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

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

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Introduction

Human activities have altered nearly all ecosystems on the planet, disrupting ecological functions

and threatening biological diversity in myriad ways (Vitousek et al. 1997). However, not all of these changes have resulted in population declines or extinctions of native species; some species benefit and even thrive under conditions created by human-induced change (see Sih et al. 2010, 2011). A key challenge for conservation, and ecology in general, is to understand how variation in species' responses to shifting conditions can predict which organisms will be winners and which will be losers in the face of anthropogenic change (Colles et al. 2009; Sih et al. 2010; 2011).

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

Most frameworks for predicting invader impacts on native species recognize that alignment between the traits of native and invading species is central to understanding native species responses to invaders (e.g., Ricciardi et al. 2013; Sih et al. 2010, 2011). However, existing frameworks do not sufficiently address the importance of ecological context (see McGill et al. 2006, Catford et al. 2021), referred to here as context dependence or conditionality. This context dependence establishes the specific conditions that determine how well the native species is aligned with invader traits and invader-induced changes within a given system. Some frameworks ignore context entirely, proposing that the degree of specialization of native species can predict their response to invaders across systems, under the premise that generalist species will have a greater likelihood of aligning with or rapidly adapting to new conditions than specialists (Colles et al. 2009). However, while generalists are more likely to fit invader-driven change on average, specialists can benefit far more than generalists when invaders happen to alter conditions in ways that align with their specific niche requirements (Colles et al. 2009; Hansen et al. 2009; Smith et al. 2016). Other frameworks have attempted to incorporate basic aspects of conditionality without explicitly addressing context. For example, Martin and Murray (2011) introduced a framework that incorporates general understandings of wildlife-habitat relationships to predict responses of native fauna to plant invasions. Although this approach incorporates some degree of context dependence, resulting predictions were not widely supported because they were too generic. For example, when they applied their framework to specific case studies that explicitly incorporated community context, it seemed to predict outcomes reasonably well, but when applied across many species and conditions without accounting for community-specific context, general predictions were not borne out.

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

A Framework for understanding invader-driven change: incorporating ecological context

Community assembly theory (Keddy 1992; Weiher and Keddy 1999) offers a framework for delineating

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

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

Historically, the niche concept evolved separately in the plant and consumer realms, but merging these perspectives is necessary to understand how changes induced by invasive plants may affect the niche space and success of native animals. Theoretically, niches of consumers relative to their food and habitat dimensions are depicted as resource utilization curves (MacArthur and Levins 1967), with the breadth of these curves delineating the relative specialization of different consumers and the peak of each curve identifying the resource optima for each species (Fig. 1c). Hence, narrower utilization curves reflect greater specialization (see species x and z in Fig. 1c) and broader curves reflect greater generalization (species y in Fig. 1c). These niche dimensions translate to relative success of different species as measured by relative abundance or species-level fitness (sensu Chesson 2000; see also HilleRisLambers et al. 2012) (Fig. 1d). Here, we assume that bottom-up processes provide the basis for understanding food webs (sensu Odum and Odum 1953) and later address other biotic drivers (e.g., competition, predation, see Conclusions). For plants, niche dimensions have commonly been expressed as curves quantifying fitness/abundance relative to abiotic axes (Whittaker 1965; Whittaker et al. 1973). However, because we are interested in how plants provide the resources to consumers that structure consumer niches, we must translate the abundance distribution of plant species into plant-derived resources relevant to the consumers by focusing on important "functional effect traits" of the plants (sensu Violle et al. 2007; see Fig. 1b). For example, focusing on plant traits like leaf nitrogen content or seed size provides a direct linkage between plant traits and consumer feeding niches. By integrating traits measured at the individual plant level, we can obtain community-level metrics (see Violle et al. 2007). Here, we propose that individual traits are averaged for each species and the abundance of each species is then quantified (via cover or biomass estimates) to map out the distribution and relative abundance of community-level functional effect traits (Fig. 1b). Re-conceptualizing the plant niche in this way provides a common denominator directly linking resource production to consumer utilization, allowing us to evaluate how changes induced by an invasive plant can shift the resource base to affect consumers (Fig. 1). Moreover, when such functional effect traits double as plant performance traits that are strongly tied to plant life-history tradeoffs, these linkages can provide powerful insights into plant-animal interactions (e.g., Dylewski et al. 2020).

The community assembly processes described above therefore establishes the essential context that defines the native plant and animal communities, their realized niches, and their inter-relationships. This (Fig. 1b, c) provides the starting point to understand how plants affect the composition and relative abundance of native consumers (Fig. 1d). The same concepts can then be used to delineate how
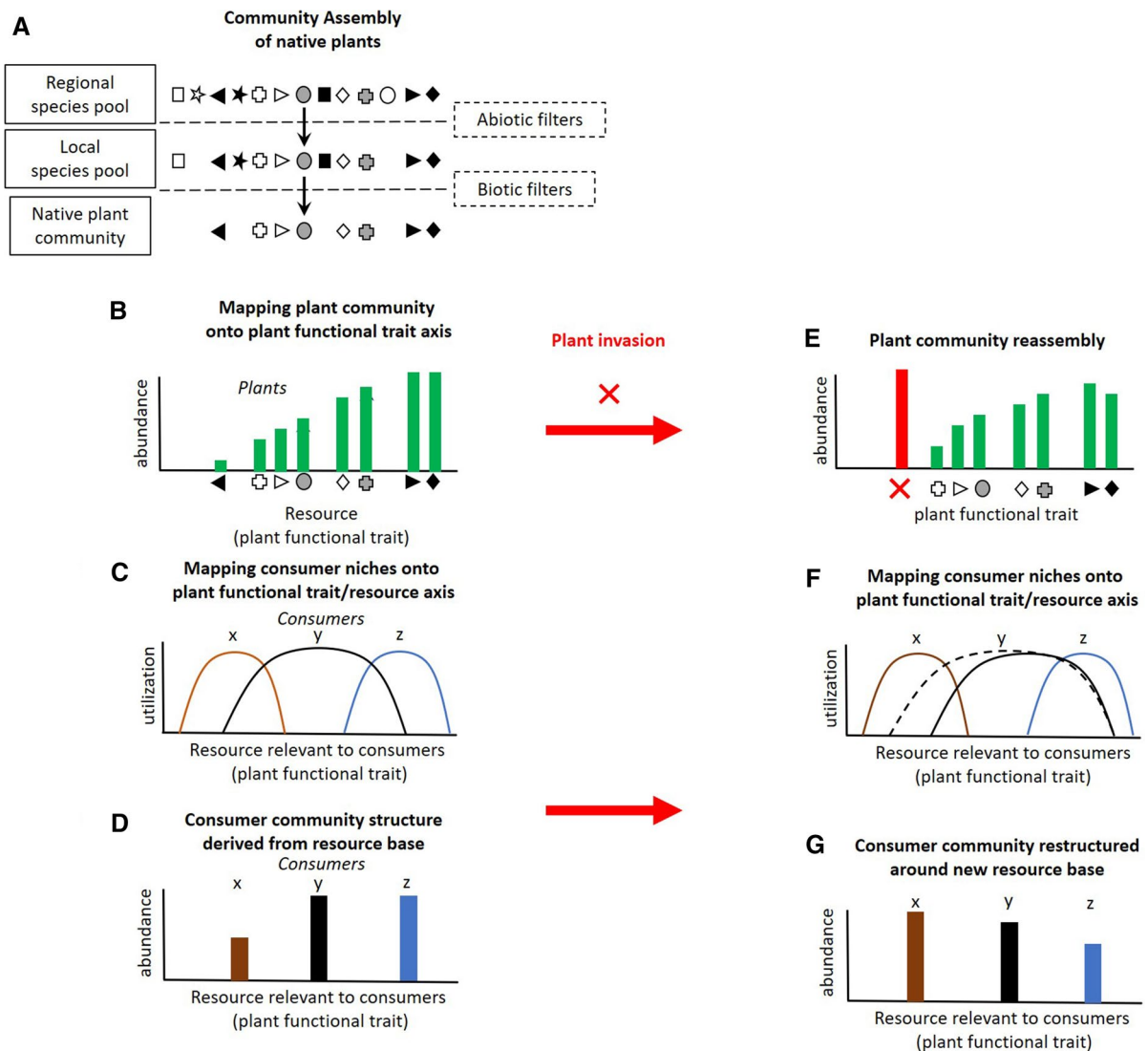
Fig. 1 Community assembly theory provides the context for understanding native community structure and interpreting the relationship between native plant traits and native consumer abundance. **a** Species from the regional species pool pass through abiotic and biotic filters to determine the composition and relative abundance of plant species, as well as the distribution of native plant functional traits. **b** The abundance distribution of the resulting community of native plants is mapped out along a trait axis of functional effect traits relevant to consumers. **c** Niches of three consumers, expressed as resource utilization curves relative to their plant-derived resource base, with two specialists (x and z) and one generalist (y). **d** Consumer community structure expressed as the relative abundance of each species as a function of the relevant plant-derived resource base. **e** Exotic plant invasion reassembles or restructures the plant community and thereby the abundance-distribution of functional effect traits relevant to consumers. **f** Consumer niches along the plant-derived resource base, which are a product of the historical ecological/evolutionary context that formed them. With altered resources, some species may express broader niches than previously possible (dotted line, species y). **g** Consumer niches are mapped onto the altered plant resource base to understand or predict restructuring of the consumer community following plant invasion. In this example, the invader became more abundant than the native plants and strongly shifted the community-level distribution of plant functional effect traits and the associated relative abundance of resources for consumers, especially suppressing plant species (and associated resources) at the upper end of the trait value range and increasing plants and associated resources at the lower end of the range. The result is a shift in the consumer community with an increased abundance of specialist x, modestly decreased abundance of generalist y, and strongly decreased abundance of specialist z, as a function of the shift in plant functional effect traits and corresponding resources relevant to the consumers

plant invasion restructures or reassembles the plant community and associated resource axes (Fig. 1e) to restructure consumer communities (Fig. 1g). By comparing the resource base of both the native and invaded plant communities (Fig. 1b, e) and linking these to the niche space of the native animals (Fig. 1c, f), we can articulate more explicitly which system components are changing and how. Based on this information, we can identify which native animals are most likely to be affected, as well as how and why they might respond to exotic plant invasion (Fig. 1g). This approach integrates many critical elements of trait-based ecology and community assembly theory, allowing us to consider how plant invasions can affect consumer assemblages by incorporating the underlying ecological context that is so often a primary obstacle to understand and ultimately predict community outcomes (McGill et al. 2006; Agrawal et al. 2007; Meyerson et al. 2019).

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

Applying the framework

Adapting this community-based framework requires that certain baseline information about the system is available and applied in a stepwise manner. Because different faunal species or guilds will have different relationships with the native flora, the first step is to identify the fauna of interest and their linkage (e.g., food, habitat) to the native plant community to determine the plant functional effect traits relevant for the native fauna and to approximate resource utilization curves of the fauna along that resource axis (Fig. 1c). Importantly, the focus here is not necessarily on plant species (unless fauna are highly specialized), but rather on plant functional effect traits relevant to the consumer (sensu Violle et al. 2007), that might be expressed similarly among subsets of functionally similar plant species. Next, the abundance distribution of the relevant functional effect trait(s) is mapped onto the resource axis by (1) averaging the effect traits for a representative subsample of individuals to obtain a community-level value for each plant species or functional group and (2) quantifying the relative abundance of the plant species or functional group in the community (e.g., cover or biomass, Fig. 1b). Then, the relative abundance of the fauna of interest can be plotted along the resource axis (Fig. 1d) and ideally supported with appropriate empirical data (e.g., habitat models). Finally, information is needed to understand how the invader will alter the resource axis by impacting native plants and distributions of their associated functional effect traits and potentially introducing novel traits (Fig. 1e) that might alter the faunal community (Fig. 1g).

We apply this framework to three empirical case studies to demonstrate the process and explore its utility for explaining how plant invasions shift native faunal communities. Each example focuses on a

different taxonomic group of native fauna and a different invading plant: spiders and rodents (below), and warblers (Appendix S1).

Spiders in invaded grasslands

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

Many web-building spiders use plants as the primary substrates for anchoring their webs, rendering them susceptible to the effects of exotic plant invasions that alter vegetation architecture (Smith-Ramesh 2017; Balkenhol et al. 2018). Within these Intermountain grasslands, native spiders fall into two distinct web-building strategies, such that plant architecture defines the general linkage between the plant and spider communities (Pearson 2009). Smaller, irregular-web spiders, like *Dictyna* spp., tend to construct their webs entirely within a single plant. In contrast, larger orb weavers tend to use multiple plants to suspend their larger webs. Hence, the architectural complexity of individual plants is highly relevant to the irregular-web spiders, as they can build larger webs in plant species possessing more complex, expansive architectures (generally greater branching and/or longer branches of the flowering stalks). In contrast, the orb weavers are less sensitive to individual plant architecture, responding more to the emergent complexity of the vegetation community derived from the many different species (Pearson 2009). Therefore, the plant functional effect trait most relevant in defining this spider community is complexity of plant architecture which readily links to plant functional groups within the system (Fig. 2a).

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

The dominant plant invaders in this system are the annual grass, cheatgrass, and numerous exotic perennial and annual forbs (Pearson et al. 2016). Cheatgrass (*Bromus tectorum*) provides a similar, but shorter substrate than the native grasses that largely replaces the dominant native grasses with a similar, though more diminutive architecture. However, the exotic forbs, which can collectively invade at levels comparable to cheatgrass, tend to have taller, more complex and expansive flowering stalks than the native forbs (Pearson et al. 2012). Hence, invasion by the exotic forbs strongly shifts the community-level distribution of the key functional effect trait toward greater structural complexity by replacing the dominant, but structurally simplistic, native grasses, as well as the more diminutive native forbs (Fig. 2d). These changes increased the abundance of both spider groups, but the specialists, whose utilization optima aligned more closely with the new conditions, increased far more than the generalists (Pearson 2009; Smith et al. 2016; Fig. 2f). An added insight from applying the framework to this invasion was that both spider groups appeared to expand their realized niches in response to invasion; by incorporating the novel plants, both groups demonstrated the ability to use a broader range of plant architectures than was available in the native system. For the irregular web spiders, this expanded niche was linked to phenotypic plasticity—the spiders constructed larger webs (an extended phenotype sensu Dawkins 1983) on exotic forbs leading to higher prey capture rates and increased per capita fitness (Pearson 2009; Smith et al. 2016). This phenotypic shift was attributed to plasticity, given
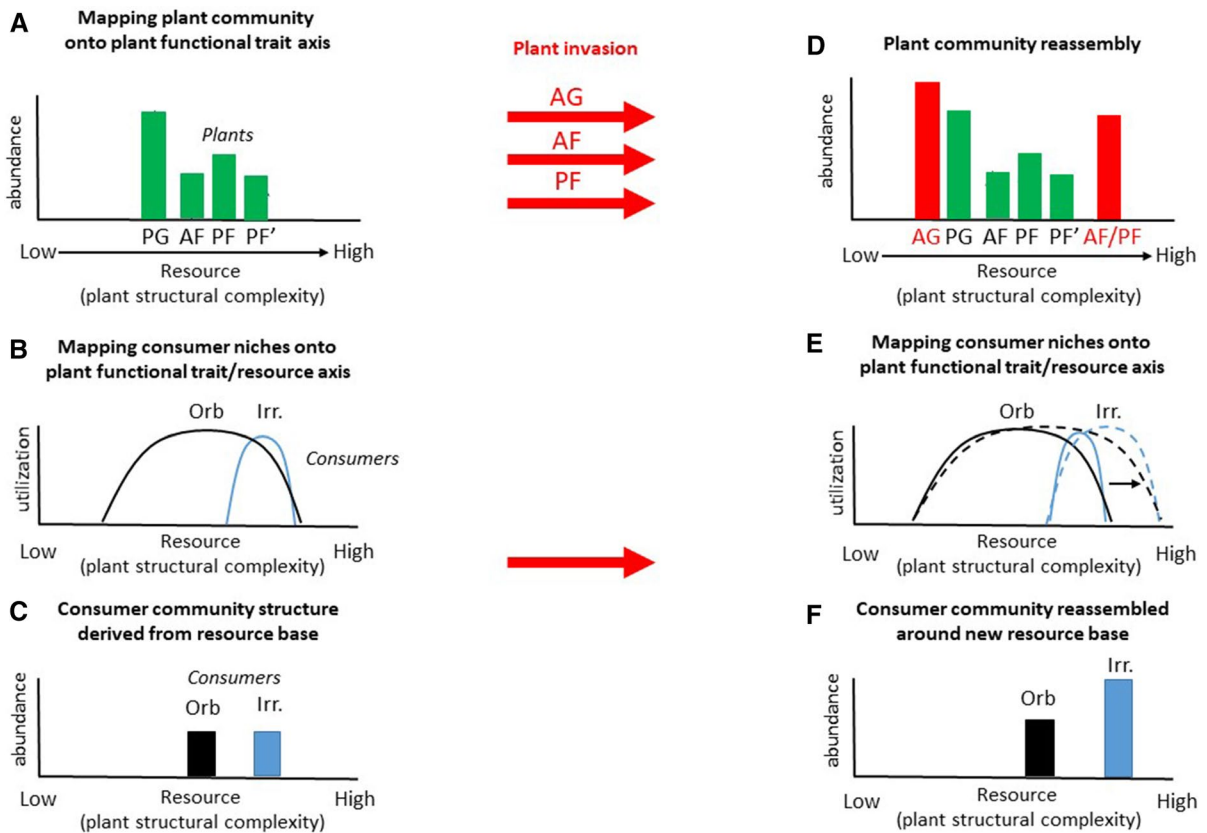
Fig. 2 The plant trait of greatest relevance to native web-building spiders in Intermountain grasslands of the western United States is plant architecture and overall structural complexity of the plant community. This community-level functional effect trait can be mapped out (**a**) as a function of structural differences (low to high complexity) among plant functional groups. **b** The habitat niches of the two primary spider guilds can be mapped onto this niche space to show that the orb weavers are generalists capable of utilizing a range of plant architectures, whereas the irregular web spiders are more specialized, using primarily the most structurally complex perennial forbs. These niche requirements, given the available habitat resource base, translate to (**c**) comparable abundance of the two spider guilds. **d** Overall, plant invaders differ from the native plants in having more complex architectures, shifting the resource axis toward greater structural complexity. **e** Mapping this new resource axis onto the spider niches shows that this shift aligns more with the specialists with the overall result that (**f**) while both spider groups increase in abundance, the specialists increase much more than the generalists. Note, given that the new resource base extends beyond the former system and yet is incorporated into both niches, this suggests a shift in realized niches (indicated by dotted vs solid curves in (**e**) to incorporate this new resource base, a shift which is linked to phenotypic plasticity for the irregular web spiders

that these behaviors were found in newly invaded areas where spiders had no time to evolve (Pearson 2009).

Rodents in semi-desert grasslands invaded by Lehmann lovegrass

In semi-desert grasslands of the southwestern United States, native grasses and forbs provide the food and habitat for a diverse assemblage of rodents (Litt and Steidl 2011). Hence, seed size and vegetative cover are two important functional effect traits that structure this rodent community (Figs. 3b and 4b). There are 3 main feeding guilds: granivores, opportunists, and insectivores. In its native state, this community is dominated by heteromyids (*Chaetodipus*, *Dipodomys*, and *Perognathus* spp.) that are mainly granivorous, generally preferring larger seeds, but *Dipodomys* is more opportunistic (Hoffmeister 1986). Cricetid rodents (*Baiomys*, *Onychomys*, *Reithrodontomys*,
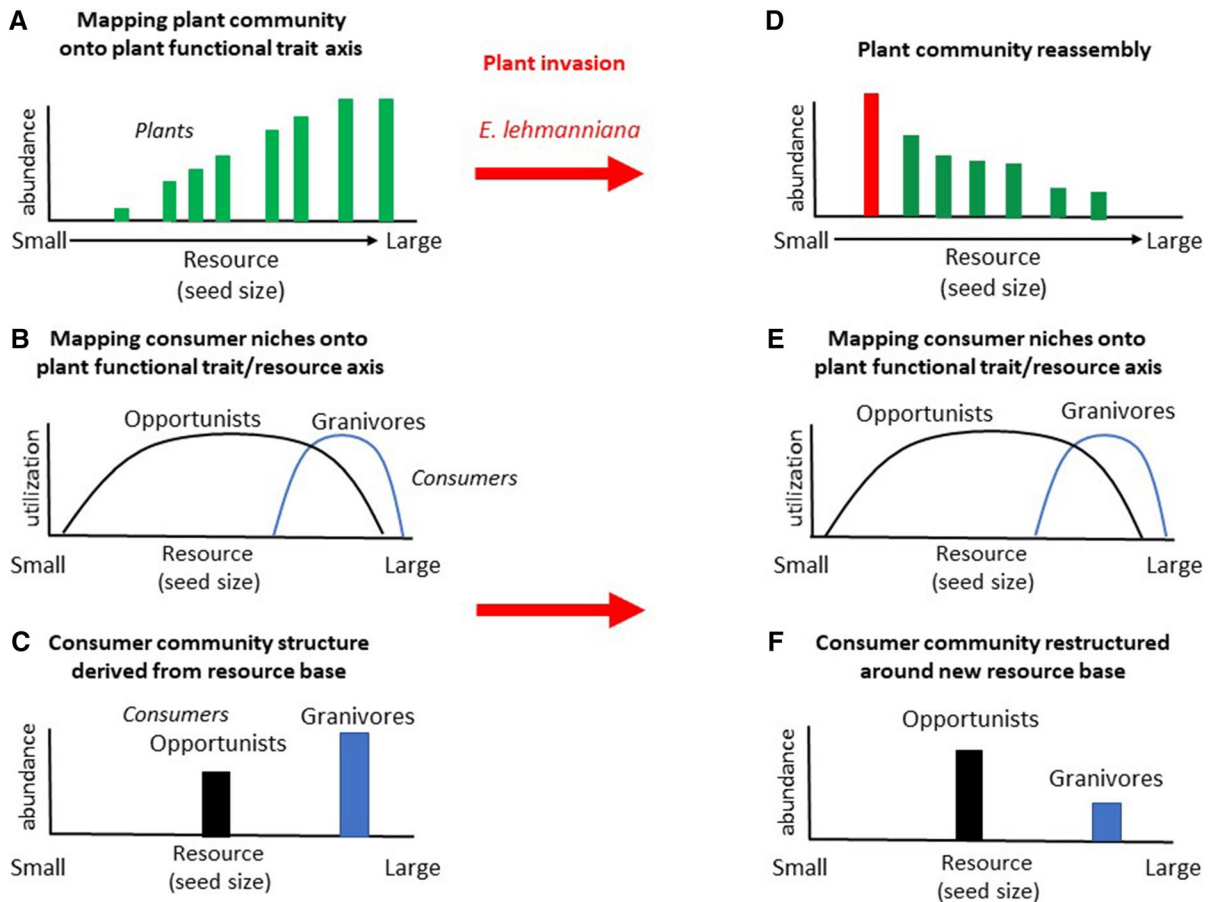
Fig. 3 a The abundance distribution of native plants in an Arizona semi-desert grassland mapped out along a gradient of seed size, one of the functional effect traits relevant to rodent consumers (see also Fig. 4). **b** Rodents in this community can be categorized by feeding guild (opportunists: *Baiomys taylori*, *Dipodomys merriami*, *Reithrodontomys fulvescens*, *Sigmodon arizonae*, and *S. ochrognathus*, and granivores: *Chaetodipus hispidus*, *C. penicillatus*, and *Perognathus flavus*), whose niches can be expressed as resource utilization curves relative to the resource base of seed sizes (small to large). **c** Rodent community structure can be expressed as the relative fitness/ abundance of each feeding guild as a function of seed size. **d**

Invasion by *Eragrostis lehmanniana* restructures the plant community and the abundance-distribution of seed sizes, now dominated by small seeds. **e** Rodent niches along the seed size resource base. Based on this information (in d and e), we can map the rodent niches (**f**) onto the altered resource base (seed size) to understand restructuring of the rodent community as a function of plant invasion. In this example, as the invading grass becomes dominant, it shifts the seed resource axis toward smaller seed sizes by suppressing large-seeded plants and producing small seeds. The result is a decline in abundance of the granivores, particularly those favoring larger seeds, and increased abundance of opportunists

Sigmodon spp.) also are present, but less abundant in this community (Litt and Steidl 2011). These species are more opportunistic feeders, consuming a diversity of plants, seeds, and insects (Schmidly 1994), but *Onychomys* feeds mainly on arthropods (Hoffmeister 1986; Schmidly 1994). From the habitat perspective, these rodents also can be partitioned into guilds preferring sparse, moderate, or dense cover. Heteromyids typically occur in areas with sparse and patchy

vegetation, but *Chaetodipus hispidus* occurs where grasses are moderately dense (Hoffmeister 1986). Several cricetids (*B. taylori*, *R. fulvescens*, *S. arizonae*) prefer dense grassy cover (Schmidly 1994), whereas others (*O. leucogaster*, *S. ochragnathus*) occur in more sparse cover (Hoffmeister 1986).

In southern Arizona, the native plant community is dominated by grasses (e.g., *Aristida* spp., *Bothriochloa barbinodis*, *Bouteloua* spp., *Digitaria*
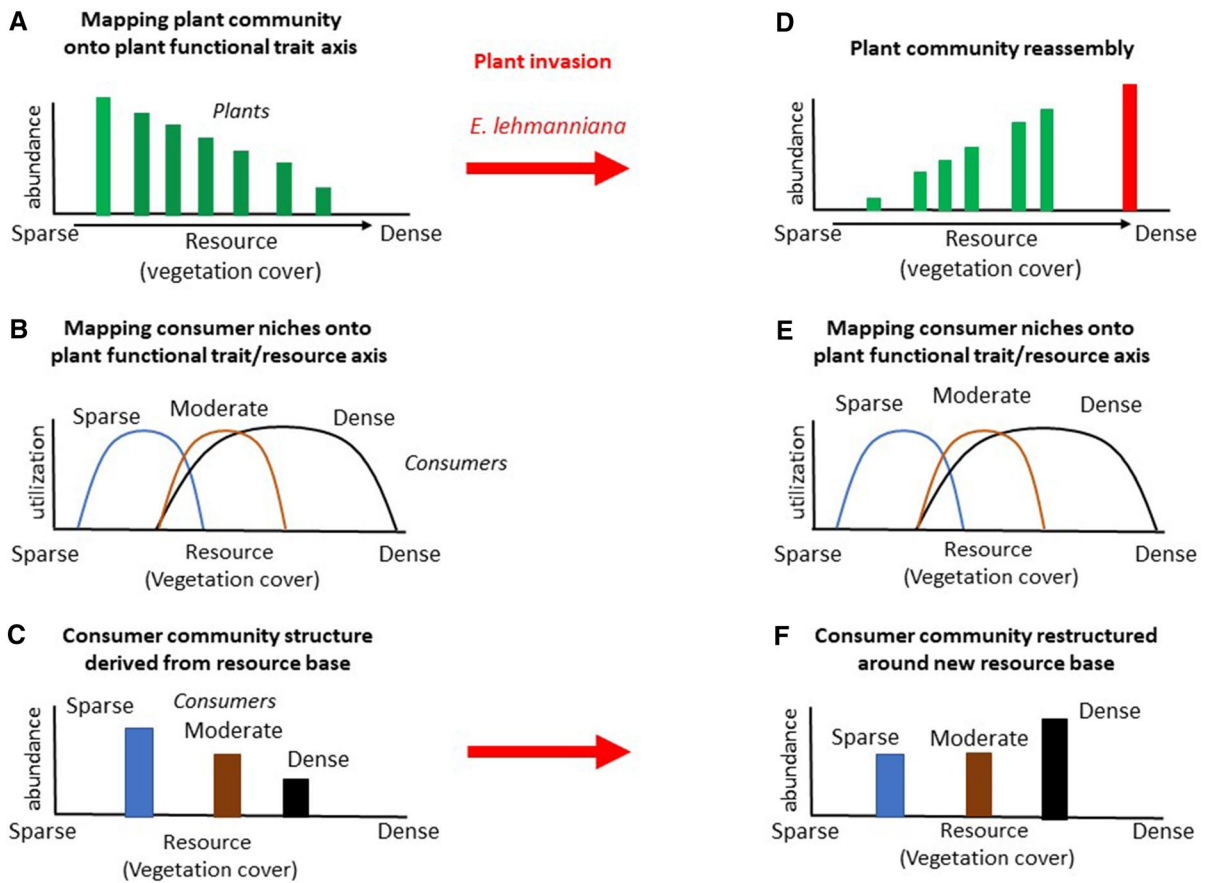
Fig. 4 **a** Vegetation cover provides another functional effect trait relevant to the rodents in the same Arizona semi-desert grassland (Fig. 3), such that we also can plot the abundance distribution of native plants along this resource axis. **b** Niches of three guilds of rodents can be expressed as resource utilization curves relative to the resource axis of vegetation cover (sparse cover: *C. penicillatus*, *D. merriami*, *P. flavus*, and *S. ochrognathus*, moderate cover: *C. hispidus*, and dense cover: *B. taylori*, *R. fulvescens*, and *S. arizonae*). **c** Rodent community structure expressed as the relative fitness/abundance of each species' guild as a function of vegetation cover (sparse to dense). **d** Invasion by *Eragrostis lehmanniana* restructures the plant community and the abundance-distribution of veg-

etation cover, now dominated by dense cover. **e** Rodent niches can be integrated with the altered vegetation cover resource base (**d**) to understand (**f**) restructuring of the rodent community as a function of plant invasion. In this example, the invading grass becomes dominant and produces more cover, shifting the relative abundance of resources for rodents, especially suppressing the guild that prefers sparse cover. The result is a decline in abundance of the sparse cover rodents and increased abundance of the dense cover species. Combining the effects of the shifts in this resource axis with the changes in the seed resource axis (Fig. 3) help to explain overall patterns of the impacts of *E. lehmanniana* invasion on the rodent community

californica, *Eragrostis intermedia*, and *Panicum* spp.) and herbaceous dicots (Geiger 2006); with most species producing relatively large seeds (Fig. 3a). Vegetation cover is generally low, but variable (Fig. 4a, total biomass ranged from 200 to 600 g/m^2, Geiger 2006) and can be patchy (Litt and Steidl 2011). Hence, the distribution of these two functional effect traits in native grasslands translates to rodent communities dominated by granivores that

prefer sparse cover (Figs. 3c and 4c, Litt and Steidl 2011).

When these grasslands are invaded by Lehmann lovegrass (*Eragrostis lehmanniana*), overall vegetative cover increases (total biomass ranged from 400 to 700 g/m^2, Geiger 2006). This increase in cover is dominated by Lehmann lovegrass (~77% of the total biomass, Geiger 2006), which produces very small seeds that likely provide little to no food for the

rodent community. Lehmann lovegrass also reduces cover of native grasses and herbaceous dicots (Geiger 2006), thereby reducing the abundance of the larger seeds produced by these plants. As such, the nonnative lovegrass shifts the habitat resource axis toward higher vegetation cover (Fig. 4d) and the food resource axis toward smaller seeds (Fig. 3d), favoring different rodent species. Additionally, the overall abundance of arthropods also decreases in invaded sites, including decreases in Orthoptera and Coleoptera (Litt and Steidl 2010); these groups are important for the most insectivorous species, *O. leucogaster.*

The effects of lovegrass invasion on this rodent community can largely be explained as a function of how invasion altered resources axes relative to the resource optima for each guild. The two more specialized heteromyid species, *Chaetodipus penicillatus* and *Perognathus flavus*, whose resource needs were linked to both lower cover and larger seeds decreased in abundance (Litt and Steidl 2011), as these resource axes both shifted away from their optima (Figs. 3f and 4f). Similarly, *Onychomys leucogaster,* which favors lower vegetative cover and larger invertebrates, declined along with both of these resources (Litt and Steidl 2010). In contrast, abundance of the cricetid species, *Reithrodontomys fulvescens* and *Sigmodon arizonae*, that prefer more dense cover and are more opportunistic in their feeding, increased (Figs. 3f and 4f) (Litt and Steidl 2011). Surprisingly, abundance of *Dipodomys merriami* also increased, despite the fact that this species favors more open environments (Hoffmeister 1986; Figs. 3f and 4f). This counterintuitive result suggests that other functional effect traits or biotic interactions are important for understanding this species' response to lovegrass invasion. No change in abundance was detected in three other species (*B. taylori*, *C. hispidus*, *S. ochragnathus*), suggesting either a lack of statistical power (*B. taylori* and *S. ochragnathus* were less abundant) or that these rodents were able to persist through a balance of positive and negative changes in food and habitat characteristics.

Conclusions

Prediction is the Holy Grail of science (Houlahan et al. 2017), but this goal has largely eluded ecology (Webb et al. 2010; Maris et al. 2018) and invasion ecology (Dick et al. 2014). This situation is attributable to the fact that ecological systems are not only highly complex but also very dynamic, with many outcomes dependent on context and stochasticity (McGill et al. 2006; Agrawal et al. 2007; Meyerson et al. 2019). From a functional ecology perspective, the first step toward predicting ecological outcomes involves identifying processes with potential to explain recurring natural phenomena. This establishes viable, mechanistic hypotheses that can be initially tested experimentally and ultimately vetted by predicting future outcomes. Here, we have drawn from basic theory linking species autecology and community ecology to develop a trait-based, functional ecology framework for mechanistically explaining the effects of exotic plant invasions on native fauna, while explicitly integrating ecological context. In applying this framework to three case studies representing an array of native fauna, we find that this approach holds promise for helping to interpret and understand past invasion outcomes with potential for predicting future outcomes. However, the framework has inherent limitations linked to the dynamic nature of ecological systems.

The framework we propose is based on two key assumptions that establish the context for its efficacy. First, we assume that bottom-up forces fuel ecological processes. This assumption is fundamental to the economics of ecology (sensu Odum and Odum 1953): (a) the sun provides the energy that charges ecological systems, (b) plants capture and fix that energy into forms available to consumers, and (c) consumers make that energy available to predators. While it is well-established that consumers and predators can have strong top-down effects on ecosystems (e.g., Paine 1980; Milchunas and Lauenroth 1993), these are secondary, restructuring forces that vary in their strength from negligible to profound depending on abiotic and biotic factors (e.g., Strong 1992; Hunter and Price 1992). Our framework will more readily explain and predict community outcomes when systems are predominantly structured by bottom-up forces. As top-down forces increase their restructuring roles via feedbacks, or when invasive plants directly and differentially affect multiple dimensions of the consumer niche space, it will be more challenging to track and predict outcomes, as our rodent example demonstrates.

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

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

Authors' contributions ARL and DEP developed the ideas and wrote the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

Declarations

Conflict of interest The authors' declared that they have no conflict of interest.

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