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Pollinator-friendly flora in rangelands following control of cheatgrass (*Bromus tectorum*): a case study

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Case Study

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Abstract

Invasive winter annual grasses, such as cheatgrass (*Bromus tectorum* L.) are considered serious threats to regional biodiversity. Pollinator populations that depend on the native flora are likely to be negatively impacted as these native species may be displaced by the invasive grass species. Colonization by cheatgrass is also predicted to increase risk of wildfires, as dead plant parts provide fuel in the already dry and arid regions of the western United States. Biocontrol, grazing, prescribed burning, or use of broad-spectrum nonselective herbicides have been suggested as possible means to control *B. tectorum*. Efficient control may facilitate regrowth of native flora that could in turn support other ecosystem functions. Reporting our findings as a case study, we describe here the results of the application of a preemergent herbicide, indaziflam, that limits germination of *B. tectorum* seeds. Herbicide was applied to the study locations during the months of December 2016, January 2017, and February 2017. The data reported here on the diversity of flowering plants were collected between May through September 2018. Herbicide-treated plots showed an increase in diversity and abundance of flowering plants compared to the untreated control within two seasons after cheatgrass control was implemented, suggesting that effective reduction of the population of the invasive annual cheatgrass may help facilitate the growth of native forbs. Further studies are necessary to understand mechanisms that facilitate reestablishment of native flowering species, the long-term consequences of reducing invasive annual grasses and to document any residual effects of the herbicide on ground-nesting pollinators.

Introduction

Invasive annual grasses have been shown to have devastating consequences on native biodiversity, environmental quality, and ecosystem services (Bartz and Kowarik 2019; Jones and McDermott 2018; Kumar Rai and Singh 2020; Pejchar and Mooney 2009). These invasive annual grasses effectively displace native vegetation (Pyšek et al. 2012), thus altering decomposition cycles and soil food webs (Lenz et al. 2003), disrupting ecosystem networks such as the plant–pollinator reproductive mutualisms (Schweiger et al. 2010; Traveset and Richardson 2006), altering historic fire regimes (D'Antonio and Vitousek 1992), and displacing ecosystem diversity and stability (Musil et al. 2005). Although controlling invasive species has received global and regional attention, the success of control measures and the positive impacts on the ecosystems following control may not always be uniform or generalizable (Adams et al. 2020; Skurski et al. 2013) and may vary across different levels of ecological complexity (Vilà et al. 2011). It has been suggested that effective control measures for invasive species, should also emphasize ecological processes that prevent reinvasion, possibly combining control with simultaneous restoration to retain broader ecosystem functions (D'Antonio et al. 2004; Flory and Clay 2009; Monaco et al. 2017).

Invasive species contribute to biodiversity losses by compounding effects of habitat destruction, agricultural intensification, and climate change, as recently discussed by Wagner (2020) in a report on global decline in insect biodiversity. Although the extent of impact may vary across different ecosystems, declining populations of insects, specifically pollinators, could compromise reproductive success of native flora (Gilgert and Vaughan 2011) and affect ecosystem functioning (Blüthgen and Klein 2011). While the impact of invasive species on native vegetation is relatively well described, and studies demonstrate targeted ecosystem trade-offs resulting from controlling invasive species (Adams et al. 2020; Pyšek et al. 2012; Skurski et al. 2013), few studies explore the relation between control of invasive plants and the subsequent impact on pollinator-friendly forbs. In the rangelands of Colorado, this relationship is especially critical, as the well-documented bee diversity of this region (Goldstein and Scott 2015) is important for the reproductive success of the native forbs. While studies indicate that the bee populations in these rangelands may not be currently experiencing concerning declines (Kearns and Oliveras 2009b) and have been conserved over several decades (Kearns and Oliveras 2009a), the spread of invasive annual grasses could compromise the habitat quality of these rangelands, negatively impacting bee populations in the long run.

It has also been suggested that winter annual invasives such as cheatgrass or downy brome (*Bromus tectorum* L.) affect regional ecosystem functions (Boyte et al. 2016; Knapp 1996). A systematic review spanning 64 yr (Monaco et al. 2017) suggests that of the different methods of control currently available, only one method, herbicide application, decreased *B. tectorum* and increased perennial grass abundance over the long term, lending support to herbicide-based control methods. Recent research reports from this region describe the efficient control of *B. tectorum* following winter application of a preemergent herbicide, indaziflam, a chemical whose cellulose biosynthesis-inhibiting action inhibits root development following seed germination, a mechanism different from previously used herbicides (Clark et al. 2019; Sebastian et al. 2016, 2017a). These studies also report that the residual effects of indaziflam application may last up to nearly three years, allowing for further reduction of *B. tectorum* seedbank in the soil (Sebastian et al. 2017b), improving the potential for native forbs to reestablish after continued germination suppression of the invasive grass seeds. Taken together, the inhibited seed germination and longer residual effect suggest that controlling *B. tectorum* during the winter months could improve reestablishment of the spring-emerging native flora in these rangelands (Sebastian et al. 2016). With this in mind, we test the hypothesis that herbicide-mediated control of *B. tectorum* has a positive impact on the native flora in the rangelands of Colorado by identifying the diversity and abundance of pollinator-friendly flora in the herbicide-treated and control plots. We report the findings as a case study.

Materials and Methods

Study Locations and Treatments

Three geographic locations within Boulder County, CO, shown in Figure 1 were identified for the study such that each location had paired herbicide-treated and untreated plots. Plot sizes depended on the terrain, but all plots had at least one side measuring 100 m in length. During the winter months, between December 2016 through February 2017, the area where the treated plots were demarcated received application of the preemergent herbicide indaziflam (Esplanade™, Bayer Crop Science, St. Louis, MO 63167, USA) at the rate of 102 g ai ha^{-1}. The exact dates of application varied based on accessibility over the terrain and weather conditions. The paired treated and untreated plots were in similar habitat types with vegetation cover dominated by *B. tectorum* and field brome (*Bromus arvensis* L.; syn.: *Bromus japonicus* Thunb.) and 0% to 10% canopy cover of scattered co-occurring species (for a list of co-occuring species, see Sebastian et al. 2017a). The coordinates of the three locations, Rabbit Mountain Open Space West (RM 1, herbicide applied to treated plots in January 2017), Rabbit Mountain Open Space East (RM 2, herbicide applied to treated plots in February 2017), and Colp (herbicide applied to treated plots in December 2016) are shown in Figure 1. Every effort was made to ensure that the treated and control plots were in the same vicinity, but in the case of Colp, this was not feasible due to the lack of suitable locations of the required size close to the treated location. Therefore, as shown in Figure 1, the treated and control plots at Colp are farther apart than at the other two study locations, and the control plot at the Colp measured 80 by 100 m. Based on our observations during the 2018 study season, we are confident that this did not significantly affect the results being presented here.

Transect Sampling

Eight permanent 100-m belt transects were established at each survey plot, spaced evenly across the vertical and horizontal axes of the plots. A meter tape was stretched between the ends of the transects to demarcate the transect line. A 1-m^2 frame was placed 1 m away from the tape at 10-m intervals, on alternating sides of the transect line. All flowering plants within the frame were identified and the number of plants of each species were counted before moving to the next frame-stop that was 10 m away. Plants that were not flowering during the sampling weeks were not recorded. When frames landed in areas with no flowering individuals, researchers moved to the next 10-m stop. For data analysis, the number of plant species in bloom was pooled across all quadrats for each transect. Sampling was conducted for a period of 8 wk (9 wk in Colp) beginning in May through September. Through the season, there were a total of 48 belt transects completed across all locations and plots. Each of the three study locations had a total of 16 belt transects, with 8 each in the treated and control plots.

Random Walk Sampling

Flowering plants that did not fall within the sampling frames of the belt transects could not be recorded during the entire study period. We conducted focal-flowering plant sampling in the entire plot using random walk sampling to obtain a census or inventory of all flowering plants that were not counted in the transect sampling. We walked the plot in an organized fashion beginning at one end spanning the entire plot, specifically targeting all flowering plants that did not fall into the frames, recording all blooming species in the plot on any given sampling day. The data collected by random walk sampling were used to create an inventory of all flowering plants recorded in our study.

Data Analyses

Standard ecological indices for plant species diversity, richness, and abundance were calculated for the treated and untreated plots for each sample event in each geographic location. Species richness is simply the total number of unique species during each sampling event. Shannon diversity index ($H' = -\sum_{i=1}^{R} p_i ln p_i$) and Simpson's diversity index ($D = 1/\sum_{i=1}^{R} {p_i}^2$) were calculated as the diversity measures for pollinator-friendly flora in the three geographic locations (Magurran 2013; Ortiz-Burgos 2016; Pielou 1966; Simpson 1949; Whittaker 1972). The Shannon diversity index combines evenness and richness into a single measure and assumes that all species are represented in a sample, while Simpson's diversity index gives more weight to common species and assumes that the few rare ones with only a few representatives will not affect the diversity values.

Data from the belt transect sampling were analyzed using a general linear model for multiple dependent variables. Treatments and geographic locations were fixed effects; sampling week was a covariate; and species richness, Shannon diversity index, and Simpson's diversity index values were dependent variables. Treatment by location interaction was also determined to analyze any location-specific response. As needed, logarithmic transformations were performed for nonnormal species richness data before analysis.

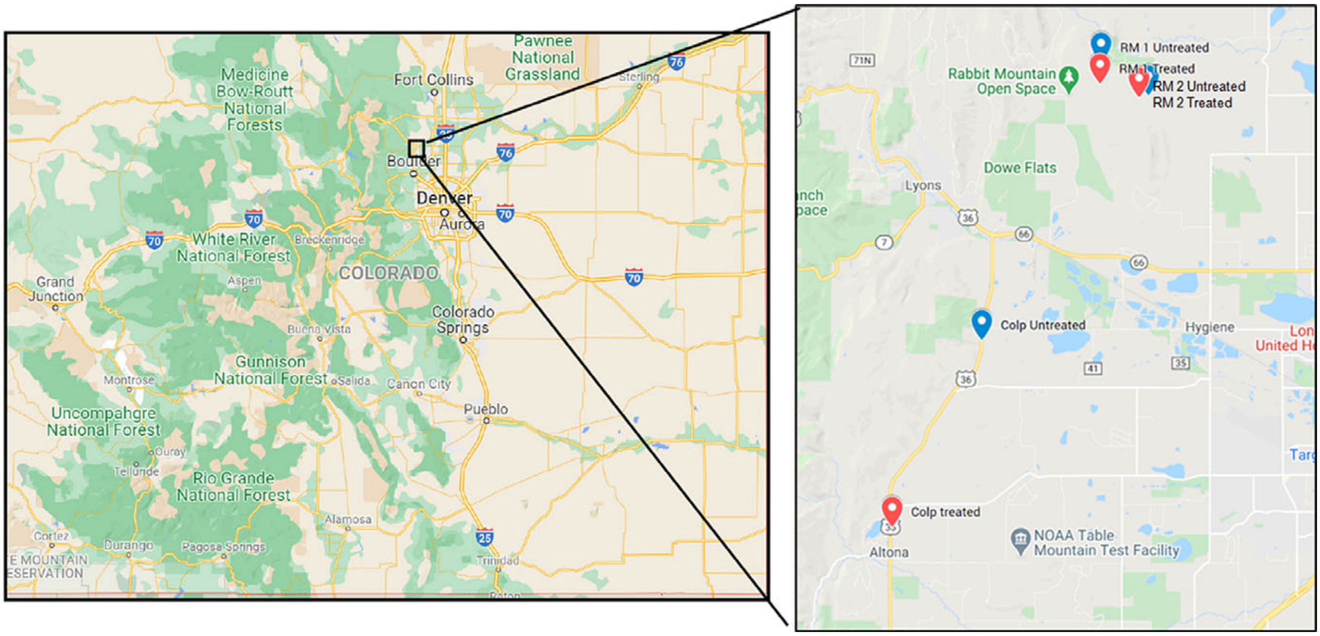

Figure 1. Study locations in Boulder County Parks and Open Space area in Colorado. State map of Colorado on the left and the inset study area on the right. The locations and their coordinates: RM 1, Rabbit Mountain 1 (Untreated: 40.2547°N, 105.2139°W; Treated: 40.2495°N, 105.2143°W); RM 2, Rabbit Mountain 2 (Untreated: 40.2468°N, 105.1984°W; Treated: 40.2463°N, 105.2015°W); Colp (Untreated: 40.1861°N, 105.2526°W; Treated: 40.1396°N, 105.2819°W).

Results and Discussion

Here we present a case study showing the richness and diversity of pollinator-friendly flora in three locations where a preemergent herbicide, indaziflam, was applied to control the invasive annual grass *B. tectorum*. There was a significant treatment effect on the different diversity measures. Herbicide-treated plots had higher richness and alpha-diversity measures across all three locations (Table 1; Figure 2; species richness: $F(1, 41) = 23.25$, $P = < 0.0001$; Shannon diversity index: $F(1, 41) = 20.29$, $P = 0.001$; Simpson's diversity index: $F(1, 41) = 15.87$, $P = 0.001$), suggesting that the control of *B. tectorum* could result in reduced competition allowing for the reestablishment of native flowering plants. There was no significant effect of location on these measures (species richness: $F(2, 41) = 0.61$; Shannon diversity index: $F(2, 41) = 0.08$; Simpson's diversity index: $F(2, 41) = 1.09$) and no significant interaction effect between treatment and location (species richness: $F(2, 41) = 3.58$; Shannon diversity index: $F(2, 41) = 2.96$; Simpson's diversity index: $F(2, 41) = 1.81$).

To visualize these diversity measures across seasons, the data were grouped into early (May to early June), mid (June to July), and late (August to September) seasons, as presented in Figures 3 and 4. Table 2 provides the list of pollinator-friendly plant species that were blooming during the study period in the three locations. The impact of herbicide application was consistent in the three locations, suggesting the possibility that previously demonstrated herbicide-mediated control of the invasive grass, *B. tectorum* (Clark et al. 2019, 2020; Sebastian et al. 2016, 2017a) could be responsible for the growth of pollinator-friendly flora. A noteworthy caveat is that our study did not measure the abundance of *B. tectorum* in the study plots. Therefore, reduced competitive pressure as a possible means for reestablishment of flowering plant species is a proposed mechanism.

Invasive annual grasses have been shown to impact community composition in ecosystems where they are invasive, leading to potential reductions in abundance and diversity of native species in these ecosystems. However, the intensity of displacement likely depends on the ecological context, specifically the ability of one species to preempt another (Fridley et al. 2021; Lenz et al. 2003; MacArthur and Levins 1967; Pyšek et al. 2012). A decrease in the richness of native species and reduced ecosystem functionality in the presence of invasive species is evident even at smaller spatial scales (Bernard-Verdier and Hulme 2019). Decrease in species richness has also been previously described in rangelands experiencing *B. tectorum* invasion (Clark 2020; Clark et al. 2019, 2020). Our results support this premise that controlling the invasive annual grass *B. tectorum* can have beneficial impacts on the rangelands by improving the richness and abundance of native flora in the region. It is to be noted that the results of the case study we present is from one flowering season immediately following the winter application of the herbicide.

Ongoing studies on biological invasions and their control suggest that the long-term impact of invasive species removal on native species richness needs further investigation. The benefits of increased species richness and diversity observed soon after control may be modest and may not be long lasting (Adams et al. 2020; Kettenring and Adams 2011). In regions experiencing long-term establishment of invasive plant species, it is likely that the diversity of native species in the ecosystem has been compromised (Duncan et al. 2004), though communities with native annual forbs can be impacted (Meyer-Morey et al. 2021). Our study shows that flowering species reappearing in the year following indaziflam application include annuals, biennials, and perennials (Table 2), many of which are native to the region, agreeing with the earlier report that indaziflam application for *B. tectorum* control does not appear to negatively impact native species richness in the natural areas and rangelands of Colorado (Clark et al. 2019). It has been suggested that implementing control measures when there is still remaining native vegetation may yield better success in restoration of native

Table 1. Multivariate general linear model showing the effect of treatment on diversity measures calculated from belt transect data.

Source		df	Mean Sum of Squares	*F*	P
Treatment[a]	Species richness	1	105.02	23.25	**
	Shannon diversity index	1	3.45	20.29	*
	Simpson's diversity index	1	21.97	15.87	*
Geographic location[b]	Species richness	2	2.77	0.61	NS
	Shannon diversity index	2	0.01	0.08	NS
	Simpson's diversity index	2	1.52	1.09	NS
Treatment × geographic location	Species richness	2	16.15	3.58	NS
	Shannon diversity index	2	0.50	2.96	NS
	Simpson's diversity index	2	2.50	1.81	NS
Week	Species richness	1	100.95	22.35	**
	Shannon diversity index	1	3.88	22.84	**
	Simpson's diversity index	1	22.09	15.96	**
Error	Species richness	41	4.52		
	Shannon diversity index	41	0.17		
	Simpson's diversity index	41	1.38		

[a] Treatments: herbicide-treated and untreated control.
[b] Geographic location: Colp, Rabbit Mountain 1, and Rabbit Mountain 2.
[c] Statistical significance at: **$P < 0.0001$; * $P = 0.001$; NS, nonsignificant.

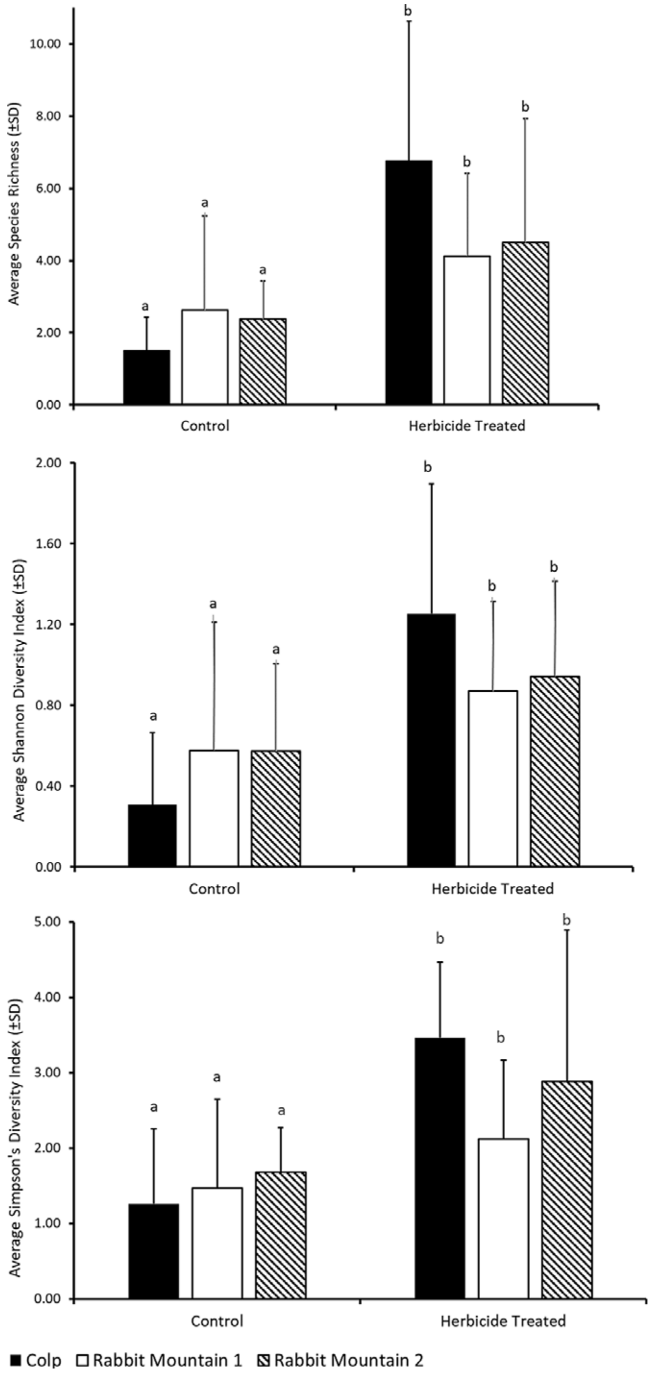

Figure 2. Average (±SD) of floral diversity measures from belt transects. Statistical comparison is across treatments within each location. Different letters indicate significant differences at $P < 0.001$ using a post hoc Bonferroni comparison (Table 1).

species (Davies and Sheley 2011). Our case study shows reduced flowering plant species diversity in control plots (Figure 2), reiterating the possibility that controlling *B. tectorum* populations in these rangelands could improve native flowering plant populations. In addition, planning restorative actions needed for assisted reestablishment of native forbs in combination with the application of herbicide for invasive grass control may further promote flowering plant reestablishment.

As mentioned earlier, one limitation of our case study is that we focused on diversity of flowering plants and did not determine the abundance of *B. tectorum* in the control and treated plots. While there are few studies that explore the direct impacts of invasion by nonnative plant species on pollinators, it is evident that abundance of native flowering species is reduced when ecosystems are dominated by invasive species (Bernard-Verdier and Hulme 2019). Thus, there is a high likelihood that plants that support the nutritional and nesting needs of pollinators (Blüthgen and Klein 2011; Giannini et al. 2015; Soliveres et al. 2016; Tscharntke et al. 2012) are reduced in such invaded areas. Although this report is a single case study from three locations in the rangelands of Colorado, the immediate benefits of controlling the invasive annual grass *B. tectorum* are compelling. An earlier study conducted in the same geographic region suggests very little if any residual effects of the herbicide indaziflam (Clark et al. 2019). However, the nesting biology of the pollinators previously reported in this rangeland ecosystem (Goldstein and Scott 2015; Kearns and Oliveras 2009a; Scott et al. 2011) indicates that many of the bee species are ground nesting, wherein the female bees tunnel into the soil, lay eggs, and provision the larvae with pollen that is consumed over the larval developmental period

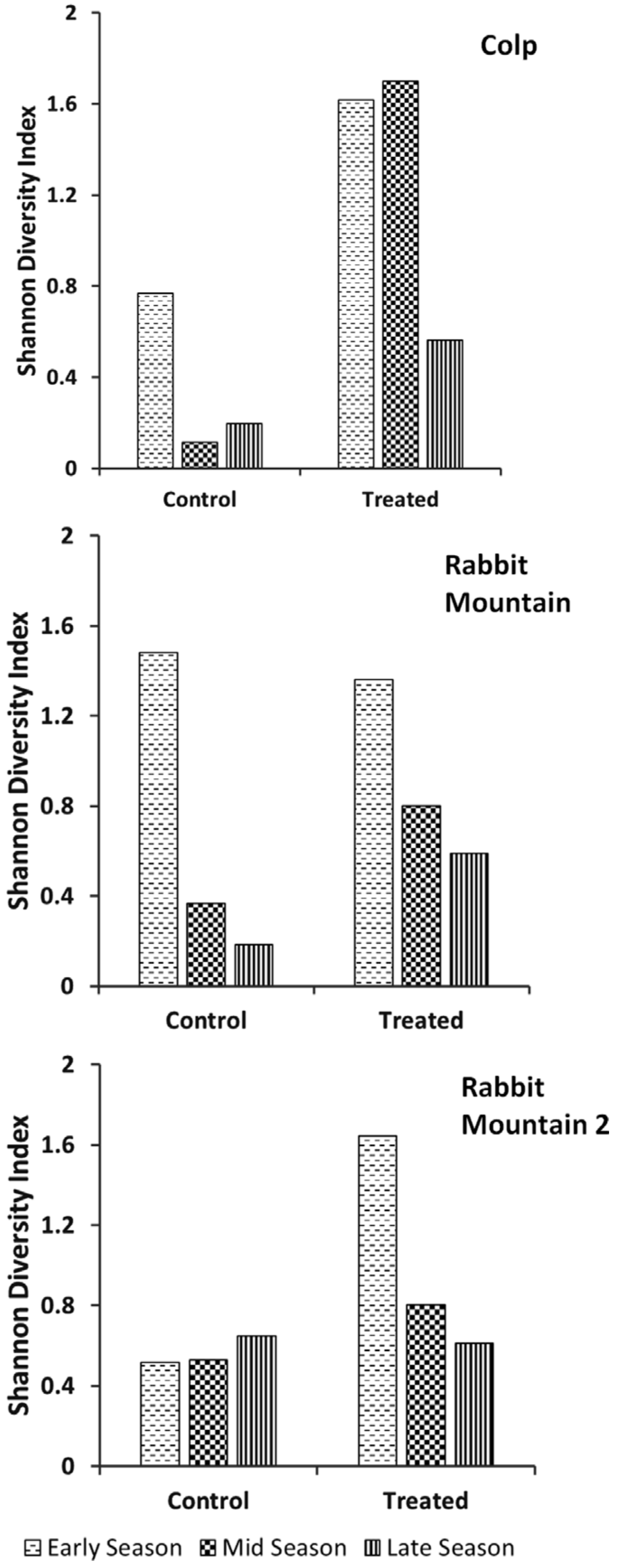

Figure 3. Shannon diversity index values from belt transects for treated and untreated control plots across the season in the different geographic locations.

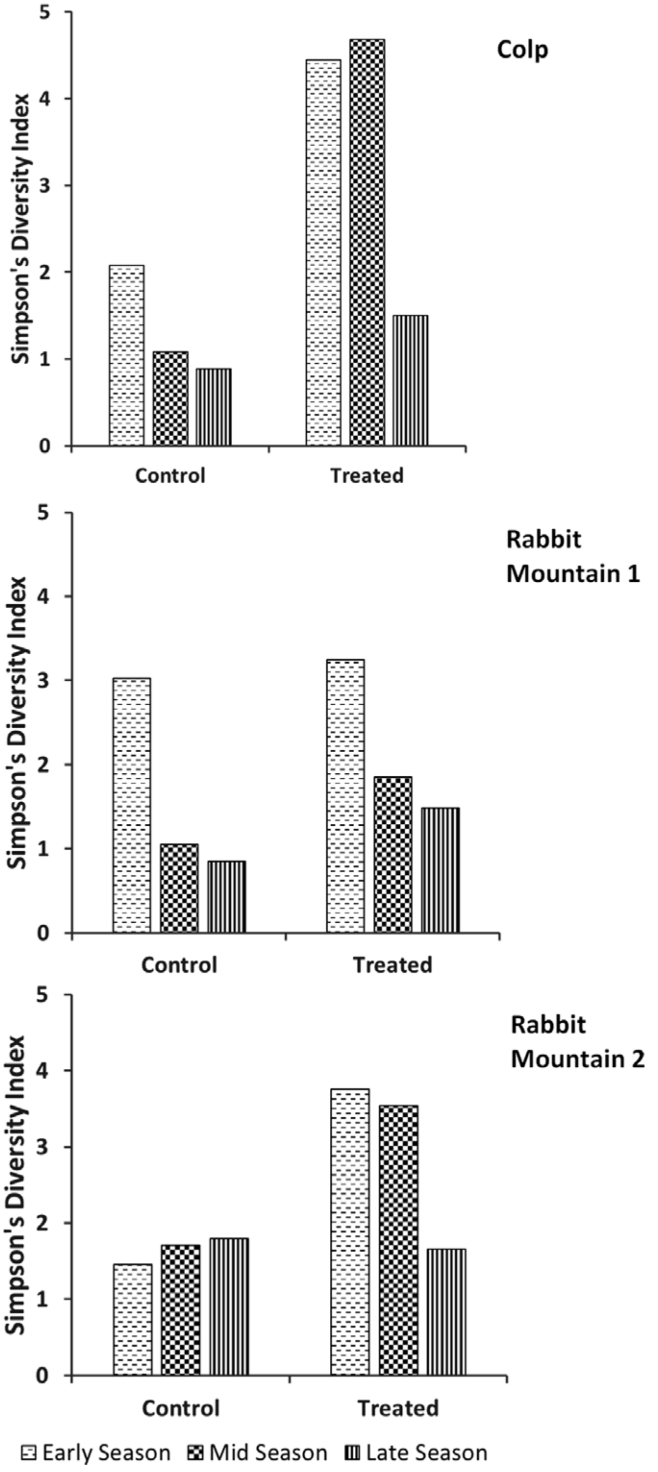

Figure 4. Simpson's diversity index values from belt transects for treated and untreated control plots across the season in the different geographic locations.

(Buchmann and Nabhan 1996; Michener 1974). It would be critical to determine the extent of herbicide residue in the soil and its potential to impact the development of ground-nesting bee larvae (Buckles and Harmon-Threatt 2019; Harmon-Threatt 2020). Continued monitoring of these locations will help strengthen

Table 2. List of flowering pollinator-friendly forb species from random walk sampling in the three geographic locations.[a]

		Colp		Rabbit Mountain 1		Rabbit Mountain 2	
Plant family	Plant species[b]	Control	Herbicide treated	Control	Herbicide treated	Control	Herbicide treated
Agavaceae	*Yucca glauca* Nutt.	X	X		X	X	X
Apiaceae	*Lomatium orientale* J.M. Coult. & Rose		X		X		X
Apocynaceae	*Asclepias viridiflora* Raf.	X	X				
Asteraceae	*Antennaria parvifolia* Nutt.						X
	Arnica fulgens Pursh				X		X
	[B/P]*Carduus nutans* L.			X		X	X
	[A/P]*Centaurea diffusa* Lam.		X				
	Chondrilla juncea L.		X				
	[B/P]*Cirsium undulatum* Nutt.	X	X		X		X
	[A/P]*Crepis occidentalis* Nutt.						X
	Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & Baird			X		X	X
	[B]*Erigeron divergens* Torr. & A. Gray	X	X	X	X	X	
	[B]*Erigeron flagellaris* A. Gray	X	X	X	X	X	X
	Erigeron pumilus Nutt.		X				
	[B/P]*Erigeron* sp.			X	X	X	X
	Gaillardia aristata Pursh		X	X	X	X	X
	[A/B/P]*Grindelia squarrosa* (Pursh) Dunal	X	X	X	X	X	X
	Gutierrezia sarothrae (Pursh) Britton & Rusby	X	X			X	X
	[A]*Helianthus annuus* L.				X		X
	Helianthus pumilus Nutt.		X				X
	Heterotheca villosa (Pursh) Shinners	X	X	X	X	X	X
	Hymenopappus filifolius Hook.		X		X	X	X
	[A/B]*Lactuca serriola* L.	X	X			X	
	Liatris punctata Hook.		X	X	X	X	X
	Lygodesmia juncea (Pursh) D. Don ex Hook.					X	
	Machaeranthera pinnatifida (Hook.) Shinners					X	
	Nothocalais cuspidata (Pursh) Greene		X		X		X
	Packera fendleri (A. Gray) W.A. Weber & Á. Löve	X	X		X	X	X
	Ratibida columnifera (Nutt.) Wooton & Standl.	X	X	X	X	X	X
	Scorzonera laciniata L.		X	X		X	
	Senecio spartioides Torr. & A. Gray		X		X	X	X
	Solidago missouriensis Nutt.			X			X
	Solidago nana Nutt.		X				
	Symphyotrichum ericoides (L.) G.L. Nesom	X	X	X	X	X	X
	Symphyotrichum porteri (A. Gray) G.L. Nesom	X		X	X		X
	Taraxacum officinale F.H. Wigg		X	X	X	X	
	Tetradymia canescens DC			X		X	X
	[A/B]*Tragopogon dubius* Scop.	X	X	X	X	X	X
Boraginaceae	[B/P]*Cryptantha virgata* (Porter) Payson		X				
	[A/B]*Lappula occidentalis* (S. Watson) Greene	X	X		X		
	Lithospermum incisum Lehm.			X	X	X	X
	Mertensia lanceolata (Pursh) DC.		X		X		X
	Onosmodium molle Michx.	X	X				X
Brassicaceae	[A]*Alyssum simplex* Rudolphi	X	X	X		X	X
	Arabis fendleri (S. Watson) Greene			X			X
	[B/P]*Arabis drummondii* A. Gray					X	
	[A/B]*Camelina microcarpa* Andrz. ex DC.			X		X	
	Descurainia sp.						X
	[A]*Draba nemorosa* L.					X	
	[B/P]*Erysimum asperum* (Nutt.) DC.		X		X	X	X
	[A/B]*Lepidium campestre* (L.) W.T. Aiton		X				X
	[A/B]*Lepidium perfoliatum* L.			X			
	Lesquerella montana (A. Gray) S. Watson		X		X	X	X
	[A/B]*Sisymbrium altissimum* L.	X	X			X	
	[A/B]*Sisymbrium* sp.			X			
Cactaceae	*Echinocereus viridiflorus* Engelm.		X		X		
	Opuntia phaeacantha Engelm.	X	X	X	X		X
	Opuntia polyacantha Haw.	X			X	X	X
Campanulaceae	[A]*Triodanis perfoliata* (L.) Nieuwl.	X					
Caryophyllaceae	*Cerastium arvense* L.		X	X	X	X	X
	[A]*Silene antirrhina* L.		X				
Clusiaceae	*Hypericum perforatum* L.	X		X	X	X	X
Commelinaceae	*Tradescantia occidentalis* (Britton) Smyth	X	X		X		
Convolvulaceae	*Convolvulus arvensis* L.	X	X	X	X	X	
	Evolvulus nuttallianus Schult.		X				
Euphorbiaceae	*Euphorbia brachycera* Engelm.						X
	[A]*Euphorbia dentata* Michx.	X					

(*Continued*)

Table 2. (*Continued*)

Plant family	Plant species^{b}	Colp Control	Colp Herbicide treated	Rabbit Mountain 1 Control	Rabbit Mountain 1 Herbicide treated	Rabbit Mountain 2 Control	Rabbit Mountain 2 Herbicide treated
Fabaceae	*Astragalus agrestis* Douglas ex G. Don			X		X	X
	Astragalus drummondii Douglas ex Hook.						X
	Astragalus flexuosus Douglas ex G. Don	X			X		X
	Astragalus shortianus Nutt.		X				X
	Dalea purpurea Vent.		X		X		X
	$^{A/P}$*Medicago sativa* L.	X					
	Oxytropis lambertii Pursh		X		X		X
	Oxytropis sericea Nutt.		X				
	Pediomelum esculentum (Pursh) Rydb.		X				
	Psoralidium tenuiflorum (Pursh) Rydb.	X	X	X	X	X	X
	Vicia americana Muhl. ex Willd.			X			
Geraniaceae	*Geranium caespitosum* James			X	X		
	$^{A/B}$*Erodium cicutarium* (L.) L'Hér. ex Aiton.	X	X	X		X	
Hydrophyllaceae	$^{B/P}$*Phacelia heterophylla* Pursh		X				
Lamiaceae	^{A}*Monarda pectinata* Nutt.	X	X				
	Nepeta cataria L.						X
	Scutellaria brittonii Porter				X		X
Liliaceae	*Allium textile* A. Nelson & J.F. Macbr.		X	X	X	X	X
	Calochortus gunnisonii S. Watson			X	X		X
	Leucocrinum montanum Nutt. ex A. Gray						X
	Linum lewisii Pursh		X				X
	^{A}*Linum pratense* (Norton) Small.	X					
Malvaceae	$^{B/P}$*Sphaeralcea coccinea* (Nutt.) Rydb.		X			X	X
Nyctaginaceae	*Mirabilis linearis* (Pursh) Heimerl.		X		X		
Onagraceae	*Calylophus serrulatus* (Nutt.) P.H. Raven.		X		X		
	Oenothera howardii (A. Nelson) W.L. Wagner						X
	Oenothera suffrutescens (Ser.) W.L. Wagner & Hoch.	X	X		X	X	X
Orobanchaceae	*Castilleja sessiliflora* Pursh		X				
	^{A}*Orobanche fasciculata* Nutt.		X		X		X
Oxalidaceae	*Oxalis dillenii* Jacq.	X					
Papaveraceae	$^{A/B/P}$*Argemone polyanthemos* (Fedde) G.B. Ownbey	X	X				
Plantaginaceae	*Linaria dalmatica* (L.) Mill.	X	X	X	X	X	X
	Penstemon secundiflorus Benth.		X		X		X
	Penstemon virens Pennell ex Rydb.		X		X		X
	^{A}*Plantago patagonica* Jacq.					X	
	^{B}*Verbascum blattaria* L.			X		X	
	^{B}*Verbascum thapsus* L.					X	
Polygonaceae	*Eriogonum alatum* Torr.		X		X		X
	Eriogonum effusum Nutt.		X			X	
	Eriogonum umbellatum Torr.			X	X	X	X
Ranunculaceae	*Delphinium carolinianum* Walter	X	X		X		X
Rhamnaceae	*Ceanothus herbaceus* Raf.		X				
	Rhus trilobata Nutt.		X	X	X		X
Rosaceae	*Potentilla fissa* Nutt.		X		X		
	Prunus virginiana L.						X
	Rosa woodsii Lindl.						X
Solanaceae	*Physalis hederifolia* A. Gray					X	X
	Physalis virginiana Mill.					X	
Verbenaceae	$^{A/P}$*Glandularia bipinnatifida* (Nutt.) Nutt.	X				X	
Violaceae	*Viola nuttallii* Pursh		X		X		X

[a] Plant species are grouped by families. X indicates species seen in the plot during the study period. Only plants that were blooming were recorded in the study. The letters A/B/P preceding the names of some species indicate annual/biennial/perennial life histories, and those without letters preceding their names are all perennials (https://plants.usda.gov/home).
[b] USDA nomenclature: https://plants.usda.gov/home.

data on the diversity of native plant species as invasive grasses continue to be controlled. This would also provide critical information on the long-term effectiveness of herbicide use and invasive species control on ecosystem functions.

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References

Adams SN, Jennings S, Warnock N (2020) Plant invasion depresses native species richness, but control of invasive species does little to restore it. Plant Ecol Divers 13:257–266

Bartz R, Kowarik I (2019) Assessing the environmental impacts of invasive alien plants: a review of assessment approaches. NeoBiota 43:69–99

Bernard-Verdier M, Hulme PE (2019) Alien plants can be associated with a decrease in local and regional native richness even when at low abundance. J Ecol 107:1343–1354

Blüthgen N, Klein A-M (2011) Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. Basic Appl Ecol 12:282–291

Boyte SP, Wylie BK, Major DJ (2016) Cheatgrass percent cover change: comparing recent estimates to climate change−driven predictions in the Northern Great Basin. Rangeland Ecol Manag 69:265–279

Buchmann SL, Nabhan GP (1996) The Forgotten Pollinators. Washington, DC: Island Press/Shearwater Books. 292 p

Buckles BJ, Harmon-Threatt AN (2019) Bee diversity in tallgrass prairies affected by management and its effects on above- and below-ground resources. J Appl Ecol 56:2443–2453

Clark SL (2020) Using herbicides to restore native species and improve habitat on rangelands and wildlands. Outlooks Pest Manag 31:57–60

Clark SL, Sebastian DJ, Nissen SJ, Sebastian JR (2019) Effect of indaziflam on native species in natural areas and rangeland. Invasive Plant Sci Manag 12:60–67

Clark SL, Sebastian DJ, Nissen SJ, Sebastian JR (2020) Evaluating winter annual grass control and native species establishment following applications of indaziflam on rangeland. Invasive Plant Sci Manag 13:199–209

D'Antonio CM, Jackson NE, Horvitz CC, Hedberg R (2004) Invasive plants in wildland ecosystems: merging the study of invasion processes with management needs. Front Ecol Environ 2:513–521

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Davies KW, Sheley RL (2011) Promoting native vegetation and diversity in exotic annual grass infestations. Restor Ecol 19:159–165

Duncan CA, Jachetta JJ, Brown ML, Carrithers VF, Clark JK, Ditomaso JM, Lym RG, McDaniel KC, Renz MJ, Rice PM (2004) Assessing the economic, environmental, and societal losses from invasive plants on rangeland and wildlands. Weed Technol 18:1411–1416

Flory SL, Clay K (2009) Invasive plant removal method determines native plant community responses. J Appl Ecol 46:434–442

Fridley JD, Jo I, Hulme PE, Duncan RP (2021) A habitat-based assessment of the role of competition in plant invasions. J Ecol 109:1263–1274

Giannini TC, Garibaldi LA, Acosta AL, Silva JS, Maia KP, Saraiva AM, Guimarães PR Jr, Kleinert AMP (2015) Native and non-native supergeneralist bee species have different effects on plant-bee networks. PLoS ONE 10:e0137198

Gilgert W, Vaughan M (2011) The value of pollinators and pollinator habitat to rangelands: connections among pollinators, insects, plant communities, fish, and wildlife. Rangelands 33:14–19

Goldstein PZ, Scott VL (2015) Taxonomic and behavioral components of faunal comparisons over time: the bees (Hymenoptera: Anthophila) of Boulder County, Colorado, Past and Present. Proc Entomol Soc Wash 117:290–346

Harmon-Threatt A (2020) Influence of nesting characteristics on health of wild bee communities. Annu Rev Entomol 65:39–56

Jones BA, McDermott SM (2018) Health impacts of invasive species through an altered natural environment: assessing air pollution sinks as a causal pathway. Environmental and Resource Economics 71:23–43

Kearns CA, Oliveras DM (2009a) Boulder County Bees revisited: a resampling of Boulder Colorado Bees a century later. J Insect Conserv 13:603

Kearns C, Oliveras D (2009b) Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. J Insect Conserv 13:655–665

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. J Appl Ecol 48:970–979

Knapp PA (1996) Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: history, persistence, and influences to human activities. Global Environ Change 6:37–52

Kumar Rai P, Singh JS (2020) Invasive alien plant species: their impact on environment, ecosystem services and human health. Ecol Indic 111:106020

Lenz TI, Moyle-Croft JL, Facelli JM (2003) Direct and indirect effects of exotic annual grasses on species composition of a South Australian grassland. Austral Ecol 28:23–32

MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. Am Nat 101:377–385

Magurran AE (2013) Measuring Biological Diversity. Hoboken, NJ: Wiley. 272 p

Meyer-Morey J, Lavin M, Mangold J, Zabinski C, Rew LJ (2021) Indaziflam controls nonnative *Alyssum* spp. but negatively affects native forbs in sagebrush steppe. Inv Plant Sci Manag:1–9. DOI: 10.1017/inp.2021.31

Michener CD (1974) The Social Behavior of the Bees: A Comparative Study. Cambridge, MA: Belknap Press of Harvard University Press. 418 p

Monaco TA, Mangold JM, Mealor BA, Mealor RD, Brown CS (2017) Downy brome control and impacts on perennial grass abundance: a systematic review spanning 64 years. Rangeland Ecol Manag 70:396–404

Musil CF, Milton SJ, Davis GW (2005) The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies: research in action. S Afr J Sci 101:337–344

Ortiz-Burgos S (2016) Shannon-Weaver diversity index. Pages 572–573 *in* Kennish MJ, ed. Encyclopedia of Estuaries. Dordrecht, Netherlands: Springer

Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. Trends Ecol Evol 24:497–504

Pielou EC (1966) The measurement of diversity in different types of biological collections. J Theor Biol 13:131–144

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biol 18:1725–1737

Schweiger O, Biesmeijer JC, Bommarco R, Hickler T, Hulme PE, Klotz S, Kühn I, Moora M, Nielsen A, Ohlemüller R, Petanidou T, Potts SG, Pyšek P, Stout JC, Sykes MT, et al. (2010) Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. Biol Rev 85:777–795

Scott VL, Ascher JS, Griswold T, Nufio CR (2011) The Bees of Colorado. Boulder, CO: University of Colorado Museum of Natural History. 100 p

Sebastian DJ, Fleming MB, Patterson EL, Sebastian JR, Nissen SJ (2017a) Indaziflam: a new cellulose-biosynthesis-inhibiting herbicide provides long-term control of invasive winter annual grasses. Pest Manag Sci 73:2149–2162

Sebastian DJ, Nissen SJ, Sebastian JR, and Beck KG (2017b) Seed bank depletion: the key to long-term downy brome (*Bromus tectorum* L.) management. Rangeland Ecol Manag 70:477–483

Sebastian DJ, Sebastian JR, Nissen SJ, Beck KG (2016) A potential new herbicide for invasive annual grass control on rangeland. Rangeland Ecol Manag 69:195–198

Simpson EH (1949) Measurement of diversity. Nature 163:688

Skurski TC, Maxwell BD, Rew LJ (2013) Ecological tradeoffs in non-native plant management. Biol Conserv 159:292–302

Soliveres S, van der Plas F, Manning P, Prati D, Gossner MM, Renner SC, Alt F, Arndt H, Baumgartner V, Binkenstein J, Birkhofer K, Blaser S, Blüthgen N, Boch S, Böhm S, et al. (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459

Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mututalisms. Trends Ecol Evol 21:208–216

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, et al. (2012) Landscape moderation of biodiversity patterns and processes—eight hypotheses. Biol Rev 87:661–685

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702–708

Wagner DL (2020) Insect declines in the Anthropocene. Annu Rev Entomol 65:457–480

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251