “functional effect  
128 traits” of the plants (*sensu* Violle et al. 2007; see Fig. 1b). For example, focusing on plant traits  
129 like leaf nitrogen content or seed size provides a direct linkage between plant traits and consumer  
130 feeding niches. By integrating traits measured at the individual plant level, we can obtain  
131 community-level metrics (see Violle et al. 2007). Here, we propose that individual traits are  
132 averaged for each species and the abundance of each species is then quantified (via cover or  
133 biomass estimates) to map out the distribution and relative abundance of community-level  
134 functional effect traits (Fig 1b). Re-conceptualizing the plant niche in this way provides a  
135 common denominator directly linking resource production to consumer utilization, allowing us  
136 to evaluate how changes induced by an invasive plant can shift the resource base to affect  
137 consumers (Fig. 1). Moreover, when such functional effect traits double as plant performance  
138 traits that are strongly tied to plant life-history tradeoffs, these linkages can provide powerful  
139 insights into plant-animal interactions (e.g., Dylewski et al. 2020).

140 The community assembly processes described above therefore establishes the essential  
141 context that defines the native plant and animal communities, their realized niches, and their  
142 inter-relationships. This (Fig. 1b and c) provides the starting point to understand how plants  
143 affect the composition and relative abundance of native consumers (Fig. 1d). The same concepts  
144 can then be used to delineate how plant invasion restructures or reassembles the plant community  
145 and associated resource axes (Fig. 1e) to restructure consumer communities (Fig. 1g). By  
146 comparing the resource base of both the native and invaded plant communities (Fig. 1b and e)  
147 and linking these to the niche space of the native animals (Fig. 1c and f), we can articulate more  
148 explicitly which system components are changing and how. Based on this information, we can  
149 identify which native animals are most likely to be affected, as well as how and why they might  
150 respond to exotic plant invasion (Fig. 1g). This approach integrates many critical elements of  
151 trait-based ecology and community assembly theory, allowing us to consider how plant invasions

152 can affect consumer assemblages by incorporating the underlying ecological context that is so  
153 often a primary obstacle to understand and ultimately predict community outcomes (McGill et al.  
154 2006; Agrawal et al. 2006; Meyerson et al. 2019).

155 As an example, a community of animals might be comprised of several granivores  
156 expressing the following foraging niches: one readily consumes a range of seed sizes (species y),  
157 one specializes on small seeds (x), and another specializes on large seeds (z) (Fig. 1c). The  
158 abundance/fitness of each consumer (Fig. 1d) will be dictated by its niche constraints (Fig. 1c)  
159 relative to the availability of resources, as expressed along the axis for the community-level  
160 functional effect traits (Fig. 1b). This mapping of the plant community onto the animal resource  
161 space defines the linkage between plant conditions and animal niches and associated traits in a  
162 manner that incorporates ecological context. When a highly invasive nonnative plant invades, it  
163 reassembles the plant community (Fig. 1e), as well as the animal community (Fig. 1g), based on  
164 the specific changes in the resource base relevant to native fauna. Within this framework,  
165 understanding how functional effect traits of the invader alter the conditions (Fig. 1e) and how  
166 these changes align with the resource niche for the native species of interest (Fig. 1f) can help to  
167 explain and predict effects of invasive plants on native fauna (Fig. 1g). Although this example  
168 illustrates only one resource axis, invader-caused changes along multiple resource axes could be  
169 similarly conceptualized to more fully understand effects on native fauna (see rodent case study  
170 below). Importantly, in this simple scenario, we assume that the consumer niches are entirely  
171 resource driven and consumer traits are fixed (i.e., the niche space observed reflects the  
172 fundamental niche and is not plastic). However, adding novel resources into a system may allow  
173 some species to express broader niches than previously possible (see spider case study below).  
174 Such outcomes would indicate that biotic conditions previously constrained or veiled the  
175 fundamental niche spaces of the native organisms, which will complicate prediction of invasion  
176 outcomes.

### 177 **Applying the Framework**

178 Adapting this community-based framework requires that certain baseline information  
179 about the system is available and applied in a stepwise manner. Because different faunal species  
180 or guilds will have different relationships with the native flora, the first step is to identify the  
181 fauna of interest and their linkage (e.g., food, habitat) to the native plant community to determine



182 the plant functional effect traits relevant for the native fauna and to approximate resource  
183 utilization curves of the fauna along that resource axis (Fig. 1c). Importantly, the focus here is  
184 not necessarily on plant species (unless fauna are highly specialized), but rather on plant  
185 functional effect traits relevant to the consumer (*sensu* Violle et al. 2007), that might be  
186 expressed similarly among subsets of functionally similar plant species. Next, the abundance  
187 distribution of the relevant functional effect trait(s) is mapped onto the resource axis by 1)  
188 averaging the effect traits for a representative subsample of individuals to obtain a community-  
189 level value for each plant species or functional group and 2) quantifying the relative abundance  
190 of the plant species or functional group in the community (e.g., cover or biomass, Fig. 1b).  
191 Then, the relative abundance of the fauna of interest can be plotted along the resource axis (Fig.  
192 1d) and ideally supported with appropriate empirical data (e.g., habitat models). Finally,  
193 information is needed to understand how the invader will alter the resource axis by impacting  
194 native plants and distributions of their associated functional effect traits and potentially  
195 introducing novel traits (Fig. 1e) that might alter the faunal community (Fig. 1g).

196 We apply this framework to three empirical case studies to demonstrate the process and  
197 explore its utility for explaining how plant invasions shift native faunal communities. Each  
198 example focuses on a different taxonomic group of native fauna and a different invading plant:  
199 spiders and rodents (below), and warblers (Appendix S1).

## 200 **Spiders in invaded grasslands**

201 Intermountain grasslands of western Montana are highly susceptible to exotic plant  
202 invasions with invaders comprising 25-60% of average total plant cover and 40-57% of average  
203 species richness in the dominant community type (Pearson et al. 2016). The impacts of these  
204 invasions on native plant community composition and structure are well documented (Ortega and  
205 Pearson 2005; Pearson et al. 2012, 2016). Although these impacts are known to spill over to  
206 native fauna, the mechanisms are poorly understood (Litt and Pearson 2013).

207 Many web-building spiders use plants as the primary substrates for anchoring their webs,  
208 rendering them susceptible to the effects of exotic plant invasions that alter vegetation  
209 architecture (Smith-Ramesh 2017; Balkenhol et al. 2018). Within these Intermountain  
210 grasslands, native spiders fall into two distinct web-building strategies, such that plant  
211 architecture defines the general linkage between the plant and spider communities (Pearson

212 2009). Smaller, irregular-web spiders, like *Dictyna* spp., tend to construct their webs entirely  
213 within a single plant. In contrast, larger orb weavers tend to use multiple plants to suspend their  
214 larger webs. Hence, the architectural complexity of individual plants is highly relevant to the  
215 irregular-web spiders, as they can build larger webs in plant species possessing more complex,  
216 expansive architectures (generally greater branching and/or longer branches of the flowering  
217 stalks). In contrast, the orb weavers are less sensitive to individual plant architecture, responding  
218 more to the emergent complexity of the vegetation community derived from the many different  
219 species (Pearson 2009). Therefore, the plant functional effect trait most relevant in defining this  
220 spider community is complexity of plant architecture which readily links to plant functional  
221 groups within the system (Fig. 2a).

222         Within these grasslands, natural plant communities are generally dominated by perennial  
223 grasses, with forb cover about 1/3 that of grasses (Mueggler and Stewart 1980). The grasses  
224 offer very simple architecture, with relatively small, compact flowerheads and flimsy culms and  
225 foliage (pers. obs., DEP). In contrast, the forbs offer more robust and complex architectures,  
226 particularly in terms of their flower stalks (Fig. 2a; Pearson 2009). The irregular-web spiders  
227 can use grasses, but strongly favor forbs, particularly those with the most complex flowering  
228 structures (Pearson 2009). The orb weavers in this system function as substrate generalists using  
229 the full range of plant architectures simply by incorporating multiple plants and plant species into  
230 their webs (Pearson 2009); they also tend to favor forbs over grasses as substrates, presumably  
231 because they are more robust (Fig. 2b). These niche differences between spider species translate  
232 to similar abundances within the system, with the orb weavers broadly distributed across plant  
233 species and the irregular web spiders restricted primarily to more structurally complex forbs (Fig.  
234 2c).

235         The dominant plant invaders in this system are the annual grass, cheatgrass, and  
236 numerous exotic perennial and annual forbs (Pearson et al. 2016). Cheatgrass (*Bromus*  
237 *tectorum*) provides a similar, but shorter substrate than the native grasses that largely replaces the  
238 dominant native grasses with a similar, though more diminutive architecture. However, the  
239 exotic forbs, which can collectively invade at levels comparable to cheatgrass, tend to have  
240 taller, more complex and expansive flowering stalks than the native forbs (Pearson et al. 2012).  
241 Hence, invasion by the exotic forbs strongly shifts the community-level distribution of the key

242 functional effect trait toward greater structural complexity by replacing the dominant, but  
243 structurally simplistic, native grasses, as well as the more diminutive native forbs (Fig. 2d).  
244 These changes increased the abundance of both spider groups, but the specialists, whose  
245 utilization optima aligned more closely with the new conditions, increased far more than the  
246 generalists (Pearson 2009; Smith et al. 2016; Fig. 2f). An added insight from applying the  
247 framework to this invasion was that both spider groups appeared to expand their realized niches  
248 in response to invasion; by incorporating the novel plants, both groups demonstrated the ability  
249 to use a broader range of plant architectures than was available in the native system. For the  
250 irregular web spiders, this expanded niche was linked to phenotypic plasticity - the spiders  
251 constructed larger webs (an extended phenotype *sensu* Dawkins 1983) on exotic forbs leading to  
252 higher prey capture rates and increased per capita fitness (Pearson 2009; Smith et al. 2016). This  
253 phenotypic shift was attributed to plasticity, given that these behaviors were found in newly  
254 invaded areas where spiders had no time to evolve (Pearson 2009).

#### 255 **Rodents in semi-desert grasslands invaded by Lehmann lovegrass**

256 In semi-desert grasslands of the southwestern United States, native grasses and forbs  
257 provide the food and habitat for a diverse assemblage of rodents (Litt and Steidl 2011). Hence,  
258 seed size and vegetative cover are two important functional effect traits that structure this rodent  
259 community (Figs. 3b and 4b). There are 3 main feeding guilds: granivores, opportunists, and  
260 insectivores. In its native state, this community is dominated by heteromyids (*Chaetodipus*,  
261 *Dipodomys*, and *Perognathus* spp.) that are mainly granivorous, generally preferring larger  
262 seeds, but *Dipodomys* is more opportunistic (Hoffmeister 1986). Cricetid rodents (*Baiomys*,  
263 *Onychomys*, *Reithrodontomys*, *Sigmodon* spp.) also are present, but less abundant in this  
264 community (Litt and Steidl 2011). These species are more opportunistic feeders, consuming a  
265 diversity of plants, seeds, and insects (Schmidly 1994), but *Onychomys* feeds mainly on  
266 arthropods (Hoffmeister 1986, Schmidly 1994). From the habitat perspective, these rodents also  
267 can be partitioned into guilds preferring sparse, moderate, or dense cover. Heteromyids typically  
268 occur in areas with sparse and patchy vegetation, but *Chaetodipus hispidus* occurs where grasses  
269 are moderately dense (Hoffmeister 1986). Several cricetids (*B. taylori*, *R. fulvescens*, *S.*  
270 *arizonae*) prefer dense grassy cover (Schmidly 1994), whereas others (*O. leucogaster*, *S.*  
271 *ochragnathus*) occur in more sparse cover (Hoffmeister 1986).

272 In southern Arizona, the native plant community is dominated by grasses (e.g., *Aristida*  
273 spp., *Bothriochloa barbinodis*, *Bouteloua* spp., *Digitaria californica*, *Eragrostis intermedia*, and  
274 *Panicum* spp.) and herbaceous dicots (Geiger 2006); with most species producing relatively large  
275 seeds (Fig. 3a). Vegetation cover is generally low, but variable (Fig. 4a, total biomass ranged  
276 from 200-600 g/m<sup>2</sup>, Geiger 2006) and can be patchy (Litt and Steidl 2011). Hence, the  
277 distribution of these two functional effect traits in native grasslands translates to rodent  
278 communities dominated by granivores that prefer sparse cover (Figs. 3c and 4c, Litt and Steidl  
279 2011).

280 When these grasslands are invaded by Lehmann lovegrass (*Eragrostis lehmanniana*),  
281 overall vegetative cover increases (total biomass ranged from 400-700 g/m<sup>2</sup>, Geiger 2006). This  
282 increase in cover is dominated by Lehmann lovegrass (~77% of the total biomass, Geiger 2006),  
283 which produces very small seeds that likely provide little to no food for the rodent community.  
284 Lehmann lovegrass also reduces cover of native grasses and herbaceous dicots (Geiger 2006),  
285 thereby reducing the abundance of the larger seeds produced by these plants. As such, the  
286 nonnative lovegrass shifts the habitat resource axis toward higher vegetation cover (Fig. 4d) and  
287 the food resource axis toward smaller seeds (Fig. 3d), favoring different rodent species.  
288 Additionally, the overall abundance of arthropods also decreases in invaded sites, including  
289 decreases in Orthoptera and Coleoptera (Litt and Steidl 2010); these groups are important for the  
290 most insectivorous species, *O. leucogaster*.

291 The effects of lovegrass invasion on this rodent community can largely be explained as a  
292 function of how invasion altered resources axes relative to the resource optima for each guild.  
293 The two more specialized heteromyid species, *Chaetodipus penicillatus* and *Perognathus flavus*,  
294 whose resource needs were linked to both lower cover and larger seeds decreased in abundance  
295 (Litt and Steidl 2011), as these resource axes both shifted away from their optima (Figs. 3f and  
296 4f). Similarly, *Onychomys leucogaster*, which favors lower vegetative cover and larger  
297 invertebrates, declined along with both of these resources (Litt and Steidl 2010). In contrast,  
298 abundance of the cricetid species, *Reithrodontomys fulvecens* and *Sigmodon arizonae*, that prefer  
299 more dense cover and are more opportunistic in their feeding, increased (Figs. 3f and 4f) (Litt  
300 and Steidl 2011). Surprisingly, abundance of *Dipodomys merriami* also increased, despite the  
301 fact that this species favors more open environments (Hoffmeister 1986; Figs. 3f and 4f). This

302 counterintuitive result suggests that other functional effect traits or biotic interactions are  
303 important for understanding this species' response to lovegrass invasion. No change in  
304 abundance was detected in three other species (*B. taylori*, *C. hispidus*, *S. ochragnathus*),  
305 suggesting either a lack of statistical power (*B. taylori* and *S. ochragnathus* were less abundant)  
306 or that these rodents were able to persist through a balance of positive and negative changes in  
307 food and habitat characteristics.

## 308 **Conclusions**

309 Prediction is the Holy Grail of science (Houlahan et al. 2017), but this goal has largely  
310 eluded ecology (Webb et al. 2010; Maris et al. 2018) and invasion ecology (Dick et al. 2014).  
311 This situation is attributable to the fact that ecological systems are not only highly complex but  
312 also very dynamic, with many outcomes dependent on context and stochasticity (McGill et al.  
313 2006; Agrawal et al. 2006; Meyerson et al. 2019). From a functional ecology perspective, the  
314 first step toward predicting ecological outcomes involves identifying processes with potential to  
315 explain recurring natural phenomena. This establishes viable, mechanistic hypotheses that can  
316 be initially tested experimentally and ultimately vetted by predicting future outcomes. Here, we  
317 have drawn from basic theory linking species autecology and community ecology to develop a  
318 trait-based, functional ecology framework for mechanistically explaining the effects of exotic  
319 plant invasions on native fauna, while explicitly integrating ecological context. In applying this  
320 framework to three case studies representing an array of native fauna, we find that this approach  
321 holds promise for helping to interpret and understand past invasion outcomes with potential for  
322 predicting future outcomes. However, the framework has inherent limitations linked to the  
323 dynamic nature of ecological systems.

324 The framework we propose is based on two key assumptions that establish the context for  
325 its efficacy. First, we assume that bottom-up forces fuel ecological processes. This assumption  
326 is fundamental to the economics of ecology (*sensu* Odum and Odum 1953): a) the sun provides  
327 the energy that charges ecological systems, b) plants capture and fix that energy into forms  
328 available to consumers, and c) consumers make that energy available to predators. While it is  
329 well-established that consumers and predators can have strong top-down effects on ecosystems  
330 (e.g., Paine 1980; Milchunas and Lauenroth 1993), these are secondary, restructuring forces that  
331 vary in their strength from negligible to profound depending on abiotic and biotic factors (e.g.,

332 Strong 1992; Hunter and Price 1992). Our framework will more readily explain and predict  
333 community outcomes when systems are predominantly structured by bottom-up forces. As top-  
334 down forces increase their restructuring roles via feedbacks, or when invasive plants directly and  
335 differentially affect multiple dimensions of the consumer niche space, it will be more challenging  
336 to track and predict outcomes, as our rodent example demonstrates.

337         We also assume that exotic plant invasions will most strongly influence bottom-up  
338 processes. When exotic plants invade, they directly affect native plants by displacing them and  
339 shifting the balance away from native plant traits and toward invader traits. These changes  
340 directly affect consumers by altering the quality and quantity of food and habitat resources.  
341 However, they can also affect predators directly and indirectly via 1) interaction chains (density-  
342 mediated indirect effects) that change predator abundance (e.g., invader reduces native food  
343 abundance reducing consumer abundance and predator abundance), 2) habitat alterations that  
344 directly affect predator abundance (direct density-mediated effects on predators), 3) habitat  
345 alterations that influence predator-prey interactions (trait-mediated indirect interactions  
346 influencing the per capita strength between predators and prey), or 4) changes in food quality,  
347 quantity, or spatial distribution that alter predator-prey interactions (also trait-mediated indirect  
348 interactions). When invading plants directly or indirectly affect predator abundance and/or their  
349 per capita effects on prey, these processes may create feedbacks that can complicate interpreting  
350 and predicting invasion outcomes.

351         These challenges derive not from failures of the framework, but rather from the inherent  
352 complexity of ecological systems – complexities that have long hindered understanding and  
353 prediction in ecology. Despite these limitations, we propose that the framework we introduce  
354 here offers a valuable heuristic tool for understanding how mechanistic, trait-based processes  
355 influence invasion outcomes and for predicting bottom-up effects of plant invaders on native  
356 fauna across a wide range of systems. We build on prior efforts by defining the relevant  
357 ecological context as the basis for deriving trait-based, mechanistic understanding. Applying this  
358 framework to previous invasion outcomes can identify hypotheses for experimental testing that  
359 can refine these understandings. Developing mechanistic explanations also provide the potential  
360 to predict changes that may result from future invasions.

361

362 **Figure Captions**

363 **Fig. 1** Community assembly theory provides the context for understanding native community  
364 structure and interpreting the relationship between native plant traits and native consumer  
365 abundance. a) Species from the regional species pool pass through abiotic and biotic filters to  
366 determine the composition and relative abundance of plant species, as well as the distribution of  
367 native plant functional traits. b) The abundance distribution of the resulting community of native  
368 plants is mapped out along a trait axis of functional effect traits relevant to consumers. c) Niches  
369 of three consumers, expressed as resource utilization curves relative to their plant-derived  
370 resource base, with two specialists (x and z) and one generalist (y). d) Consumer community  
371 structure expressed as the relative abundance of each species as a function of the relevant plant-  
372 derived resource base. e) Exotic plant invasion reassembles or restructures the plant community  
373 and thereby the abundance-distribution of functional effect traits relevant to consumers. f)  
374 Consumer niches along the plant-derived resource base, which are a product of the historical  
375 ecological/evolutionary context that formed them. With altered resources, some species may  
376 express broader niches than previously possible (dotted line, species y). g) Consumer niches are  
377 mapped onto the altered plant resource base to understand or predict restructuring of the  
378 consumer community following plant invasion. In this example, the invader became more  
379 abundant than the native plants and strongly shifted the community-level distribution of plant  
380 functional effect traits and the associated relative abundance of resources for consumers,  
381 especially suppressing plant species (and associated resources) at the upper end of the trait value  
382 range and increasing plants and associated resources at the lower end of the range. The result is  
383 a shift in the consumer community with an increased abundance of specialist x, modestly  
384 decreased abundance of generalist y, and strongly decreased abundance of specialist z, as a  
385 function of the shift in plant functional effect traits and corresponding resources relevant to the  
386 consumers

387 **Fig. 2** The plant trait of greatest relevance to native web-building spiders in Intermountain  
388 grasslands of the western United States is plant architecture and overall structural complexity of  
389 the plant community. This community-level functional effect trait can be mapped out a) as a  
390 function of structural differences (low to high complexity) among plant functional groups. b)  
391 The habitat niches of the two primary spider guilds can be mapped onto this niche space to show

392 that the orb weavers are generalists capable of utilizing a range of plant architectures, whereas  
393 the irregular web spiders are more specialized, using primarily the most structurally complex  
394 perennial forbs. These niche requirements, given the available habitat resource base, translate to  
395 c) comparable abundance of the two spider guilds. d) Overall, plant invaders differ from the  
396 native plants in having more complex architectures, shifting the resource axis toward greater  
397 structural complexity. e) Mapping this new resource axis onto the spider niches shows that this  
398 shift aligns more with the specialists with the overall result that f) while both spider groups  
399 increase in abundance, the specialists increase much more than the generalists. Note, given that  
400 the new resource base extends beyond the former system and yet is incorporated into both  
401 niches, this suggests a shift in realized niches (indicated by dotted vs solid curves in e) to  
402 incorporate this new resource base, a shift which is linked to phenotypic plasticity for the  
403 irregular web spiders



404 **Fig. 3** a) The abundance distribution of native plants in an Arizona semi-desert grassland  
405 mapped out along a gradient of seed size, one of the functional effect traits relevant to rodent  
406 consumers (see also Figure 4). b) Rodents in this community can be categorized by feeding  
407 guild (opportunists: *Baiomys taylori*, *Dipodomys merriami*, *Reithrodontomys fulvescens*,  
408 *Sigmodon arizonae*, and *S. ochrognathus*, and granivores: *Chaetodipus hispidus*, *C. penicillatus*,  
409 and *Perognathus flavus*), whose niches can be expressed as resource utilization curves relative to  
410 the resource base of seed sizes (small to large). c) Rodent community structure can be  
411 expressed as the relative fitness/abundance of each feeding guild as a function of seed size. d)  
412 Invasion by *Eragrostis lehmanniana* restructures the plant community and the abundance-  
413 distribution of seed sizes, now dominated by small seeds. e) Rodent niches along the seed size  
414 resource base. Based on this information (in d and e), we can map the rodent niches f) onto the  
415 altered resource base (seed size) to understand restructuring of the rodent community as a  
416 function of plant invasion. In this example, as the invading grass becomes dominant, it shifts the  
417 seed resource axis toward smaller seed sizes by suppressing large-seeded plants and producing  
418 small seeds. The result is a decline in abundance of the granivores, particularly those favoring  
419 larger seeds, and increased abundance of opportunists

420 **Fig. 4** a) Vegetation cover provides another functional effect trait relevant to the rodents in the  
421 same Arizona semi-desert grassland (Figure 2), such that we also can plot the abundance  
422 distribution of native plants along this resource axis. b) Niches of three guilds of rodents can be  
423 expressed as resource utilization curves relative to the resource axis of vegetation cover (sparse  
424 cover: *C. penicillatus*, *D. merriami*, *P. flavus*, and *S. ochrognathus*, moderate cover: *C. hispidus*,  
425 and dense cover: *B. taylori*, *R. fulvescens*, and *S. arizonae*). c) Rodent community structure  
426 expressed as the relative fitness/abundance of each species' guild as a function of vegetation  
427 cover (sparse to dense). d) Invasion by *Eragrostis lehmanniana* restructures the plant  
428 community and the abundance-distribution of vegetation cover, now dominated by dense cover.  
429 e) Rodent niches can be integrated with the altered vegetation cover resource base (d) to  
430 understand f) restructuring of the rodent community as a function of plant invasion. In this  
431 example, the invading grass becomes dominant and produces more cover, shifting the relative  
432 abundance of resources for rodents, especially suppressing the guild that prefers sparse cover.  
433 The result is a decline in abundance of the sparse cover rodents and increased abundance of the  
434 dense cover species. Combining the effects of the shifts in this resource axis with the changes in

435 the seed resource axis (Figure 3) help to explain overall patterns of the impacts of *E.*  
436 *lehmanniana* invasion on the rodent community

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