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Role of invasive *Melilotus officinalis* in two native plant communities

Laura C. Van Riper · Diane L. Larson

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Abstract This study examines the impact of the exotic nitrogen-fixing legume *Melilotus officinalis* (L.) Lam. on native and exotic species cover in two Great Plains ecosystems in Badlands National Park, South Dakota. *Melilotus* is still widely planted and its effects on native ecosystems are not well studied. *Melilotus* could have direct effects on native plants, such as through competition or facilitation. Alternatively, *Melilotus* may have indirect effects on natives, e.g., by favoring exotic species which in turn have a negative effect on native species. This study examined these interactions across a 4-year period in two contrasting vegetation types: Badlands sparse vegetation and western wheatgrass (*Pascopyrum smithii*) mixed-grass prairie. Structural equation models were used to analyze the pathways through which *Melilotus*,

native species, and other exotic species interact over a series of 2-year time steps. *Melilotus* can affect native and exotic species both in the current year and in the years after its death (a lag effect). A lag effect is possible because the death of a *Melilotus* plant can leave an open, potentially nitrogen-enriched site on the landscape. The results showed that the relationship between *Melilotus* and native and exotic species varied depending on the habitat and the year. In Badlands sparse vegetation, there was a consistent, strong, and positive relationship between *Melilotus* cover and native and exotic species cover suggesting that *Melilotus* is acting as a nurse plant and facilitating the growth of other species. In contrast, in western wheatgrass prairie, *Melilotus* was acting as a weak competitor and had no consistent effect on other species. In both habitats, there was little evidence for a direct lag effect of *Melilotus* on other species. Together, these results suggest both facilitative and competitive roles for *Melilotus*, depending on the vegetation type it invades.

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Introduction

When exotic nitrogen-fixing plants become abundant in natural areas, they have been shown to increase

nitrogen (N) levels and accelerate the rate of N cycling (Haubensak and Parker 2004; Vitousek and Walker 1989; Vitousek et al. 1987; Wheeler et al. 1987). Nitrogen is a limiting resource in many ecosystems, and the changes in competitive dynamics between plant species due to increased N can potentially cause broad changes in the composition of native communities (Vitousek and Walker 1989). Native species often are better adapted to lower N levels present in the unaltered ecosystem (Arendt 1997; Hobbie 1992; McLendon and Redente 1992). In contrast, many invasive exotic species are well adapted to exploiting high N sites and have high dispersal rates that allow rapid colonization (Cousens and Mortimer 1995; Maron and Connors 1996; Rejmanek and Richardson 1996). Once at a N-rich site, exotic species can exploit N more quickly than later successional natives by increasing growth rates in response to higher nutrient availability (Carson and Barrett 1988; Fogarty and Facelli 1999). Nitrogen enrichment by exotic N-fixing species can facilitate the further invasion by other exotic species (Adler et al. 1998; Carino and Daehler 2002; Maron and Jefferies 1999; Sher and Hyatt 1999), moving the system toward an “invasional meltdown” (Simberloff 2006; Simberloff and Von Holle 1999).

Melilotus officinalis (L.) Lam. (hereafter *Melilotus*) is a biennial legume (Fabaceae) native to Eurasia that has become naturalized throughout the world (Klebesadel 2001; Turkington et al. 1978; Wu et al. 2003) and has been recognized as a conservation problem in natural areas in North America (Lesica and DeLuca 2000; Turkington et al. 1978; Weaver et al. 2001; Wolf et al. 2003). The effects of *Melilotus* on native species and ecosystems in the North American Great Plains are largely unknown. *Melilotus* may cause ecosystem-level changes due to its association with *Sinorhizobium meliloti* bacteria, which allows it to fix atmospheric N and thus potentially enrich the soil (Turkington et al. 1978; Wivstad 1999; Zakhia and de Lajudie 2001). Great Plains habitats invaded by *Melilotus* are historically low-N systems (Clark et al. 1980; Woodmansee 1978). Competition with living *Melilotus* may decrease the cover of both native and exotic species (Wolf et al. 2003), but if N-rich patches remain after the death of *Melilotus*, exotics could be favored over natives (Carino and Daehler 2002; Maron and Jefferies 2001).

Native species diversity also can decline through interactions with *Melilotus*. Increased N often reduces evenness, resulting in the replacement of a diverse community by one or a few dominant species (Carson and Barrett 1988; Tilman 1987; Willems et al. 1993). Monoculture-forming exotic species also may out-compete native species (Mack et al. 2000; Mooney and Drake 1986; Wilcove et al. 1998). *Melilotus*'s effects on native species diversity may therefore be direct, via competition (e.g., space, water, nutrients, or light), and/or indirect via alteration of the N cycle.

Melilotus is still widely planted, despite uncertainties in its effect on native species and ecosystems (Lesica and DeLuca 2000; Turkington et al. 1978; Weaver et al. 2001). The purpose of this study is to evaluate the effects of *Melilotus* on native and exotic species cover; the interactions between *Melilotus*, native, and other exotic species; and the variations in those interactions from year-to-year. Specifically, we use structural equation modeling (Grace 2006) to address the following questions: (1) Is there an association between live *Melilotus* cover and the cover of native and other exotic species? (2) Can we detect a lag in the association between *Melilotus* cover and cover of native and other exotic species (i.e., has *Melilotus* left some legacy in the soil after its death)? (3) Do other exotic species present in our study influence native cover in the current year or as a lag effect? (4) Can we detect an association in cover between consecutive years within each group (*Melilotus*, native species, and other exotic species)? (5) Can we detect an effect of native and exotic species cover on *Melilotus* cover?

Methods

Study site

Badlands National Park is located in the northern Great Plains in southwestern South Dakota, USA. The region has a semiarid climate with short, hot summers (22°C average) and cold winters (−4°C average) (Nielsen 1996). The average total precipitation is 39.5 cm, of which 75% falls between April and September (Nielsen 1996). During the years of our study, precipitation varied >1 standard deviation above and below the 30-year mean (Fig. 1). The park is dominated by two ecosystems, western

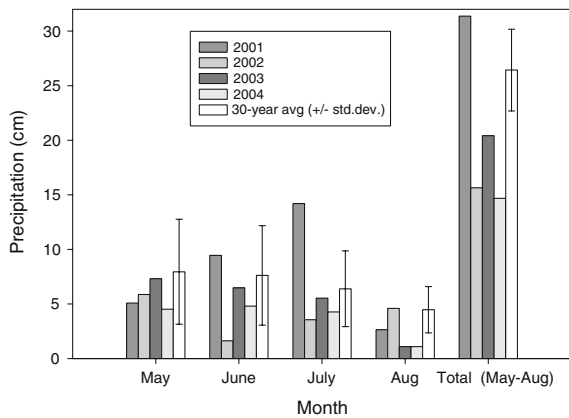


Fig. 1 Precipitation at Badlands National Park in southwestern South Dakota during the 2001–2004 growing seasons. The 30-year average (\pm standard deviation) also is included. Precipitation data are from the National Oceanic and Atmospheric Administration (NOAA) weather station in Interior, SD

wheatgrass—green needlegrass (*Pascopyrum smithii* (Rydb.) A. Löve—*Nassella viridula* (Trin.) Barkworth) mixed-grass prairie (hereafter, wheatgrass prairie) and Badlands sparse vegetation (hereafter, sparse vegetation). Wheatgrass prairie covers 36.6% of the park and has plant cover levels of 45–100% (Von Loh et al. 1999). Sparse vegetation covers 45.5% of the park, occurs in areas with highly erodible soils, and has plant cover levels of 5–10%.

Wheatgrass prairie and sparse vegetation differ in their dominant species. Common species in wheatgrass prairie include perennial native grasses such as western wheatgrass, green needlegrass, blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, Poaceae), and buffalograss (*Buchloe dactyloides* Nutt. Englem., Poaceae), the annual exotic grass Japanese brome (*Bromus japonicus* Thunb. ex Murr., Poaceae), and the perennial native forb scarlet globemallow (*Sphaeralcea coccinea* (Nutt.) Rydb., Malvaceae). Common species in sparse vegetation include perennial native forbs such as broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt. & Rusby, Asteraceae) and fewflower buckwheat (*Eriogonum pauciflorum* Pursh, Polygonaceae), the native shrub fourwing saltbush (*Atriplex canescens* (Pursh) Nutt., Chenopodiaceae), the biennial native forb curlycup gumweed (*Grindelia squarrosa* (Pursh) Dunal, Asteraceae), and the annual exotic forb Russian thistle (*Salsola tragus* L., Chenopodiaceae). Taxonomy follows USDA Plants (www.plants.usda.gov; accessed 1/2/08).

Soils and associated ecosystem properties also differ between wheatgrass prairie and sparse ecosystems (all soil information from U.S. Department of Agriculture soil surveys: Nielsen 1996; Schleppe 1987). The mollisols on which wheatgrass prairie species grow are characterized as deep, well drained, and nearly level with low organic content and slow water runoff. The soils are generally calcareous loams and some are sodium rich. At Badlands National Park, the soils on which the sparse vegetation grows are aridisols and entisols. The soils can be very shallow and often are composed of mudstone, siltstone, and shale. These soils vary from calcareous clay loams to calcareous clays and have low organic matter content, low fertility, low water capacity, and very slow permeability. The Badlands areas where most sparse vegetation is located are steep with many drainage channels and have high runoff potential and active erosion.

Vegetation sampling

Vegetation sampling occurred during May, June and July on permanent plots in the two ecosystems. Random points within each vegetation type were generated using ArcView (ESRI 2001) and up to three permanent plots were established at each randomly located point. The number of plots sampled varied from year-to-year due to differences in field crew availability. There were up to 50 random points in each vegetation type and a maximum of 107 plots in wheatgrass prairie and 119 plots in sparse vegetation. At each random point, one permanently marked 2 m \times 6 m plot was located at the random point and up to two permanently marked 2 m \times 6-m plots were located near the random point (within 100 m). The nearby plots were chosen to represent the range of *Melilotus* cover at the site (from low to high percent cover of *Melilotus*). To quantify the plant community within a plot, all plant species and their Daubenmire (1959) cover classes were recorded in each of 12 0.5 m \times 2-m segments (this covers the entire plot). The cover classes for the 12 segments were averaged, resulting in a cover class for each species for the plot and a total species list. Native and exotic species cover class midpoints were summed for total cover of native and exotic species per plot. The number of native and exotic species was summed to give native and exotic species richness per plot. The exotic species category refers to all exotic species present except *Melilotus*.

Data from the random plots provide general trends for the study site over the course of the study. Native versus exotic status of the plant species follow the Great Plains Flora Association (1986).

Statistical analysis

The percent cover data are reported as proportional data. Mean cover and richness values for each vegetation type in each year were determined. Although we report species richness as part of our site characterization, we do not statistically analyze these data due to space limitations. Model results were similar for species richness and cover (Van Riper 2005).

We used structural equation models (Chapter 30, McCune and Grace 2002) to analyze the multivariate relationships in the plant cover data (Fig. 2, explained below). Proportional data were arcsine square root transformed to increase normality and reduce kurtosis. We structured the data into time steps (2001–2002 and 2002–2003 for wheatgrass prairie and 2001–2002, 2002–2003, and 2003–2004 for sparse vegetation) so that each time step was a group, and used multi-group analysis in Amos v. 7 (Arbuckle 2006) to ask (1) if the same model fit the data for each time step; and (2) if path (standardized regression) coefficients were the same for all time steps, given that the same model fit each time step. For a discussion of multigroup analysis using structural equation models, see Grace (2006). Because data were collected prior to model formulation, the models presented are considered exploratory rather than “strictly confirmatory” (Jöreskog and Sörbom 1996).

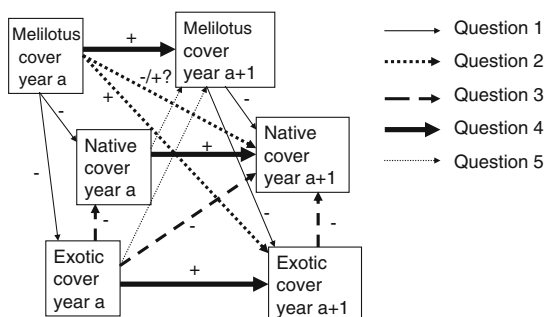


Fig. 2 The hypothesized model. The sign (+ or -) indicates the hypothesized relationship (positive or negative) of the variable at the origin of the arrow to the variable at the point of the arrow. The different line formats of the arrows refer to the different questions posed in our study (see “Introduction” section)

The model (Fig. 2) was used to examine the relationship between *Melilotus* cover and native and exotic species cover. In the model, single-headed (unidirectional) arrows represent causal pathways (Hatcher 1994). The output of Amos provides a χ^2 significance test for the null hypothesis that the data fit the model. If $P < 0.05$ the null hypothesis is rejected, indicating that the data are inconsistent with the model (Hatcher 1994). The significance of the coefficient of each path also is determined. Paths with $P > 0.05$ ($t < 1.96$) are considered to have coefficients that are not different from zero. For paths with significant coefficients, the standardized path coefficients, which indicate the strength of the relationship between the variables, are reported. For example, if the path from Variable 1 to Variable 2 has a standardized path coefficient of 0.50, then there is an increase of 0.50 standard deviations in Variable 2 for an increase of 1 standard deviation in Variable 1, while holding constant the effects of other variables (Hatcher 1994). The R^2 values, showing the total explained variance, are presented for the dependent variables (Mitchell 1993).

Our goal was to assess the influence of *Melilotus* in each vegetation type. We hypothesized that *Melilotus* cover was influencing the covers of native species and other exotic species. The sign and significance of path coefficients between *Melilotus* and native and exotic species covers, as determined by structural equation models, can support or counter our hypothesis. The focal questions, corresponding to the arrows in the model (Fig. 2), are:

1. Does *Melilotus* in year a inhibit natives and other exotics in year a and/or does *Melilotus* in year $a + 1$ inhibit natives and other exotics in year $a + 1$?
2. Is there a lag effect of *Melilotus*? This examines the effect of *Melilotus* in year a on natives and other exotics in year $a + 1$.
3. Does the cover of other exotic species in year a inhibit natives in year a or $a + 1$, and/or does the cover of other exotic species in year $a + 1$ inhibit natives in year $a + 1$?
4. Does the cover of *Melilotus*, natives or other exotics in year a influence their cover in year $a + 1$? Measurements were made on permanent plots, so we expect that *Melilotus*, other exotic, and native cover in year $a + 1$ will be strongly

related to *Melilotus*, other exotic, and native cover, respectively, in year a .

5. Does the cover of native and other exotic species in year a influence *Melilotus* cover in year $a + 1$? We anticipate that *Melilotus* is not strongly inhibited by native or exotic species cover as *Melilotus* populations can invade a variety of habitats.

Observational data from two vegetation types at Badlands National Park were used to address the study questions. Because the two vegetation types, wheatgrass prairie and sparse vegetation, differ dramatically in the processes that shape them, the relationship between each vegetation type and *Melilotus* could also differ. In wheatgrass prairie, we hypothesized that live *Melilotus* cover would inhibit growth of natives and other exotics in year a due to competition, but the N rich patches left behind the next year (i.e., year $a + 1$) would disproportionately favor exotic species over natives. (Because not all *Melilotus* plants measured in year a will die by year $a + 1$, this effect is predicted to be relatively weak.) Native species would be disfavored if exotics can better exploit the increased N. There is potential for year-to-year variation in the strength of these effects due to environmental factors, such as varying amounts of precipitation. *Melilotus* itself can vary widely in population abundance from year-to-year, with large *Melilotus* populations found in years of high precipitation (Von Loh et al. 1999).

The same model applies for sparse vegetation, but it is less clear what effect *Melilotus* would have in year a . In this harsher, less vegetated environment, *Melilotus* may act as a nurse plant in year a for both native and exotic plants (O'Connor 1995; Walker and Vitousek 1991), unlike the competitive relationship hypothesized for the more densely vegetated wheatgrass prairie habitat.

Results

Site characterization

Throughout Badlands National Park, *Melilotus* presence in our plots varied substantially among years and vegetation types, ranging from 29% of individual plots occupied in sparse vegetation in 2004 to >80%

of individual plots occupied in wheatgrass prairie in 2001; *Melilotus* always occurred more frequently in wheatgrass prairie than in sparse vegetation (Table 1). Although frequency of occurrence was generally high, *Melilotus* cover averaged only 2–8% in wheatgrass prairie and 1–3% in sparse vegetation (Table 1). In all plots (not only those at the random points), *Melilotus* cover ranged from 0 to 50–75% cover in wheatgrass prairie and from 0 to 25–50% cover in sparse vegetation. While other exotic species were common in both habitats, native species cover and richness exceeded other exotic species cover and richness. Native and other exotic species richness was higher in wheatgrass prairie plots than sparse vegetation plots (Table 1). In total, 22 exotic species were found in wheatgrass prairie plots and nine exotic species were found in sparse vegetation plots (species are listed in Van Riper 2005).

Model evaluation

We used our hypothesized model (Fig. 2) to examine the effect of *Melilotus* cover on native and exotic species cover in wheatgrass prairie and sparse vegetation. The models for wheatgrass prairie (Fig. 3) and sparse vegetation (Fig. 4) were examined to determine the answers to the initial questions (summarized in Table 2).

Q1 Does *Melilotus* cover in year a inhibit native and other exotic species cover in year a ?

Model results for wheatgrass prairie were inconsistent both within and between 2-year time steps (Table 2). For example, although *Melilotus* cover had a fairly strong negative association with native cover in 2001, there were no significant associations in the other years (Fig. 3). Only in 2003 did we find any association of *Melilotus* cover with exotic species cover, and it was negative (Table 2, Fig. 3). In contrast, we found consistent positive associations of *Melilotus* cover with both native and exotic species in sparse vegetation (Table 2, Fig. 4).

Q2 Does *Melilotus* cover in year a promote other exotic cover and reduce native cover in year $a + 1$? (Does *Melilotus* have a lag effect?)

There was slight evidence for a lag effect in wheatgrass prairie, but none in sparse vegetation (Table 2, Figs. 3 and 4). Only in the 2002–2003 wheatgrass

Table 1 *Melilotus* frequency and mean percent cover of *Melilotus*, native species and other exotic species in western wheatgrass prairie and Badlands sparse vegetation from plots at random points

	2001	2002	2003	2004
Wheatgrass prairie				
<i>Melilotus</i> frequency (%)	83 (39/47)	67 (34/51)	53 (24/45)	NA
<i>Melilotus</i> cover	8.3 ± 2.6	3.6 ± 0.9	2.4 ± 0.9	NA
Native cover	100.2 ± 4.0	73.7 ± 4.0	67.7 ± 3.8	NA
Exotic cover	18.9 ± 2.8	10.7 ± 1.5	26.1 ± 3.5	NA
Bare ground cover	1.6 ± 0.9	4.0 ± 1.2	10.3 ± 2.1	NA
Native richness	8.5 ± 0.7	10.8 ± 0.7	14.4 ± 0.9	NA
Exotic richness	2.8 ± 0.2	2.6 ± 0.3	4.2 ± 0.3	NA
Sparse vegetation				
<i>Melilotus</i> frequency (%)	55 (24/44)	46 (23/50)	54 (22/41)	29 (14/49)
<i>Melilotus</i> cover	3.3 ± 0.9	1.7 ± 0.5	1.8 ± 0.4	1.0 ± 0.4
Native cover	43.6 ± 12.5	24.2 ± 3.1	25.6 ± 3.1	16.6 ± 2.4
Exotic cover	4.1 ± 1.0	3.1 ± 0.5	5.5 ± 1.0	2.1 ± 0.4
Bare ground cover	68.3 ± 4.1	84.6 ± 2.1	84.9 ± 2.3	87.1 ± 1.7
Native richness	5.6 ± 0.6	6.5 ± 0.7	8.2 ± 0.8	5.6 ± 0.7
Exotic richness	1.0 ± 0.2	1.2 ± 0.2	1.7 ± 0.2	0.8 ± 0.2

Melilotus frequency is the percent of plots with *Melilotus* (number of plots with *Melilotus* divided by total number of plots). Mean percent cover and richness (\pm SE) for *Melilotus*, natives, and other exotics are presented for each year. NA = not available, data were not collected in that year

prairie model did *Melilotus* in one year have a positive association with exotic species in the next year, but there was no association with native species.

Q3 Is there a negative relationship between other exotic species cover and native species cover in either year *a* or between years?

There was little evidence for a relationship between other exotic and native species cover in the wheatgrass prairie vegetation, with only one weak negative association in 2001 (Fig. 3). Significant associations were more numerous and generally positive in the sparse vegetation; we found only one negative association, between other exotic cover in 2002 and native cover in 2003 (Fig. 4).

Q4 Does the cover of *Melilotus*, natives, or other exotics in year *a* influence cover of *Melilotus*, natives, or other exotics, respectively, in year *a* + 1?

Of all potential pathways, the cover of each group in year *a* had the largest effect on the cover of the same group in year *a* + 1. All associations were positive and strong (Figs. 3 and 4), with one exception: the pathway between native cover in 2001 and 2002 in wheatgrass prairie was nonsignificant (Fig. 3a).

Q5 Does the cover of native and other exotic species in year *a* influence *Melilotus* cover in year *a* + 1?

Melilotus cover was not strongly affected by the cover of native and other exotic species in the previous year. In wheatgrass prairie, there was no association between native or other exotic species cover and *Melilotus* cover in the second year (Fig. 3). In sparse vegetation, the association between native species cover and *Melilotus* cover in the second year ranged from weakly negative in 2001–2002, to weakly positive in 2002–2003 and 2003–2004 (Fig. 4). There was no association detected between the cover of other exotic species and *Melilotus* cover in the sparse vegetation models (Fig. 4).

Strength of associations

In general, we accounted for less of the variance in our response variables in the wheatgrass prairie model than in the sparse vegetation model; R^2 in wheatgrass prairie ranged from 0.001 to 0.36 while in sparse vegetation it ranged from 0.06 to 0.77. Typically, the models accounted for more of the

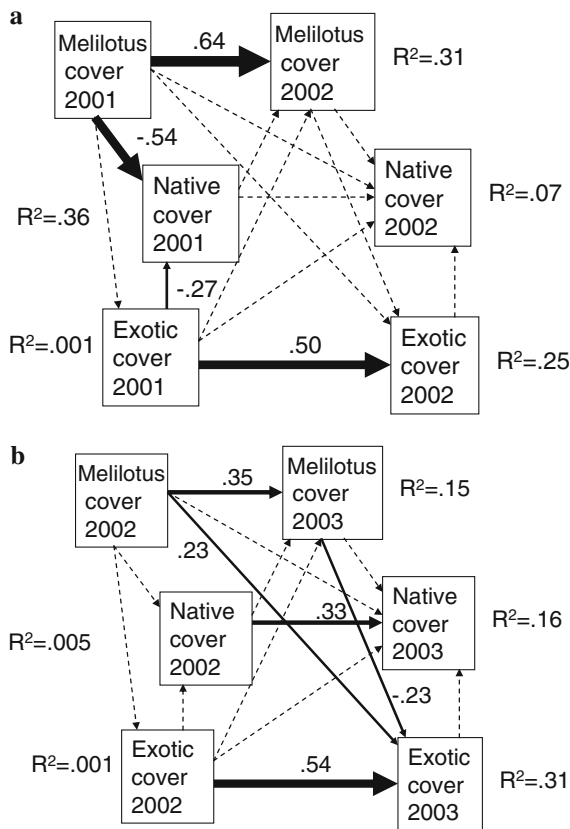


Fig. 3 Results of structural equation models of western wheatgrass prairie cover data, (a) 2001–2002; (b) 2002–2003. The model was consistent with the data ($N = 107$ plots, $\chi^2 = 1.397$, $df = 2$, $P = 0.50$). The thickness of the arrows corresponds to the magnitude of the standardized coefficients. Dashed lines with no coefficient indicate nonsignificant pathways. R^2 is reported for each dependent variable

variance in year $a + 1$ than in year a . The only exception was in wheatgrass prairie, where the pathways from both *Melilotus* and other exotics resulted in a relatively high R^2 in 2001 native cover; notably, the pathway from 2001 native cover to 2002 native cover was nonsignificant and R^2 was only 0.07 for native cover in 2002.

Discussion

Contrasting roles of *Melilotus*: competitor or facilitator

Our results suggest a competitive interaction between *Melilotus* and native species in the mesic wheatgrass

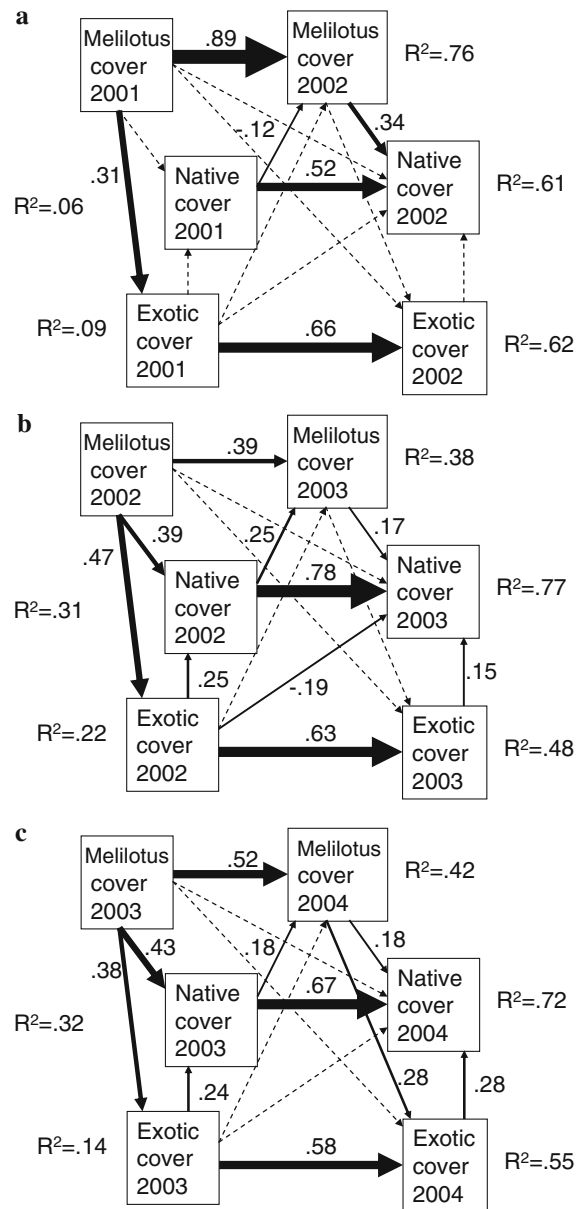


Fig. 4 Results of structural equation models of sparse vegetation cover data, (a) 2001–2002; (b) 2002–2003; (c) 2003–2004. The model was consistent with the data ($N = 119$ plots, $\chi^2 = 3.845$, $df = 3$, $P = 0.28$). See Fig. 3 for description of notation

prairie, but a positive (perhaps facilitative) interaction in the more stressful sparse vegetation. Although we did not design our study to test the stress gradient hypothesis, in which positive interactions dominate in more stressful environments (Bertness and Callaway 1994; Brooker et al. 2008; Callaway et al. 2002),

Table 2 Summary of significant *Melilotus* associations from structural equation models (+ = positive association with *Melilotus*; – = negative association with *Melilotus*)

Model	Same year association of <i>Melilotus</i> and:				Second year association of <i>Melilotus</i> and:			
	Natives		Exotics		Natives		Exotics	
	+	–	+	–	+	–	+	–
Wheatgrass								
2001–2002		1						
2002–2003				1			1	
Sparse								
2001–2002	1		1					
2002–2003	2		1					
2003–2004	2		2					

For same year associations, the maximum possible number of statistically significant (at the $P < 0.05$ level) effects is 2. For example, if both the association of *Melilotus* in year a with native cover in year a and the association of *Melilotus* in year $a + 1$ with native cover in year $a + 1$ were significant, then there would be two significant effects. For second year associations, the maximum possible number of statistically significant associations is 1 (for example, the association of *Melilotus* cover in year a with native cover in year $a + 1$)

these results are consistent with its predictions. In the harsh sparse vegetation environment, we found a facilitative role for *Melilotus*, which had a consistent, positive relationship with cover of native and exotic species within a given year (Table 2). *Melilotus* has been shown to increase soil N in sparse vegetation soils (Van Riper 2005), and other species may benefit from this enrichment. Additionally, in dry environments, nurse plants can facilitate species growth by protecting other species from desiccation, wind, and erosion (Bruno et al. 2003; O'Connor 1995; Shumway 2000; Smith et al. 2004). Alternatively, the limited number of hospitable locations within the sparse vegetation may be responsible for the associations among *Melilotus*, native and other exotic vegetation, consistent with other observational studies in which relatively richer sites support more exotics as well as more natives (Chaneton et al. 2002; Lonsdale 1999; Stohlgren et al. 1999).

Lag effects

Although we expected to find a weak lag effect of *Melilotus* on exotic vegetation because of its N-fixing abilities, we found virtually no effect. The only exception was a positive relationship between sweet-clover cover in 2002 and other exotic cover in 2003 in the wheatgrass prairie vegetation. Nitrogen enrichment from *Melilotus* apparently did not create a more favorable environment for exotic species in the

subsequent year, or N enrichment did not occur at a scale that would benefit other exotics. The lack of a lag effect may mean that native and exotic species responded similarly to increased N (Thomsen et al. 2006) or that *Melilotus* is not substantially changing the nutrient environment of the site, at least at the low densities we observed in this study. A fertilization experiment at Badlands National Park showed that N was not limiting in wheatgrass prairie (Van Riper 2005), so effects of N addition are unlikely there. In contrast, this same fertilization experiment indicated that N was limiting in sparse vegetation, but propagule pressure determined the effect of N addition on vegetation (Van Riper 2005). Because the effect was dependent on propagule pressure, which would be expected to produce a patchy expression on the landscape, our observational study would be unlikely to detect it.

Effect size

The best predictor for cover of natives, other exotics, and *Melilotus* in each vegetation type was that cover type in the previous year. The effect size of *Melilotus* and exotic species on native species was less than the effect size of the cover of native species in the previous year, although generally not less than half as strong. While sweetclover associations with natives and exotics were smaller than associations of natives and exotics with themselves, the associations with

sweetclover are not insignificant. Many of the common species in these ecosystems are perennials (Great Plains Flora Association 1986), so continuity from year-to-year outweighs the effects of *Melilotus*, at least in the short term. However, studies of long-term N addition find shifts in the plant community, even in communities originally dominated by perennials (Carson and Barrett 1988; Samuel and Hart 1998; Wedin and Tilman 1996). Because we do not have information on plant communities at our study sites prior to *Melilotus* invasion, we do not know how these communities may have changed in the long term.

Generality of the model relationships

Our data were found to be consistent with our hypothesized model over the time steps examined for each vegetation type. This suggests the general utility of the modeled relationships for this system. We note that, even though some hypothesized pathways never differed significantly from 0 (e.g., *Melilotus* cover in yr a to native cover in yr $a + 1$), we have retained them in the model because they are biologically sensible; to drop them would risk over-fitting the model to the data we collected in this relatively short study.

The strength of the modeled relationships varied from year-to-year, perhaps reflecting variability in environmental conditions, such as precipitation and temperature. The lowest R^2 values were in the wheatgrass prairie models, indicating that factors not explicit in our models, such as precipitation, likely had a large impact on the observed cover values, while this may not be the case for sparse vegetation. Seedling establishment of *Melilotus* has been shown to be sensitive to water availability (Tobe and Gao 2007). As a result of relatively dry years in 2002–2004 (Fig. 1), there were few plots with >25% *Melilotus* cover. If wetter years result in higher *Melilotus* cover, stronger effects may be expected. Increased water has been shown to make N fixation more favorable under N-limited conditions and to increase legume competitive ability over non-legumes (Lauenroth and Dodd 1979). In drier years, water may be limiting to *Melilotus*, natives, and other exotics; when water is no longer limiting, N limitation may make effects of *Melilotus* more apparent (Lorenz and Rogler 1972; Samuel and Hart 1998; Wight and Black 1979).

Management implications

Melilotus is having an effect on vegetation at Badlands National Park, even at the relatively low cover levels we observed in this study. Because *Melilotus* is well-known for its episodic “boom” years, we would anticipate stronger effects during these outbreaks. Unfortunately, its widespread distribution throughout the park and outside park boundaries, as well as its economic value to beekeepers and livestock producers, makes control of *Melilotus* at landscape scales unlikely. Because effects were most pronounced in sparse vegetation, where presence of *Melilotus* generally was associated with enhanced cover of both natives and exotics, management might best focus on these other exotics, which may prove more amenable to control.

Although we found a positive association between *Melilotus* and native plant cover in the sparse vegetation, the accumulation of plant biomass—whether native or exotic—may result in a fundamental change to an emblematic feature of Badlands National Park. As the stark spires of the Badlands gradually become more vegetated, soil will be stabilized and erosion may slow, eventually adding enough organic matter to the soils to favor the prairie species currently surrounding them. *Melilotus* seems likely to speed this process.

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