Ecological consequences of dead wood extraction in an arid ecosystem[1]

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Abstract
Coarse woody debris (CWD) plays a key role in ecosystems, reducing erosion and affecting soil development, storing nutrients and water, providing a major source of energy and nutrients, serving as a seedbed for plants and as habitat for decomposers and heterotrophs. We asked whether removal of CWD affected the structure and functioning of an arid woodland ecosystem in mid-western Argentina. These woodlands are protected by national laws and inhabited by indigenous local pastoralists who have land rights to use natural resources, including wood for fuel and construction material. We hypothesized that removal of CWD affected negatively the populations of wood-nesting pollinators, the reproductive performance of *Prosopis flexuosa* (the dominant tree species), plant cover, richness and composition, and nutrient cycling in the soil. We conducted a manipulative experiment consisting of four pairs of 70 m radius circular plots, each pair with an experimental (CWD removal) and a control (no removal) plots. Experimental CWD extraction affected negatively flower visitor abundance, although the magnitude of this effect decreased over time. In contrast, extraction had a significant, positive effect on seed production of *P. flexuosa*. No significant effects of extraction were found on cover, richness and composition of understory plants and soil properties. Thus, CWD did not have the generally negative effects expected under our hypotheses.

Keywords: Argentina, Monte desert, plant reproduction, pollination, soil properties, wood extraction, wood-nesting bees

Introduction

Extraction activities such as mining, fisheries, logging and harvesting are among the main causes of degradation of natural ecosystems, not only affecting the target resources but also having a variety of unwanted secondary effects (Groom, Meffe, & Carroll, 2006). One major resource extracted from natural ecosystems is wood, used by human populations as a

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source of raw material for construction of buildings and other structures, manufacturing of furniture and utensils, and fuel, particularly in rural areas. This extracting activity has major impacts on natural ecosystems. For example, habitat degradation by fuelwood consumption affects 137 million hectares throughout the world (United Nations Environment Programme, 2002). In turn, habitat loss and degradation are major threats to biodiversity (Vié, Hilton-Taylor, & Stuart, 2009). Thus, extractive activities represent a management dilemma, in which the economic benefits of exploitation must be weighed against their potential ecological consequences.

In this paper we are concerned with the ecological impacts of extraction of coarse woody debris (CWD), which includes a wide variety of material: standing dead trees (also called snags or stags), stumps, dead branches, whole fallen trees, coarse roots, and wood pieces that have resulted from fragmentation of larger snags and logs. CWD plays a key role in ecosystems, reducing erosion and affecting soil development, storing nutrients and water, providing a major source of energy and nutrients, serving as a seedbed for plants and as a major habitat for decomposers and heterotrophs (Grove, 2002; Harmon, Franklin, Swanson, Sollins, Gregory, et al., 2002; Jonsson, Kruys, & Ranius, 2005).

There is a large body of literature evaluating the ecological effects of extraction of CWD. These studies come mostly from northern Europe (particularly Fennoscandia), North America and Australia. Evidence for the effects of removal of CWD is mixed. Some studies show negative effects on multiple ecosystem components and ecological processes (Bader, Jansson, & Jonsson, 1995; Lohr, Gauthreaux, & Kilgo, 2002; Mac Nally, Horrocks, & Pettifer, 2002; McCay & Komoroski, 2004; Rothermel & Luhring, 2005; Heinemann & Kitzberger, 2006; Kappes, 2006; Todd, Rothermel, Reed, Luhring, Schlatter, et al., 2008). Other studies, however, show nil or even positive effects of CWD extraction (He & Barclay, 2000; Spears, Holub, Harmon, & Lajtha, 2003; Hocking & Semlitsch, 2007; Owens, Moseley, McCay, Castleberry, Kilgo, et al., 2008; Ulyshen & Hanula, 2009). The general conclusion that can be drawn from this body of work is that dead wood management should be included in ecosystem management of forests (Grove, 2002; Jonsson et al., 2005; Langor, Hammond, Spence, Jacobs, & Cobb, 2008; Simberloff, 2001; Woldendorp & Keenan, 2005), but at the same time that more rigorous experimentation at broad spatial and temporal scales is needed (Davies, Tyler, Stewart, & Pullin, 2008; Mac Nally et al., 2002; Simberloff, 2001), with a greater coverage of ecosystem types throughout the World (Langor et al., 2008).

Here we report the results of an experimental study evaluating the ecological effects of CWD in an arid woodland ecosystem in the Monte desert of Argentina. We worked in Telteca Forest Reserve, an area dominated by the tree *Prosopis flexuosa* D.C. (algarrobo dulce), the main tree species in the Monte desert. Telteca is a natural and cultural reserve, inhabited by local pastoralist communities of Huarpe ancestry, who rely on natural resources for their economic activities and daily subsistence. Woody plant species, particularly *P. flexuosa*, have been harvested in the Monte region since the origins of human settlements, peaking in the early 20th century with the expansion of railroads and the development of the wine industry (Abraham & Prieto, 1999; Villagra, Defossé, del Valle, Tabeni, Rostagno, et al., 2009). Yet, the difficult access imposed by sand dunes in our study area meant that substantial portions of it have been used only sparingly by the sparse local population (Roig 1982), and have remained unimpacted by the massive extraction occurring in many other areas. Today, *Prosopis* woodlands are protected by national and regional laws, and dead wood extraction is done exclusively by the local settlers, who use wood for construction of houses, corrals, and frames for groundwater wells, their only source of water for domestic animals. Surprisingly, although the Telteca Reserve's goal is to preserve the natural environment and the local culture, the important management question of how local human activities affect the woodland ecosystem has not been evaluated. This is the question we address here. In a broader context, our study may help to complete the catalogue of studies on the ecology and management of CWD, as arid ecosystems are notoriously underrepresented in this catalogue, even though dead wood extraction is one of the main subsistence activities in many arid regions around the world, particularly those with low economic development.

Our general question is whether removal of CWD affected the structure and functioning of this woodland ecosystem in the Telteca region. Our first specific question concerns wood-nesting pollinators, which use dead wood of *P. flexuosa* as nesting sites and are among the main pollinators of this tree species. Thus, we hypothesized that removal of CWD could affect negatively the populations of wood-nesting pollinators, and indirectly affect the reproductive performance of *P. flexuosa*. A second specific question concerns understory vegetation, which is likely to suffer from extracting activities, both directly (e.g., trampling during the extraction process) and indirectly (e.g., changes in soil conditions). Thus, we hypothesized that extraction of CWD would lead to modified cover, richness and composition of understory plants. A final question concerns the biological processes associated with nutrient cycling in the soil. We hypothesized that the increased fine debris and nutrient cycling and the lower nutrient demand for decomposition caused by CWD extraction led to increased soil nutrients and fine organic matter under tree canopies in the short term. To evaluate these questions we conducted a manipulative experiment consisting of four pairs of 70 m radius circular plots (ca. 1.5 ha), removing most CWD in one plot per pair, and studying wood-nesting bee abundance, reproductive success of *P. flexuosa*, understory vegetation and soil properties in three study years.

Methods

Study system

The study area is located in Telteca Forest Reserve, in the Monte desert of northeastern Mendoza, Argentina (32–33 S, 67–68 W; 500–550 m elevation). The climate is arid, with total annual precipitation ca. 156 mm concentrated mostly in summer (December-March), and wide daily and annual thermal amplitudes. Mean annual temperature is 18.5 ºC, with absolute maximum and minimum of 48 ºC and -10 ºC, respectively (Estrella, Heras, & Guzzeta, 1979). The area is located in a sedimentary basin. The aeolian reworking originated a system of transverse sand dunes of up to 20 m in height, separated by 100–200 m wide troughs (González Loyarte, 1992).

The *Prosopis flexuosa* woodland is the characteristic arboreal community of the Monte region (Rundel, Villagra, Dillon, Roig-Juñent, & Debandi, 2007). As other species of *Prosopis*, this legume produces soil enrichment via nitrogen fixation. Density of *P. flexuosa* ranges 155–233 trees ha^{-1}, biomass 4,000–15,000 kg ha^{-1} (Alvarez, Villagra, Cony, Cesca, & Boninsegna, 2006), and mean annual wood productivity (121–170 kg ha^{-1} year^{-1}) is low compared to other woodlands in the Monte (Alvarez et al. under review). Previous studies have reported that the total woody debris produced by *P. flexuosa* ranged from 4,424 to 8,692 kg ha^{-1} (Alvarez, 2008). *P. flexuosa* is self-incompatible and is entirely dependent on pollinators for pollination and seed production (Aschero & Vázquez, 2009).

P. flexuosa provides many important services to local human settlers. Its fruits have been used by indigenous communities since prehispanic times (Roig, 1993) and are still collected mainly to feed livestock, but also for human consumption. The shade provided by the forest is important for the establishment and subsistence of human settlements and their livestock. The Telteca reserve hosts approximately 34 family units in an area of 20 400 ha (Bosch, 2008). Inhabitants from surrounding areas may also use some resources from the reserve, such as wood and fruits. Land use intensity in different areas should vary according to the spatial aggregation of livestock posts, and the type of use given by their owners (i.e., amount of animals, size and number of corrals). The study area is also important for biodiversity conservation, as it harbors several endemic and threatened taxa (Roig-Juñent, Flores, Claver, Debandi, & Marvaldi, 2001).

Experimental design

We worked in four pairs of CWD extraction and no-extraction sites, each pair consisting of two circular plots of 1.5 ha and 70 m radius. The distance between the edges of paired extraction/no-extraction plots within a site was 37-111 m, while the distance between plots at different sites was 0.86-1.1 km. We removed all CWD of woody species (mostly *P. flexuosa*, *Bulnesia retama* and *Geoffroea decorticans*), including large and small logs, dead standing trees (snags), dead branches on the ground and in the canopies, and any other reachable pieces of dead wood that were at least 5 cm thick. We decided to remove all CWD from our study plots so as to simulate the maximum possible intensity of CWD removal effects. We used power saws to remove and cut large logs, and transported CWD by hand, horse and trucks to the nearest settlements, located at 2–4 km from the plots. Focal trees for measurement of bee abundance and seed production were located within 10 m radius from the center of the plot. The choice of the size of the plots was made considering a trade-off between typical foraging distances of bees and logistic and management constraints. The plot size was agreed with the controlling authority for the protected areas of the Government of Mendoza. Although some wood-nesting bee species are known to fly distances that greatly exceed the dimensions of our plots, particularly large carpenter bees (Beekman & Ratnieks, 2000; Pasquet, Peltier, Hufford, Oudin, Saulnier, et al., 2008), smaller bees typically fly shorter distances, with average flight distances well within the size of our plots (Gathmann & Tscharntke, 2002; Steffan-Dewenter, 2004). Dispersal kernels of moving organisms or their propagules are typically right-skewed, or leptokurtic, with a sharp peak near the point of origin and a long tail towards long distances (Turchin, 1998; Kot et al., 1996; Gómez & Zamora, 1999); this shape of the dispersal kernel means that most movements occur at short distances, even though animals can fly much longer distances.

Field and laboratory methods

Flower visitor sampling

To evaluate CWD extraction effects on pollinators, we sampled insects visiting flowers of *P. flexuosa* trees within the inner 15 m radius of our plots during 4 consecutive days in early November in 2006, 2007 and 2009; in 2008 we were unable to conduct flower visitor observations because a heavy hail storm destroyed most flowers of *P. flexuosa* in our study populations. We chose to work with *P. flexuosa* as the focal plant species because it is abundant and flowers profusely at our study sites. The identity and number of insects visiting flowers of *P. flexuosa* were sampled in 5 min observation periods. Paired sites were sampled simultaneously by different observers from dawn till dusk (7:00–20:00 h). Observers were switched between sites in each sampling period (morning, noon and afternoon) to avoid observer bias. In each sampling period we recorded the number and identity of flower visitors. An average of 22 sampling periods per site were conducted in 2006, 27 in 2007 and 16 in 2009.

Seed production

To study the effects of CWD extraction on seed production, we selected four individuals of *P. flexuosa* within 10 m radius of the center of each plot. At the peak of the flowering season (early November) we tagged five branches of each tree and recorded the number of inflorescences (I) per branch. In mid December, once seeds had developed but before pod maturation, we counted the number of pods per branch (P) and the number of seeds per pod in five pods per branch. We then calculated the average number of seeds per pod (S_P) for each branch, and estimated the number of seeds per inflorescence (S_I) as $S_I = S_P P/I$. In 2008, we could not study seed production because a heavy hail storm had destroyed most *P. flexuosa* flowers.

Plant cover, richness and composition

We used the point-quadrat method to characterize the effects of deadwood extraction on plant cover, richness and composition (Kent & Coker, 1992). We worked along three fixed 30 m transects per plot, with measurement points every 0.30 m (i.e., 100 points per transect). We recorded the identity of species intercepting each point, collecting herbarium specimens when identification was not possible in the field.

Soil properties

Soil samples were obtained at two microsites in each plot: under *P. flexuosa* canopies and at exposed areas without vegetation. Soil samples were obtained in March 2007 and 2008 for organic matter analysis and in October-November 2007 for nutrient availability.

Soil samples for organic matter analyses were collected along three transects per microsite per plot. At each transect, at least 5 sub-samples were taken and later pooled for analyses. Samples were dried at 60 °C and sieved with a 2 mm mesh before the analysis. Organic matter was analyzed with the Walkley-Black method of wet oxidation (Nelson & Sommers, 1982).

Samples for nutrient availability were taken under four trees and their exposed adjacent areas within a 15-m radius of the center of each site. Under each tree, four subsamples were taken 1 m from the trunk in different directions; subsamples were later pooled for the analyses. Each sample from exposed areas was also a composite of four subsamples. Soil nitrate, ammonium, and orthophosphate concentrations in soil extracts were used as indicators of nutrients available to plants. Samples were sieved with a 2 mm mesh, extracted with a 2 N solution of KCl immediately after return from the field (20 g of soil in 60 ml of 2 M KCl), and frozen until chemical analyses. Nitrate and ammonium concentrations were determined by spectrophotometry of the soil KCl extracts. Nitrate was determined with the spongy cadmium method (Jones, 1984), and ammonium with the phenol-hypochlorite method (Weatherburn, 1967). Soil samples for available P determinations were dried at 60 °C before the analysis. Available soil phosphate was determined in Olsen soil extracts (4 g of soil in 10 ml of 0.5 M $NaHCO_3$) and spectrophotometry after reaction with ammonium molybdate (Okalebo, Gathua, & Woomer, 1993).

Statistical analyses

We used generalized mixed models (GLMM) to evaluate the effect of CWD extraction on flower visitor abundance (no. visitors in each 5 min observation period), seed production and soil properties, with “treatment” as a fixed factor with two levels (extraction and no-extraction) and “site” as a random factor with four levels (sites A-D); the models for soil properties had an additional fixed factor, microsite, with two levels (under *P. flexuosa* and exposed areas). Models for visitor abundance and seed production had a Poisson error distribution and a log link function, whereas the models for soil properties used log-transformed data and assumed a normal error distribution. We used the Akaike information criterion (AIC) to compare the fit of mixed models with and without the interaction between fixed and random factors. GLMM analyses were conducted using the lmer function of the lme4 package of R statistical software, version 2.11 (R Development Core Team, 2010). We also compared the effect size of extraction on seed production among years using Hedges's *d* statistic, calculated as the difference between treatment and control means of the response variable (seeds per inflorescence) in units of standard deviations while correcting for small sample bias (Gurevitch, Curtis, & Jones, 2001).

The effect of CWD on plant cover was evaluated with a *t* test, using function t.test of the stats package of R; a *t* test is appropriate here because we had only one cover measurement per plot coming from the point quadrats. Species richness was compared between extraction and non-extraction sites using sample-based rarefaction, rescaling richness estimates to individuals (Gotelli & Colwell, 2001); rarefaction analyses were done using an add hoc function written in R (available from D.P. Vázquez upon request). Finally, the effect of CWD extraction on plant composition was assessed grafically using non-metric multidimensional scaling (NMDS) and statistically using a Mantel permutation (Legendre & Legendre, 1998). For NMDS we used the isoMDS function in the MASS package of R; the Mantel permutation was done using the Mantel function in the vegan package of R.

Results

Flower visitors

Considering all study sites and years, the main flower visitors were *Centris* spp. (28% of all visits), *Megachile* spp. (19%), *Apis mellifera* (10%), several coleopteran species (6%) and other species of bees, other hymenopterans and dipterans. Wood extraction had a significantly negative effect on the abundance of all flower visitors in 2006 and 2007, but not in 2009 (Fig. 1, Table 1). Incorporating the treatment × site interaction improved the GLMM significantly in 2007 but not in the other years. A similar trend was observed for all years when only wood-nesting bees were considered, although it was never statistically significant (Fig. 1, Table 1).

Seed production

Contrary to our expectations, wood extraction had a significantly positive effect on seed production in 2006 and 2009; no signficant effect was found in 2007 (Fig. 2, Table 1). In all three years, adding the treatment × site interaction did not improve the fit of the GLMM, indicating that the interaction did not have a significant effect. The correlation between the amount of wood extracted and effect size of extraction treatment varied among years and was never statistically significant. The effect size of CWD extraction on seed production was substantially greater in 2006 (Hedge's $d = 1.21$) than in subsequent years (2007: $d = 0.05$; 2009: $d = 0.39$).

Plant cover, richness and composition

A total of 50 plant species was recorded during the study. The most frequent species included *Trichloris crinita* (6%), *Setaria leucophila* (6%), *Lycium tenuispinosum* (5.7%), *Bulnesia retama* (4.3%), *Suaeda divaricata* (3.9%), *Capparis atamisquea* (3.8%) and *Bouteloua barbata* (3.5%). There were no significant differences in plant cover between treatments for any year of study (2007: $t = -1.79$, $p = 0.1712$; 2008: $t = -0.61$, $p = 0.5871$; 2009: $t = -0.37$, $p = 0.7383$). Similarly, rarefaction analyses indicate that there were no effects on plant richness, as the results of *t* tests on rarefied means were always non-significant (2007: $t = 0.25$, $p = 0.8204$; 2008: $t = -1.03$, $p = 0.3800$; 2009: $t = -0.09$, $p = 0.9334$). Finally, there was no effect of treatment on plant composition for any year (Fig. 3), as the Mantel test statistic (r_o)

was always small and non-signficant for the three study years (2007: $r_o = -0.13$, $p = 0.847$; 2008: $r_o = -0.18$, $p = 0.825$; 2009: $r_o = -0.13$, $p = 0.733$).

Soil properties

Wood extraction did not affect soil organic matter, nitrate, ammonium and available phosphorous concentrations (Table 1). The factor microsite had significant effects on all soil variables, with soils under *P. flexuosa* having higher contents of soil nutrients and organic matter than soils from exposed areas (1.6 ± 0.7 vs 0.4 ± 0.2 % weight for organic matter, 6.1 ± 4.1 vs 2.3 ± 3.7 μg N g^{-1} for ammonium, 6 ± 1.5 vs 1.5 ± 0.7 μg N g^{-1} for nitrate, and 15.3 ± 7.6 vs 9.2 ± 6.6 μg P g^{-1} for available phosphorus). The addition of the interaction among fixed and random factors did not improve the models for any soil variable (Table 1).

Discussion

As we expected, experimental CWD extraction had a negative effect on flower visitor abundance. However, this effect was significant only when all flower visitors were considered, and became statistically non-significant three years after extraction. There was also a significant effect of extraction on seed production of *P. flexuosa*, but the effect was opposite to the prediction of our first hypothesis. No significant effects of extraction were found on cover, richness and composition of understory plants and soil properties, contradicting our second and third hypotheses. Taken together, our results indicate that removal of CWD did not have the generally negative effects expected under our hypotheses.

What could explain the above results? One possibility is that our hypotheses are indeed incorrect and that CWD extraction has little effect on the functioning of this arid forest ecosystem. This conclusion should not come as a surprise, as ours is not the first study to fail to find effects of CWD removal (see references in *Introduction*). However, several alternative explantions must also be considered. First, the generally non-significant results may have resulted from lack of statistical power associated with low level of replication in our study. We had only four replicates (four pairs of sites), which is likely to result in low power, as has been pointed out in other studies with a similar design (Vázquez & Simberloff, 2004). Unfortunately, logistic constraints prevented us from achieving greater replication (see *Methods: Study area and experimental design*). However, low replication is unlikely to explain the results for seed production, as the effect was highly significant and in a direction opposite to the prediction of our hypothesis; other alternative explanations of this striking result should be considered (see below).

A second explanation of the results for flower visitors, weak effects for wood-nesting bees and decreased effect size with time for all visitors may have also resulted from the presence of unharvested dead wood in our experimental sites. This is because we are likely to have missed some dead wood, especially dead branches of live trees, and thus bees may have colonized this wood after their nests were removed. Furthermore, additional dead wood may have been produced after our experimental removal, and bees may have colonized these newly available nesting sites, leading to decreased effect of CWD extraction with time.

The effect of CWD extraction on flower visitors was detected for all flower visitors but not when only wood nesting bees were considered. This result suggests that the mechanism involved in this effect is different from that hypothesized above and is not directly related to CWD extraction. For example, ground-nesting flower visitors could be affected by the physical soil disturbance caused by the extraction and transport of CWD in our experimental plots. In any event, this effect became non-significant by the end of the study, suggesting that, if real, the effect is unimportant in the long term.

For reproduction of *P. flexuosa*, it is striking that, contrary to our prediction, CWD had a positive effect on seed production in two of the three years for which we have data (2006 and 2009). One explanation of this result concerns increased reproductive success in response to removal of vegetative tissue. When removing dead branches from live trees, we did our best not to damage live branches; however, as they fell, dead branches usually produced some damage in live branches; this damage may have enhanced reproduction, as occurs with overcompensation to herbivore damage in some plants (Agrawal, 2000). Another possible explanation is increased nutrient availability in soils resulting from sawdust and other fine woody debris, including leaves, added to the soil as a consequence of CWD removal; however, this possibility is unlikely, given that our soil analyses failed to detect any effects of CWD removal on soil properties. As to the lack of effect on seed production for 2007, heavy showers during the peak of flowering destroyed most flowers in some sites, leading to extremely low seed production.

Finally, the lack of effects on soil properties may have resulted from the slow rate of decomposition of dead wood in arid environments, so that the content of organic material and nutrients in the soil did not increase in spite of the addition of fine debris resulting from extraction activities. Alternatively, the copious inputs of fine material annually (Alvarez, Villagra, Rossi, & Cesca, 2009), may buffer in the short term the possible effects of wood removal on soil organic matter.

In summary, our results suggest that CWD removal practiced by local pastoralists does not have a negative effect on the ecosystem properties analyzed, especially considering that removal of CWD by local communities is usually less intense than in our experiment, as CWD is removed without power saws or mechanical tools and transported by hand, horse or mule (L. Saldi and J.A. Alvarez personal observations). Wood extraction also alternates among different areas, which may allow recovery of dead wood stocks. However, increasing land use pressure resulting from the growth of the human population, accompanied by a higher density of livestock ranches, may increase the demand for forest products in the future, bringing the level of CWD extraction closer to that simulated in our study. It is also important to consider other ecological processes besides those considered here before drawing the general conclusion that traditional practices have no negative effects on the woodland ecosystem.

Put in a broader context, results reported here come to fill an important knowledge gap, as arid ecosystems have received little attention in the study of effects of CWD extraction. Our study is also unique in that it considers multiple ecosystem processes, some of which (e.g., pollination and plant reproduction) had not been considered previously in studies of CWD extraction. Of course, one study is not enough to allow general conclusions on the effects of CWD extraction on this type of biome and ecological processes; clearly, more studies like ours are needed, with rigurous experimentation at the ecologically relevant spatial and temporal scales. Furthermore, future progress in understanding and managing CWD will benefit from a greater effort for synthesis, as available reviews are too narrowly focussed on particular taxa or functional groups, regions or processes (Grove, 2002; Jonsson et al., 2005; Woldendorp et al., 2005; Langor et al., 2008; Davies et al., 2008).

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Table 1. Fit statistics for generalized linear mixed model analyses.

Response variable	Year	Extraction × site interaction	dAIC*	Test statistic¶	*P*
Abundance of all visitors	2006	Absent	0.00	**2.93**	**0.0034**
		Present	2.00		
	2007	Absent	15.13		
		Present	0.00	**2.71**	**0.0067**
	2009	Absent	1.27	-0.52	0.6020
		Present	0.00		
Abundance of wood-nesting bees	2006	Absent	0.00	0.77	0.4400
		Present	2.00		
	2007	Absent	0.00	1.56	0.1180
		Present	1.41		
	2009	Absent	0.00	0.19	0.8480
		Present	2.00		
Seeds per inflorescence	2006	Absent	0.00	**-2.61**	**0.0091**
		Present	3.47		
	2007	Absent	2.65		
		Present	0.00	-0.64	0.5240
	2009	Absent	0.00	-1.65	0.0984
		Present	2.00		
Organic matter	2007	Absent	0.00	-0.45	0.3416
		Present	4.40		
	2008	Absent	0.00	0.25	0.4094
		Present	4.30		
Ammonium	2007	Absent	0.00	2.06	0.0657
		Present	4.00		
Nitrate	2007	Absent	0.00	1.01	0.1934
		Present	0.60		
Available Phosphorus	2007	Absent	0.00	-0.39	0.3613
		Present	4.33		

* Difference of AIC for models with and without interaction for a given response variable and year. Models with dAIC > 2 are considered to fit worse then the competing model. When $dAIC < 2$ the simplest model with no interaction is selected.

¶ Test statistic for fixed effect of extraction, reported for the model with lowest dAIC for each response variable and year. Test statistic was Student's *t* for all soil variables, assumed to be normally distributed, and *z* for other variables, assumed to be Poisson distributed. Significant test statistcs at $\alpha = 0.05$ are highlighted in bold.

Figure legends

Fig. 1. Abundance of flower visitors in flowers of *Prosopis flexuosa* in the study plots for three years of study, measured as number of bee individuals recorded in a focal tree during 5-min intervals. Solid circles indicate treatment means; horizontal line dividing each box in two indicates the median; box limits are the first and third quartiles of the distribution; whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range from the box; circles indicate outlying data points falling beyond whisker limits. See Table 1 for GLMM fit statistics.

Fig. 2. Number of seeds per inflorescence of *Prosopis flexuosa* in study plots for three years of study. Conventions as in Fig. 1. See Table 1 for GLMM fit statistics.

Fig. 3. Reduced-space plot of first two coordinates resulting from non-metric multidimensional scaling (NMDS) of plant species composition. Black symbols, extraction sites; white symbols, control sites. Symbol shape indicates site pair, as shown in legend.

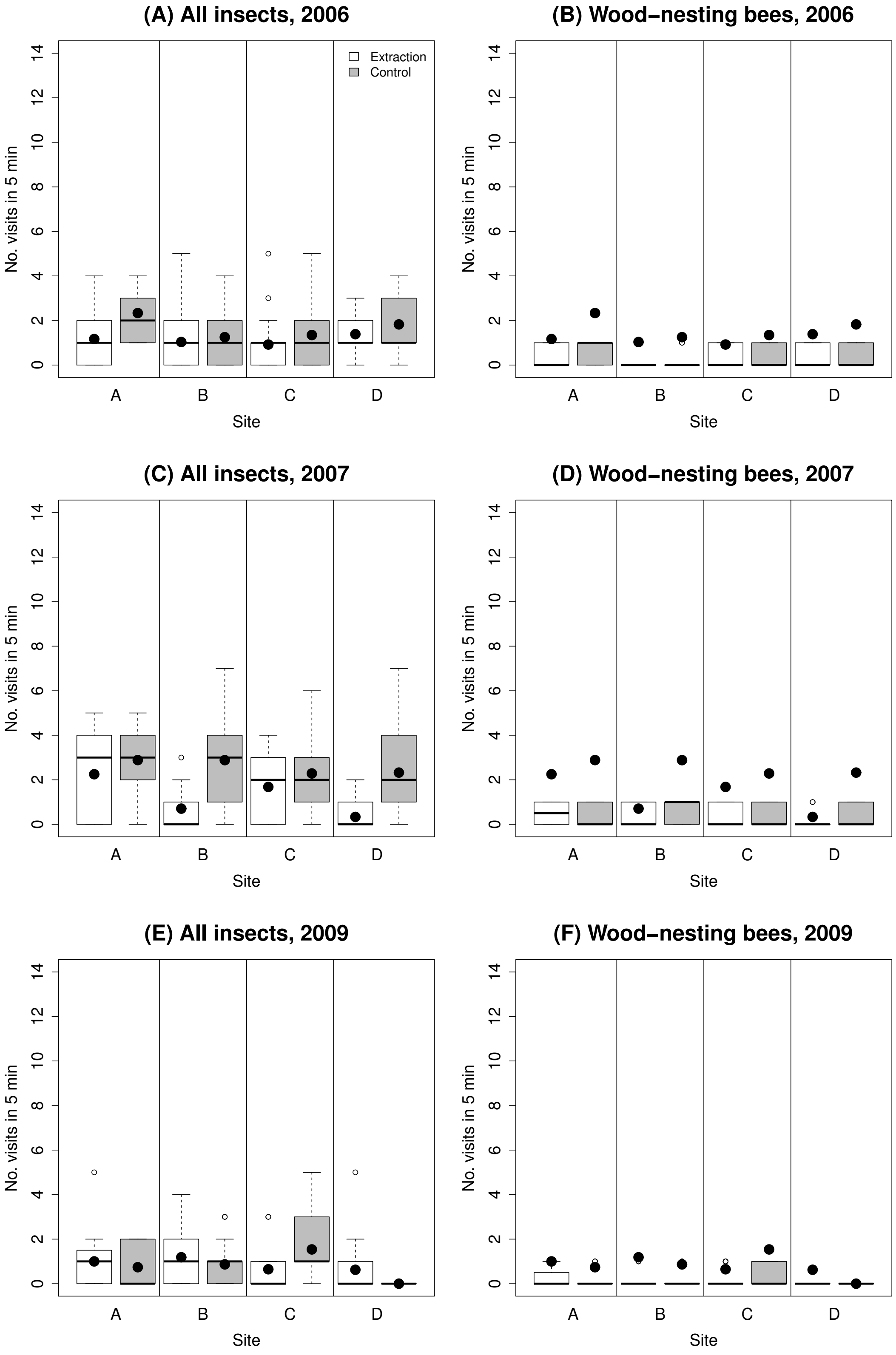
(A) All insects, 2006
(B) Wood−nesting bees, 2006
(C) All insects, 2007
(D) Wood−nesting bees, 2007
(E) All insects, 2009
(F) Wood−nesting bees, 2009
☐ Extraction
▨ Control
No. visits in 5 min
0
2
4
6
8
10
12
14
A
B
C
D
Site

Figure 1

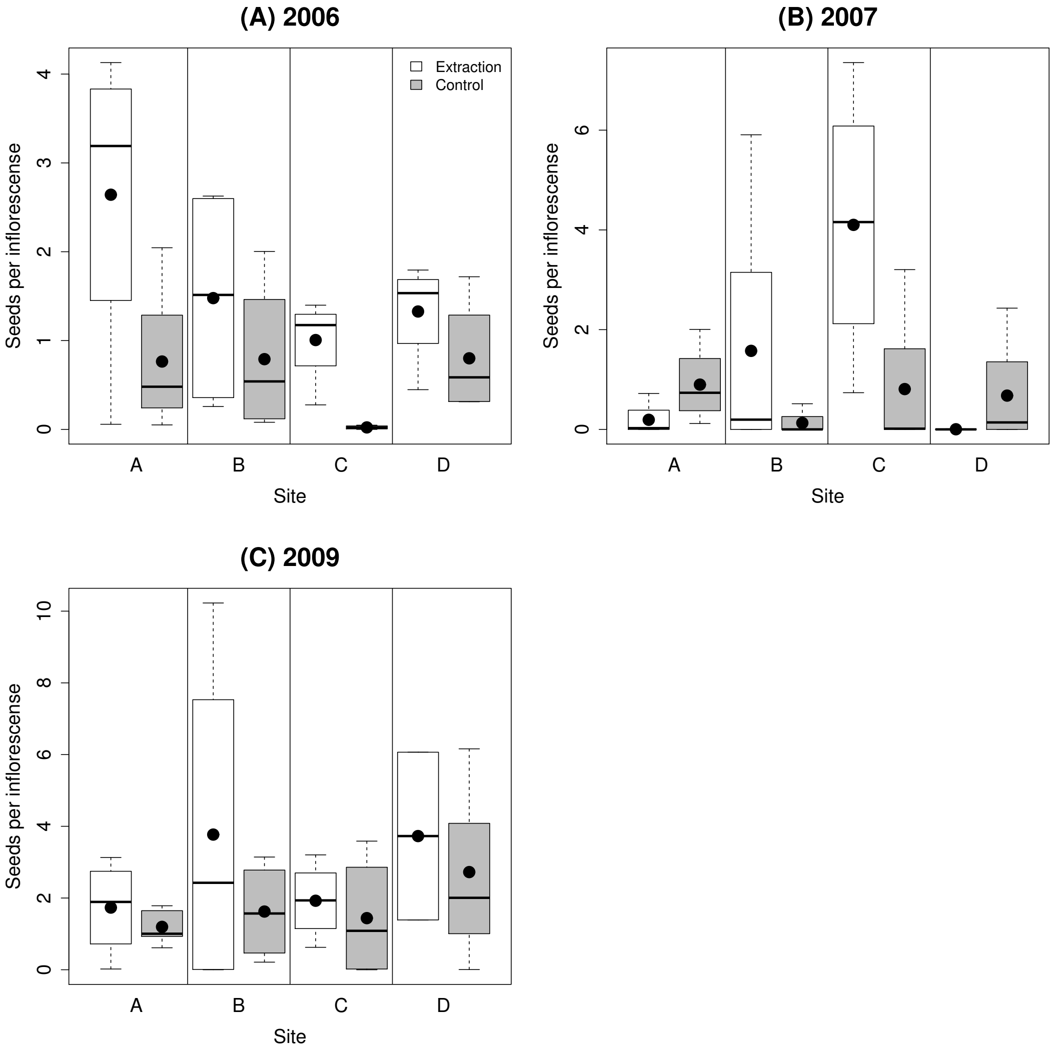
(A) 2006
(B) 2007
(C) 2009
Extraction
Control
Seeds per inflorescense
Site
A
B
C
D
0
1
2
3
4
6
8
10

Figure 2

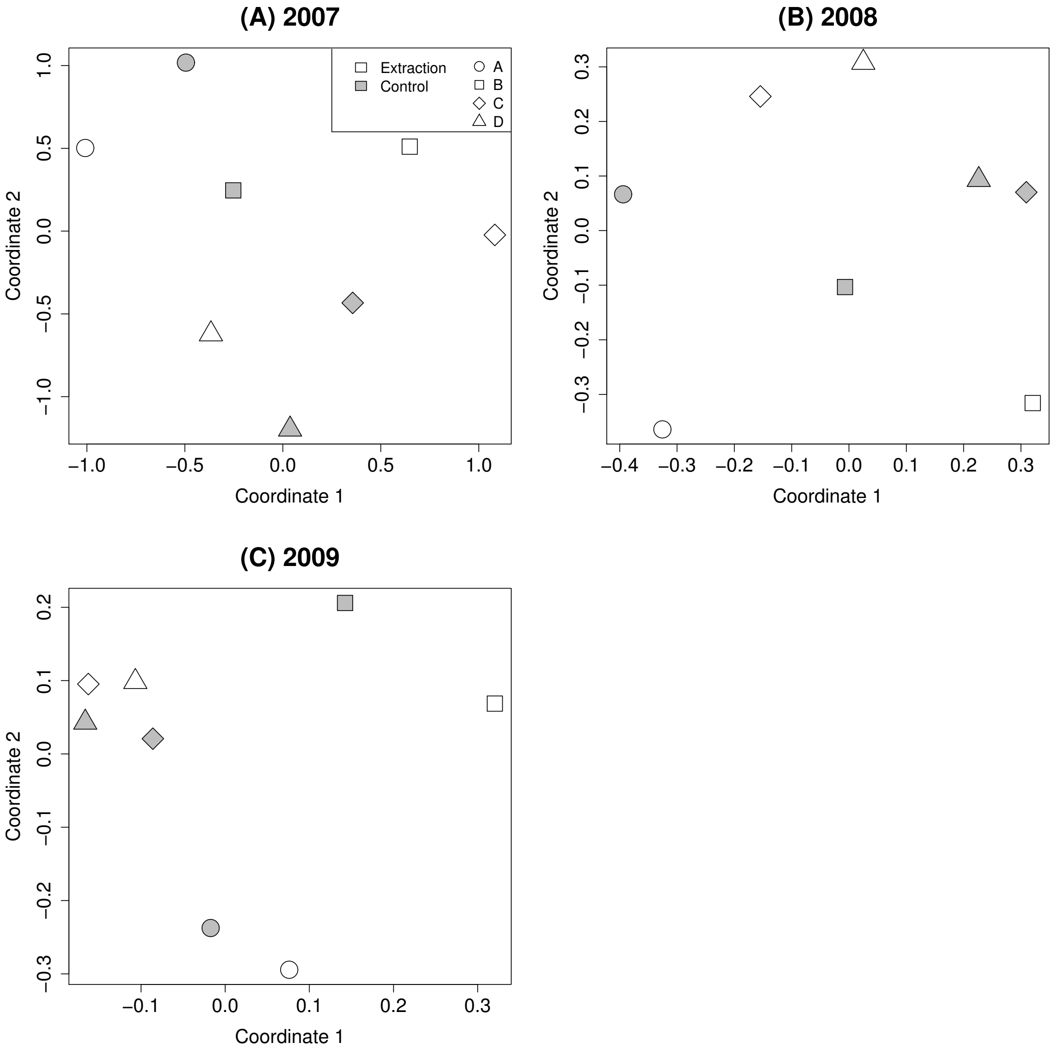
(A) 2007
(B) 2008
(C) 2009
Extraction
Control
A
B
C
D
Coordinate 1
Coordinate 2
−1.0
−0.5
0.0
0.5
1.0
−0.4
−0.3
−0.2
−0.1
0.1
0.2
0.3

Figure 3