Responses of grassland arthropods to an invasion by nonnative grasses

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Abstract

In grassland ecosystems, invasions by nonnative grasses typically decrease floristic diversity and structural heterogeneity in ways that alter the quantity and quality of habitat for animals. Grassland arthropods that rely directly on herbaceous plants for food, shelter, or as substrates for reproduction are especially vulnerable to these invasions because many have evolved specialized relationships with host plants that might be displaced. We evaluated how invasions by nonnative grasses affected abundance and richness of foliage-dwelling arthropods in semidesert grasslands of Arizona, USA. On 90, 3.1-ha plots established along a gradient of invasion where dominance of nonnative grasses ranged from 0 to nearly 100% of grass cover, we captured >90,000 arthropods from 11 orders during 270 surveys in 2014 and 2015. Although the invasion by nonnative grasses (primarily *Eragrostis lehmanniana* and secondarily E. *curvula*) increased the amount of herbaceous foliage available to arthropods, richness of arthropods decreased by an average of 2% and total abundance by an average of 7% for every 10% increase in nonnative-grass dominance. Responses to the plant invasion, however, varied among taxa and functional groups. As dominance of nonnative grasses increased, abundances of most predators and specialist herbivores decreased, whereas abundances of most generalist herbivores were lowest at intermediate points of the invasion gradient. The changes we observed in the arthropod community have potential to alter broad-scale ecological processes, including energy flow and nutrient cycling, and to reduce food resources for insectivores, which can have adverse, cascading effects on imperiled grassland ecosystems.

Keywords

Eragrostis lehmanniana · exotic species · insect · invasive species · invertebrate · semidesert

Introduction

Nonnative grasses have been introduced to almost every grassland or savanna ecosystem in the world, which has had significant impacts on native species (D'Antonio and Vitousek 1992; Steidl et al. 2013). Typically, as nonnative grasses invade grasslands and increase in dominance, floristic diversity and structural heterogeneity decrease (D'Antonio and Vitousek 1992; Vilà et al. 2011), and vegetation cover and biomass increase (Brooks et al. 2004; Geiger 2006). These changes in composition and structure of grassland plant communities alter ecosystem processes, including primary production, decomposition, nutrient and carbon cycling, and hydrologic and disturbance regimes (Vitousek et al. 1996; Levine et al. 2003; Bradley et al. 2006). Consequently, invasions by nonnative grasses pose a serious threat to remaining grasslands, which are among the most biologically diverse and most threatened ecosystems in the world (Wilson et al. 2012; Murphy et al. 2016).

Collectively, changes in ecosystem structure, composition, and processes associated with plant invasions can affect the quantity and quality of habitat for animals that inhabit grasslands (Steidl et al. 2013). Arthropods may be especially vulnerable to changes in the plant community that result from invasions because many have limited mobility or have evolved specialized relationships with host plants that provide food or substrates for reproduction (Bernays and Graham 1988). For example, approximately 90% of all phytophagous insects feed on plants in only one or a few plant lineages, and these host plants may be displaced or reduced in abundance when novel plants invade a community (Strong et al. 1984; Bernays and Graham 1988; Tallamy 2004). Additionally, survival, reproduction, or distributions of all arthropods, including those not associated closely with specific plants, can change in response to invasions by nonnative plants if vegetation structure is altered in ways that affect microclimatic conditions, including light intensity, temperature, and soil moisture (Wolkovich 2010; Schirmel and Buchholz 2013). These changes in abundance and community composition of arthropods can affect broad-scale ecological processes, including decomposition, nutrient cycling, and pollination

(Hladik et al. 2015; Nitschke et al. 2015), and are likely to have disproportionately strong effects on food webs because many taxa are key prey for insectivores. Grasshoppers (Orthoptera), for example, are the primary prey of many breeding grassland birds (George and McEwen 1992), a group that has declined more rapidly than any other group of birds in North America (Sauer and Link 2011).

Effects of plant invasions on arthropods may be strongest where invading plants have reduced vegetation heterogeneity markedly (Hovick et al. 2015), such as in semidesert grasslands of North America where two perennial C_4 grasses have come to dominate grasslands once characterized by a diverse flora of native grasses (Litt and Steidl 2011). *Eragrostis lehmanniana* and *E. curvula* were introduced to southeast Arizona from southern Africa in the 1930s and 1940s in an attempt to revegetate degraded rangelands and mitigate soil erosion after prolonged drought (Anable et al. 1992). These two species have spread rapidly and are predicted to expand to an area >71,000 km^2 in southern Arizona and New Mexico alone (Anable et al. 1992; Schussman et al. 2006). Compared to most native grasses, these nonnative species grow more rapidly, produce more seeds and up to four times more aboveground biomass, and are less palatable to vertebrate herbivores (Cox et al. 1990; Geiger 2006). These attributes can increase fire intensity and frequency, a primary ecological process that governs spatial and temporal patterns of biodiversity in many grassland ecosystems (McPherson 1995; Brooks et al. 2004; Steidl et al. 2013).

Although invasions by these nonnative grasses have been shown to alter richness and abundance of many vertebrate taxa, effects on grassland arthropods are less well-understood (Steidl et al. 2013; Litt et al. 2014). We know, however, that richness and abundance of epigeic (i.e., surface-dwelling) insects decrease as dominance of *E. lehmanniana* increases, although responses vary among taxa (Litt and Steidl 2010). Here, we sought to understand the effects of these invasions on arthropods that use grasses or other herbaceous plants as their primary substrate (hereafter, foliage-dwelling arthropods). This group may be especially vulnerable to changes in grassland structure or floristics that

accompany invasions because of their direct reliance on herbaceous plants for food, shelter, or reproduction (Gleditsch 2016). Specifically, we evaluated how abundance and richness of foliage-dwelling arthropods changed along a gradient of dominance by nonnative grasses in semidesert grasslands. This gradient represents a space-for-time substitution for the process by which nonnative-grass invasions transform grassland plant communities once composed of a diverse assemblage of native grass species into near-monocultures with few native species.

Methods

Study area

We surveyed arthropods and vegetation in southeastern Arizona, USA at three sites that span the range of variation in vegetation structure and management of semidesert grasslands in North America: Appleton-Whittell Research Ranch (31.6° N, 110.5° W), Fort Huachuca Military Reservation (31.6° N, 110.3° W), and Las Cienegas National Conservation Area (31.8° N, 110.6° W). Sites are located within a 40 x 55 km area where semidesert grasslands occur between 1350 and 1550 m elevation and annual precipitation averages 350 to 450 mm, most of which falls during a monsoon season between July and September that is preceded by two to three months that are hot and dry (McClaran 1995). Livestock have been excluded from Fort Huachuca Military Reservation since 1950 and Appleton-Whittell Research Ranch since 1968. Grasslands at Las Cienegas National Conservation Area are grazed by cattle, therefore we excluded areas that were scheduled to be grazed during the study.

Vegetation composition at all sites was dominated by a variety of C_4 perennial grasses. Common native grasses included *Aristida* spp., *Bothriochloa barbinodis*, *Bouteloua* spp., *Digitaria californica*, and *Eragrostis intermedia*. At each site, composition of perennial grasses ranged from 0 to nearly 100% nonnative species, with areas dominated by nonnative species occurring throughout each site. Of the nonnative grasses, *E. lehmanniana* was the most widespread and often dominated large areas, although

E. curvula was abundant locally. Woody plants were composed almost entirely of native species (>99% of woody cover), especially *Baccharis* spp., *Isocoma tenuisecta*, *Mimosa* spp., and *Prosopis velutina*, which has encroached many grasslands in this region transforming them to shrub savannas (Archer et al. 2017).

Arthropod sampling

We established 90, 100-m-radius circular plots (3.1-ha) at random throughout upland areas of the three sites. We excluded areas with obvious anthropogenic features (e.g., roads or buildings), those that were scheduled to be grazed, and those that had been burned or otherwise manipulated to reduce woody vegetation during the previous three years. We surveyed 50 plots in 2014 and 40 different plots in 2015; 12 plots were located at Appleton-Whittell, 29 at Fort Huachuca, and 49 at Las Cienegas.

We surveyed arthropods on each plot three times between mid-June and mid-August. This period typically encompasses most monsoon precipitation, which coincides with the growing season for grasses and peak abundance of many arthropod taxa in semidesert grasslands (Whitford et al. 1995). To target foliage-dwelling arthropods, we used a 38-cm sweep net constructed of heavy sailcloth canvas to capture arthropods along three 60-m transects radiating from plot center at 120° intervals. Sweep sampling is well-suited for surveying these arthropods (Gardiner et al. 2005; Yi et al. 2012) and characterizes relative abundance and community composition accurately (Larson et al. 1999; Kati et al. 2004). To minimize variation among surveyors and variation induced by heterogeneity in vegetation density or height (Doxon et al. 2011), we standardized our sweeping procedure. Surveyors traversed each transect at a constant pace and made 30 fast sweeps (one 2-m sweep per pace) as close to the ground as permitted by vegetation (Neill et al. 2002). We emptied the contents of the net into a labeled 3.8 L freezer bag that we stored on ice soon after collection and transferred to a freezer within three days.

In the lab, we counted and classified individuals to morphospecies based on recognizable visual characteristics, an efficient approach that produces estimates of richness similar to those obtained by specialists who identify specimens to species (Oliver and Beattie 1993, 1996). Additionally, we classified most (99.3%) individuals to order and individuals from the three most abundant orders to suborder (Hemiptera) or family (Coleoptera and Orthoptera). We classified taxa thought to be functionally homogeneous into functional groups for analysis (Table 1). Specifically, we classified taxa as generalist herbivores, specialist herbivores, and predators based on information provided in Triplehorn and Johnson (2005) and Litt et al. (2014).

Vegetation sampling

Although our primary objective was to evaluate responses of arthropods to variation in dominance of nonnative grasses, arthropod populations also reflect other vegetation features. Therefore, we characterized species composition and structure of the entire plant community on each plot using a design that complemented the approach we used to sample arthropods. We surveyed vegetation by establishing eight 10-m diameter subplots systematically on each plot, two along each cardinal axis with one 25 m and another 75 m from plot-center. On each subplot, we estimated canopy cover and composition (as percent of total cover) of grasses, canopy cover of woody plants and forbs (i.e., herbaceous dicots), and surface cover of ground litter and bare ground by combining visual estimates from four quadrants. Additionally, we measured grass height at eight points spaced systematically on the periphery of each subplot. We surveyed vegetation in September, when presence of grass inflorescences aided identification. Although we surveyed vegetation later in the season than arthropods, composition of C_4 perennial grasses remains stable during summer months (Geiger 2006), therefore dominance of nonnative grasses likely changed little between surveys. To reduce observer-induced variation, only two observers measured vegetation each year and each measured half of the

subplots on every plot. For analysis, we averaged estimates of vegetation cover, composition, and grass height across the eight subplots on each plot.

Data analysis

For all analyses, we quantified dominance of nonnative grasses as the proportion of perennial grass cover comprised by nonnative species. We used simple linear regression to evaluate how vegetation features on plots varied with dominance of nonnative grasses; we used Shannon's Index to characterize diversity of grasses. To reduce the number of non-focal vegetation variables in models, we considered only cover of woody plants, forbs, and grasses as covariates because grass cover was correlated with cover of bare ground (r = -0.90), litter (r = -0.53), and grass height (r = 0.61).

Our overarching approach to analysis was to evaluate the effect of dominance of nonnative grasses on each arthropod response after accounting for other sources of variation among plots. As responses, we considered richness of orders, richness of morphospecies for all taxa combined and the three orders with highest abundances, and abundance of all orders combined (hereafter 'total abundance'), each taxa individually, and each functional group. For each response, we began with a generalized linear mixed model that included all vegetation covariates except for nonnative grasses, plus site, plot, and three covariates to describe timing of surveys: year, Julian day, and time-of-day; we considered both linear and quadratic effects for Julian day and time-of-day. We treated all terms as fixed effects except for plot, which we treated as a random effect. We then used backwards elimination to eliminate vegetation and temporal covariates with little explanatory power ($P > 0.10$ based on Wald Z-tests). Lastly, we added terms for dominance of nonnative grasses (both linear and quadratic forms) to a model that included all remaining covariates, which provided a direct test of the influence of nonnative grasses on each response variable after accounting for other important features (Ramsey and

186 Schafer 2002). We standardized all covariates to *Z*-scores (mean = 0, standard deviation = 1) to improve
187 numerical convergence of models.
188 To model abundance, we specified a log link function and a negative binomial error distribution
189 because counts of arthropods were overdispersed. To model richness, we specified a log link function
190 and a Poisson error distribution. We fit models with the R package lme4 (Bates et al. 2015). To aid
191 interpretation, we report the percentage change in each response for every 10% increase in dominance
192 of nonnative grasses (Ramsey and Schafer 2002).
193
194 **Results**
195 Vegetation
196 Sites were dominated by perennial grasses and our plots spanned the gradient of invasion by nonnative
197 grasses on each site (Table 2, Fig. 1). Across all sites and plots, composition of perennial grasses
198 averaged 48% native species and 49% nonnative species (3% were unidentified), and ranged from 0 to
199 99% nonnative species (Table 2). Native grasses were represented by 27 species, none of which
200 comprised >10% of perennial grass cover, which illustrates the high degree of diversity in this category.
201 Nonnative grasses were represented by three species that were locally abundant (Table 2). *Eragrostis*
202 *lehmanniana* was by far the most common, comprising 95% of nonnative grass cover and 47% of
203 perennial grass cover across all plots (Table 2). As dominance of nonnative grasses increased, grass
204 diversity decreased markedly, simplifying the plant community (Fig. 1c). In addition to altering species
205 composition, nonnative grasses also altered vegetation structure and reduced vegetation heterogeneity.
206 For every 10% increase in dominance of nonnative grasses, mean grass height increased by 1.5 cm (SE =
207 0.34, t_{88} = 4.59, P < 0.0001) and total grass cover increased by 1.4% (SE = 0.58, t_{88} = 2.47, P = 0.015; Fig.
208 1a, b). Cover of bare ground averaged 18% (Table 2) and decreased by an average of 0.8% (SE = 0.40, t_{88}
209 = 1.98, P = 0.051) for every 10% increase in dominance of nonnative grasses. Cover of forbs averaged

10% and woody plants 8% across plots (Table 2), neither of which varied systematically with dominance of nonnative grasses ($t_{88} < 0.95$, $P > 0.35$).

Arthropods

We captured 93,418 arthropods from 11 orders during 270 surveys on 90 plots (Table 1). Four orders comprised 94% of individuals captured: 75% were Hemiptera (true bugs), 9% Orthoptera (grasshoppers, crickets and katydids), 5% Coleoptera (beetles), and 5% Araneae (spiders).

Total abundance of arthropods decreased by an average of 7% for every 10% increase in dominance of nonnative grasses (Table 1). Excluding the two most abundant Hemipteran morphospecies, which represented 43% of all individuals captured, did not change the direction of this effect but did reduce its magnitude to 5% (SE = 1.51, $X^2 = 8.92$, $P = 0.003$) for every 10% increase in dominance of nonnative grasses.

Although total abundance of arthropods decreased as dominance of nonnative grasses increased, effects varied widely among orders. Abundance of 3 of 11 (27%) orders decreased as dominance of nonnative grasses increased (Table 1). Abundance decreased by an average of 9% in Coleoptera, Hemiptera, and Diptera for every 10% increase in dominance of nonnative grasses (Table 1). For Coleoptera, the decrease was driven by decreases in four of the five most common families (Table 1). Abundance decreased by an average of 16% in Melyridae (flower beetles), 11% in Cleridae (checkered beetles), 8% in Curculionidae (weevils), and 6% in Chrysomelidae (leaf beetles) for every 10% increase in dominance of nonnative grasses (Table 1, Fig. 2). Among suborders within Hemiptera, abundance decreased by an average of 9% for Auchenorrhyncha (cicadas, hoppers, spittlebugs) and 8% for Heteroptera (true bugs) for every 10% increase in dominance of nonnative grasses (Table 1, Fig. 2).

Abundance of 4 of 11 (36%) orders increased as dominance of nonnative grasses increased (Table 1). Abundance increased by an average of 32% in Parasitiformes (ticks), 15% in Mantodea

234 (mantises), 14% in Neuroptera (net-winged insects), and 5% in Hymenoptera (bees and ants) for every
235 10% increase in dominance of nonnative grasses (Table 1).

236 Abundances did not vary linearly with dominance of nonnative grasses for 3 of 11 (36%) orders:
237 Araneae, Phasmatodea (stick insects), Lepidoptera (butterflies and moths; 86% of which were larvae),
238 and Orthoptera (Table 1). Phasmatodea and Orthoptera, however, varied nonlinearly along the invasion
239 gradient, with abundances being similar at the gradient extremes and lowest at intermediate levels of
240 nonnative grass dominance (Fig. 2, Appendix 1 of Electronic Supplementary Material). For Orthoptera,
241 this pattern was driven by nonlinear responses in two of three families: Acrididae (grasshoppers) and
242 Tettigoniidae (bush crickets; Fig. 2, Appendix 1 of Electronic Supplementary Material).

243 Among functional groups, abundance decreased by an average of 9% for specialist herbivores
244 and 4% for predators for every 10% increase in dominance of nonnative grasses (Table 1, Fig. 3).
245 Abundance of generalist herbivores changed nonlinearly along the invasion gradient, with abundances
246 similar at the gradient extremes and lowest where composition of nonnative grasses was approximately
247 50% (Fig. 3, Appendix 1 of Electronic Supplementary Material).

248 Richness decreased as dominance of nonnative grasses increased for three of the five taxonomic
249 groups we considered (Table 3). Specifically, richness of morphospecies decreased by an average of 2%
250 for all taxa combined, 5% within Coleoptera, and 4% within Orthoptera for every 10% increase in
251 dominance of nonnative grasses (Table 3). Richness of orders and richness within Hemiptera did not
252 vary along the invasion gradient (Table 3).

253

254 **Discussion**

255 In the grasslands we studied, height and cover of grasses increased as nonnative grasses increased in
256 dominance, a pattern similar to that observed in many other invaded grasslands (Brooks et al. 2004).
257 Although these changes increased the quantity of substrate available to foliage-dwelling arthropods,

258 total abundance and richness decreased as dominance of nonnative grasses increased. This suggests
259 that any benefits from increased foliage to this community of arthropods were outweighed by costs
260 associated with changes in vegetation composition or structure, such as reduced structural
261 heterogeneity or grass diversity (Fig. 1).

262 Changes in abundance of foliage-dwelling arthropods along the invasion gradient varied
263 considerably among taxa, as some orders decreased in abundance as the invasion intensified
264 (Coleoptera, Diptera, Hemiptera), whereas others increased (Hymenoptera, Mantodea, Neuroptera,
265 Parasitiformes) or were unaffected (Araneae, Lepidoptera, Orthoptera, Phasmatodea). A spectrum of
266 responses has been reported for studies that considered the effects of plant invasions on multiple
267 arthropod taxa, which may be attributable to how different functional groups respond to changes in
268 plant composition and structure (Litt et al. 2014).

269 Relative to other groups, herbivorous insects are especially vulnerable to floristic changes from
270 plant invasions because 90% feed only on plants from one or a few lineages and may not use novel
271 plants as food, at least for species whose diets are known (Strong et al. 1984; Bernays and Graham 1988;
272 Tallamy 2004). In the grasslands we studied, as dominance of nonnative grasses increased, abundance
273 of specialist herbivores decreased more steeply than the other functional groups (Fig. 3). Among taxa in
274 this group, which are characterized largely by monophagous or oligophagous herbivores, we found that
275 abundance of Curculionidae and both suborders of Hemiptera decreased markedly as dominance of
276 nonnative grasses increased, a pattern consistent with other studies (reviewed in Litt et al. 2014).
277 Similarly, many Lepidoptera require specific plants for feeding or reproduction, therefore their
278 abundances typically decrease when nonnative plants invade a community (Tallamy and Shropshire
279 2009; Burghardt et al. 2010). In Arizona grasslands, however, we and others observed no systematic
280 variation in abundance of lepidopterans with dominance of nonnative grasses (Litt and Steidl 2010). This
281 finding was not an artifact of a bias towards adults, which are vagile and more likely than larvae to be

282 captured on plants that they do not use for food or reproduction, because 86% of lepidopterans that we
283 captured were caterpillars. We acknowledge, however, that larvae of many species, including those that
284 bore into stems or feed within leaf sheaths, were likely underrepresented in our sample and might
285 respond to invasions differently than other groups. The lack of an effect for Lepidoptera may be
286 attributable to the way that grass invasions affect forbs, which are the focus of many lepidopteran-plant
287 specializations (Futuyma 1976). Typically, forbs decrease in abundance and diversity as dominance of
288 nonnative plants increase (Geiger 2006), but we found no systematic changes in forb cover along the
289 invasion gradient. The absence of a decrease in forbs along the invasion gradient might also explain why
290 abundance of Hymenoptera, an important pollinator taxa, did not decrease in our study. Like specialist
291 herbivores, pollinators typically are less common in invaded areas because the flowering plants they rely
292 on for food generally are less abundant (Montero-Castaño and Vilà 2012; Litt et al. 2014).

293 Generalist herbivores may be more likely to feed on novel plant species than forage-specialized
294 arthropods (Strong et al. 1984; Tallamy 2004). Consequently, taxa dominated by polyphagous species
295 might be less vulnerable to invasions that displace their native food sources, especially if nonnative
296 grasses lack effective defenses against evolutionarily novel herbivores (Parker et al. 2006; Avanesyan
297 and Culley 2015). They might even increase in abundance if nonnative plants produce more biomass
298 than native species. In our study, abundances of generalist herbivores were similar (Orthoptera,
299 Phasmatodea) or lower (Chrysomelidae) in areas dominated by nonnative grasses relative to areas
300 dominated by native grasses. Interestingly, though, we found that abundances of Phasmatodea and
301 Orthoptera (including two of three families, Acrididae and Tettigoniidae) were nonlinear, with lower
302 abundances at intermediate levels of nonnative dominance than at the gradient extremes (Fig. 2).

303 Nonlinear variation in abundance along the invasion gradient likely reflects species-level
304 variation in responses of generalist herbivores. The decrease in abundance associated with early stages
305 of invasion suggests that some species were unable to use nonnative grasses, which generally are

306 considered less palatable to herbivores than native species because of lower tissue nitrogen and higher
307 lignin content (Haddad et al. 2001; Geiger 2006). As nonnative grasses continued to increase in
308 dominance, however, abundance of generalist herbivores increased, suggesting that other species may
309 have been preadapted to use nonnative grasses, the most common of which are congeners of a locally
310 common native species (*Eragrostis intermedia*). These species may have benefitted from the increased
311 quantity of foliage in invaded areas or from structural changes that accompanied invasion by nonnative
312 grasses. For example, some orthopterans are associated closely with habitat features common to areas
313 dominated by nonnative grasses, such as increased litter depth or vegetation biomass, which increase
314 humidity and moderate temperature extremes (Samways 1990; Szinwelski et al. 2012). Conversely,
315 other species are associated with habitat features common to areas dominated by native grasses, such
316 as high structural heterogeneity, patches of bare ground, or areas open to direct sunlight (Whitford et
317 al. 1995; Chambers and Samways 1998). Collectively, these species-specific responses could explain the
318 nonlinear changes in abundance that we observed.

319 Because their diets are less specialized than herbivores, predaceous arthropods are thought to
320 respond more to changes in vegetation structure than to floristics (Pearson 2009; Litt et al. 2014).
321 Consequently, their abundance and richness often increase with height and complexity of vegetation
322 (Tscharntke 1995; Haddad et al. 2009). In our study, however, predator abundance decreased as
323 dominance of nonnative grasses increased, despite increases in grass height and density (Fig. 1a, b).
324 When taxa were considered individually, abundances of the four most common predator-dominated
325 taxa remained consistent (Araneae, Meloidae, which have predatory larvae) or decreased (Melyridae,
326 Cleridae) along the invasion gradient, likely reflecting decreased abundance of herbivore prey. This
327 suggests that decreases in abundance of herbivorous arthropods are unlikely the result of top-down
328 pressure from predators exploiting increased habitat along the invasion gradient.

329 Arthropods in semidesert grasslands of Arizona have been sampled with sweep nets (this study)
330 and pitfall traps (Litt and Steidl 2010), with each method chosen to target a subset of arthropods that
331 use different primary substrates. Taxonomic composition differed between these two subsets, but
332 among those taxa well represented in both studies, the direction of responses of foliage- and surface-
333 dwelling (i.e., epigeic) arthropods to invasions by nonnative grasses were generally similar (Litt and
334 Steidl 2010). For both groups abundances of Coleoptera and all taxa combined decreased similarly as
335 dominance of nonnative grasses increased, whereas abundances of foliage-dwelling Hemiptera and
336 Diptera decreased more sharply than their surface-dwelling counterparts. Responses to the plant
337 invasion differed directionally across studies for only two well-represented taxa. Abundance of surface-
338 dwelling Orthoptera decreased markedly as dominance of nonnative grasses increased (Litt and Steidl
339 2010) whereas abundance of foliage-dwelling Orthoptera was similar at the extremes of the invasion
340 gradient and lowest at intermediate levels of nonnative grass dominance. The decrease in abundance of
341 surface-dwelling Orthoptera may be attributable to the importance of open ground or microclimatic
342 conditions for many species, features that likely change when larger, denser-growing grasses invade
343 grasslands (Fig. 1a, b). Conversely, abundance of foliage-dwelling Hymenoptera increased as dominance
344 of nonnative grasses increased whereas abundance of ground-dwelling Hymenoptera did not change
345 (Litt and Steidl 2010). The response of ground-dwelling Hymenoptera was driven strongly by Formicidae
346 (ants), however, which comprised 63% of total individuals captured by pitfall trap (Litt and Steidl 2010)
347 but that we captured only rarely on foliage.
348 In summary, total abundance and richness of foliage-dwelling arthropods decreased as
349 dominance of nonnative grasses increased, although abundances of some groups increased or largely
350 were unaffected by invasions of nonnative grasses. As nonnative grasses continue to expand into
351 grassland and savanna systems as predicted (Schussman et al. 2006), the abundance and distribution of
352 many arthropods is likely to continue to change. Changes in arthropod communities in response to

changes in the plant community could have far-reaching consequences for imperiled grassland ecosystems and the native organisms they support. For example, changes in populations of pollinators or herbivores could influence composition and structure of grassland plant communities (Bezemer et al. 2014). Additionally, decreases in abundance of foliage-dwelling arthropods have the potential to disrupt food webs because these arthropods are the primary prey for many insectivorous species, including groups of high-conservation concern, such as breeding grassland birds (George and McEwen 1992; Rzanny and Voigt 2012). Further, given their key role in ecological processes, including energy flow and nutrient cycling, changes to arthropod communities would be expected to alter how grassland ecosystems function (Whiles and Charlton 2006). Consequently, understanding how arthropod communities change in response to invasions by nonnative grasses will become increasingly important for guiding conservation and restoration strategies for grasslands and the organisms and ecological processes they support.

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Table 1 Number of individuals or taxa captured (No.), non-focal vegetation and temporal covariates included in final model, and linear effect of dominance of nonnative grasses on abundance and richness of arthropod taxa and functional groups (*n* = 90 plots). Estimates reported on the log scale and back transformed as the percentage change in abundance for every 10% increase in dominance of nonnative grasses (10% increase). Letters in parenthesis indicate functional groups (G = generalist herbivores, P = predators, S = specialist herbivores). Estimates for non-focal covariates provided in Appendix 1 of Electronic Supplementary Material

Response	Taxa or functional group	No.	Covariates	Estimate	SE	*Z*	*P*	10% increase
Abundance	Araneae (P)	4,690	year, day^2, time^2, forb	-0.03	0.05	-0.47	0.64	-0.8
	Coleoptera	4,765	year, day^2	-0.30	0.07	-4.47	<0.001	-9.4
	Chrysomelidae (G)	2,128	day^2, forb, grass	-0.20	0.09	-2.19	0.03	-6.2
	Cleridae (P)[a]	482	day, wood, grass	-0.35	0.13	-2.57	0.01	-10.7
	Curculionidae (S)	703	year, day^2, wood	-0.26	0.11	-2.48	0.01	-8.3
	Meloidae	116	day^2, wood	0.02	0.22	0.08	0.94	0.6
	Melyridae (P)	1,279	year, day	-0.53	0.18	-2.89	0.004	-16.1
	Diptera	861	year, day^2, time^2	-0.28	0.09	-3.05	0.002	-8.7
	Hemiptera (S)	69,698	year, forb, grass	-0.30	0.09	-3.16	0.002	-9.3
	Auchenorrhyncha (S)	56,945	year, day, time, forb, grass	-0.30	0.11	-2.70	0.007	-9.4
	Heteroptera (S)	12,753	year, day^2, grass	-0.24	0.09	-2.83	0.005	-7.7
	Hymenoptera	1,911	year, day^2, time^2, forb	0.15	0.09	1.69	0.09	5.0
	Lepidoptera (S)	1,532	year, day^2, grass	0.10	0.08	1.19	0.23	3.4
	Mantodea (P)	42	day, time, wood	0.43	0.21	1.99	0.05	15.1
	Neuroptera (P)	55	day, wood	0.39	0.18	-2.89	0.03	13.6
	Orthoptera (G)[a]	8,702	year, day, forb	-0.03	0.09	-0.35	0.73	-1.0
	Acrididae (G)[a]	5,869	year, day^2, time, wood, forb, grass	-0.05	0.09	-0.56	0.58	-1.7

	Gryllidae (G)	121	day^2, time, forb, grass	-0.04	0.22	-0.18	0.86	-1.3
	Tettigoniidae[a]	2,712	year, day^2, forb	0.04	0.15	-0.27	0.79	-1.3
	Parasitiformes	29	year, day^2, wood, grass	0.85	0.32	2.67	0.007	32.2
	Phasmatodea (G)[a]	512	year, time, wood, grass	-0.05	0.11	-0.50	0.62	-1.8
	All taxa combined	93,418	year, day, forb, grass	-0.21	0.07	-3.07	0.002	-6.8
	Generalist herbivores[a]	11,342	year, day, forb	-0.05	0.07	-0.64	0.52	-1.5
	Specialist herbivores	71,933	year, day^2, forb, grass	-0.27	0.09	-2.98	0.003	-8.5
	Predators	6,548	year, day^2, time^2	-0.13	0.06	-2.27	0.02	-4.2
Richness	Orders	11	year, day, time	0.01	0.03	0.54	0.59	0.5
	All taxa	131	year, day, time^2, forb, grass cover	-0.21	0.07	-3.07	0.002	-1.9
	Coleoptera	32	year, day^2, time^2, grass cover	-0.14	0.04	-4.08	<0.001	-4.6
	Hemiptera	31	year, day^2, forb, grass cover	-0.04	0.03	-1.36	0.18	-1.4
	Orthoptera	38	year, day, forb	-0.12	0.04	-2.69	0.007	-3.8

[a] Taxa for which there was evidence for a nonlinear response to nonnative dominance ($P < 0.05$); see Appendix 1 of Electronic Supplementary Material

Table 2 Mean, standard error, minimum and maximum cover of vegetation and composition of perennial grasses, including the three most common nonnative species across sites, plots, and years (*n* = 90 plots)

Measure	Category	Mean	SE	Min	Max
Cover (%)	Bare	18.4	1.2	2.5	51.7
	Forbs	9.8	1.0	0.3	52.5
	Litter	4.3	0.3	0.3	12.9
	Woody plants	7.8	0.8	0.0	33.5
	Annual grasses	6.6	1.1	0.0	44.2
	Perennial grasses	64.7	1.8	29.6	95.4
Composition (%)[a]	Native grasses	48.3	3.1	1.3	100.0
	Nonnative grasses	49.1	3.2	0.0	98.8
	Eragrostis lehmanniana	46.7	3.2	0.0	98.8
	Eragrostis curvula	1.9	0.9	0.0	66.3
	Bothriochloa ischaemum	0.5	0.2	0.0	14.3

[a] 2.6% of perennial grasses could not be classified as native or nonnative

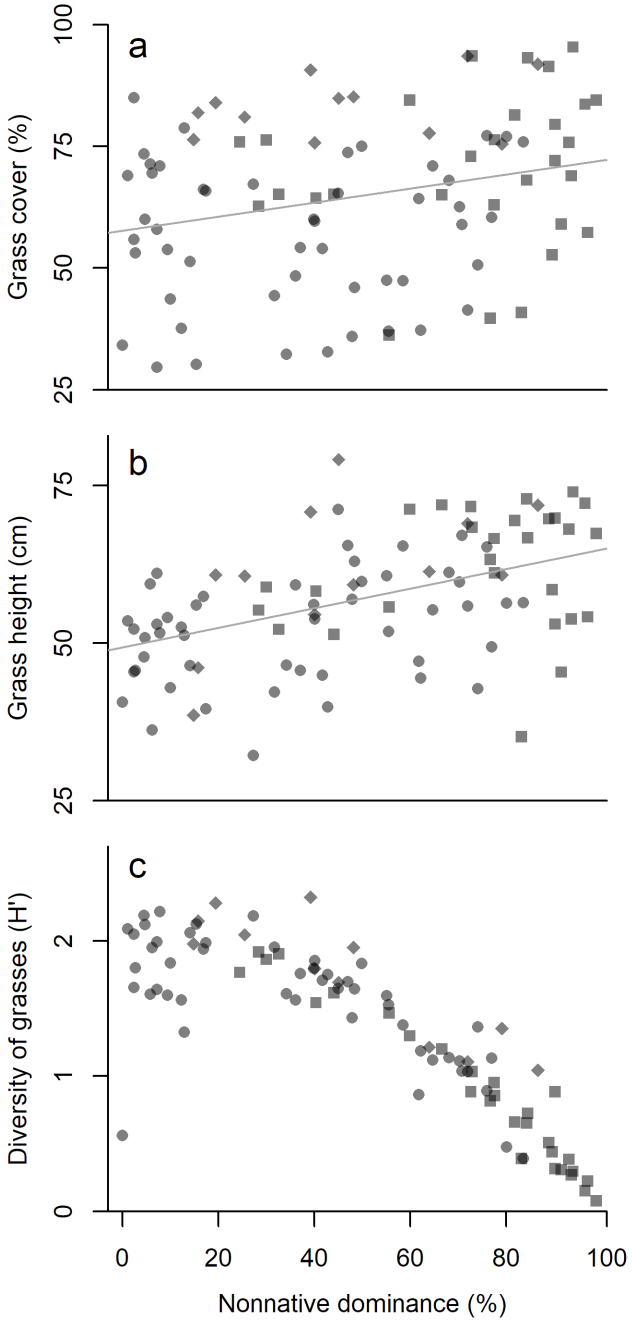

Fig. 1 Grass cover (a), grass height (b), and diversity (Shannon's Index) of perennial grasses (c) versus dominance of nonnative grasses. Point shapes represent the three different sites we surveyed and demonstrate the range of nonnative grass dominance at each site

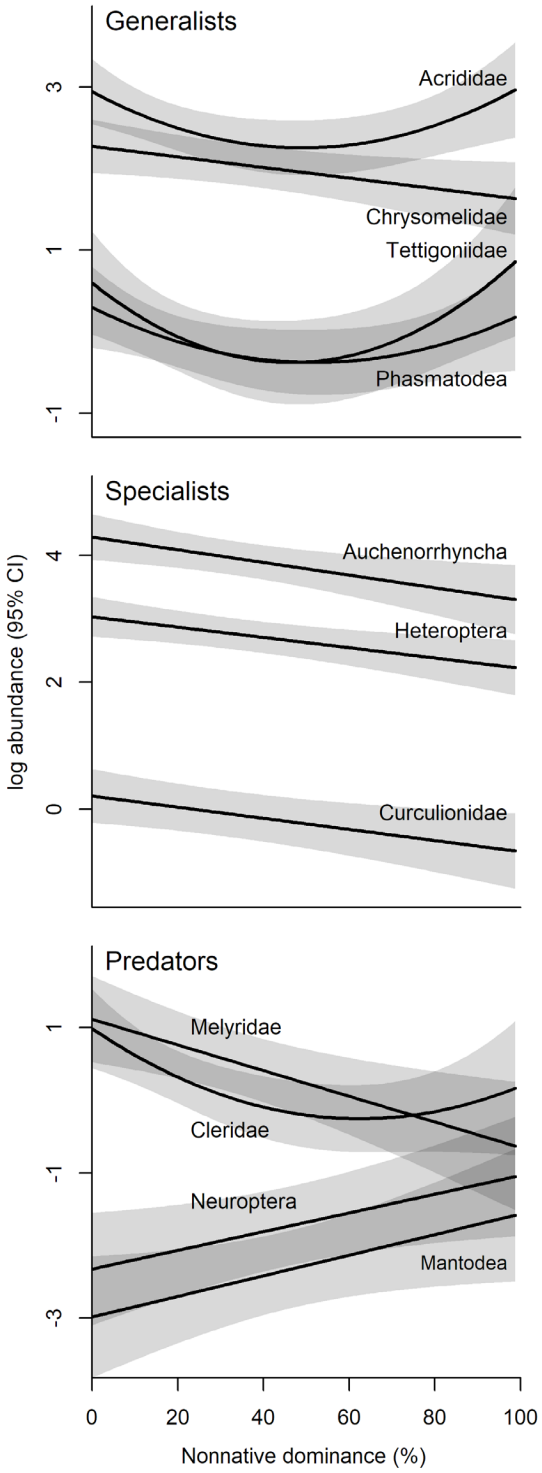

Fig. 2 Log abundance (95% CI) of arthropod taxa versus dominance of nonnative grasses for generalist herbivores (top panel), specialist herbivores (middle panel) and predators (bottom panel). Only those taxa where abundance varied appreciably are shown (Table 1)

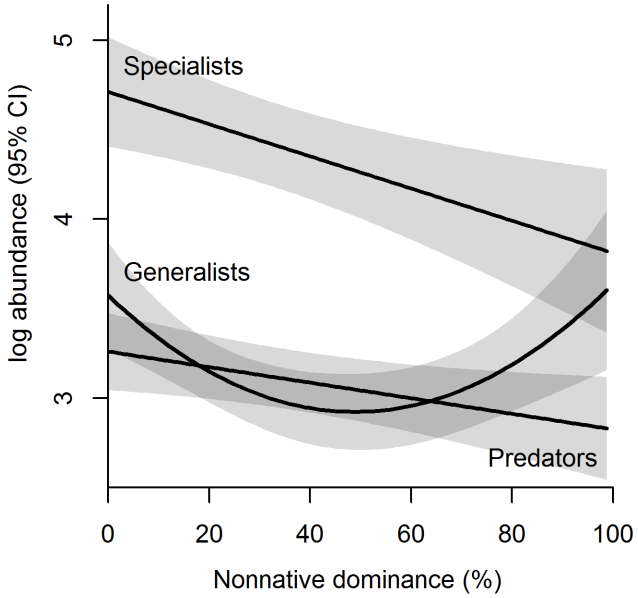

Fig. 3 Log abundance (95% CI) of arthropod functional groups versus dominance of nonnative grasses.

Taxa comprising each group are shown in Table 1

Appendix 1 Estimates reported on the log scale with standard errors (SE), test statistics (*Z*), and *P*-values for fixed effects from final models of arthropod abundance and richness by functional group and taxa. All models included plot as a random effect. For nonnative-dominance effect, quadratic term included when supported ($P < 0.05$). For site effect, FH = Fort Huachuca Military Reservation, LC = Las Cienegas National Conservation Area, and the reference level is Appleton-Whittell Research Ranch

Metric	Functional group or taxa	Covariates	Estimate	SE	*Z*	*P*
Abundance	Generalist herbivores	intercept	3.17	0.17	18.94	<0.001
		site FH	-0.08	0.21	-0.37	0.714
		site LC	-0.24	0.18	-1.35	0.177
		year	0.27	0.06	4.45	8.410
		Julian day	0.86	0.05	17.59	<0.001
		forb cover	0.21	0.06	3.57	<0.001
		nonnative dominance	0.00	0.07	0.07	0.946
		nonnative dominance^2	0.25	0.07	3.43	<0.001
	Specialist herbivores	intercept	5.61	0.22	25.56	<0.001
		site FH	-0.15	0.26	-0.58	0.560
		site LC	-1.34	0.26	-5.24	<0.001
		year	0.73	0.09	7.82	<0.001
		Julian day	0.09	0.04	2.28	0.023
		Julian day^2	0.11	0.05	2.33	0.020
		forb cover	0.13	0.09	1.42	0.155
		grass cover	0.17	0.11	1.54	0.124
		nonnative dominance	-0.27	0.09	-2.98	0.003
	Predators	intercept	3.65	0.14	25.44	<0.001
		site FH	-0.30	0.16	-1.85	0.065
		site LC	-0.60	0.15	-4.08	<0.001
		year	0.43	0.05	8.77	<0.001
		Julian day	0.19	0.04	5.41	<0.001
		Julian day^2	-0.17	0.04	-4.11	<0.001
		time-of-day	-0.02	0.04	-0.42	0.676
		time-of-day^2	-0.07	0.04	-1.92	0.055
		nonnative dominance	-0.13	0.06	-2.27	0.023
	Araneae	intercept	3.45	0.13	25.91	<0.001

	site FH	-0.33	0.16	-2.12	0.034
	site LC	-0.54	0.14	-3.97	<0.001
	year	0.49	0.05	10.67	<0.001
	Julian day	0.01	0.03	0.27	0.791
	Julian day^2	-0.29	0.04	-7.39	<0.001
	time-of-day	0.03	0.04	0.69	0.494
	time-of-day^2	-0.09	0.04	-2.59	0.010
	forb cover	0.08	0.05	1.80	0.072
	nonnative dominance	-0.03	0.05	-0.47	0.642
Coleoptera	intercept	3.00	0.17	17.79	<0.001
	site FH	-0.22	0.19	-1.16	0.246
	site LC	-0.60	0.17	-3.48	<0.001
	year	0.10	0.06	1.70	0.090
	Julian day	0.77	0.05	14.73	<0.001
	Julian day^2	-0.12	0.06	-1.84	0.066
	nonnative dominance	-0.30	0.07	-4.47	<0.001
Chrysomelidae	intercept	2.09	0.23	9.25	<0.001
	site FH	-0.20	0.25	-0.80	0.421
	site LC	-0.13	0.25	-0.54	0.588
	Julian day	0.73	0.07	10.11	<0.001
	Julian day^2	-0.30	0.08	-3.69	<0.001
	forb cover	0.19	0.09	2.13	0.034
	grass cover	0.18	0.09	2.00	0.046
	nonnative dominance	-0.20	0.09	-2.19	0.029
Cleridae	intercept	1.01	0.29	3.44	<0.001
	site FH	-1.36	0.38	-3.57	<0.001
	site LC	-1.21	0.34	-3.53	<0.001
	year	0.22	0.13	1.68	0.092
	Julian day	0.53	0.11	4.77	<0.001
	woody plant cover	-0.19	0.13	-1.48	0.138
	grass cover	0.24	0.14	1.66	0.097
	nonnative dominance	-0.26	0.14	-1.86	0.063
	nonnative dominance^2	0.29	0.14	2.09	0.036
Curculionidae	intercept	0.89	0.27	3.35	<0.001
	site FH	0.00	0.30	0.01	0.992
	site LC	-1.12	0.26	-4.36	<0.001

	year	0.34	0.09	3.72	<0.001
	Julian day	0.70	0.09	7.87	<0.001
	Julian day^2	0.23	0.11	2.15	0.032
	woody plant cover	0.43	0.09	4.83	<0.001
	nonnative dominance	-0.26	0.11	-2.48	0.013
Meloidae	intercept	-3.85	0.76	-5.06	<0.001
	site FH	2.59	0.74	3.51	<0.001
	site LC	0.58	0.72	0.80	0.423
	Julian day	5.92	1.40	4.23	<0.001
	Julian day^2	-3.62	1.03	-3.51	<0.001
	woody plant cover	-0.60	0.21	-2.79	0.005
	nonnative dominance	0.02	0.22	0.08	0.937
Melyridae	intercept	0.32	0.44	0.72	0.470
	site FH	-0.18	0.52	-0.34	0.734
	site LC	-0.07	0.48	-0.14	0.886
	year	0.25	0.16	1.57	0.116
	time-of-day	0.07	0.13	0.53	0.597
	Julian day	1.04	0.14	7.58	<0.001
	nonnative dominance	-0.53	0.18	-2.89	0.004
Diptera	intercept	0.46	0.26	1.77	0.077
	site FH	0.37	0.26	1.41	0.159
	site LC	0.16	0.24	0.64	0.521
	year	0.34	0.08	4.46	<0.001
	Julian day	0.94	0.09	10.36	<0.001
	Julian day^2	-0.29	0.10	-2.82	0.005
	time-of-day	-0.19	0.08	-2.42	0.016
	time-of-day^2	0.25	0.07	3.63	<0.001
	nonnative dominance	-0.28	0.09	-3.05	0.002
Hemiptera	intercept	5.70	0.22	25.85	<0.001
	site FH	-0.19	0.27	-0.72	0.472
	site LC	-1.42	0.26	-5.38	<0.001
	year	0.79	0.10	8.12	<0.001
	forb cover	0.14	0.09	1.46	0.145
	grass cover	0.17	0.12	1.41	0.158
	nonnative dominance	-0.30	0.09	-3.16	0.002
Auchenorrhyncha	intercept	5.48	0.26	21.03	<0.001

	site FH	-0.36	0.32	-1.12	0.261
	site LC	-1.68	0.31	-5.38	<0.001
	year	0.79	0.12	6.82	<0.001
	Julian day	-0.22	0.04	-6.31	<0.001
	time-of-day	-0.07	0.04	-1.75	0.080
	forb cover	0.19	0.11	1.71	0.088
	grass cover	0.26	0.14	1.90	0.057
	nonnative dominance	-0.30	0.11	-2.70	0.007
Heteroptera	intercept	2.75	0.22	12.26	<0.001
	site FH	0.63	0.25	2.54	0.011
	site LC	-0.12	0.25	-0.46	0.644
	year	1.02	0.08	12.11	<0.001
	Julian day	0.75	0.06	12.85	<0.001
	Julian day^2	0.22	0.07	3.34	<0.001
	grass cover	0.24	0.09	2.62	0.009
	nonnative dominance	-0.24	0.09	-2.83	0.005
Hymenoptera	intercept	2.16	0.22	9.65	<0.001
	site FH	-0.36	0.25	-1.43	0.153
	site LC	-0.11	0.22	-0.50	0.618
	year	-0.27	0.08	-3.52	<0.001
	Julian day	0.12	0.07	1.69	0.091
	Julian day^2	-0.45	0.08	-5.29	<0.001
	time-of-day	-0.11	0.08	-1.40	0.160
	time-of-day^2	0.18	0.07	2.38	0.017
	nonnative dominance	0.15	0.09	1.69	0.090
Lepidoptera	intercept	0.16	0.23	0.68	0.494
	site FH	0.68	0.25	2.71	0.007
	site LC	0.35	0.25	1.41	0.160
	year	0.18	0.08	2.14	0.032
	Julian day	0.97	0.08	12.73	<0.001
	Julian day^2	0.50	0.10	5.22	<0.001
	grass cover	0.37	0.10	3.84	<0.001
	nonnative dominance	0.10	0.08	1.19	0.233
Mantodea	intercept	-2.06	0.51	-4.03	<0.001
	site FH	0.07	0.60	0.11	0.914
	site LC	-0.23	0.58	-0.40	0.691

	Julian day	-0.34	0.16	-2.18	0.029
	time-of-day	-0.34	0.19	-1.83	0.067
	forb cover	0.18	0.13	1.43	0.152
	woody plant cover	0.28	0.15	1.87	0.061
	nonnative dominance	0.43	0.21	1.99	0.047
Neuroptera	intercept	-2.21	0.50	-4.43	<0.001
	site FH	-0.18	0.56	-0.32	0.748
	site LC	0.52	0.51	1.01	0.311
	Julian day	0.73	0.17	4.27	<0.001
	woody plant cover	0.30	0.13	2.34	0.019
	nonnative dominance	0.39	0.18	2.14	0.033
Orthoptera	intercept	2.57	0.21	12.37	<0.001
	site FH	0.08	0.26	0.29	0.774
	site LC	-0.08	0.23	-0.36	0.721
	year	0.39	0.08	5.11	<0.001
	Julian day	1.01	0.06	17.24	<0.001
	forb cover	0.23	0.07	3.12	0.002
	nonnative dominance	0.02	0.09	0.26	0.797
	nonnative dominance^2	0.25	0.09	2.82	0.005
Acrididae	intercept	2.08	0.23	9.12	<0.001
	site FH	0.00	0.27	-0.01	0.989
	site LC	0.17	0.26	0.66	0.508
	year	0.27	0.10	2.66	0.008
	Julian day	0.86	0.06	13.68	<0.001
	Julian day^2	0.12	0.07	1.69	0.092
	time-of-day	0.14	0.06	2.33	0.020
	forb cover	0.29	0.09	3.21	0.001
	woody plant cover	0.16	0.08	2.08	0.038
	grass cover	0.14	0.12	1.20	0.230
	nonnative dominance	0.00	0.09	0.02	0.980
	nonnative dominance^2	0.26	0.09	2.76	0.006
Gryllidae	intercept	-2.35	0.58	-4.04	<0.001
	site FH	0.42	0.57	0.74	0.459
	site LC	-2.33	0.66	-3.55	<0.001
	Julian day	1.17	0.13	8.98	<0.001
	Julian day^2	0.80	0.20	4.06	<0.001

	time-of-day	0.23	0.12	1.89	0.058
	forb cover	-0.44	0.20	-2.19	0.028
	grass cover	-1.21	0.25	-4.91	<0.001
	nonnative dominance	-0.04	0.22	-0.18	0.861
Tettigoniidae	intercept	0.71	0.37	1.91	0.056
	site FH	-0.07	0.44	-0.17	0.864
	site LC	-1.09	0.39	-2.81	0.005
	year	0.85	0.13	6.49	<0.001
	Julian day	1.87	0.15	12.48	<0.001
	forb cover	0.22	0.12	1.77	0.076
	nonnative dominance	0.07	0.14	0.51	0.612
	nonnative dominance^2	0.41	0.15	2.75	0.006
Parasitiformes	intercept	-1.36	0.55	-2.48	0.013
	site FH	-1.75	0.71	-2.46	0.014
	site LC	-1.36	0.77	-1.76	0.079
	year	0.89	0.30	2.98	0.003
	Julian day	-0.19	0.26	-0.76	0.450
	Julian day^2	-0.80	0.25	-3.20	0.001
	woody plant cover	0.58	0.29	2.00	0.046
	grass cover	0.85	0.43	1.99	0.047
	nonnative dominance	0.85	0.32	2.67	0.007
Phasmatodea	intercept	0.32	0.25	1.28	0.202
	site FH	0.12	0.30	0.40	0.689
	site LC	-0.70	0.30	-2.31	0.021
	year	0.32	0.11	2.85	0.004
	time-of-day	-0.33	0.08	-4.28	<0.001
	woody plant cover	-0.21	0.11	-2.00	0.046
	grass cover	0.21	0.13	1.63	0.104
	nonnative dominance	-0.04	0.11	-0.39	0.700
	nonnative dominance^2	0.23	0.12	1.98	0.047
All taxa	intercept	6.00	0.16	36.60	<0.001
	site FH	-0.10	0.20	-0.52	0.601
	site LC	-0.97	0.20	-4.92	<0.001
	year	0.59	0.07	8.20	<0.001
	Julian day	0.18	0.03	5.42	<0.001
	forb cover	0.18	0.07	2.54	0.011

		grass cover	0.18	0.09	2.02	0.044
		nonnative dominance	-0.21	0.07	-3.07	0.002
Richness	Orders	intercept	2.03	0.06	33.43	<0.001
		site FH	-0.05	0.08	-0.68	0.496
		site LC	-0.10	0.07	-1.39	0.163
		year	0.05	0.02	2.04	0.041
		Julian day	0.07	0.02	3.17	0.002
		time-of-day	-0.05	0.02	-2.13	0.034
		nonnative dominance	0.01	0.03	0.54	0.590
	Morphospecies	intercept	6.00	0.16	36.60	<0.001
		site FH	-0.10	0.20	-0.52	0.601
		site LC	-0.97	0.20	-4.92	<0.001
		year	0.59	0.07	8.20	<0.001
		Julian day	0.18	0.03	5.42	<0.001
		forb cover	0.18	0.07	2.54	0.011
		grass cover	0.18	0.09	2.02	0.044
		nonnative dominance	-0.21	0.07	-3.07	0.002
	Coleoptera	intercept	1.56	0.09	16.85	<0.001
		site FH	0.04	0.10	0.39	0.697
		site LC	-0.16	0.10	-1.71	0.087
		year	0.09	0.03	2.60	0.009
		Julian day	0.40	0.03	11.91	<0.001
		Julian day^2	-0.15	0.04	-3.77	<0.001
		time-of-day	-0.01	0.03	-0.25	0.805
		time-of-day^2	0.04	0.03	1.55	0.121
		grass cover	0.07	0.04	1.91	0.056
		nonnative dominance	-0.14	0.04	-4.08	<0.001
	Hemiptera	intercept	1.69	0.08	20.92	<0.001
		site FH	0.07	0.09	0.81	0.418
		site LC	-0.20	0.09	-2.19	0.029
		year	0.14	0.03	4.23	<0.001
		Julian day	0.20	0.03	7.64	<0.001
		Julian day^2	0.08	0.03	2.43	0.015
		forb cover	0.08	0.03	2.60	0.009
		grass cover	0.07	0.04	1.54	0.123
		nonnative dominance	-0.04	0.03	-1.36	0.175

Orthoptera	intercept	1.34	0.10	12.97	<0.001
	site FH	0.32	0.13	2.50	0.012
	site LC	0.06	0.11	0.51	0.609
	year	0.07	0.04	2.00	0.046
	Julian day	0.45	0.03	15.05	<0.001
	forb cover	0.13	0.03	3.83	<0.001
	nonnative dominance	-0.12	0.04	-2.69	0.007