

Ecological Mechanisms Underlying Arthropod Species Diversity in Grasslands

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Annu. Rev. Entomol. 2013. 58:19–36

First published online as a Review in Advance on
July 20, 2012

The *Annual Review of Entomology* is online at
ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-120811-153540

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Keywords

fire-grazing interactions, landscape fragmentation, network and food web dynamics, spatial heterogeneity, species-energy relationships

Abstract

Arthropods are an important component of grassland systems, contributing significantly to biodiversity and ecosystem structure and function. Climate, fire, and grazing by large herbivores are important drivers in grasslands worldwide. Arthropod responses to these drivers are highly variable and clear patterns are difficult to find, but responses are largely indirect with respect to changes in resources, species interactions, habitat structure, and habitat heterogeneity resulting from interactions among fire, grazing, and climate. Here, we review these ecological mechanisms influencing grassland arthropod diversity. We summarize hypotheses describing species diversity at local and regional scales and then discuss specific factors that may affect arthropod diversity in grassland systems. These factors include direct and indirect effects of grazing, fire, and climate, species interactions, above- and belowground interactions, and landscape-level effects.

NPP: net primary production

γ -(regional)

diversity: total species diversity across all communities over a broad geographic area; also known as regional species pool

INTRODUCTION

Understanding patterns of arthropod species diversity worldwide is a grand challenge. A hierarchical approach is required to determine how ecological processes filter regional species pools, resulting from historical and biogeographic processes, to shape local species composition and diversity (41, 95, 101). In grasslands, local arthropod diversity is influenced largely by ecological factors associated with grazing, fire, and climate, the primary ecological and evolutionary drivers shaping grassland systems (67). We review primary ecological mechanisms that determine species diversity of grassland arthropods, and link them to contributions from intermediate- to large-scale ecological factors acting over broad landscapes (37, 114, 121).

Grasslands and savannas cover approximately 35%–40% of Earth's surface (103), although human activities over the past century (especially agriculture) have greatly diminished their actual land cover and increased the degree of fragmentation. Grasslands are dominated by nonwoody vegetation, where grasses make up about 80% of the aboveground biomass (net primary production, NPP), but plant species richness is about 80% forbs (67). Moreover, most grasslands experience variable weather patterns, leading to big swings in NPP and plant foliar quality between years (82), and arthropod abundances can show large swings (12). The legacy of variable climatic history associated with Pleistocene glacial-interglacial cycles caused significant shifts in range distributions in northern latitudes, leading to altered taxonomic composition of communities and associated species interactions (54). However, significant differences in the history of grasslands worldwide challenge our ability to fully understand local ecological determinants of arthropod diversity and search for common mechanisms.

Arthropods contribute significantly to grassland biodiversity (30, 116, 124), community-level trophic dynamics (46, 47, 106), and ecosystem function (7, 81, 124) while providing critical goods and services to society (124). In general, arthropod communities exhibit wide-ranging patterns of taxonomic composition, body size distributions, feeding modalities, abundances, and lifestyles (32, 108, 109). Despite incredible arthropod diversity worldwide, evidence suggests the existence of repeatable, self-similar patterns across spatial scales for diversity-related patterns such as rank-abundance distributions, species-area curves, and size-frequency distributions (32). Because arthropod species are quite responsive to changing environments, including those resulting from human management practices (22, 48, 84), densities and diversity can be highly variable within and among years and sites. The striking variability among grassland arthropod communities worldwide begs the question: Are there common ecological mechanisms and processes for understanding arthropod biodiversity in grasslands, especially for comparisons among grasslands with no historical affinity? Understanding mechanisms underlying the maintenance of arthropod diversity in grasslands can also serve as an important model for understanding the ecological factors determining species diversity more generally, while providing a framework for developing conservation plans. Although no sufficient data exist to answer this question directly, we incorporate information from grasslands throughout the world to develop a general picture and framework.

To organize contributions of ecological factors to arthropod species diversity in grasslands, we address the following topics. (*a*) We start with species diversity–area/productivity relationships (101, 110), which provide a backdrop for understanding γ -(regional) diversity and appropriate spatial scale by defining the characteristics of species pools from which contemporary communities draw species (32). General hypotheses describing species diversity at local and regional scales are briefly discussed. (*b*) Primary drivers of grassland ecosystem development and maintenance (fire, grazing, climate) underlie arthropod diversity, acting either directly or indirectly through changes in vegetation characteristics (60, 67, 84) or in response to interactions resulting from habitat heterogeneity in the landscape mosaic (53, 114). Studies of fire-grazing interactions focus on

primary ecological drivers responsible for the development and maintenance of grassland ecosystems and their spatial heterogeneity (38, 39), which influence arthropod diversity. Moreover, the same underlying mechanistic factors structure local arthropod diversity worldwide and include vegetation architectural structure (59, 76, 127), plant community taxonomic composition and diversity, and food quality. Variable weather patterns, spatial heterogeneity in resource availability, and small-scale abiotic conditions and vegetation structure complement these physical contributions of habitat. (c) Biotic interactions, including species interactions and food web dynamics, further contribute to patterns of diversity, including those between hosts and parasites and between predators and pathogens. This requires a synthesis of how other biotic interactions and food web dynamics regulate local patterns of diversity (1, 92). Interesting insights into community-level stability are emerging (46). (d) Above- and belowground compartments of grasslands are typically treated separately, but linking the two compartments into interactive components mediated through effects on host plants is clearly warranted (8, 55). (e) Landscape-level processes can be important because they link patterns of α -(local) diversity across multiple spatial and temporal scales, and the spatial arrangement and size of habitat templates greatly alter actions of underlying mechanisms determining species diversity (29, 59). (f) Finally, we place these results into a broader perspective, including discussion of the influence of arthropod diversity on ecosystem function and conservation.

REGIONAL INFLUENCES ON ARTHROPOD DIVERSITY (AREA AND ENERGY)

Species diversity varies predictably with area in a scale-dependent fashion—the canonical species-area curve (101), in which species-area and species-energy (productivity) relationships are often linked (128). Including energy (productivity) explicitly adds a metric of resource availability and heterogeneity to the analysis, as recognized in standard species-area evaluations over latitudinal gradients (26, 27, 101). Energy is a fundamental currency in ecology and varies greatly over broad geographic gradients as temperature (through influences on metabolism or seasonality), incidence of solar radiation, or primary production (by determining the resource base to support multiple trophic levels), each covarying with species diversity although mechanistic understanding is often elusive (27). Several mechanisms can explain the patterns (27, 119, 128), and outcomes often lead to unimodal patterns of diversity with respect to productivity in local comparisons or monotonic relationships at global scales (15). Spatially, outcomes that may be confounded with area are highly scale dependent; at least nine mechanisms with nonexclusive predictions exist to explain general patterns of species diversity as affected by productivity (27).

Species-energy theory posits a critical role of increased population size as a primary reason to explain why species increase with productivity (the More Individuals Hypothesis; 128). Increased energy availability should increase population sizes, which in turn reduces local extinction rates of species and thus maintains diversity. Moreover, complex food webs with more trophic levels should result as NPP increases among habitats (36, 106), leading to more coexisting species. On the basis of the thermoregulatory load hypothesis, temperature-dependent metabolism determines the fate of energy allocation as it switches from maintenance to growth and reproduction with implications for population sizes (26). Small individuals should be more sensitive to low temperatures and respond more strongly to population increases at higher temperatures. Kaspari et al. (62, 63) test key predictions of species-energy theory using litter ants across a broad gradient of primary productivity. For scrub, tundra, and grasslands, NPP limits taxocene density, and density limits species richness (63). In ground-dwelling ants, nest density varied as a function of NPP, although the response was negatively decelerating, and thus change was less striking at higher NPP levels.

α -(local) diversity: species diversity in a single type of habitat at a site

Species-area relationship: the number of species found increases with the size of the area examined, as indicated by the formula $\log(\text{number of species})/z \log(\text{Area}) + \log(c)$, where z is the slope of the relationship and $\log(c)$ is the y -intercept

Taxocene: a taxonomically related set of interacting species within a community

Shifting mosaic of vegetation: results from management practices that use fire-grazing interactions to promote heterogeneity in the landscape over space and time

NPP ultimately influenced species richness, which showed a negatively decelerating relationship with nest density at three spatial scales (63). Energy limitation was more profound at sites with lower NPP, and sites with higher average temperatures tended to have ants with smaller body size (61). Although mechanisms underlying species-energy theory as a general explanation are currently unresolved, species-energy theory as a general approach is clearly a highly promising approach for understanding arthropod diversity, and available evidence from insect groups suggests more study is warranted.

Other hypotheses, in addition to regional energy/area explanations, have been proposed for understanding patterns of species diversity at local and regional scales (**Table 1**). These include hypotheses that focus on abiotic aspects of the habitat, time, temperature, and disturbance regimes. Other hypotheses suggest that biotic interactions determine diversity, and focus on particular species interactions as well as resource diversity, heterogeneity and complexity, and how network connectance determines stability (**Table 1**).

FIRE, GRAZING, AND ARTHROPOD DIVERSITY

Interactions between fire and grazing by large herbivores act as dominant proximate ecosystem drivers in grasslands worldwide (2, 3, 35, 37, 39, 66). These ecosystem drivers create shifting mosaics of vegetation, which shape the landscape to influence consumer distribution, abundance, and diversity, ultimately maintaining grassland structure and function. In addition to effects on vegetation structure, plant species diversity, and taxonomic composition, grazers worldwide exhibit a preference for recently burned areas (3), which further creates spatial heterogeneity of habitat suitable for arthropods.

Fire and grazing influence arthropod diversity in grassland systems, especially in North America and Europe (**Supplemental Tables 1** and **2**; follow the Supplemental Material link from the Annual Reviews home page at <http://www.annualreviews.org>). Understandably, studies vary among experimental treatments, methodologies, and level of taxonomic interest, so comparisons and conclusions are necessarily coarse. Arthropod responses to fire and grazing are often species specific and vary with patch size, phenological timing, intensity, and frequency of burning or grazing (5, 34, 50, 73). Experimental studies indicate that the species and breed of grazer may interact with vegetation type to determine arthropod responses to grazing (98–100). Finally, arthropod responses to fire and grazing are highly variable among years and sites (90), an outcome that makes it difficult to generalize about effects of fire and grazing on arthropod communities.

A wide range of responses result from studies assessing how grazing intensity affects arthropod diversity. Unimodal responses of arthropod species richness, consistent with the intermediate disturbance hypothesis, sometimes result (58, 59, 96). Other studies conclude that grazing leads to increased species richness (4, 123), decreased species richness (74), or no effect on arthropod species richness (5, 94), and these responses may vary among sites and years. For example, species richness was often higher in ungrazed and winter grazed plots than in summer grazed plots in desert grassland (34), but no consistent responses of arthropod populations over the five-year study resulted. Furthermore, arthropod responses to grazing are often species specific, obscuring our ability to generalize community-wide patterns.

Different species of grazers differentially influence arthropod community composition and diversity as grazer identity interacts with vegetation type to influence the outcome. In field experiments from northwestern Spain using different species (cattle, sheep, goats) and breeds of grazers at multiple grazing intensities, Rosa García et al. (98–100) found that arthropod responses may be highly dependent on grazer and vegetation type. For example, ground-dwelling arthropod

Table 1 Representative hypotheses explaining the promotion of arthropod species diversity in grasslands

Hypothesis	Description of hypothesis	Operational scale	References
Species-area relationship	Species diversity increases with area.	Regional/local	101
Productivity hypotheses	Species diversity increases with productivity.	Regional/local	128
Metabolic theory hypothesis	Molecular evolution scales with metabolic rate. Speciation should be highest in small-bodied species and for species in warm environments.	Regional	13
Time/stability hypothesis	Species diversity is higher in areas that are older and have been undisturbed for longer periods than in younger/more recently disturbed areas.	Regional	112
Niche partitioning and resource diversity hypothesis	Species diversity is highest when resources are diverse; species can partition resources to reduce competition and competitive exclusion.	Local	77
Habitat complexity hypothesis	Species diversity increases with habitat complexity; there is heterogeneity of microhabitat types within a habitat.	Local	77
Habitat diversity hypothesis	Species diversity increases with the number of types of habitats within a region (as opposed to microhabitats within a habitat type as in the habitat complexity hypothesis).	Regional	37
Intermediate disturbance hypothesis	Species diversity is highest at intermediate levels of disturbance.	Local	56
Theory of island biogeography	Species diversity on islands or habitat fragments is a dynamic equilibrium dependent on the island size and distance to mainland.	Regional/local	78
Diversity increases with predation	Species diversity is higher when predation reduces competition or reduces abundance of competitively dominant species (keystone predator).	Local	89
Diversity cascade hypothesis	Species diversity in food webs increases as dominant members of the food web increase in abundance (diversity cascades up the food web). This effect is more pronounced in heterogeneous than in homogeneous habitats.	Local	28
Foliar resource synchronization hypothesis	Synchronous flushes of foliar nutrients alter states at which different herbivore species do best; for gall makers, increased phenolics may fend off pathogens and parasitoids.	Local	45
Pulsed plant nutrient/productivity hypothesis	Unpredictable drought stress/relief alters foliar nutritional status to generate storage effect.	Local	14, 93

communities varied in pastures grazed by goats versus sheep, with a significant interaction between vegetation type and grazer identity (100).

As with the effects of grazing, comprehensive reviews indicate that insect responses to prescribed burning in grasslands defy our ability to identify repeatable responses (113). In general, arthropod responses to fire are often species specific and vary with fire frequency, time since burn, taxa examined, and species traits. Kerstyn & Stiling (65) found no effect of burn frequency on abundances of leaf miners, but grasshoppers were more abundant in plots burned more

frequently. Nadeau et al. (85) found no consistent responses among plots for grasshopper responses to burning, but other studies show clear, species-specific effects (58, 59). Long-term studies indicate that general responses can be uncovered (60), but the taxonomic level examined may be critical to uncovering general patterns. For example, Panzer (90) showed that arthropod responses to fire at 21 sites over a seven-year period were consistent year to year at the species level, but patterns disappeared after lumping species into higher taxonomic levels.

Fire has the potential to negatively affect very rare species that cannot recover from fire in highly fragmented landscapes (113). However, Panzer (90) found that 68% of insect species that responded negatively to fire recovered to prefire levels within 1 year of a burn, and 94% of species recovered within 2 years of a fire; very rare species may have been missed in this study. Ultimately, fire seems essential for maintaining grassland habitat necessary for grassland invertebrates despite the potential for negative effects on individual arthropod species populations. For example, arthropod diversity was higher in burned plots than in unburned plots because reduced presence of woody vegetation in burned plots favored increased arthropod diversity (50).

Arthropod diversity reflects mostly fire-grazing interactions rather than the effect of either factor alone (37, 60, 120). Analyses of a long time-series of grasshopper abundances and communities in tallgrass prairie at Konza Prairie (Kansas) (60) document such relationships. Fire, weather, and grazing by bison all influenced grasshopper responses, and different feeding guilds responded differently. Mixed and forb-feeding taxa were more abundant on grazed watersheds, and grass-feeders were more abundant on watersheds burned annually in the spring. The interaction between the length of time since the last burn and bison grazing was most predictive, as were long-term climate signals (North Atlantic Oscillation and Palmer Drought Severity Index) (60). The mechanisms by which fire and grazing influence grassland arthropods remain unresolved.

MECHANISMS STRUCTURING GRASSLAND ARTHROPOD ASSEMBLAGES

Vegetation in grasslands provides the physical habitat for most consumer species and the nutritional base for arthropod food webs. Disturbance from grazing, fire, and their interactions alter vegetation, structuring arthropod community responses through indirect paths emanating from the altered plant community. As such, key vegetation attributes that could influence arthropod diversity include overall primary production, degree and heterogeneity of structural architecture, plant species richness, floristic composition, chemical attributes of foliage from both defensive and nutritional viewpoints, and factors affecting mutualistic relationships between plants and insects (e.g., flower density/diversity, pollinator diversity, and plant-microbe interactions) or competitive and/or exploitive interactions among species from multiple trophic levels.

Fire, grazing, and weather in a landscape context interact simultaneously on habitat structure (**Figure 1**), influencing arthropod diversity through several mechanisms also acting simultaneously. An increase in host plant species resulting from fire and grazing regimes should increase the number of insect herbivore species that coexist locally as seen in many systems worldwide (18, 87), the heterogeneity in local vegetation structure (73, 121), and, in some cases, the responses corresponding to the availability of specific host plants needed by insect herbivores (see below). In terms of diet, insect herbivores range from strict specialists to generalists, where host plant selection is mediated by nutritional and defensive chemicals in plant tissues (9). If plant taxa or nutritional blends represent unique resources for exclusive use by different insect herbivores, one then expects more resources to yield greater species diversity (6).

Species composition of the plant community defines its physical structure, which influences important ecological responses by arthropods. Insect populations respond dramatically to thermal

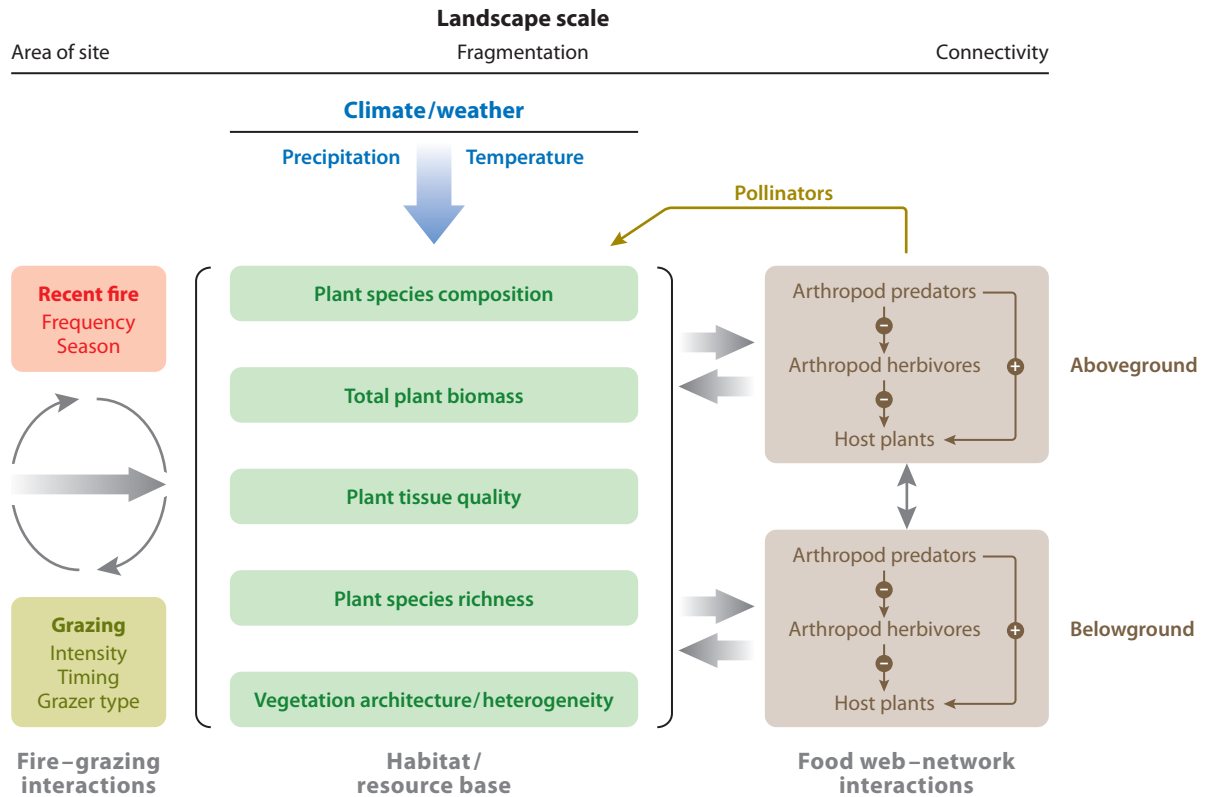


Figure 1

An overview framework of factors contributing to arthropod diversity in grasslands is shown. In addition to climate (weather), fire-grazing interactions structure the habitat template that determines resource availability and architectural structure for coexisting arthropods at a site. Resources and habitat characteristic influence direct and indirect species interactions among multiple trophic levels in both aboveground and belowground compartments. Landscapes operating at a regional level with respect to area, degree of fragmentation, and connectivity influence the available species pool and likelihood of local extinction. Detailed interaction networks are not indicated for simplicity.

characteristics of their habitats (20). Thermoregulation is important for many individual activities and is especially important for maintaining digestion efficiency and resource acquisition in insects (129). Spatially heterogeneous habitat structures with a variety of canopy options, including open microhabitat, facilitate opportunities for thermoregulation by insects without exposing them to predators as much as closed-canopy habitats do (68, 127). Altered habitat structure affects the availability of enemy-free space, where the number of microhabitats that minimize detection and capture by predators should lead to increased arthropod diversity (57, 75). As habitat conditions and resources diversify in response to fire and grazing, more taxa and trophic complexity should result at the local scale. Variable grassland vegetation structure coupled to increased plant species richness increases the availability of limiting resources, microhabitats, and suitability of abiotic conditions necessary to support arthropod taxa.

Overall arthropod abundances vary with plant species richness, but responses show both positive and negative associations (70). Grasshopper species richness varied negatively with grass biomass and canopy height, and positively with heterogeneous canopy height and plant species richness, in North American tallgrass prairie managed long-term with controlled burns and bison grazing

Path analysis model:
multiple regression
analysis used to
evaluate causal
schemes depicted as
path diagrams that
influence critical
responses (e.g., species
richness)

at watershed scales (59). No significant relationships existed between grasshopper species richness and either forb biomass or variability in plant species richness, even though a number of generalist feeding species eat forbs. Total insect herbivore and combined insect predator/parasitoid richness varied positively with plant species richness in experimental plots from Minnesota grasslands (69).

Well-studied butterfly assemblages include taxa with host ranges that vary from extreme specialists to generalists, providing another opportunity to test the basic assumption that increased plant diversity provides more resources, supporting more butterfly species. In a regional comparison across California, plant species richness is not a strong predictor of butterfly diversity, even though statistically significant positive correlations exist between plant and butterfly species richness for all “butterfly species combined” and for “host specialists only” (52). Rather, a path analysis model that included environmental variables associated with effects of temperature and plant productivity appeared causal; no additional goodness of fit to predict the number of butterfly species was achieved with the inclusion of plant species richness. A challenge is to reconcile regional, spatially scaled responses to expectations at local levels.

Belowground responses to increasing plant species and functional diversity are idiosyncratic in the sense that all manner of responses have been recorded, including no detectable response. In experimental temperate grasslands established for four years, soil collembolan species diversity and overall density increased positively with plant species richness and plant functional diversity (102). Short-term experimental studies (122) often showed opposite responses, suggesting that results are context dependent or idiosyncratic, that more details remain to be uncovered, or that ecosystem dynamics were still in flux from the establishment phase.

Floristic composition of plant communities is less often investigated as a determinant of arthropod diversity but may be important (33, 49), particularly because floristic composition integrates a range of biotic and abiotic factors. Schaffers et al. (104) showed that plant species composition consistently outperformed vegetation structure to predict diversity of multiple arthropod groups examined in seminatural grasslands in The Netherlands. Vegetation structure strongly influenced the diversity of bees and spiders, but diversity of grasshoppers, carabid ground beetles, weevils, delphacid planthoppers, spittlebugs, and hover flies responded most strongly to plant species composition. Influences from abiotic factors (e.g., soil characteristics, soil chemistry, temperature) did not predict arthropod diversity in this case, unlike some other studies in grazed grasslands and heathlands (51). Rather, the conclusions in this study (104) shifted to contributions of individual plant species on arthropod diversity and food web structure, as they collectively determine vegetation structure, host plant diversity, and the landscape of defensive chemical and nutritional characteristics affecting insect herbivores. Given the structure of arthropod food webs, this approach makes sense because many insect herbivores show restricted diets, or nearly so (9).

Trophic position is central to understanding communities, fostering continued efforts to understand bottom-up versus top-down dynamics, and the relative contributions of direct and indirect interactions. Does plant diversity influence diversity differentially among trophic levels and by what mechanism? Separate experimental studies provide insights, but results are not consistent. Insect herbivores and combined predators and parasitoids increased with plant species richness in Minnesota (69). Mixed results were observed for arthropod abundances in BIODDEPTH experiments that manipulated plant species richness in both Switzerland and Sweden (70). Consumer species richness is usually positively associated with overall abundance (see above). Abundances of specialist leafhoppers and wingless aphids varied with plant species richness and functional group diversity, but leafhoppers responded negatively and aphids positively with respect to plant species diversity. No trend with plant species richness was observed for generalist insect herbivores (70). Abundances of generalist spider and carabid beetle predators were negatively associated with

the number of plant species or plant functional groups, and specialist hymenopteran parasitoids showed no relationship.

ABOVEGROUND AND BELOWGROUND LINKAGES

Diversity of grassland arthropods reflects feedbacks between aboveground and belowground compartments of the food web (8, 21, 55), which can change as plant diversity or plant quality varies (8). The effects of one compartment on the other may influence higher-order trophic interactions, including predator-prey and host-parasite interactions.

Belowground interactions may influence aboveground arthropod populations by modulating plant chemistry and thus nutrition to aboveground consumers, ultimately altering herbivore abundances and traits such as body size or fecundity (11, 105). These interactions are often species and guild specific. Scheu et al. (105) found that earthworms and collembolans had different effects on nitrogen content and root versus shoot biomass in two species of plants, leading to context-dependent responses in aphid reproduction that varied with plant species and soil fauna treatment. The addition of protozoa increased plant nitrogen content, thus altering aphid abundance and biomass (11).

Belowground interactions may affect aboveground species interactions at higher trophic levels such as predators and parasites (10, 40, 79). Bezemer et al. (10) grew plants in separate pots and inoculated the soil with nematodes, microbes, or both. Plant quality (amino acid composition) was lower when nematodes were added, leading to decreased aphid abundance and increased parasitoid survival. This resulted partly from the larger size of aphids in the nematode-added treatments, which promoted higher levels of parasitoid survival. Gange et al. (40) found that fungal arbuscular mycorrhizal fungi could increase, decrease, or have no effect on parasitism by a dipteran seed predator, but the effect depended on the species of arbuscular mycorrhizal fungi used. Reduced root herbivory using insecticide led to fewer invertebrate seed predators and parasites compared to plants with root herbivory (79). Fewer studies examined how aboveground species interactions influence belowground interactions, but a manipulative laboratory experiment involving aphids and two species of predators showed that aboveground trophic cascades increased abundance and diversity of primary consumers in belowground communities (122). Abundance and diversity of belowground predators also responded to the addition of aboveground consumers, but the effect varied over time among treatments.

Other mechanisms further indicate the richness inherent in interactions between belowground and aboveground compartments. In the rhizosphere, top-down regulation of belowground prey by top predators altered the release of nutrients that regulate bottom-up plant productivity, which in turn altered aboveground species webs (83). Moreover, natural food webs include slow and fast food web energy channels, which contribute differentially to nutrient cycling and differ in productivity and turnover rates. Top-down predation belowground can couple slow and fast channels to confer stability to natural grassland food webs (97).

Species interactions in aboveground compartments of the food web affect species interactions in the belowground food web compartments, and vice versa, which may ultimately influence arthropod diversity. Hooper et al. (55) hypothesized that linkages between diversity aboveground and belowground are mediated through plant diversity, which increases the diversity of resource types and quality (for example, increased litter diversity and litter quality may increase arthropod diversity of decomposers). However, the nature of the correlations between aboveground and belowground diversity likely depends on the nature of species interactions between aboveground and belowground compartments and on the scale of ecological factors that affect these communities (55). Additional studies are needed to test these predictions in grassland habitats.

Trophic cascade: an indirect interaction in which predators increase plant biomass by altering herbivore traits or herbivore density, which decreases the amount eaten

NETWORKS, FOOD WEB STRUCTURE, AND ARTHROPOD DIVERSITY

NSF LTER

Program: long-term, site-based ecological research at multiple sites to understand dynamic ecological processes that occur over multidecadal time frames

Food webs or species interaction webs describe multiple-level relationships among coexisting arthropod species that ultimately reflect basal plant taxa and their diversity, effects that propagate throughout the community network (1, 46, 47, 91). Reducing the number of plant species in aphid-parasitoid communities, for example, decreased species richness at all trophic levels primarily through indirect paths (91). Aphids and primary parasitoids showed the highest species richness at intermediate levels of plant species richness, whereas secondary parasitoids declined linearly with plant species richness resulting from shorter food chains in communities with the highest plant species richness. Similar results were observed in a North American field experiment in Minnesota (46, 47). As plant species richness increased from 1 to 16 species in long-term field experiments in the NSF LTER Program study at Cedar Creek, Minnesota, cumulative species richness of herbivorous arthropods increased by an average of ~40% and predator richness increased by ~35%.

In a comparative study, Albrecht et al. (1) tested the hypothesis that declining plant species diversity led to decreased interaction diversity and decreased quantitative changes in food web structure of trap-nesting insects from restored Swiss grassland meadows. Intensively managed meadows contain lower plant species diversity than restored sites do. Reduced plant species richness was associated with reduced diversity at all trophic levels. Increased linkage density and interaction diversity, enhanced compartment diversity, and decreased interaction evenness were observed in restored meadows (1), reflecting increased generalism in host-prey species interactions.

Experiments from Cedar Creek, Minnesota, on arthropod responses to plant diversity also document the important role of basal plant species richness in overall food web stability (measured as lower year-to-year variability in responses) (46). Theory predicts that food web stability results from the connectivity of trophic interactions, including the degree of specialist feeding (80). As plant diversity increases consumer diversity and habitat structure, food web connectivity decreases as the number of potential species interactions and potential for prey escape from predators increase (80). In this study, population stability and community stability responded differently. Population stability of specialists largely decreased as plant species richness increased, but population-level stability of generalist herbivores was not affected. Low-diversity treatments had greater than 40% more herbivore individuals, significantly higher abundances of specialist herbivores, and higher levels of population fluctuation (47). In contrast, plant species diversity stabilized responses by the entire herbivore community, resulting largely from bottom-up control (46) and the “portfolio effect” (24), wherein statistical averaging according to power-law relationships ensures diversity-stability relationships. The stability of predator and parasitoid to species richness over the range investigated increased by ~30%, but again the variability in abundance responses of populations increased with plant species richness. Overall, community stability at all trophic levels increased with plant species diversity as food web complexity increased, and interspecific interactions were less tightly coupled (lower connectivity) as predicted by theory (46, 80).

In communities, multiple species interactions among trophic levels set up many possible contrasts between bottom-up and top-down control of overall food web structure, which can affect species diversity of the system. However, the indirect contributions of predator-prey interactions to community and ecosystem processes are often poorly appreciated (106, 107), despite their fundamental roles in the reticulated network of direct and indirect pathways that influence community and ecosystem dynamics (106). For example, trophic cascades (indirect increases in vegetation caused by predator-induced reductions in herbivore feeding or density) vary with many factors, such as predator diversity, abiotic conditions, and herbivore density (31, 44, 88), and indicate the relative importance of top-down versus bottom-up processes.

More generally, local community assemblages can be represented as complex ecological interaction networks and webs to document the local robustness of species diversity and its sensitivity to species loss depending on the nature of the network interaction for trophic and mutualistic networks (92, 115). From theory and empirical analyses of arthropod assemblages, highly connected and nested sets of species interactions are expected to promote stability of mutualistic networks (e.g., pollination), and trophic network stability (e.g., herbivory) is enhanced most likely by compartmented and weakly connected architectures (115). Intensely sampled networks that depend on plant species from spatially distributed managed grasslands embedded within an otherwise agroecosystem landscape (92) revealed (a) much variability in the robustness of different networks to loss of plant species, (b) that components did not covary such that activities that benefitted a particular functional network did not inevitably benefit others, and (c) that mutualistic networks were highly sensitive to plant species loss. Aphids, seed-feeding insects, and seed-feeder parasitoids were most vulnerable to sequential loss of plant species in simulations (92).

Ecological landscape:
an area that includes heterogeneous ecosystems or habitats whose spatial arrangement in the area affects ecological processes

β -diversity:
interhabitat component of species diversity as sampling crosses boundaries of habitat types

LANDSCAPE-LEVEL PROCESSES AND DIVERSITY

Landscape-level processes influence ecological processes responsible for the origin and maintenance of local arthropod diversity, and a variety of mechanisms contribute to their influence on species diversity. Habitat fragmentation and habitat modification are major anthropogenic processes that affect ecosystems at the global level (19, 29, 71, 119), modifying rates of extinction and colonization of species at local scales. The resulting size and spatial distribution of suitable habitats, including dispersal corridors, thus contribute to local arthropod diversity.

Fragmentation, Available Habitat Areas, and Corridors

Mechanisms underlying community responses to fragmentation are difficult to assess because of inherent complexity from biotic and abiotic interactions at multiple scales (126). Landscape structure can influence spatial patterns of diversity. Diekotter et al. (23) partitioned the additive diversity for three arthropod functional groups (pollinators: bees, herbivores: true bugs, and predators: carabid beetles) within and among patches that differed in connectivity in a Swiss-managed grassland landscape. Increased connectivity led to a greater contribution of β -diversity to overall γ -diversity, and the effect was greater in carabid beetles that could not disperse as effectively as bees and true bugs.

Habitat area was most important for understanding species diversity at all trophic levels in controlled experiments of arthropod responses to planted clover plots (126). Plots with increased habitat sampled the regional source pool to a greater degree and accumulated more species than plots with less habitat area. Using data from 24 independent studies, Ockinger et al. (86) showed that increased habitat area and connectivity consistently increased arthropod species richness in cross-continent comparisons. Life-history traits proved important for understanding responses to landscape, as species with low mobility, specialized diets, and low reproductive capability were most affected by habitat loss. Other studies show reduced extinction risk by generalist feeders (43, 111).

Arthropod species respond differentially to habitat fragmentation and area (16–18), often depending on the feeding guilds and whether they specialize on few or many host species. Generalist feeding species are more likely than specialists to find sufficient resources within a fragment and are also more likely to utilize corridors that could provide nourishment and additional habitat (16). Local food sources, compared with regional, geographical factors, often contribute a strong, direct impact to herbivores in fragmented studies (18, 64, 71). If food is scarce, specialists must

move among fragments to acquire specific resources and are limited by landscape-scale factors that inhibit dispersal. Simulations (125) showed that specialists were less likely than generalists to aggregate at resources and continue random searching.

Trophic Level Susceptibility to Fragmentation Hypothesis

Predators may respond to landscape-scale factors in accordance with the Trophic Level Susceptibility to Fragmentation Hypothesis (71). Because reestablishment of predator populations requires the prior establishment of prey populations, predators are more susceptible to fragmentation.

Insect species from different trophic levels often respond differently to fragment isolation, area, or both (42, 71, 118, 130). Arthropods associated with top trophic levels respond to both fragment isolation and area, while arthropods associated with lower trophic levels are less affected (25). The Trophic Level Susceptibility to Fragmentation Hypothesis (71, 72, 117, 118) predicts that species richness of predators and parasitoids should decrease as habitat fragments become isolated and area is reduced.

Herbivorous insects from lower trophic levels are not greatly affected by regional fragmentation factors directly but rather respond indirectly, possibly reflecting changes in the plant community due to regional fragmentation. Plant community changes include attributes such as plant species richness, plant height diversity, and blooming flower community. Local extinction as a result of disturbance in prairie remnants may be common, because fragments are often managed for hay production or grazing by large mammals. Arthropods associated with higher trophic levels such as parasitoids and predators rely on the prior establishment of prey populations and may be slow to successfully reestablish in disturbed fragments after extirpation (72).

CONCLUSIONS

Many ecological factors operating at different spatial scales contribute simultaneously to the origin and maintenance of local arthropod diversity in grasslands. In each case, species interactions are important, and these interactions are usually poorly understood in single systems, let alone in multiple grasslands, which would facilitate comparative studies. Much can be gained by linking existing comparative studies of grassland arthropod diversity with long-term experiments aimed at teasing apart specific ecological mechanisms, especially when couched in a strong conceptual and theoretical framework.

SUMMARY POINTS

1. Species-area and species-energy relationships predict scale-dependent patterns of arthropod diversity. Diversity increases with productivity, in support of the “more individuals hypothesis,” in which greater population size leads to lower extinction rates of coexisting species in higher productivity systems.
2. Fire, grazing, and climate are dominant ecosystem drivers that structure grasslands. Each factor alone can affect arthropod diversity, but the results of individual studies are idiosyncratic. Ultimately, fire-grazing interactions are more important than either factor alone, largely because of the resulting habitat and landscape heterogeneity that contributes to increased arthropod diversity.
3. Local arthropod diversity varies with vegetation attributes, including richness and composition of plant species, plant architectural heterogeneity, total productivity, and abiotic conditions. Multiple indirect interactions are expected.

4. Aboveground and belowground communities are compartmentalized, where they interact primarily via responses of plant species to herbivory or via effects on nutrient cycling; higher trophic levels are also affected through this linkage.
5. Local communities represent complex interaction networks, supporting a variety of indirect interactions among species, including trophic cascades, compartmentalized and nested architectures, and variable connectedness, each of which contributes to patterns of arthropod diversity and possible system stability.
6. At the landscape level, habitat fragmentation and area explain major shifts in arthropod diversity in grasslands. Higher trophic levels appear more sensitive to these effects.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The preparation of this manuscript occurred under the support of the National Science Foundation (Division of Environmental Biology 1020485). This paper is a contribution of the Kansas Agricultural Experiment Station (manuscript number 12-370-J).

LITERATURE CITED

1. Albrecht M, Duelli P, Schmid B, Muller CB. 2007. Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *J. Anim. Ecol.* 76:1015–25
2. Anderson TM, Ritchie ME, Mayemba E, Eby S, Grace JB, McNaughton SJ. 2007. Forage nutritive quality in the Serengeti ecosystem: the roles of fire and herbivory. *Am. Nat.* 170:343–57
3. Archibald S, Bond WJ, Stock WD, Fairbanks DHK. 2005. Shaping the landscape: fire-grazer interactions in an African savanna. *Ecol. Appl.* 15:96–109
4. Balmer O, Erhardt A. 2000. Consequences of succession on extensively grazed grasslands for central European butterfly communities: rethinking conservation practices. *Conserv. Biol.* 14:746–57
5. Batary P, Baldi A, Samu F, Szuts T, Erdos S. 2008. Are spiders reacting to local or landscape scale effects in Hungarian pastures? *Biol. Conserv.* 141:2062–70
6. Behmer ST, Joern A. 2008. Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proc. Natl. Acad. Sci. USA* 105:1977–82
7. Belovsky GE, Slade JB. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proc. Natl. Acad. Sci. USA* 97:14412–17
8. Bennett A. 2010. The role of soil community biodiversity in insect biodiversity. *Insect Conserv. Divers.* 3:157–71
9. Bernays E, Chapman R. 1994. *Host Plant Selection by Phytophagous Insects*. New York: Chapman & Hall
10. Bezemer TM, De Deyn GB, Bossinga TM, van Dam NM, Harvey JA, Van der Putten WH. 2005. Soil community composition drives aboveground plant-herbivore-parasitoid interactions. *Ecol. Lett.* 8:652–61
11. Bonkowski M, Geoghegan IE, Birch ANE, Griffiths BS. 2001. Effects of soil decomposer invertebrates (protozoa and earthworms) on an above-ground phytophagous insect (cereal aphid) mediated through changes in the host plant. *Oikos* 95:441–50
12. Branson DH, Joern A, Sword GA. 2006. Sustainable management of insect herbivores in grassland ecosystems: new perspectives in grasshopper control. *Bioscience* 56:743–55

1. Examines species interaction diversity in differently managed sites.

13. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–89
14. Chesson P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31:343–66
15. Clarke A, Gaston KJ. 2006. Climate, energy and diversity. *Proc. R. Soc. Biol. Sci.* 273:2257–66
16. Collinge SK. 2000. Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. *Ecology* 81:2211–26
17. Collinge SK, Palmer TM. 2002. The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. *Landscape Ecol.* 17:647–56
18. Collinge SK, Prudic KL, Oliver JC. 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conserv. Biol.* 17:178–87
19. Collinge SK, Ray C. 2009. Transient patterns in the assembly of vernal pool plant communities. *Ecology* 90:3313–23
20. Coxwell CC, Bock CE. 1995. Spatial variation in diurnal surface temperatures and the distribution and abundance of an alpine grasshopper. *Oecologia* 104:433–39
21. De Deyn GB, Van der Putten WH. 2005. Linking aboveground and belowground diversity. *Trends Ecol. Evol.* 20:625–33
22. di Giulio M, Edwards P, Meister E. 2001. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *J. Appl. Ecol.* 38:310–19
23. Diekötter T, Billeter R, Crist TO. 2008. Effects of landscape connectivity on the spatial distribution of insect diversity in agricultural mosaic landscapes. *Basic Appl. Ecol.* 9:298–307
24. Doak DF, Bigger D, Harding EK, Marvier MA, O'Malley RE, Thomson D. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.* 151:264–76
25. Dubbert M, Tschamtké T, Vidal S. 1998. Stem-boring insects of fragmented *Calamagrostis* habitats: herbivore-parasitoid community structure and the unpredictability of grass shoot abundance. *Ecol. Entomol.* 23:271–80
26. Evans KL, Greenwood JJD, Gaston KJ. 2005. Dissecting the species-energy relationship. *Proc. R. Soc. Biol. Sci.* 272:2155–63
27. Evans KL, Warren PH, Gaston KJ. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biol. Rev.* 80:1–25
28. Eveleigh ES, McCann KS, McCarthy PC, Pollock SJ, Lucarotti CJ, et al. 2007. Fluctuations in density of an outbreak species drive diversity cascades in food webs. *Proc. Natl. Acad. Sci. USA* 104:16976–81
29. Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Syst.* 34:487–515
30. Fay PA. 2003. Insect diversity in two burned and grazed grasslands. *Environ. Entomol.* 32:1099–104
31. Finke DL, Denno RF. 2004. Predator diversity dampens trophic cascades. *Nature* 429:407–10
32. Finlay BJ, Thomas JA, McGavin GC, Fenchel T, Clarke RT. 2006. Self-similar patterns of nature: insect diversity at local to global scales. *Proc. R. Soc. Biol. Sci.* 273:1935–41
33. Foord SH, Ferguson JWH, Van Jaarsveld AS. 2003. Coleopteran assemblages in afro-montane grasslands reflect fine-scale variation in vegetation. *Environ. Entomol.* 32:797–806
34. Forbes GS, Van Zee JW, Smith W, Whitford WG. 2005. Desert grassland canopy arthropod species richness: temporal patterns and effects of intense, short-duration livestock grazing. *J. Arid Environ.* 60:627–46
35. Frank DA, Evans RD. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology* 78:2238–48
36. Fretwell SD. 1987. Food-chain dynamics: the central theory of ecology. *Oikos* 50:291–301
37. Fuhlendorf SD, Engle DM. 2001. **Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns.** *Bioscience* 51:625–32
38. Fuhlendorf SD, Engle DM, Kerby J, Hamilton R. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conserv. Biol.* 23:588–98
39. Fuhlendorf SD, Harrell WC, Engle DM, Hamilton RG, Davis CA, Leslie DM. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecol. Appl.* 16:1706–16
40. Gange AC, Brown VK, Aplin DM. 2003. Multitrophic links between arbuscular mycorrhizal fungi and insect parasitoids. *Ecol. Lett.* 6:1051–55

37. Describes how interactions between fire and grazing may be used to create habitat heterogeneity and a shifting mosaic of vegetation in grassland systems.

41. Gaston K, Blackburn T. 2000. *Pattern and Process in Macroecology*. Oxford: Blackwell Publ.
42. Golden DM, Crist TO. 2000. Experimental effects of habitat fragmentation on rove beetles and ants: patch area or edge? *Oikos* 90:525–38
43. Goulson D, Derwent LC, Hanley ME, Dunn DW, Abolins SR. 2005. Predicting calyptrate fly populations from the weather, and probable consequences of climate change. *J. Appl. Ecol.* 42:795–804
44. Gratton C, Denno RF. 2003. Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. *Oecologia* 134:487–95
45. Gutbrodt B, Mody K, Dorn S. 2011. Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. *Oikos* 120:1732–40
- 46. Haddad N, Crutsinger G, Gross K, Haarstad J, Tilman D. 2011. Plant diversity and the stability of foodwebs. *Ecol. Lett.* 14:42–46**
47. Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecol. Lett.* 12:1029–39
48. Haddad NM, Haarstad J, Tilman D. 2000. The effects of long-term nitrogen loading on grassland insect communities. *Oecologia* 124:73–84
49. Haddad NM, Tilman D, Haarstad J, Ritchie M, Knops JMH. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. *Am. Nat.* 158:17–35
50. Hartley MK, Rogers WE, Siemann E, Grace J. 2007. Responses of prairie arthropod communities to fire and fertilizer: balancing plant and arthropod conservation. *Am. Midl. Nat.* 157:92–105
51. Hartley SE, Gardner SM, Mitchell RJ. 2003. Indirect effects of grazing and nutrient addition on the hemipteran community of heather moorlands. *J. Appl. Ecol.* 40:793–803
52. Hawkins BA, Porter EE. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. *Am. Nat.* 161:40–49
53. Hendrickx F, Maelfait JP, Van Wingerden W, Schweiger O, Speelmans M, et al. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J. Appl. Ecol.* 44:340–51
54. Hewitt G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405:907–13
55. Hooper DU, Bignell DE, Brown VK, Brussaard L, Dangerfield JM, et al. 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. *Bioscience* 50:1049–61
56. Huston M. 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge, UK: Cambridge Univ. Press
57. Joern A. 2002. Context-dependent foraging and enemy-free space: Grasshopper sparrows (*Ammodramus savannarum*) searching for grasshoppers (Acrididae). *Ecoscience* 9:231–40
58. Joern A. 2004. Variation in grasshopper (Acrididae) densities in response to fire frequency and bison grazing in tallgrass prairie. *Environ. Entomol.* 33:1617–25
59. Joern A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology* 86:861–73
60. Jonas JL, Joern A. 2007. Grasshopper (Orthoptera: Acrididae) communities respond to fire, bison grazing and weather in North American tallgrass prairie: a long-term study. *Oecologia* 153:699–711
61. Kaspari M. 2005. Global energy gradients and size in colonial organisms: worker mass and worker number in ant colonies. *Proc. Natl. Acad. Sci. USA* 102:5079–83
- 62. Kaspari M, Alonso L, O'Donnell S. 2000. Three energy variables predict ant abundance at a geographical scale. *Proc. R. Soc. Lond. Ser. B* 267:485–89**
63. Kaspari M, O'Donnell S, Kercher JR. 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. *Am. Nat.* 155:280–93
64. Kemp W, Harvey S, O'Neill K. 1990. Habitat and insect biology revisited: the search for patterns. *Am. Entomol.* 3:44–49
65. Kerstyn A, Stiling P. 1999. The effects of burn frequency on the density of some grasshoppers and leaf miners in a Florida sandhill community. *Fla. Entomol.* 82:499–505
66. Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, et al. 1999. The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *Bioscience* 49:39–50

46. Results of long-term study manipulating plant species richness assess contribution to food web stability of consumer levels.

62. Empirical test of species-energy theory using ants along broad geographic gradients.

67. Knapp AK, Briggs JM, Hartnett DC, Collins SL, eds. 1998. *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*. New York, NY: Oxford Univ. Press. 364 pp.
68. Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, et al. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–5
69. Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, et al. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.* 2:286–93
70. Koricheva J, Mulder CPH, Schmid B, Joshi J, Huss-Danell K. 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125:271–82
71. Kruess A, Tscharntke T. 1994. Habitat fragmentation, species loss, and biological control. *Science* 264:1581–84
72. Kruess A, Tscharntke T. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122:129–37
73. Kruess A, Tscharntke T. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biol. Conserv.* 106:293–302
74. Kruess A, Tscharntke T. 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conserv. Biol.* 16:1570–80
75. Lawton J. 1979. Between the devil and the deep blue sea: on the problem of being an herbivore. In *Population Dynamics*, ed. R Anderson, B Turner, L Taylor, pp. 223–44. Oxford, UK: Blackwell Sci.
76. Lawton JH. 1983. Plant architecture and the diversity of phytophagous insects. *Annu. Rev. Entomol.* 28:23–39
77. MacArthur R. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. New York: Harper & Row. 269 pp.
78. MacArthur R, Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton Univ. Press. 203 pp.
79. Masters GJ, Jones TH, Rogers M. 2001. Host-plant mediated effects of root herbivory on insect seed predators and their parasitoids. *Oecologia* 127:246–50
80. McCann K, Rasmussen J, Umbanhowar J. 2005. The dynamics of spatially coupled food webs. *Ecol. Lett.* 8:513–23
81. Meyer CK, Whiles MR, Charlton RE. 2002. Life history, secondary production, and ecosystem significance of acridid grasshoppers in annually burned and unburned tallgrass prairie. *Am. Entomol.* 48:52–61
82. Milchunas DG, Varnamkhasti AS, Lauenroth WK, Goetz H. 1995. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. *Oecologia* 101:366–74
83. Moore J, McCann K, Setälä H, de Ruiter P. 2003. Top-down is bottom-up: Does predation in the rhizosphere regulate aboveground dynamics? *Ecology* 84:846–57
84. Morris MG. 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biol. Conserv.* 95:129–42
85. Nadeau L, Cushing PE, Kondratieff BC. 2006. Effects of fire disturbance on grasshopper (Orthoptera: Acrididae) assemblages of the Comanche National Grasslands, Colorado. *J. Kans. Entomol. Soc.* 79:2–12
86. Ockinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecol. Lett.* 13:969–79
87. Otte D. 1976. Species richness patterns of New World desert grasshoppers in relation to plant diversity. *J. Biogeogr.* 3:197–209
88. Ovadia O, Schmitz OJ. 2004. Weather variation and trophic interaction strength: sorting the signal from the noise. *Oecologia* 140:398–406
89. Paine RT. 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. *Ecology* 50:951–61
90. Panzer R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. *Conserv. Biol.* 16:1296–307
91. Petermann JS, Muller CB, Weigelt A, Weisser WW, Schmid B. 2010. Effect of plant species loss on aphid-parasitoid communities. *J. Anim. Ecol.* 79:709–20
92. Pocock M, Evans D, Memmott J. 2012. The robustness and restoration of a network of ecological networks. *Science* 335:973–77

91. Shows how plant species richness affects abundance and species richness of arthropod herbivores and parasitoids through direct and indirect mechanisms.

92. Identifies unique functional groups, their relative robustness to loss of plant species, and the lack of covariance among many functional groups.

93. Price PW. 1992. The resource based organization of communities. *Biotropica* 24:273–82
94. Rambo JL, Faeth SH. 1999. Effect of vertebrate grazing on plant and insect community structure. *Conserv. Biol.* 13:1047–54
95. Ricklefs R, Schluter D, eds. 1993. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago: Univ. Chicago Press
96. Roberts RJ, Morton R. 1985. Biomass of larval Scarabaeidae (Coleoptera) in relation to grazing pressures in temperate, sown pastures. *J. Appl. Ecol.* 22:863–74
97. Rooney N, McCann K, Gellner G, Moore J. 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442:265–69
98. Rosa García R, García U, Osoro K, Celaya R. 2011. Ground-dwelling arthropod assemblages of partially improved heathlands according to the species of grazer and grazing regime. *Eur. J. Entomol.* 108:107–15
99. Rosa García R, Jauregui BM, García U, Osoro K, Celaya R. 2009. Responses of arthropod fauna assemblages to goat grazing management in northern Spanish heathlands. *Environ. Entomol.* 38:985–95
100. Rosa García R, Ocharan FJ, Jauregui BM, García U, Osoro K, Celaya R. 2010. Ground-dwelling arthropod communities present in three types of Cantabrian (NW Spain) heathland grazed by sheep or goats. *Eur. J. Entomol.* 107:219–27
101. Rosenzweig ML. 1995. *Species Diversity in Space and Time*. Cambridge, UK: Cambridge Univ. Press
102. Sabais ACW, Scheu S, Eisenhauer N. 2011. Plant species richness drives the density and diversity of Collembola in temperate grassland. *Acta Oecol. Int. J. Ecol.* 37:195–202
103. Sala O. 2001. Temperate grasslands. In *Global Biodiversity in a Changing Environment: Scenarios for the 21st Century*, ed. F Chapin, O Sala, E Huber-Sannwald, pp. 121–37. New York: Springer
104. Schaffers AP, Raemakers IP, Sykora KV, Ter Braak CJF. 2008. Arthropod assemblages are best predicted by plant species composition. *Ecology* 89:782–94
105. Scheu S, Theenhaus A, Jones TH. 1999. Links between the detritivore and the herbivore system: effects of earthworms and Collembola on plant growth and aphid development. *Oecologia* 119:541–51
- 106. Schmitz OJ. 2008. Herbivory from individuals to ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 39:133–52**
107. Schmitz OJ, Post E, Burns CE, Johnston KM. 2003. Ecosystem responses to global climate change: moving beyond color mapping. *Bioscience* 53:1199–205
108. Siemann E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057–70
109. Siemann E, Tilman D, Haarstad J, Ritchie M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Nat.* 152:738–50
110. Steffan-Dewenter I, Munzenberg U, Burger C, Thies C, Tscharntke T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83:1421–32
111. Stoner KJL, Joern A. 2004. Landscape versus local habitat scale influences to insect communities from tallgrass prairie remnants. *Ecol. Appl.* 14:1306–20
112. Strong D, McCoy E, Rey J. 1977. Time and the number of herbivore species: the pests of sugarcane. *Ecology* 58:167–75
113. Swengel AB. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodivers. Conserv.* 10:1141–69
114. Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, et al. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31:79–92
115. Thebault E, Fontaine C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853–56
116. Tscharntke T, Greiler HJ. 1995. Insect communities, grasses, and grasslands. *Annu. Rev. Entomol.* 40:535–58
117. Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C. 2002. Characteristics of insect populations on habitat fragments: a mini review. *Ecol. Res.* 17:229–39
118. Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecol. Appl.* 12:354–63
119. Turner JRG. 2004. Explaining the global biodiversity gradient: energy, area, history and natural selection. *Basic Appl. Ecol.* 5:435–48

106. Provides a comprehensive review of how diversity interacts with herbivore performance.

122. Examines the effects of aboveground predator-prey interactions on the belowground food web.

126. Tests the relative role of area versus fragmentation on arthropod diversity using a simplified plant community.

120. Vogel JA, Debinski DM, Koford RR, Miller JR. 2007. Butterfly responses to prairie restoration through fire and grazing. *Biol. Conserv.* 140:78–90
121. WallisDeVries MF, Bakker JP, Van Wieren SE, eds. 1998. *Grazing and Conservation Management*. Dordrecht, The Netherlands: Kluwer Acad. Publ.
122. **Wardle DA, Williamson WM, Yeates GW, Bonner KI. 2005. Trickle-down effects of above-ground trophic cascades on the soil food web. *Oikos* 111:348–58**
123. Wettstein W, Schmid B. 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. *J. Appl. Ecol.* 36:363–73
124. Whiles MR, Charlton RE. 2006. The ecological significance of tallgrass prairie arthropods. *Annu. Rev. Entomol.* 51:387–412
125. With KA, Crist TO. 1995. Critical thresholds in species responses to landscape structure. *Ecology* 76:2446–59
126. **With KA, Pavuk DM. 2011. Habitat area trumps fragmentation effects on arthropods in an experimental landscape system. *Landscape Ecol.* 26:1035–48**
127. Woodcock BA, Potts SG, Westbury DB, Ramsay AJ, Lambert M, et al. 2007. The importance of sward architectural complexity in structuring predatory and phytophagous invertebrate assemblages. *Ecol. Entomol.* 32:302–11
128. Wright DH. 1983. Species-energy theory: an extension of species-area theory. *Oikos* 41:496–506
129. Yang YL, Joern A. 1994. Influence of diet quality, developmental stage, and temperature on food residence time in the grasshopper *Melanoplus differentialis*. *Physiol. Zool.* 67:598–616
130. Zabel J, Tscharrntke T. 1998. Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia* 116:419–25



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