

Insect assemblages change along a gradient of invasion by a nonnative grass

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Received: 16 April 2009 / Accepted: 2 March 2010 / Published online: 14 March 2010
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Abstract Because invasions by nonnative plants alter the structure and composition of native plant communities, invasions can alter the function of ecosystems for animals that depend on plants for food and habitat. We quantified effects of an invasion by a nonnative grass on the insect community in grasslands of southeastern Arizona. We sampled insects on 54 1-ha plots established across a gradient of invasion by Lehmann lovegrass (*Eragrostis lehmanniana* Nees), a perennial species native to southern Africa. Between 2000 and 2004, we captured 94,209 insects representing 13 orders, 91 families, and 698 morphospecies during 2,997 trap nights. Richness of families, richness of morphospecies, and overall abundance of insects decreased as dominance of nonnative grass increased. With every 100 g/m² increase in biomass of nonnative grass, the average number of insect families decreased by 5%, morphospecies decreased by 6%, and overall abundance decreased by 14%. In areas dominated by nonnative grass, 2 of 8 orders and 6 of 27 families of insects were present less frequently and one family was

present more frequently; 5 of 8 orders and 6 of 27 families of insects were less abundant and 3 families were more abundant than in areas dominated by native grasses. As a result, this plant invasion altered the structure of the insect community, which has consequences for animals at higher trophic levels and for ecosystem processes, including decomposition and pollination. Because complete eradication of nonnative plants might be possible only rarely, maintaining stands of native vegetation in invaded areas may be an important practical strategy to foster persistence of animals in grasslands invaded by nonnative plants.

Keywords *Eragrostis lehmanniana* · Grasslands · Invertebrates · Lehmann lovegrass · Nonnative plants · Phytophagous insects

Introduction

Nonnative plants are established in nearly all terrestrial ecosystems, affecting ecosystem structure and ecological processes at all spatial and temporal scales, from the rate at which essential nutrients cycle (Vitousek et al. 1987) to the frequency and intensity of disturbances that govern patterns of biodiversity (Mack and D'Antonio 1998). Because invasions by nonnative plants alter the structure and composition of native plant communities, these changes can alter the quantity and quality of habitat for animals, causing compositional shifts in faunal

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communities that inhabit these areas. Relative to other taxa, effects of plant invasions on insects have been studied little, yet their limited mobility, dependence on plants for food, cover, and sites for reproduction, and their specialized relationships with particular plant species (Kremen et al. 1993) make insects vulnerable to changes driven by plant invasions. Given their short generation times, insects are also likely to respond rapidly to ecological changes, making them ideal subjects for research on the effects of plant invasions.

Insects are important components of many ecosystems in part because they comprise the highest biomass and species richness of any animal group (Wilson 1987). Therefore, changes to insect communities resulting from invasions by nonnative plants are likely to affect a number of important ecological processes, including pollination (Jennersten 1988), decomposition (Klein 1989), and nutrient cycling (Kitchell et al. 1979), as well as altering abundance and richness of food resources for insectivorous organisms (e.g., Burke and Nol 1998). The diversity of species, functional groups, and degree of specialization represented by insects provides the opportunity to explore a wide range of responses to invasion by nonnative plants.

Lehmann lovegrass (*Eragrostis lehmanniana* Nees) is a perennial bunchgrass native to southern Africa that was introduced to grasslands in the southwestern United States to revegetate and reduce erosion after a prolonged period of drought (Crider 1945). Since its introduction in the 1930s, dominance and distribution of this nonnative grass have increased rapidly throughout the southwestern United States and Mexico, with predictions for its potential distribution to exceed 71,000 km² in southern Arizona and New Mexico alone (Cox and Ruyle 1986; Anable et al. 1992; Schussman et al. 2006). Invasion by *E. lehmanniana* has strong implications for the structure of these grassland plant communities because it grows rapidly and produces up to four times more aboveground biomass than native grass species (Crider 1945; Cable 1971; Cox et al. 1990). These changes in structure and composition of the plant community have been associated with corresponding reductions in richness and abundance of native plants and animals (Cable 1971; Bock et al. 1986; Geiger 2006; Litt 2007).

Grasslands are among the most endangered plant communities in North America, in part due to

widespread invasions by nonnative plants (Noss et al. 1995). To evaluate the effects of a plant invasion into native grasslands, we quantified characteristics of the insect community on plots established along a gradient of nonnative-grass invasion, from areas dominated entirely by native grasses to areas dominated almost entirely by *E. lehmanniana*. We quantified how presence, abundance, richness, and evenness of orders, families, and morphospecies of insects varied along the invasion gradient after accounting for existing variation among plots in other vegetation and soil attributes. Changes to the insect community in response to plant invasions have broad implications for conservation of other native flora and fauna, and for maintaining ecosystem processes.

Materials and methods

Study area

We studied semi-desert grasslands in southeastern Arizona on Fort Huachuca Military Reservation (31°N, 110°W) where elevations ranged from 1,420 to 1,645 m. Annual precipitation averaged 391 mm (SE = 17 mm, $n = 39$ years, 1955–1998, Air Force Combat Climatology Center), about two-thirds of which falls during a monsoonal period between July and October that is preceded by a hot, dry period between late March and early July. Common native grasses were *Aristida* spp., *Bothriochloa barbinodis*, *Bouteloua* spp., *Digitaria californica*, *Eragrostis intermedia*, and *Panicum* spp., and common shrubs were *Baccharis pteronioides*, *Baccharis sarothroides*, *Dasyllirion wheeleri*, *Isocoma tenuisecta*, *Mimosa culeaticarpa* var. *biuncifera*, and *Mimosa dysocarpa*. Livestock have been excluded from the study area since 1950 and none of the areas we sampled burned for at least 9 years prior to sampling.

Sampling

We established 54 1-ha plots (100 m × 100 m) across a gradient of nonnative-grass invasion where *E. lehmanniana* comprised 0–91% of the total live biomass (mean = 44.2%, SE = 2.8). We established 27 plots in 2000 and an additional 27 plots in 2001. We sampled each spring (May–June), summer (July–August), and winter (February–March) from spring

2000 through spring 2004. We sampled the first set of 27 plots for 13 consecutive seasons (Spring 2000–Spring 2004) and the second set of plots for 10 consecutive seasons (Spring 2001–Spring 2004). Sample sizes in each season varied from 18 to 45 plots due to the staggered initiation of sampling and because some plots burned during the study period, after which we excluded them from the study. Between 2000 and 2004, we collected a total of 333 plot-level samples for all plots and seasons (mean = 6.2 samples/plot).

Insects

We sampled insects on each plot with a 3×3 array of pitfall traps spaced 25 m apart. Traps were 0.27-l tapered plastic cups set in the ground so that the rim was flush with the soil surface. At dusk, we filled each trap approximately three-quarters full with propylene glycol and left traps undisturbed for 24 h. We combined contents of all nine traps upon collection to create a single composite sample per plot. All sampling within a season was completed during a period of 3–4 weeks.

We counted, sorted, and classified all individuals to morphospecies based on visual characteristics (Oliver and Beattie 1993, 1996). We identified each morphospecies to order and family based on the classification in Borror et al. (1992); we included immature forms when they were identifiable at least to order. We focused on members of the class Insecta (or Hexapoda) and excluded arachnids (Class Arachnida) because identifying them reliably is difficult (Derraik et al. 2002). Although insects in the orders Homoptera and Hemiptera have been combined into a single order (Johnson and Triplehorn 2005), we treated them separately reflecting an earlier classification (Borror et al. 1992). This approach provided higher taxonomic and functional resolution as homopterans feed nearly exclusively on plant fluids and hemipterans feed on a variety of liquid foods, from both plants and animals (von Dohland and Moran 1995).

The use of pitfall traps to quantify relative abundance of invertebrates has been criticized because the number of individuals captured can vary with factors unrelated to true abundance, including density of vegetation surrounding the trap (Greenslade 1964; Melbourne et al. 1997). This bias should

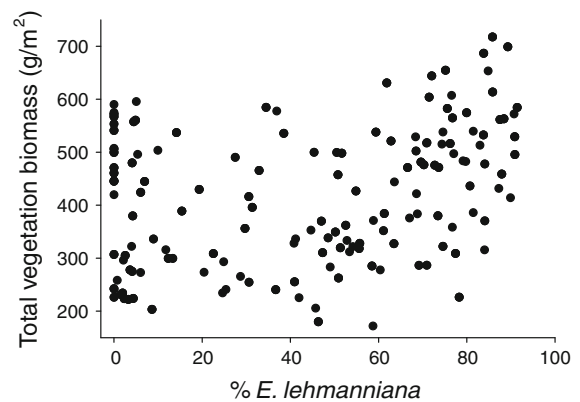


Fig. 1 Average total vegetation biomass per plot ($n = 54$) across the gradient of nonnative-grass invasion in southeastern Arizona, 2000–2004. Percentage of nonnative grass was computed as the ratio of average biomass of *E. lehmanniana* to average total biomass per plot

be minimal in our study because the nine subsamples in each composite sample spanned a range of vegetation densities on each plot and variation in biomass of vegetation was relatively consistent across the invasion gradient (Fig. 1). Efficiency of pitfall traps also may be affected by activity levels of invertebrates and because propylene glycol may attract some groups, sampling these taxa more effectively than others (Greenslade 1964; Melbourne et al. 1997). Because we sampled all plots similarly, however, any taxonomic biases should be consistent across plots.

We quantified characteristics of the insect community and of populations within the community. At the community level, we quantified richness of orders, families, and morphospecies, overall abundance of all insects, and evenness of orders and families in each composite sample based on counts of insects captured. We also estimated richness for each of these levels using the jackknife estimator (Burnham and Overton 1979), but we report only results based on counts because they were identical to results based on estimates. We computed evenness as the inverse of Simpson's diversity index divided by taxa richness (Begon et al. 1990: 616–617). At the population level, we computed presence and abundance for individual insect orders and families in each composite sample. We classified an order or family as present on a plot if we captured at least one individual in a composite sample.

Nonnative grass and other vegetation

Although our principal interest was quantifying responses of insects to variation in dominance by nonnative grass, other plot characteristics explained variation in insect populations and the insect community. Therefore, we quantified six vegetation and soil covariates on each plot in addition to dominance by nonnative grass. We estimated biomass (g/m^2) of litter, woody and herbaceous species, native grasses, and *E. lehmanniana* on each plot. *E. lehmanniana* grows mainly during summer, therefore we collected vegetation data in fall to estimate peak biomass (Cox et al. 1990). Each September from 1999 to 2003, all vegetation was clipped on 25, 0.5-m^2 quadrats on each plot (Geiger 2006). Samples were oven-dried and dry weights recorded by species for each quadrat. Percent cover of gravel ($<3''$ diameter) and cobble ($\geq 3''$ diameter) were estimated visually on each quadrat after all vegetation was clipped and collected. For litter, woody species, herbaceous species, native grass species, and *E. lehmanniana*, we computed average biomass per plot each fall. For gravel and cobble, we computed average percent cover per plot across all sampling seasons; we log-transformed cobble cover for analysis. We used biomass estimates from each fall to characterize vegetation conditions present from summer of the sampling year through winter and spring of the subsequent year (e.g., vegetation sampling from fall 2001 corresponded to insect sampling from summer 2001, winter 2002, and spring 2002). We used patchiness of vegetation biomass as a measure of heterogeneity in vegetation cover that we quantified with the coefficient of variation (CV) of total live biomass of vegetation among all 25 quadrats on each plot.

We used line transects to estimate density of all shrubs and point-centered quarter methods to estimate density of shrubs $>30\text{-cm}$ tall in summer 2004. Shrubs, which we defined as plants with multiple woody stems, were counted within a 1-m wide transect established diagonally across each plot. For point-centered quarter sampling, we measured the distance to the nearest shrub $>30\text{-cm}$ tall in each of four quadrants at four points located at random on each plot. For both sampling methods, we combined counts for all shrub species and converted counts to density ($\text{no. shrubs}/\text{m}^2$) (Thompson 2002).

Statistical analyses

Before assessing the influence of nonnative-grass dominance on each parameter, we first accounted for variation explained by the six plot-level covariates. Covariates were not highly correlated ($|r| < 0.5$ for all pairs, except woody biomass and cobble cover, where $r = 0.62$). We excluded biomass of native grass and gravel cover as potential covariates because they were correlated with biomass of *E. lehmanniana* ($r = -0.61$ and $r = -0.67$, respectively), the explanatory variable of interest. For each response variable, we used backwards variable selection to choose a subset of covariates from all plot-level covariates, sampling year (2000–2004), and sampling season (winter, spring, summer) that had explanatory power ($P \leq 0.10$ for a variable to remain in the model). We then fit a final model for inference that included the selected subset of covariates and biomass of *E. lehmanniana*, the primary variable of interest.

We used logistic regression to analyze presence of insect orders and families and negative binomial log-linear regression to analyze richness of orders, families, and morphospecies, overall abundance, and abundance of orders and families (Cameron 1998). We used likelihood-ratio chi-squared tests and confidence intervals based on the profile likelihood function to examine effects of individual parameters. We used linear regression to examine variation in evenness of insect orders and families, and in vegetation heterogeneity across the invasion gradient.

We analyzed presence and abundance data for a given order or family only if that group was present in at least 10% of composite samples ($n = 333$). Therefore, we analyzed presence of 7 orders and 27 families and excluded the order Hymenoptera ($n = 323$) and the family Formicidae (Hymenoptera, $n = 317$) as these groups were present in nearly all samples. We analyzed abundance of 8 orders and 27 families and excluded the family Reduviidae (Hemiptera) due to the small range of values observed per sample (range = 0–2).

We express the effect of nonnative-grass invasion as the multiplicative percentage change in the response variable for every $100\text{ g}/\text{m}^2$ increase in biomass of nonnative grass that we computed from back-transformed regression coefficients adjusted for selected covariates. For analyses of evenness, we express the effect of nonnative-grass invasion as the

linear change in evenness for every 100 g/m² increase in biomass of nonnative grass. Parameter estimates, test statistics, and *P*-values for all covariates are available from A.R.L.

We used principal components analysis (PCA) to examine how community composition varied with dominance of nonnative grass. We first computed mean abundance for each of the eight insect orders identified above for each plot ($n = 54$) over all sampling periods then ordinated these data based on a centered correlation matrix. We determined which orders were associated most closely with the dominant elements of the ordination by correlating each principal component with mean abundances of each order on each plot. Lastly, we used linear regression to assess how community composition, as captured by the first principal component, varied with dominance of nonnative grass on plots. We did not explore community composition based on insect families because we did not have sufficient samples relative to the number of families (McGarigal et al. 2000: 35).

Results

Variation in biomass of live vegetation was relatively homogeneous across the invasion gradient, increasing slightly in areas where nonnative grass was dominant (Fig. 1). Vegetation heterogeneity was greatest at low to intermediate levels of nonnative grass and ranged most widely across areas where native plants were dominant (Fig. 2).

During 2,997 trap nights, we captured 94,209 insects (mean per composite sample = 282.9, 95% CI = 209.5–356.3), representing 13 orders (5.2, 5.0–5.4), 91 families (8.9, 8.4–9.3), and 698 morphospecies (14.4, 13.4–15.4) (Appendix 1). Insects from the order Hymenoptera (e.g., ants, bees, wasps) were a dominant element of the community principally because Formicidae (ants) were present in 95% of samples and comprised 63% of all individuals captured (Appendix 1). Insects from the order Hemiptera (true bugs) were also abundant, especially the family Lygaeidae (seed bugs), but less widespread than Hymenoptera (Appendix 1).

Richness of families, richness of morphospecies, and overall abundance of all insects decreased as dominance of nonnative grass increased; richness of orders also decreased along the invasion gradient, but

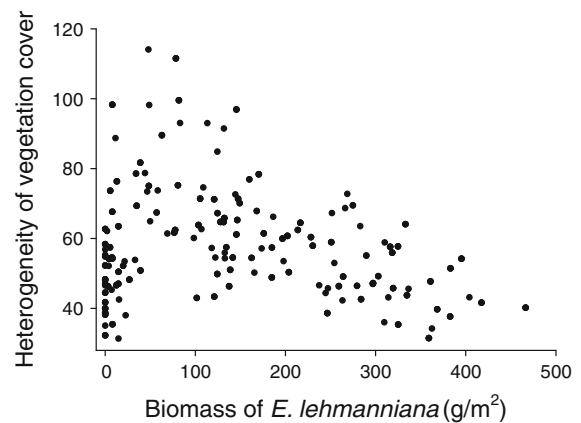


Fig. 2 Vegetation heterogeneity per plot ($n = 54$), measured as the coefficient of variation (%) of live vegetation biomass, across the gradient of nonnative-grass invasion

evidence for the decrease was less strong than for other parameters (Table 1). For every 100 g/m² increase in biomass of nonnative grass, average richness of insect families decreased by 5% (95% CI = 1.4–8.1%), richness of morphospecies decreased by 6% (2.6–9.7%), and overall abundance of insects decreased by 14% (1.5–24.4%, Table 1). Evenness of both orders and families of insects increased as dominance of nonnative grass increased (Table 1); for every 100 g/m² increase in biomass of nonnative grass, average evenness of orders increased by 0.015 (95% CI = 0.004–0.026) and evenness of families increased by 0.012 (0.003–0.021).

The decrease in richness of insect orders as dominance of nonnative grass increased resulted from a 23% (95% CI = 7.2–35.5%) decrease in presence of Coleoptera (beetles) and a 21% (7.3–32.1%) decrease in presence of Lepidoptera (e.g., butterflies and moths) for every 100 g/m² increase in nonnative grass (Table 2). Abundance of five of eight orders also decreased as dominance of nonnative grass increased (Table 3). For every 100 g/m² increase in nonnative grass, abundance of Coleoptera decreased by 21% (13.5–27.0%), Diptera (flies) decreased by 12% (3.1–19.6%), Hemiptera decreased by 17% (7.5–25.4%), Homoptera (e.g., aphids, planthoppers, cicadas) decreased by 16% (5.5–24.7%), and Orthoptera (e.g., grasshoppers and crickets) decreased by 10% (0–18.5%; Table 3).

The decrease in richness of insect families as dominance of nonnative grass increased resulted from

Table 1 Estimated changes in community-level metrics in response to changes in dominance of nonnative grass after accounting for other important covariates, $n = 333$

Response	Covariates ^a	Effect of nonnative grass			
		Estimate ^b	SE	<i>F</i>	<i>P</i>
Richness of orders	+Herbaceous, year, season	-1.69	1.01	1.5	0.22
Richness of families	+Herbaceous, +shrubs	-4.78	1.02	7.5	0.0066
Richness of morphospecies	+Herbaceous, +litter, year, season	-6.20	1.02	11.1	0.0010
Evenness of orders ^c	-Shrubs >30 cm, season	0.02	<0.01	7.3	0.0074
Evenness of families ^c	-Shrubs >30 cm, season	0.01	<0.01	6.7	0.010
Overall abundance		-13.76	1.07	4.8	0.029

For this and subsequent tables, estimates, sample sizes, and covariates (biomass of litter, woody species, and herbaceous species, density of all shrubs [shrubs], density of shrubs >30-cm tall, cover of cobble, year, and season) are from generalized linear mixed models and are reported if they explained significant variation in the response ($P \leq 0.10$)

^a Covariates included in the model used for inference, the sign preceding each represents the direction of the individual regression coefficient given all other variables in the model

^b For analyses of richness and overall abundance, estimates and standard errors have been back-transformed to show the multiplicative percentage change for each 100 g/m² increase in biomass of nonnative grass. For analyses of evenness, estimates have been converted to represent linear changes for each 100 g/m² increase in biomass of nonnative grass

^c Three samples were omitted in the analyses of evenness, as no insects were captured on those plots during that season

Table 2 Effect of changes in nonnative grass dominance on presence of insect orders on plots after accounting for other important covariates, $n = 333$

Response	Covariates	Effect of nonnative grass			
		Estimate	SE	<i>F</i>	<i>P</i>
Coleoptera	Year, season	-22.66	1.10	7.8	0.0058
Diptera	+Shrubs	-14.02	1.12	1.8	0.18
Hemiptera	+Herbaceous, -cobble	-11.49	1.15	0.8	0.37
Homoptera	+Litter, +shrubs >30 cm, year, season	2.43	1.11	0.1	0.82
Lepidoptera		-20.63	1.08	8.6	0.0037
Microcoryphia	-Herbaceous	-11.04	1.13	0.9	0.34
Orthoptera		-10.77	1.16	0.6	0.45

Table 3 Effect of changes in nonnative grass dominance on abundance of insect orders, after accounting for other important covariates

Response	<i>n</i>	Covariates	Effect of nonnative grass			
			Estimate	SE	<i>F</i>	<i>P</i>
Coleoptera	252	Year, season	-20.55	1.04	28.6	<0.0001
Diptera	232	+Shrubs, -woody, season	-11.66	1.05	6.9	0.0093
Hemiptera	183	-Cobble	-16.89	1.06	11.6	0.0009
Homoptera	208	-Woody	-15.72	1.06	8.8	0.0035
Hymenoptera	323	+Litter, -shrubs	0.60	1.07	0.0	0.93
Lepidoptera	191	+Herbaceous	-5.92	1.10	0.5	0.50
Microcoryphia	79	+Woody	-6.48	1.15	0.2	0.64
Orthoptera	219	+Shrubs >30 cm, season	-9.61	1.05	3.8	0.054

Table 4 Effect of changes in nonnative grass dominance on presence of insect families after accounting for other important covariates, $n = 333$

Order	Family	Covariates	Effect of nonnative grass				
			Estimate	SE	<i>F</i>	<i>P</i>	
Coleoptera	Carabidae	+Herbaceous, +cobble, year, season	-3.15	1.15	0.1	0.82	
	Chrysomelidae	-Herbaceous, -cobble, season	-21.96	1.19	2.1	0.15	
	Curculionidae	+Cobble	-18.13	1.14	2.2	0.14	
	Scarabaeidae	+Herbaceous	-13.15	1.19	0.7	0.41	
	Tenebrionidae	+Herbaceous, +litter, season	-18.05	1.10	4.0	0.046	
Diptera	Bombyliidae	-Herbaceous, season	-39.71	1.18	9.6	0.0021	
	Chloropidae	+Herbaceous, +litter, season	16.98	1.20	0.8	0.38	
	Muscidae	-Woody	-28.39	1.15	5.8	0.017	
	Sarcophagidae	Year, season	-35.08	1.15	9.4	0.0024	
Hemiptera	Tachinidae	Season	-9.06	1.11	0.8	0.38	
	Coreidae	+Litter, season	-73.13	1.48	11.4	0.0009	
	Lygaeidae	-Cobble, year, season	-21.18	1.13	4.0	0.047	
Homoptera	Reduviidae	-Litter, -cobble, season	-13.58	1.15	1.1	0.29	
	Cicadellidae	+Herbaceous, +litter, year, season	22.04	1.13	2.6	0.11	
Hymenoptera	Anthophoridae	+Woody, -litter, -cobble, season	-14.02	1.15	1.1	0.29	
	Bradynobaenidae		-14.96	1.15	1.2	0.27	
	Halictidae	-Cobble, year, season	-5.64	1.11	0.3	0.56	
	Mutillidae	+Shrubs, season	-3.82	1.12	0.1	0.74	
	Pompilidae	-Herbaceous, year, season	-3.82	1.14	0.1	0.77	
	Scoliidae	-Herbaceous	-1.59	1.12	0.0	0.88	
	Sphecidae	+Woody, -cobble, year, season	-5.35	1.15	0.2	0.70	
	Vespidae	+Shrubs, year, season	32.37	1.12	5.9	0.016	
	Lepidoptera	Hesperiidae	-Litter, year, season	-1.78	1.17	0.0	0.91
	Microcoryphia	Machilidae	-Herbaceous, year, season	-11.04	1.13	0.9	0.34
Orthoptera	Acrididae	+Herbaceous, -woody, season	-2.18	1.15	0.0	0.87	
	Gryllidae	+Litter, +cobble, +shrubs, season	-3.82	1.10	0.2	0.68	
	Tettigoniidae	+Shrubs, -litter	1.66	1.07	0.1	0.82	

changes in presence in 7 of 27 families. Presence of Tenebrionidae (darkling beetles), Bombyliidae (bee flies), Muscidae (e.g., house fly), Sarcophagidae (flesh flies), Coreidae (leaf-footed bugs), and Lygaeidae decreased as dominance of nonnative grass increased, whereas presence of Vespidae (e.g., paper wasps, yellow jackets) increased (Table 4).

Abundance of 9 of 27 families changed with dominance of nonnative grass. Abundance of Scarabaeidae (scarab beetles), Tenebrionidae, Bombyliidae, Coreidae, Cicadellidae (leafhoppers), and Acrididae (short-horned grasshoppers) decreased as dominance of nonnative grass increased, whereas abundance of Sarcophagidae, Mutillidae (velvet ants) and Tettigoniidae (long-horned grasshoppers)

decreased (Table 5). As dominance of nonnative grass increased across the invasion gradient, both presence and abundance of Tenebrionidae, Bombyliidae, and Coreidae decreased (Tables 4, 5). Uniquely, Sarcophagidae decreased in presence, but increased in abundance as nonnative grass increased (Tables 4, 5).

Composition of the insect community changed markedly along the invasion gradient (Fig. 3). The first principal component (PC1) derived from abundance of insect orders explained 26% of variation in insect abundances and decreased as dominance of nonnative grass increased (slope = -0.0039, SE = 0.0020, $t_{52} = -1.96$, $P = 0.056$). Coleoptera ($r = 0.62$) and Homoptera ($r = 0.77$) were positively correlated with

Table 5 Effect of changes in nonnative grass dominance on abundance of insect families after accounting for other important covariates, $n = 333$

Order	Family	n	Covariates	Effect of nonnative grass			
				Estimate	SE	F	P
Coleoptera	Carabidae	80	–Litter, –shrubs >30 cm, season	–3.05	1.05	0.5	0.49
	Chrysomelidae	47	+Litter, –herbaceous, –shrubs >30 cm, season	–11.22	1.08	2.5	0.13
	Curculionidae	56	+Woody, +shrubs	4.56	1.09	0.3	0.59
	Scarabaeidae	40	+Woody	–17.88	1.12	3.3	0.094
	Tenebrionidae	143	+Shrubs >30 cm, –cobble, –shrubs, year, season	–15.38	1.07	7.0	0.0096
Diptera	Bombyliidae	53		–27.53	1.16	4.9	0.039
	Chloropidae	41		1.27	1.16	0.1	0.93
	Muscidae	61		–9.61	1.08	1.7	0.20
	Sarcophagidae	56	Year	15.92	1.07	4.9	0.041
	Tachinidae	77	Year	–12.89	1.09	2.6	0.12
Hemiptera	Coreidae	47	Season	–49.34	1.36	5.0	0.037
	Lygaeidae	109	–Litter, –cobble, year, season	–4.02	1.07	0.4	0.54
Homoptera	Cicadellidae	198	–Woody, –litter, year, season	–14.96	1.06	7.2	0.0082
Hymenoptera	Anthophoridae	51	–Woody, –litter	–5.73	1.11	0.3	0.58
	Bradynobaenidae	34	+Cobble, –woody, year	–8.97	1.10	1.1	0.38
	Formicidae	317	+Litter	–6.01	1.09	0.5	0.48
	Halictidae	76	+Herbaceous, –litter, season	–1.49	1.06	0.0	0.88
	Mutillidae	58	+Woody, +litter	15.87	1.05	7.6	0.013
	Pompilidae	118	–Herbaceous	–4.78	1.07	0.5	0.49
	Scoliidae	66	–Litter	3.90	1.10	0.2	0.68
	Sphecidae	84		9.06	1.31	0.1	0.75
	Vespidae	54		0.68	1.11	0.0	0.95
Lepidoptera	Hesperiidae	56	+Herbaceous, year, season	–2.08	1.11	0.0	0.85
Microcoryphia	Machilidae	79	+Woody	–6.48	1.15	0.2	0.64
Orthoptera	Acrididae	187	–Cobble, year, season	–10.33	1.05	5.5	0.021
	Gryllidae	118	+Herbaceous, +cobble, +shrubs, +shrubs >30 cm, –woody, season	–0.80	1.07	0.0	0.91
	Tettigoniidae	98	–Litter, year, season	17.30	1.07	5.0	0.032

PC1, indicating that abundances of these orders decreased with increasing nonnative grass. As dominance of nonnative grass increased, community composition of insects became increasingly homogeneous relative to community composition in areas dominated by native grasses (Fig. 3).

Discussion

In grasslands of southern Arizona, richness and abundance of insects decreased as dominance of

nonnative grass increased, a pattern observed in other ecosystems invaded by nonnative plants (Olckers and Hulley 1991; Samways et al. 1996; Collinge et al. 2003; Herrera and Dudley 2003; Burghardt et al. 2008; Yoshioka et al. 2010; but see Derraik et al. 2005). Changes in composition of the insect community, however, reflected both increases and decreases in presence and abundance of different insect groups. For most insect groups, changes in vegetation structure and composition associated with invasion by nonnative grass were detrimental; for other groups, however, these changes were beneficial.

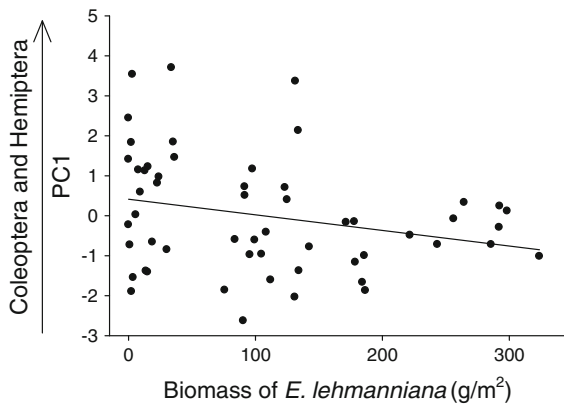


Fig. 3 Variation in community composition of insects across the gradient of nonnative-grass invasion as captured by the first principal component (PC1) in an ordination of abundances by order ($n = 54$). Abundance of Coleoptera and Hemiptera were most closely associated with these compositional changes

This pattern of both positive and negative responses to changes in the plant community has been reported for several taxa, including invertebrates, birds, and small mammals (Bock et al. 1986; Breytenbach 1986; Lagerloff and Wallin 1993; Samways et al. 1996; Wilson and Wheeler 2005; Litt 2007). Changes in richness and composition of insects we observed with changes in dominance of nonnative grass were not likely sampling artifacts associated with decreased abundance of insects on plots dominated by nonnative grass because evenness of families and orders increased as dominance of nonnative grass increased. For variation in abundance to have explained the changes we observed, evenness would have had to decrease along the invasion gradient; instead, evenness increased for both orders and families of insects as dominance of nonnative grass increased.

Vegetation structure

Habitat of many insects depends on structural features of vegetation, including height, cover, and density (Samways and Moore 1991; Lagerloff and Wallin 1993; Crisp et al. 1998; Kruess and Tschardtke 2002; Brockerhoff et al. 2005; Wilson and Wheeler 2005). Insects that inhabit sparsely vegetated areas are likely to decrease in response to invasions by plant species similar to *E. lehmanniana* that increase overall plant biomass and reduce heterogeneity of vegetation structure (Samways

et al. 1996; Kruess and Tschardtke 2002; Derraik et al. 2005). Grasshoppers, for example, are often most diverse and abundant in areas of bare ground (Whitford et al. 1995) or in areas intercepting direct sunlight (Samways and Moore 1991), which explains the decreases in abundance of Acrididae (Orthoptera) we observed as dominance of nonnative grass increased (Table 5). Further, increases in vegetation cover can impede movements of some insects, especially flight (Samways et al. 1996), which may explain decreases we observed in presence or abundance of flies (Diptera) and other volant groups in areas dominated by nonnative grass (Table 5).

Taller vegetation and more uniform cover increase soil moisture and humidity, stabilize temperatures, and increase the number of refugia from predators (Samways 1977; Lagerloff and Wallin 1993; Samways et al. 1996; Lassau et al. 2005), characteristics that may be especially important during early stages of insect development (Samways 1977). Several species of rare planthoppers, for example, use the dense grass crowns of another introduced species of *Eragrostis* for development and shelter (Wilson and Wheeler 2005). Therefore, insects in the families Mutillidae (Hymenoptera), Vespidae (Hymenoptera), and Tettigoniidae (Orthoptera) that increased in presence or abundance in areas dominated by *E. lehmanniana* likely responded positively to increases in cover, height, or other structural changes of vegetation (Tables 4, 5). Similarly, abundance of Mutillidae (Hymenoptera) increased as biomass of litter increased (Table 5). Consequently, for some groups of insects, nonnative plants can increase the quantity or quality of habitat and serve to enhance their populations. For example, an endangered species of ground beetle occurs only in plantations of nonnative pines where native habitat patches are extremely rare (Brockerhoff et al. 2005).

Changes to vegetation heterogeneity in response to invasion by nonnative plants (Fig. 2) also may affect habitat quality for insects. Some grasshoppers and beetles, for example, prefer mosaics of vegetation with patches containing a mixture of tall and short grasses and areas of bare ground (Samways 1977; Curry 1994; Chambers and Samways 1998; Kruess and Tschardtke 2002; Lassau et al. 2005). This mixture of structural features creates a variety of microclimates and allows insects to meet multiple life-history requirements, including resources for

food and shelter, and bare ground for oviposition sites (Curry 1994). Patchiness and structural heterogeneity decreased as dominance of *E. lehmanniana* increased (Fig. 2), creating simpler, more uniform vegetation structure and composition that likely contributed to declines in insect abundance and richness we and others have observed (Slobodchikoff and Doven 1977; Herrera and Dudley 2003). High heterogeneity in community composition of insects among plots in areas dominated by native grasses reflects high heterogeneity of vegetation in these areas (Fig. 3).

Vegetation composition

Many herbivorous insects have evolved close relationships with particular food plants and feed only on plants in a few families (Southwood et al. 1982; Bernays and Graham 1988; Curry 1994; Collinge et al. 2003); these insect groups may be especially vulnerable to changes in composition of the plant community (Potts et al. 2009). Phytophagous insects, for example, may be less abundant in areas dominated by nonnative plants because they do not share a lengthy evolutionary history with these plants (Strong et al. 1984; Tallamy 2004). Orders and families of insects that decreased as dominance of nonnative grass increased included Coleoptera, Hemiptera, Homoptera, Lepidoptera, and Orthoptera, all groups that include species that feed on plant material (Strong et al. 1984; Borror et al. 1992). Increased dominance of *E. lehmanniana* was associated with reductions in herbaceous plants (Geiger 2006), species that are important food resources for many native insects (Weis and Berenbaum 1989). Relative to native grasses, *E. lehmanniana* is likely less palatable for insect herbivores because its tissues become coarse and tough during the summer growing season (Crider 1945; Cable 1971). For insect groups that chew foliage, such as adult and nymph grasshoppers in the family Acrididae (Orthoptera) (Strong et al. 1984; Borror et al. 1992), lower palatability of nonnative grass may explain decreased abundance in areas dominated by *E. lehmanniana*. Although short generation times of invertebrate species may facilitate shifts in the host and food preferences of phytophagous species in response to vegetation change (Bernays and Graham 1988), we observed decreases in presence and abundance of some insect

groups decades after this nonnative grass was first established.

Omnivorous and predatory insects have less specialized diets (Southwood et al. 1982), therefore they may respond more to changes in vegetation structure than to changes in floristics. For example, abundance of ants (Formicidae) did not vary along the invasion gradient, perhaps because they tend to be omnivorous or forage on a variety of seeds (Curry 1994; Whitford et al. 1995). Similarly, neither presence nor abundance of the family Carabidae (Coleoptera) varied with dominance of nonnative grass (Tables 4, 5). Because many carabid beetles are predatory (Borror et al. 1992; Curry 1994), individuals may be able to find sufficient food resources as composition of the plant community changes in response to invasions.

Implications for conservation

Changes in abundance and composition of insects in response to invasions by nonnative plants might portend other structural and functional changes to ecosystems. Decreases in pollinators, such as Hymenoptera and Lepidoptera, and in herbivorous invertebrates in general, can alter vegetation composition over the long term (Weis and Berenbaum 1989). Decreases in many insect groups, including Coleoptera, Lepidoptera, Orthoptera, and Hymenoptera (Formicidae), can reduce food resources for other animals, from predatory and parasitic insects to herpetofauna, small mammals, and birds (Bock et al. 1986; Medina 1988; Wilson and Belcher 1989; Burke and Nol 1998; Abell 1999). Abundance of an insectivorous rodent, the northern grasshopper mouse (*Onychomys leucogaster*), decreased with increased dominance of nonnative grass (Litt 2007). This species feeds almost exclusively on invertebrates, primarily insects in the orders Coleoptera, Lepidoptera, and Orthoptera (Hoffmeister 1986), all of which feed extensively on plants and decreased in presence or abundance in areas dominated by *E. lehmanniana*. Given their dominant roles in many terrestrial ecosystems, changes in the insect community in response to invasion by nonnative plants are likely to precipitate future changes to ecosystem structure and function.

Because insects vary in the ways they depend on plants for food or structure or both, measuring responses of only one or a few taxonomic groups

may not represent changes occurring in other groups (Oliver and Beattie 1996). Several studies have focused on particular invertebrate taxa as indicators of environmental change (Kerr et al. 2000), such as ground beetles (Carabidae) (Rushton et al. 1990; Niemala et al. 1993), tiger beetles (Cicindelidae) (Pearson and Cassola 1992), or butterflies (Lepidoptera) (Burghardt et al. 2008), because they are relatively easy to collect and identify, are thought to respond rapidly to environmental changes, and might reflect changes in other taxa (Pearson and Cassola 1992; Kerr et al. 2000; but see Rykken et al. 1997). Although some insect groups may respond similarly to environmental changes (Tables 2, 3, 4, 5; Pearson and Cassola 1992; Kerr et al. 2000), we quantified both decreases and increases in presence and abundance of orders and families along the invasion gradient. If we had selected one taxon as an indicator, such as Carabidae, we might have concluded that the insect community in these semi-desert grasslands changed little in response to invasion by *E. lehmanniana*. In our study, for example, there were almost certainly additional changes occurring below the lowest taxonomic level we investigated (family). Therefore, to capture the full range of changes to the biodiversity of insects, we suggest that studies evaluate as many taxa as possible with as much resolution as is feasible.

Because the nonnative grass we studied continues to increase in distribution and dominance, we anticipate further changes to the insect community and its component groups. We observed declines in presence, and therefore changes in distribution, of multiple insect orders that were absent and therefore likely extirpated from areas where the nonnative grass predominated. Because changes in the insect community has consequences for other plant and animal communities, we anticipate changes to populations and communities of organisms at higher trophic levels and for ecosystem processes in areas invaded by nonnative plants. Complete eradication of nonnative grasses is unlikely in all but the rarest circumstances, therefore retaining mosaics of native vegetation in invaded areas will be an increasingly important strategy for conservation of biodiversity and for maintaining ecosystem structure and function in grasslands invaded by nonnative plants.

Acknowledgments We are grateful to K. Franklin, W. Moore, and C. Olson for their assistance with identifying insects, E. Geiger for providing vegetation data and other valuable assistance, and S. Stone and G. McPherson for support throughout this entire project. Our work was supported by The Department of Defense Legacy Resource Management Program (Project 03-102). We appreciate the constructive suggestions offered by A. E. Arnold and by anonymous reviewers.

Appendix 1 Presence and relative abundance by order and family of 94,209 insects, $n = 333$

Order	Family	Order		Family	
		Present in samples (%)	Total individuals (%)	Present in samples (%)	Total individuals (%)
Blatteria	Blattellidae	1.20	0.01	0.30	0.01
	Blattidae			0.30	0.00
	Polyphagidae			0.90	0.00
Coleoptera	Buprestidae	75.68	1.18	5.41	0.03
	Cantheridae			0.30	0.00
	Carabidae			24.02	0.19
	Chrysomelidae			14.11	0.09
	Cicindelidae			4.50	0.02
	Cleridae			1.80	0.01
	Coccinellidae			0.60	0.00
	Curculionidae			16.82	0.11
	Elateridae			5.11	0.04

Appendix 1 continued

Order	Family	Order		Family	
		Present in samples (%)	Total individuals (%)	Present in samples (%)	Total individuals (%)
	Histeridae			1.80	0.01
	Lagriidae			0.60	0.00
	Meloidae			3.60	0.02
	Melyridae			0.30	0.00
	Scarabaeidae			12.01	0.08
	Staphylinidae			3.90	0.01
	Tenebrionidae			42.94	0.46
Diptera	Acroceridae	69.67	1.01	1.50	0.01
	Asilidae			1.20	0.00
	Bibionidae			0.60	0.00
	Bombyliidae			15.92	0.19
	Cecidomyiidae			6.31	0.15
	Chironomidae			4.80	0.05
	Chloropidae			12.31	0.08
	Culicidae			0.60	0.00
	Dalichopodidae			0.90	0.00
	Heleomyzidae			0.60	0.00
	Muscidae			18.32	0.10
	Otitidae			0.30	0.00
	Phoridae			0.90	0.00
	Sarcophagidae			16.82	0.10
	Scathophagidae			7.51	0.05
	Scianidae			1.20	0.01
	Stratiomyidae			6.91	0.05
	Syrphidae			2.10	0.01
	Tachinidae			23.12	0.16
	Tephritidae			0.60	0.00
	Tipulidae			0.60	0.00
Hemiptera	Acanthosomatidae	54.95	24.48	0.30	0.00
	Alydidae			4.80	0.03
	Coreidae			14.11	0.32
	Cydnidae			4.20	0.02
	Largidae			5.11	0.04
	Lygaeidae			32.73	23.87
	Pentatomidae			3.90	0.01
	Reduviidae			13.81	0.06
	Rhopalidae			8.71	0.07
	Scutelleridae			0.30	0.00
	Thyreocoridae			2.10	0.02

Appendix 1 continued

Order	Family	Order		Family	
		Present in samples (%)	Total individuals (%)	Present in samples (%)	Total individuals (%)
Homoptera	Acanaloniidae	62.46	1.61	1.80	0.01
	Aphididae			1.80	0.02
	Cicadellidae			59.46	1.49
	Cicadidae			0.60	0.00
	Dictyopharidae			0.60	0.00
	Membracidae			6.01	0.09
Hymenoptera	Anthophoridae	97.00	64.25	15.32	0.10
	Apidae			4.50	0.02
	Bethylidae			1.80	0.01
	Braconidae			3.30	0.02
	Bradynobaenidae			10.21	0.08
	Ceraphronidae			0.60	0.00
	Chalcididae			0.90	0.00
	Encyrtidae			0.90	0.00
	Eupelmidae			0.30	0.00
	Formicidae			95.20	62.77
	Halictidae			22.82	0.25
	Ichneumonidae			0.60	0.00
	Megachilidae			7.51	0.06
	Mutillidae			17.42	0.09
	Pompilidae			35.44	0.31
	Scoliidae			19.82	0.17
Sphecidae			25.23	0.27	
Vespidae			16.22	0.10	
Isoptera	Termitidae	2.70	0.03	0.90	0.01
Lepidoptera	Danaidae	57.36	1.08	0.30	0.00
	Hesperiidae			16.82	0.14
	Lycaenidae			6.91	0.03
	Nymphalidae			3.60	0.02
	Pieridae			2.40	0.01
	Sphingidae			0.30	0.00
Mantodea	Mantidae	2.70	0.01	2.70	0.01
Microcoryphia	Machilidae	23.72	2.03	23.72	2.03
Neuroptera	Myrmeleontidae	4.50	0.02	0.30	0.00
	Sisyridae			0.60	0.00
Orthoptera	Acrididae	65.77	4.29	56.16	2.63
	Gryllacrididae			4.20	0.02
	Gryllidae			35.44	0.39
	Tettigoniidae			29.43	1.26
Phasmida	Heteronemiidae	0.60	0.00	0.60	0.00

We identified all individuals to order, but because we could not identify the family of some individuals, abundance of percentages for families sums to <100

References

- Abell AJ (1999) Variation in clutch size and offspring size relative to environmental conditions in the lizard *Sceloporus virgatus*. *J Herpetol* 33:173–180
- Anable ME, McClaran MP, Ruyle GB (1992) Spread of introduced Lehmann lovegrass *Eragrostis lehmanniana* nees in southern Arizona, USA. *Biol Conserv* 61:181–188
- Begon M, Harper JL, Townsend CR (1990) *Ecology: individuals, populations and communities*, 2nd edn. Blackwell, Boston
- Bernays E, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology* 69:886–892
- Bock CE, Bock JH, Jepsen KL, Ortega JC (1986) Ecological effects of planting African lovegrasses in Arizona. *Nat Geogr Res* 2:456–463
- Borror DJ, Triplehorn CA, Johnson NF (1992) *An introduction to the study of insects*, 6th edn. Saunders College Publishing, Fort Worth
- Breytenbach GJ (1986) Impacts of alien organisms on terrestrial communities with emphasis on communities of the south-western cape. In: Macdonald IAW, Kruger FJ, Ferrar AA (eds) *The ecology and management of biological invasions in southern Africa*. Oxford University Press, Cape Town
- Brockerhoff EG, Berndt LA, Jactel H (2005) Role of exotic pine forests in the conservation of the critically endangered New Zealand ground beetle *Holcaspis brevicula* (Coleoptera: Carabidae). *N Z J Ecol* 29:37–43
- Burghardt KT, Tallamy DW, Shriver WG (2008) Impact of native plants on bird and butterfly biodiversity in suburban landscapes. *Conserv Biol* 23:219–224
- Burke DM, Nol E (1998) Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk* 115:96–104
- Burnham KP, Overton WS (1979) Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60:927–936
- Cable DR (1971) Lehmann lovegrass on the Santa Rita experimental range, 1937–1968. *J Range Manag* 24:17–21
- Cameron AC (1998) *Regression analysis of count data*. Cambridge University Press, West Nyack, New York
- Chambers BQ, Samways MJ (1998) Grasshopper response to a 40-year experimental burning and mowing regime, with recommendations for invertebrate conservation management. *Biodivers Conserv* 7:985–1012
- Collinge SK, Prudic KL, Oliver JC (2003) Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conserv Biol* 17:178–187
- Cox JR, Ruyle GB (1986) Influence of climatic and edaphic factors on the distribution of *Eragrostis lehmanniana* Nees in Arizona, USA. *J Grassl Soc S Afr* 3:25–29
- Cox JR, Ruyle GB, Roundy BA (1990) Lehmann lovegrass in southeastern Arizona: biomass production and disappearance. *J Range Manag* 43:367–372
- Crider FJ (1945) Three introduced lovegrasses for soil conservation. US Department of Agriculture Circulation No. 730, Washington, DC
- Crisp PN, Dickinson KJM, Gibbs GW (1998) Does invertebrate diversity reflect native plant diversity? A case study from New Zealand and implications for conservation. *Biol Conserv* 83:209–220
- Curry JP (1994) *Grassland invertebrates: ecology, influence on soil fertility, and effects on plant growth*. Chapman and Hall, New York
- Derraik JGB, Closs GP, Dickinson KJM, Sirvid P, Barratt BIP, Patrick BH (2002) Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. *Conserv Biol* 16:1015–1023
- Derraik JGB, Rufaut CG, Closs GP, Dickinson KJM (2005) Ground invertebrate fauna associated with native shrubs and exotic pasture in a modified rural landscape, Otago, New Zealand. *N Z J Ecol* 29:129–135
- Geiger EL (2006) *The role of fire and a nonnative grass as disturbances in semi-desert grasslands*. Dissertation, University of Arizona
- Greenslade PJM (1964) Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *J Anim Ecol* 33:301–310
- Herrera AM, Dudley TL (2003) Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. *Biol Invasions* 5:167–177
- Hoffmeister DF (1986) *Mammals of Arizona*. University of Arizona Press, Tucson
- Jennersten O (1988) Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conserv Biol* 2:359–367
- Johnson NF, Triplehorn CA (2005) *Borror and DeLong's introduction to the study of insects*, 7th edn. Brooks/Cole, Belmont
- Kerr JT, Sugar A, Packer L (2000) Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. *Conserv Biol* 14:1726–1734
- Kitchell JF, O'Neill RV, Webb D, Gallop GW, Bartell SM, Koonce JF, Ausmus BF (1979) Consumer regulation of nutrient cycling. *Bioscience* 29:28–34
- Klein GC (1989) Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70:1715–1725
- Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF, Sanjayan MA (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conserv Biol* 7:796–808
- Kruess A, Tschardt T (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conserv Biol* 16:1570–1580
- Lagerlof J, Wallin H (1993) The abundance of arthropods along two field margins with different types of vegetation composition: an experimental study. *Agric Ecosyst Environ* 43:141–151
- Lassau SA, Hochuli DF, Cassis G, Reid CAM (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Divers Distrib* 11:73–82
- Litt AR (2007) *Effects of experimental fire and nonnative grass invasion on small mammals and insects*. Dissertation, University of Arizona
- Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. *Trends Ecol Evol* 13:195–198

- McGarigal K, Cushman S, Stafford S (2000) Multivariate statistics for wildlife and ecology research. Springer, New York
- Medina AL (1988) Diets of scaled quail in southern Arizona. *J Wildl Manag* 52:753–757
- Melbourne BA, Gullan PJ, Su YN (1997) Interpreting data from pitfall-trap surveys: crickets and slugs in exotic and native grasslands of the Australian Capital Territory. *Mem Mus Vic* 56:361–367
- Niemala J, Langor D, Spence JR (1993) Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conserv Biol* 7:551–561
- Noss RF, LaRoe ET, Scott JM (1995) Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. US Department of International, Nat Biol Serv, Washington, DC
- Olckers T, Hulley PE (1991) Impoverished insect herbivore faunas on the exotic bugweed *Solanum mauritianum* Scop. relative to indigenous *Solanum* species in Natal/KwaZulu and the Transkei. *J Entomol Soc S Afr* 54:39–50
- Oliver I, Beattie AJ (1993) A possible method for the rapid assessment of biodiversity. *Conserv Biol* 7:562–568
- Oliver I, Beattie AJ (1996) Invertebrate morphospecies as surrogates for species: a case study. *Conserv Biol* 10:99–109
- Pearson DL, Cassola F (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conserv Biol* 6:376–391
- Potts SG, Woodcock BA, Roberts SPM, Tscheulin T, Pilgrim ES, Brown VK, Tallwin JR (2009) Enhancing pollinator diversity in intensive grasslands. *J Appl Ecol* 46:369–379
- Rushton SP, Eyre MD, Luff ML (1990) The effects of scrub management on the ground beetles of oolitic limestone grassland at castor hanglands national nature reserve, Cambridgeshire, UK. *Biol Conserv* 51:97–111
- Rykken JJ, Capen DE, Mahabir SP (1997) Ground beetles as indicators of land type diversity in the Green Mountains of Vermont. *Conserv Biol* 11:522–530
- Samways MJ (1977) Effect of farming on population movements and acoustic behavior of two bush crickets (Orthoptera: Tettigoniidae). *Bull Entomol Res* 67: 471–481
- Samways MJ, Moore SD (1991) Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. *Biol Conserv* 57:117–137
- Samways MJ, Caldwell PM, Osborn R (1996) Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agric Ecosyst Environ* 59: 19–32
- Schussman H, Geiger E, Mau-Crimmins T, Ward J (2006) Spread and current potential distribution of an alien grass, *Eragrostis lehmanniana* Nees, in the southwestern USA: comparing historical data and ecological niche models. *Divers Distrib* 12:582–592
- Slobodchikoff CN, Doven JT (1977) Effects of *Ammophila arenaria* on sand dune arthropod communities. *Ecology* 58:1171–1175
- Southwood TRE, Moran VC, Kennedy CEJ (1982) The assessment of arboreal insect fauna: comparisons of knockdown sampling and faunal lists. *Ecol Entomol* 7:331–340
- Strong DR, Lawton JH, Southwood R (1984) Insect on plants: community patterns and mechanisms. Harvard University Press, Cambridge
- Tallamy DW (2004) Do alien plants reduce insect biomass? *Conserv Biol* 18:1689–1692
- Thompson SK (2002) Sampling, 2nd edn. Wiley, New York
- Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238:802–804
- Von Dohlen CD, Moran NA (1995) Molecular phylogeny of the Homoptera: a paraphyletic taxon. *J Mol Evol* 41:211–223
- Weis AE, Berenbaum MR (1989) Herbivorous insects and green plants. In: Abrahamson WA (ed) Plant-animal interactions. McGraw-Hill, New York, pp 123–162
- Whitford WG, Forbes GS, Kerley GI (1995) Diversity, spatial variability, and functional roles of invertebrates in desert grassland ecosystems. In: McClaran MP, Van Devender TR (eds) The desert grasslands. The University of Arizona Press, Tucson, pp 152–195
- Wilson EO (1987) The little things that run the world (the importance and conservation of invertebrates). *Conserv Biol* 1:344–346
- Wilson SD, Belcher JW (1989) Plant and bird communities of native prairie and introduced Eurasian vegetation in Manitoba, Canada. *Conserv Biol* 3:39–44
- Wilson SW, Wheeler AG Jr (2005) An African grass, *Eragrostis curvula* (Poaceae), planted in the southern United States recruits rarely collected native planthoppers (Hemiptera: Fulgoroidea: Dictyopharidae, Fulgoridae). *J N Y Entomol Soc* 113:174–204
- Yoshioka A, Kadoya T, Suda S, Washitani I (2010) Impacts of weeping lovegrass (*Eragrostis curvula*) invasion on native grasshoppers: responses of habitat generalist and specialist species. *Biol Invasions* 12:531–539