

Facilitation vs. apparent competition: insect herbivory alters tree seedling recruitment under nurse shrubs in a steppe–woodland ecotone

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Summary

1. Facilitation of recruitment by ‘nurse’ plants can play a major role in harsh environments. Yet the extent to which consumer-mediated apparent competition from habitat-forming plants may counteract facilitative interactions remains largely unexplored.
2. We examined whether seedling predation by tenebrionid beetles seeking refuge under nurse shrubs may prevent tree recruitment facilitation in a Patagonian steppe–woodland ecotone. Newly emerged seedlings of *Austrocedrus chilensis* were planted in shrub canopy, off-shrub shelter and bare soil microsites, and monitored for causes of early mortality and for overall survival under ambient and elevated beetle densities.
3. Most seedlings in open microsites died from abiotic stress, whereas shrub cover and artificial shelters decreased desiccation mortality. Herbivory was the main cause of mortality in shrub microsites. Beetle addition increased predation beneath shrubs and in off-shrub shelters, indicating that apparent competition ‘spilled over’ from shrubs with high insect densities.
4. Litter removal from shrubs prevented seedling predation suggesting that nurse plants altered recruitment by providing food as well as shelter to insects. Herbivory rates did not depend on seedling patch density but decreased with seedling age, with 1-week old plants being most vulnerable to beetle predation.
5. *Synthesis.* Apparent competition from nurse plants can strongly reduce recruitment facilitation in stressful environments, although weak herbivore density dependence and seedling growth into ontogenetic refuges may limit the strength of apparent competition. An explicit consideration of negative, as well as positive, herbivore-mediated indirect effects from habitat-forming plants would broaden the understanding of community dynamics along stress gradients.

Key-words: apparent competition, facilitation, herbivory, indirect interactions, litter, ontogeny, Patagonia, refuge, seedling predation, spatial heterogeneity

Introduction

Understanding how the nature and strength of species interactions change with biotic and abiotic context is central to community ecology (Agrawal *et al.* 2007). The outcome of plant–plant interactions reflects the balance of negative and positive effects acting simultaneously (Miller 1994; Callaway & Walker 1997; Holzapfel & Mahall 1999; Levine 2000; Maestre, Bautista & Cortina 2003a; Graff, Aguiar & Chaneton 2007). Determining what factors tip that balance may be critical for predicting community dynamics along environmental

gradients (Bertness & Callaway 1994; Michalet *et al.* 2006; Alberti *et al.* 2008; Brooker *et al.* 2008). There has been a growing recognition that positive interactions can play a significant role in shaping community structure, especially in harsh physical environments (Bertness & Callaway 1994; Bruno, Stachowicz & Bertness 2003; Brooker *et al.* 2008). Direct and indirect facilitation from benefactor plants may override the negative impacts of physical stress and resource competition on heterospecific neighbours (Callaway 1995; Levine 2000). Further, neighbours may provide ‘associational defences or refuges’ when a focal plant species experiences reduced herbivory by growing close to other plants (Hay 1986; Hämbäck, Ågren & Ericson 2000; Graff, Aguiar & Chaneton 2007;

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Craine 2008). However, evidence shows that competition (Aguilar, Soriano & Sala 1992), extreme abiotic stress (Kitzberger, Steinaker & Veblen 2000), and heavy grazing pressure (Smit *et al.* 2007) may offset facilitation by nurse plants (Michalet *et al.* 2006; Brooker *et al.* 2008). By contrast, the extent to which recruitment facilitation by habitat amelioration may be disrupted by negative, consumer-mediated indirect effects remains poorly explored (Bruno, Stachowicz & Bertness 2003).

The realized impact of herbivory depends on the focal plant and herbivore species traits, as well as on neighbourhood structure (Hay 1986; Agrawal, Lau & Hämbäck 2006). Plants may offer food or shelter to herbivores that in turn feed upon, and often kill, other plant species growing nearby (Rand 2003; Caccia, Chaneton & Kitzberger 2009). Such consumer-mediated indirect interactions have been generically termed 'apparent competition' (Holt & Kotler 1987; Connell 1990; Chaneton & Bonsall 2000), because the resulting patterns of prey abundance (e.g. local exclusion, spatial segregation) may be similar to those created by resource competition. Theory suggests that, in patchy environments, apparent competition between plants may arise through differential habitat use and food choice by mobile consumers (Holt 1984, 1987; Holt & Kotler 1987). While herbivore-mediated apparent competition has been documented in several systems (Reader 1992; Chaneton & Bonsall 2000; Rand 2003; Orrock, Witter & Reichman 2008), few studies have been designed to test its role relative to other interactions (Caccia, Chaneton & Kitzberger 2009). Little is known about the influence of apparent competition on plant recruitment in systems where facilitation is thought to prevail (see Callaway 1992; Ibañez & Schupp 2001). In harsh environments, small-sized consumers may utilize nurse plants as refuge from physical stress. By attracting herbivores, nurse plants could indirectly affect seedling species that otherwise would benefit from stress amelioration (Bruno, Stachowicz & Bertness 2003). Yet, to our knowledge, no study has explicitly assessed how apparent competition may alter the outcome of nurse plant–seedling interactions.

More generally, an empirical understanding of the factors that govern consumer-mediated indirect interactions is lacking for different biotic contexts (Chesson & Kuang 2008). Herbivore-mediated apparent competition may potentially drive susceptible plants locally extinct (Connell 1990; Chaneton & Bonsall 2000; Rand 2003). Indeed, various mechanisms may create 'virtual' prey refugia from consumers (Berryman & Hawkins 2006), thus relaxing the strength of apparent competition and allowing coexistence (Holt & Lawton 1994). These comprise habitat partitioning between alternative food plants (Holt 1984), spatio-temporal variability of herbivore pressure (Holt 1987; Caccia, Chaneton & Kitzberger 2006), weak density dependence of herbivory on focal plant species (Chesson & Kuang 2008), herbivore saturation (Holt & Kotler 1987) or limitation by non-trophic factors (e.g. ground cover; Holt & Lawton 1994), and plant growth into age or size refuges (Chase 1999; Boege & Marquis 2005). However, factors controlling the strength of apparent competition have yet to be fully examined in natural plant communities.

We investigated the balance between direct facilitation and herbivore-mediated apparent competition in a Patagonian shrub steppe–woodland ecotone. Ecotones offer interesting scenarios to assess consumer impacts on plant recruitment, as shifts in the balance of negative vs. positive interactions may alter whole-community transitions (Brown & Heske 1990; Bertness *et al.* 1999). In north-western Patagonia, semiarid shrub steppes intermingle with open woodlands dominated by the conifer *Austrocedrus chilensis*, forming wide ecotones with trees scattered on a sparse shrub matrix (Veblen *et al.* 1996). Shrub shading facilitates tree establishment by reducing abiotic stress levels for emerging seedlings (Kitzberger, Steinaker & Veblen 2000). In addition, shrub patches provide habitat and food resources to ground-dwelling arthropods, including tenebrionid beetles that feed on the litter deposited under shrub crowns (Mazía, Chaneton & Kitzberger 2006). Kitzberger, Steinaker & Veblen (2000) noted that adult beetles could inflict substantial mortality on tree seedlings suggesting that herbivory might offset facilitation.

Here, we examined the hypothesis that apparent competition arising from behavioural aggregation of adult beetles under nurse shrubs reduces the strength of facilitation on seedling survival (Fig. 1). Our general aims were to assess the extent to which insect herbivory alters early facilitation of tree recruitment, and to evaluate how beetle abundance, litter presence, seedling density and seedling age affect the magnitude of apparent competition. Specifically, we predicted that seedling predation by beetles would be higher beneath shrubs than in off-shrub microsites, and that seedling mortality by predation would increase under elevated beetle densities, even for plants surviving in off-shrub interspaces. In addition, because litter accumulation may contribute to attract beetles to shrub patches, we expected greater predation rates in the presence of litter (Fig. 1). Also, given that tenebrionids are primarily detritivores, we expected seedlings to find 'safety in numbers'

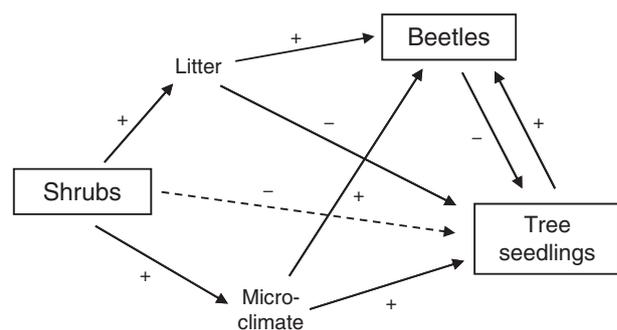


Fig. 1. Diagram of proposed interactions between nurse shrubs, tree seedlings and insect herbivores evaluated in the present study. Direct interactions (solid lines) can be either trophic (e.g. seedlings are a food source to beetles) or nontrophic (e.g. shrub facilitation of seedling survival by habitat amelioration). Indirect interactions (broken lines) between species are mediated by a third species (e.g. apparent competition between shrubs and seedlings mediated by beetle herbivory). Specifically, we hypothesized that nurse shrubs indirectly alter tree seedling recruitment by providing suitable habitat and food resources (litter) to tenebrionid beetles.

(Connell 2000), so that predation mortality would decrease in higher-density seedling patches. Lastly, susceptibility to beetle predation should decrease with tree seedling age/size, as older seedlings may be more resistant to herbivory than younger ones (Boege & Marquis 2005). Our study system was ideal to focus on the role of asymmetric apparent competition (Connell 1990; Chaneton & Bonsall 2000), because resource competition does not affect early tree survival under shrub canopies (Kitzberger, Steinaker & Veblen 2000).

Materials and methods

STUDY SYSTEM

Field experiments were conducted at Cerro Otto, 3.5 km west of Bariloche, Nahuel Huapi National Park, Argentina (41°06' S, 71°14' W). The study site was located *c.* 900 m a.s.l. on a north-east facing slope at Lake Nahuel Huapi. Soils are sandy-loam Andisols developed from volcanic ashes. Mean annual precipitation is 807 mm (SD = 193 mm, 1984–2003), mostly falling as rain and snow during autumn and winter (April–September). Summer months (December–March) are usually very dry, receiving only *c.* 12% of the total rainfall. Mean temperatures vary from 3.2 °C in July to 14 °C in January, but daily maximum summer temperatures often exceed 30 °C.

The site was representative of the transition between dry coniferous woodlands and the semiarid Patagonian steppe (Veblen *et al.* 1996). It was free of livestock grazing for > 50 years. The vegetation physiognomy corresponds to open woodland dominated by *A. chilensis* (hereafter, *Austrocedrus*). Adult trees up to 15 m tall are scattered in a sparse shrub matrix (0.5–1.5 m height) dominated by the prostrate-growing *Discaria articulata* (Rhamnaceae). Other shrub species include *Maytenus boaria*, *Schinus patagonicus*, *Lomatia hirsuta* and *Berberis buxifolia*. Shrub patches intermingle with bare soil interspaces, which account for *c.* 60% of the ground cover; herb cover is less than 10%. *Austrocedrus* produces small, wind-dispersed seeds forming transient soil banks. Juvenile *Austrocedrus* are commonly found associated with various shrub species (Kitzberger, Steinaker & Veblen 2000; Letourneau, Andenmatten & Schlichter 2004). Shrubs also create habitat for epigeal beetles and other macroarthropods (Mazia, Chaneton & Kitzberger 2006). We focussed on tenebrionid species that were known to feed on young seedlings as well as organic detritus, particularly *Nyctelia rotundipennis* (Kitzberger, Steinaker & Veblen 2000). This species is widely distributed across xeric habitats along the woodland–steppe ecotone of north-western Patagonia (Sackmann & Farji-Brener 2006).

INSECT ABUNDANCE-ACTIVITY PATTERNS

We expected that differential microhabitat use by tenebrionid beetles would lead to their numerical aggregation in shrub patches (Mazia, Chaneton & Kitzberger 2006). Beetle abundance-activity levels were measured throughout the study using pitfall traps placed under shrub canopies and in off-shrub, open microsites (see Appendix S1 in Supporting Information). All beetles trapped were identified to species and counted, but data are here reported only for the major seedling consumers, *N. rotundipennis* and *Emmalleria obesa-costata*. Differences in cumulative beetle numbers (individuals trap⁻¹ day⁻¹) between microsites were examined using generalized linear models with Poisson errors (for details, see Appendix S1).

EXPERIMENT 1: MICROSITE AND BEETLE DENSITY EFFECTS

In early summer (December) 2000, we tested the effects of shrub cover and beetle density on *Austrocedrus* seedling survival. We established 21 plots, 90 cm wide × 150 cm long, each including about one-third of a *D. articulata* shrub overhanging at one end, and a large bare-soil area (*c.* 90 × 110 cm) opposite to it. Shrubs had well-developed canopies (80–100 cm height, 1.5–2 m diameter). Plots were located at least 5 m apart and were randomly assigned to three treatments (*n* = 7): (i) fenced, ambient beetle density; (ii) fenced, elevated beetle density and (iii) unfenced, ambient beetle density. Fenced plots were enclosed by a 12-cm tall aluminium barrier, which prevented walking arthropods from entering or leaving the plots. Unfenced plots served as controls for enclosure effects.

In the fenced plots, we established three microsite treatments: shrub canopy, off-shrub artificial shelter and bare soil interspace. The off-shrub shelter and bare soil microsites were located *c.* 1 m away from the shrub crown at 30 cm from each other. The unfenced plots comprised only shrub and off-shrub shelter microsites, as we lacked enough seedlings and were primarily concerned with seedling predation in shaded microsites (where seedlings had greater chances of surviving abiotic stress). Artificial shelters (30 × 30 cm) were made of a half-shade cloth, kept 20 cm above the soil with iron pegs. Shelters reduced direct solar radiation (35% light transmittance) and midday soil temperatures by 10–15 °C, mimicking the physical effect of shrubs on microclimate but not on soil organic matter and microbial communities (Kitzberger, Steinaker & Veblen 2000; Austin & Vivanco 2006). Given their relatively small size, we assumed the artificial shelters would not provide habitat for beetles (Mazia, Chaneton & Kitzberger 2006). This treatment was intended to create suitable microsite conditions for seedlings in off-shrub areas. We assumed that shelters would ensure early seedling survival from physical stress away from shrubs, a pattern observed in wetter years (Kitzberger, Steinaker & Veblen 2000). This allowed us to evaluate predation mortality in open interspaces resulting from 'spill over' effects under elevated beetle densities (Holt 1984; Orrock, Witter & Reichman 2008).

To examine insect density effects, we augmented the local abundance of the tenebrionid *N. rotundipennis* (*Nyctelia* henceforth) (see Fig. S1). The diurnal habit, large size and high mobility of *Nyctelia* make it an ideal test insect. Eight adult beetles were added to each of seven, randomly chosen, fenced plots; the remaining plots served as controls (ambient density). Our elevated density treatment simulated episodic increases in beetle numbers observed by previous work in these communities (Kitzberger, Steinaker & Veblen 2000). Beetles were collected 24 h before the experiment and introduced in the morning (09:00–10:00) next to the transplants. Fenced controls were assumed to harbour relatively low *Nyctelia* densities under the shrub crown, which was then confirmed by the sampling of beetle populations within the study area (<0.07 beetles shrub⁻¹ day⁻¹ were trapped throughout the study; see Table S1). We avoided traditional methods of insect exclusion (cages, pesticides) because this would have likely altered other, non-target arthropods. Selective removal of beetle species was deemed unfeasible. Therefore, we chose to augment the abundance of a focal consumer in field enclosures, which permitted a tighter control of the main 'actors' in the system (Schmitz 2004). It must be noted that, by fencing the plots, we impeded beetle immigration into the shrub patches where we placed the seedlings. Furthermore, we prevented emigration from the insect-addition plots, where the beetles could reach seedlings in both shrub and off-shrub areas.

In each microsite, we placed a 10-cm diameter × 8 cm deep polystyrene pot with 20 newly emerged *Austrocedrus* seedlings (0.25 plants

cm⁻²). Pots were placed flush with the soil, had their bottom side cut off before planting and were watered to reduce initial shock. Similarly dense seedling patches occur during favourable years for emergence or high tree seed production, especially underneath or in the periphery of shrub crowns (Kitzberger 1994; Kitzberger, Steinaker & Veblen 2000). Seedlings were grown in an unheated glasshouse and were 2 cm tall with two fully expanded cotyledons (*c.* 10 days old). Seeds were subjected to 60 day cold-wet stratification and were sowed at *c.* 100 seeds per pot; seedlings were thinned to 20 plants pot⁻¹ upon emergence. Every 3–5 days, we counted living, damaged and death seedlings. The apparent causes of mortality were assessed by scoring seedlings as being killed by abiotic stress (desiccation) or insect herbivory (predation). Seedlings killed by drought or heat stress turned yellowish or brown. Seedlings killed by insects had their cotyledons missing but the hypocotyle remained in place. Mortality was computed as cumulative seedling numbers killed per pot (proportion of initial). The study ran for 27 days (mid-January) and was terminated when frequent monitoring showed that predation mortality had levelled off. Conditions for *Experiment 1* were fairly wet (rainfall = 92 mm), relative to the average for the season (mean \pm SD = 39 \pm 29 mm). Temperatures were about average (13 °C).

We evaluated seedling mortality by desiccation and insect predation, and final seedling survival, using a generalized linear modelling approach (PROC GENMOD, SAS Institute 1996). Proportional data were modelled using a binomial error structure and the logit link function. Significance of model parameters was assessed by likelihood-ratio tests. Models were checked for overdispersion but no further adjustment was needed. As the plot-level and microsite-level treatments were not fully crossed (seedlings were not planted in bare soil spaces of unfenced plots), we ran two separate analyses. The core analysis focussed on the fenced plots and included beetle density (ambient or elevated) and microsite type (shrub, shelter and bare soil) as main effects. We then tested for enclosure effects using only the plots under ambient beetle densities, with enclosure (fenced vs. unfenced) and microsite (shrub vs. off-shrub shelter) as main factors. We found that, irrespective of microsite ($P = 0.91$), seedling mortality by predation was lower inside fenced plots than in unfenced ones (6 vs. 12%, respectively; $\chi^2 = 4.43$, $P = 0.035$), which suggested that our enclosure set-up was effective at reducing predation below ambient levels. However, the enclosure increased desiccation mortality under both shrubs and artificial shelters (fenced: 30% vs. unfenced: 13%, $\chi^2 = 25.84$, $P < 0.0001$; microsite: $P = 0.72$).

EXPERIMENT 2: SHRUB COVER AND LITTER EFFECTS

To examine whether litter presence influences seedling mortality through either predation or physical stress (Fig. 1), we factorially manipulated microsite cover (shrub canopy vs. artificial shelter) and litter presence (removed vs. added) under ambient beetle densities. Only shrub and off-shrub sheltered microsites were included, since most seedlings in bare soil interspaces died from desiccation shortly after emergence (see Results), and our aim was to test for litter effects independent of shrub-canopy effects. In mid-summer (February) 2001, we selected 20 shrubs (all *D. articulata*) located at least 5 m apart. Artificial shelters identical to those of *Experiment 1* were placed in open interspaces, 2–3 m away from the nearest shrub. We manually removed all the litter material accumulated beneath half the crown of each of 10 shrubs and then added the litter to 10 off-shrub patches covered with artificial shelters (50 \times 50 cm). Ten intact shrubs (no litter removed) and off-shrub shelters (no litter added) were used as controls, for a total of 40 plots ($n = 10$). In each microsite, we placed a polystyrene pot with 20 newly emerged *Austrocedrus*

seedlings (0.25 plants cm⁻²), which were grown from seed as in *Experiment 1*. The experiment ran for 45 days (early April), until mortality by predation had levelled off. We monitored survival and apparent causes of death (desiccation or predation) on a weekly basis. Weather conditions during *Experiment 2* were relatively dry (rainfall = 39 mm, long-term mean \pm SD = 58 \pm 36 mm), with average daily temperatures (13 °C). Data for cumulative seedling mortality and final survivorship per microsite were analysed through generalized linear models assuming binomial errors (see *Experiment 1*), with cover type and litter presence as main effects.

EXPERIMENT 3: SEEDLING DENSITY EFFECTS

In early summer (December–January) 2003/04, we tested for density dependence in seedling predation under ambient beetle abundance. *Austrocedrus* seedlings were planted in shrub and off-shrub microsites at three densities, creating six treatments in a fully randomized design ($n = 8$). Treatments simulated natural variability in emergence rates associated with inter-annual climatic variation and spatial heterogeneity in seed dispersal (Kitzberger 1994; Kitzberger, Steinaker & Veblen 2000). We selected 24 shrubs (*D. articulata*, *M. boaria* and *S. patagonicus*) and added an equal number of artificial shelters (see *Experiments 1 and 2*) in bare soil interspaces, for a total of 48 microsites located at least 2 m apart. In each microsite, we placed a polypropylene pot (8 cm diameter, 15 cm height) with 2, 8 or 16 seedlings (0.04, 0.16 and 0.32 plants cm⁻²). Seeds were germinated in the glasshouse as described above; emerging seedlings (two-cotyledon stage) were thinned to obtain the desired number of plants per pot. The experiment ran for 30 days; seedling mortality sources were recorded on a weekly basis. Conditions during *Experiment 3* were quite variable; December was wetter (44 mm) and cooler (10 °C) than normal (long-term means: 27 mm, 12.4 °C), while January had no rain and was very warm (15.5 °C). Data were analysed through generalized linear modelling, as in the previous two experiments. Models tested for effects of microsite cover and seedling density on desiccation and predation mortality rates. In addition, we tested for the probability of a seedling patch being encountered by insects as a function of patch density using log-linear analysis (PROC CATMOD, SAS Institute 1996).

GLASSHOUSE EXPERIMENT: SEEDLING AGE AND HERBIVORY

To test the hypothesis that age or size class affects seedling susceptibility to beetle predation, we conducted non-choice feeding trials under early-summer glasshouse conditions. *Austrocedrus* seedlings with 1, 3 or 6 weeks from emergence (*i.e.* 5, 25 and 40 days, respectively) were planted in separate trays (20 \times 35 \times 8 cm) filled with sandy soil and a 0.5-cm deep litter layer from shrub microsites. Different seed batches were germinated at prescribed times to establish three even-aged cohorts. Hypocotyle length did not vary with age (mean \pm SD = 1.6 \pm 0.2 cm), but seedling cohorts differed in the number of needle-shaped, primary leaves; 1-, 3- and 6-week-old seedlings had two cotyledons and 0, 6 and 10 leaves, respectively. We placed 10 seedlings in each tray ($n = 10$ trays per age) and 48 h later we added one adult *Nyctelia* (length = 15–19 mm). Beetles were collected at Cerro Otto 2 days before the trials. Trays were covered with chicken wire and watered twice a week. Over a 5-day period, we measured seedling survival and damage inflicted by beetles on a daily basis. We recorded the amount of damage by scoring the number of leaves consumed per plant. Differences in proportional mortality and leaf damage were analysed using generalized linear models assuming binomial errors (logit link

function) and normal errors (identity link function), respectively (PROC GENMOD, SAS Institute 1996).

Results

BEETLE ABUNDANCE-ACTIVITY PATTERNS

Pitfall trapping during summer 2000/01 showed that mean abundance-activity levels of tenebrionid beetles were generally higher ($P < 0.05$) beneath shrub canopies than in off-shrub open and artificially sheltered microsites (see Table S1, *Experiments 1 and 2*). Overall, beetles were trapped in 85–100% of the shrub patches sampled, and in 60–80% of the off-shrub microsites. Litter manipulation in *Experiment 2* did not alter the number of beetles trapped per microsite (Table S1). On the other hand, contrary to *Experiments 1 and 2*, we found no significant difference in beetle numbers between shrub and off-shrub microsites during *Experiment 3* in the summer 2003/04 (Table S1).

SEEDLING MORTALITY AND BEETLE DENSITY EFFECTS

In *Experiment 1*, seedling mortality attributed to desiccation was much higher in bare soil than in shrub and off-shrub sheltered microsites ($\chi^2_{[2]} = 354.5$, $P < 0.00001$) and also varied with beetle density, being the lowest under shrubs with added beetles (microsite \times beetle addition: $\chi^2_{[2]} = 10.1$, $P = 0.0064$; Fig. 2a). Abiotic stress was the primary cause of mortality (93%) in open interspaces, where seedlings died within 1 week of planting. In contrast, on average, only 29% of seedlings beneath shrubs and off-shrub shelters died from desiccation after 4 weeks of experiment. Artificial shades substantially reduced desiccation mortality, relative to that observed in bare soil microsites (Fig. 2a).

Insect herbivory was the main cause of mortality beneath shrubs, whereas it was generally low in off-shrub shelters and bare soil interspaces ($\chi^2_{[2]} = 89.83$, $P < 0.00001$; Fig. 2b). *Nyctelia* addition markedly influenced seedling mortality ($\chi^2_{[1]} = 8.63$, $P = 0.0033$) by increasing predation rates under both shrub canopies and artificial shelters, but did not affect seedling fate in open microsites (beetle addition \times microsite: $\chi^2_{[2]} = 11.85$, $P = 0.0027$). Thus, microsite differences in seedling predation were most apparent under elevated beetle densities (Fig. 2b).

As a result of the above mortality patterns, *Austrocedrus* seedling survival was significantly lower in bare soil interspaces than in both types of sheltered microsites ($\chi^2_{[2]} = 175.1$, $P < 0.00001$; Fig. 2c). Beetle addition decreased survivorship mostly under shrub canopies and artificial shelters ($\chi^2_{[1]} = 22.65$, $P < 0.00001$), but the beetle density \times microsite interaction was not significant ($P = 0.13$). Overall seedling survival was highest beneath shrubs, irrespective of beetle addition (see Fig. 2c).

MICROSITE COVER AND LITTER EFFECTS

In *Experiment 2*, microsite cover (shrub vs. artificial shelter) affected seedling mortality by desiccation ($\chi^2_{[1]} = 7.66$,

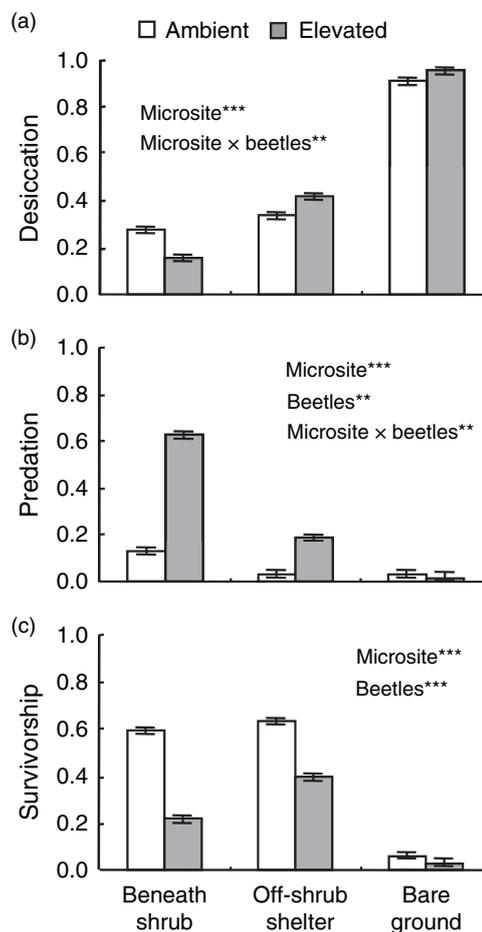


Fig. 2. *Austrocedrus chilensis* seedling mortality by (a) desiccation and (b) predation and (c) overall seedling survival across shrub and off-shrub microsites under ambient and elevated beetle densities. Bars show means \pm 95% confidence limits ($n = 7$). Asterisks denote significant effects: ** $P < 0.01$, *** $P < 0.001$.

$P = 0.0056$; Fig. 3a). This reflected the increased mortality that resulted from adding litter to off-shrub shelters (litter \times microsite: $\chi^2_{[1]} = 17.84$, $P < 0.00001$; litter: $\chi^2_{[1]} = 13.36$, $P = 0.00026$). Overall, seedling predation was higher beneath shrubs than artificial shelters (microsite: $\chi^2_{[1]} = 5.55$, $P = 0.018$), while litter presence increased predation rates in both microsites ($\chi^2_{[1]} = 17.29$, $P < 0.00001$). Litter removal from shrubs reduced seedling predation, whereas litter addition slightly increased predation under off-shrub shelters (Fig. 3b). This resulted in predation mortality being highest under intact shrubs. Overall, final survival did not differ between microsites ($P = 0.53$), but litter decreased survival ($\chi^2_{[1]} = 47.67$, $P < 0.00001$), especially in off-shrub, sheltered microsites (litter \times microsite: $\chi^2_{[1]} = 6.44$, $P = 0.011$; Fig. 3c).

SEEDLING DENSITY EFFECT

In *Experiment 3*, neither desiccation mortality ($\chi^2_{[2]} = 4.42$, $P = 0.11$; Fig. 4a) nor seedling loss to herbivory ($\chi^2_{[2]} = 3.06$, $P = 0.22$; Fig. 4b) depended on initial patch

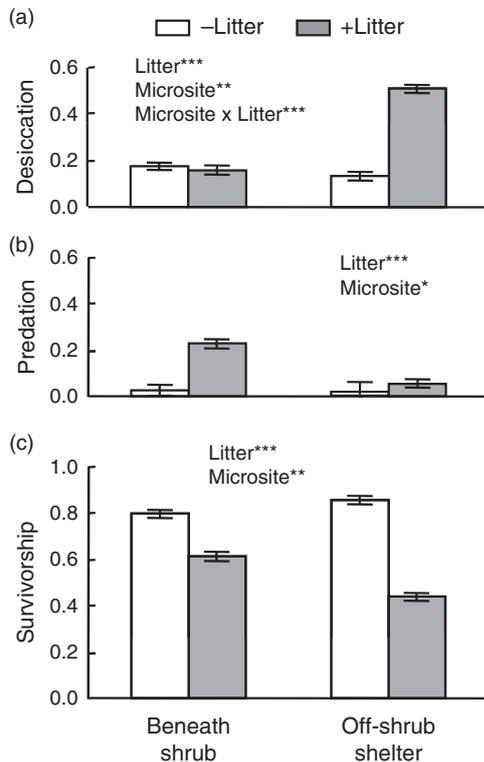


Fig. 3. Litter effects on *Austrocedrus chilensis* seedling mortality by (a) desiccation and (b) predation, and (c) overall seedling survival, under ambient beetle densities. Bars show means \pm 95% confidence limits ($n = 10$). Asterisks denote significant effects: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

density. Nevertheless, high-density patches with 8–16 seedlings were more frequently encountered by insects (> 80%) than two-seedling patches (50%) ($\chi^2_{[1]} = 7.51$, $P = 0.0063$), irrespective of microsite type. Predation mortality in shrub microsites was twice as high as in off-shrub shelters ($\chi^2_{[1]} = 17.63$, $P < 0.00001$; microsite \times density, $P = 0.14$), whereas desiccation mortality was higher under artificial shelters ($\chi^2_{[1]} = 11.73$, $P = 0.00061$; Fig. 4). Thus, pooling over seedling densities, final survival was similar in shrub and off-shrub sheltered microsites (20.5 vs. 23.9%, $P = 0.64$), and final recruitment (number of surviving seedlings) increased with initial patch density.

SEEDLING SUSCEPTIBILITY TO HERBIVORY

In non-choice feeding trials, newly emerged, 1-week-old seedlings experienced higher mortality by *Nyctelia* herbivory than 3-week-old plants ($\chi^2_{[1]} = 51.37$, $P < 0.00001$), whereas not one 6-week-old plant was killed (Fig. 5a). For surviving seedlings, both the relative leaf damage ($\chi^2_{[2]} = 26.72$, $P < 0.00001$, Fig. 5b) and absolute number of leaves consumed by *Nyctelia* ($\chi^2_{[2]} = 28.5$, $P < 0.00001$) were higher in 3-week-old seedlings (2.2 ± 0.2 leaves per plant). The larger, 6-week-old plants suffered very little herbivory (0.9 ± 0.3 leaves per plant). Mortality was produced by beetles clipping the hypocotyle or consuming all green tissues (see Fig. S1).

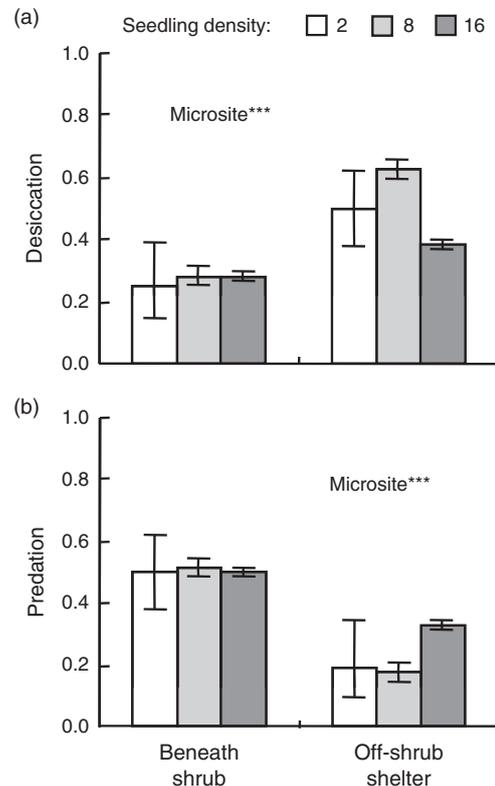


Fig. 4. Effect of initial patch density on *Austrocedrus chilensis* seedling mortality by (a) desiccation stress and (b) predation, under ambient beetle densities. Bars show means \pm 95% confidence limits ($n = 8$). Mortality was density independent and overall survival did not differ among treatments ($P > 0.10$). Asterisks denote significant effects: *** $P < 0.001$.

Seedlings damaged or killed in laboratory trials had the same marks attributed to beetle herbivory in the field experiments.

Discussion

Herbivory has long been recognized as a major factor modifying plant competitive interactions (Harper 1977; Hämbäck & Beckerman 2003). Yet the role of herbivores in mediating apparent competition in plant communities has not received much attention (Chaneton & Bonsall 2000; Rand 2003; Caccia, Chaneton & Kitzberger 2006, 2009; Orrock, Witter & Reichman 2008). Here, we showed that consumers seeking refuge under habitat-forming plants may strongly alter the strength of recruitment facilitation in harsh environments. We found that shrubs exerted opposing impacts on tree seedlings by facilitating survival through physical stress alleviation and by simultaneously increasing the risk of insect herbivory. Noteworthy, apparent competition increased mortality to varying degrees but did not fully override seedling facilitation by shrubs in this ecotonal community (Figs 2–4). A few studies had observed similar consumer-mediated effects of nurse plants on their protégés (Callaway 1992; Rousset & Lepart 2000; Ibañez & Schupp 2001), although the underlying mechanisms remained unexplored.

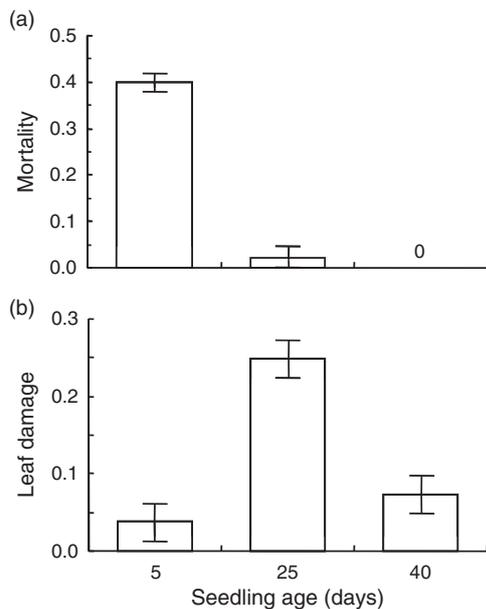


Fig. 5. Effect of herbivory by *Nyctelia rotundipennis* on *Austrocedrus chilensis* seedlings of different age in non-choice feeding trials. (a) Proportion of plants killed by predation. (b) relative damage (leaves eaten divided by total number of leaves) for surviving plants. Bars show means \pm 95% confidence limits ($n = 10$ trays). Each tray had 10 even-aged seedlings and one adult beetle. Age: days since emergence.

DIRECT AND INDIRECT EFFECTS OF NURSE SHRUBS ON SEEDLING SURVIVAL

Abiotic stress was the overwhelming cause of seedling mortality in open, bare-soil interspaces. This was observed in other stressful environments where shrubs also enhanced woody seedling survival through habitat amelioration (e.g. Callaway 1992; Gómez-Aparicio *et al.* 2004). We found that survivorship increased when seedlings in off-shrub microsites were protected from direct solar radiation. However, desiccation mortality differed between shrub canopies and off-shrub shelters, being higher under the shelters (see Figs 2–4). Our results suggest that shrubs may protect *Austrocedrus* seedlings against heat stress or photoinhibition (Callaway 1995), although other microsite factors such as soil organic matter and moisture levels may be also involved. Shrub shade reduces soil temperatures (Mazia, Chaneton & Kitzberger 2006) creating moister microsites relative to bare soil patches. By manipulating water availability, Kitzberger, Steinaker & Veblen (2000) were able to show that buffering of drought stress contributed to enhance tree recruitment in shrub patches. While facilitation of *Austrocedrus* survival can remain important through later life stages (Letourneau, Andenmatten & Schlichter 2004), shrub competition may still decrease tree seedling growth (Holzapfel & Mahall 1999; Kitzberger, Steinaker & Veblen 2000; Rousset & Lepart 2000).

In agreement with our initial hypothesis, numerical aggregation of beetles led to increased seedling mortality under shrub canopies (Fig. 1). Insect herbivory was the pre-eminent factor limiting survivorship in shrub microsites. Similar forms of

apparent competition have been reported for other systems in which plants giving refuge to invertebrate (Reader 1992; Facelli 1994; Ibañez & Schupp 2001) or vertebrate (Gill & Marks 1991; Lambrinos 2006; Caccia, Chaneton & Kitzberger 2009) herbivores indirectly inhibited recruitment of a focal species. Thus, asymmetric apparent competition between plants induced by habitat selection by mobile herbivores appears to be more pervasive than previously thought (Connell 1990). Because most tree seedlings in open interspaces were rapidly killed by physical stress (Fig. 2a), there was little chance for beetles to prey on them. Yet, even when seedlings escaped desiccation under off-shrub shelters, beetle predation remained a greater mortality source beneath shrubs. This finding supports the assumption that shrub patches offered resources other than tree seedlings to attract tenebrionid beetles. The spatial segregation of biotic and abiotic causes of seedling mortality may generate species regeneration patterns reflecting the local distribution of dominant plants that create adequate habitat for both other plants and resident consumers (De la Cruz *et al.* 2008; Caccia, Chaneton & Kitzberger 2009).

FACTORS INFLUENCING THE STRENGTH OF APPARENT COMPETITION

The magnitude of seedling predation, and hence the extent to which apparent competition counteracted facilitation, depended on insect abundance. Beetle addition increased predation beneath shrubs by threefold. It is possible that predation rates under elevated beetle densities may not give a realistic measure of the tree seedling–beetle interaction strength (Schmitz 2004). However, similarly high predation mortality was recorded under natural beetle densities during *Experiment 3* (cf. Figs 2b,4b), perhaps reflecting enhanced beetle activity due to the wetter and cooler conditions of early summer 2003. The consistency of experimental results obtained in different years under contrasting climatic conditions and beetle activity levels suggest that mortality patterns were not an artefact of the experimental set-up. Although beetles aggregated in shrub patches, predation also altered seedling survival in off-shrub microsites. As predicted, the addition of *Nyctelia* increased mortality of seedlings protected by artificial shelters (Fig. 2b). Thus apparent competition ‘spilled over’ from nurse-plant zones onto adjacent, open interspaces, and this spatial effect was magnified by high insect densities. Similar neighbourhood interactions can be expected in other spatially structured plant communities (Orrock, Witter & Reichman 2008). These results concur with spatial models of apparent competition predicting that high predator abundances homogenize the risk of attack across patches of different prey productivity (Holt 1984; Holt & Kotler 1987). Seedling predation in off-shrub shelters was nonetheless relatively low, probably because shelters did not provide adequate microhabitat to retain beetles (Mazia, Chaneton & Kitzberger 2006). As such spatial indirect effects depend on predator habitat use and activity levels (Holt 1984; Holt & Kotler 1987), we expect them to vary in magnitude among climatically different

years (Caccia, Chaneton & Kitzberger 2006). Apparent competition via insect spill-over from shrub crowns should be stronger in wetter years, when seedlings have greater chances of surviving in bare soil patches (Kitzberger, Steinaker & Veblen 2000) and beetles would be more active (see Fig. 4b).

Plant litter can influence recruitment through a variety of direct and indirect mechanisms (Facelli 1994; Suding & Goldberg 1999). We found that litter generally had a negative impact on tree seedling survival (Fig. 1), yet the nature of the interaction was conditional on the microsite. In off-shrub microsites, litter did not affect seedling predation but increased mortality by desiccation. It is possible that litter cover reduced air movement at the soil surface, increasing heat stress for seedlings. On the other hand, litter presence increased predation beneath shrubs and thus contributed to the apparent competitive effect of nurse shrubs on tree recruitment. Shrubs provide beetles with shelter from physiological stress and also accumulate large amounts of plant debris, a major food source for tenebrionids (Mazia, Chaneton & Kitzberger 2006). By feeding on tree seedlings insect detritivores may obtain water or nutrient resources less available from litter (McCluney & Sabo 2009). So far, few studies had focussed on the importance of trophic (food-mediated) and nontrophic (habitat-mediated) linkages mediating apparent competition (Caccia, Chaneton & Kitzberger 2006). Our findings indicate that shrubs indirectly altered seedling survival by providing food (Holt & Kotler 1987; Rand 2003) as well as shelter (Connell 1990; Orrock, Witter & Reichman 2008) to tenebrionids (Fig. 1). Local heterogeneity in litter production among shrub patches could create transient refuges for tree recruitment through spatial variation in apparent competition (Holt 1987; Facelli 1994).

Seedling emergence under nurse plants can vary widely in both space and time (Kitzberger, Steinaker & Veblen 2000; Brooker *et al.* 2008), which may in turn affect the likelihood of predation (Agrawal, Lau & Hämbäck 2006). Seedlings could find refuge in low-emergence microsites, if herbivores forage in a density-dependent fashion and aggregate numerically in high-density food patches (Holt 1987; Holt & Kotler 1987). Alternatively, survival could increase in high-density patches if predator saturation (Holt & Kotler 1987) or prey 'crowding' decrease the per-capita risk of attack (Connell 2000). In the study system, beetles operate as donor-controlled consumers, which are maintained by a large, non-living food base, but also feed opportunistically on a living, low-density prey. Thus, beetle activity levels may not be linked to seedling dynamics in a density-dependent manner, which should relax apparent competition (Holt 1987; Holt & Lawton 1994; Chesson & Kuang 2008). Our experimental results were consistent with the latter scenario, as predation mortality did not change with seedling patch density (Fig. 4b). Intriguingly, high-density seedling patches were more readily encountered by insects. This suggests that other factors (e.g. handling time, seedling age) may have constrained the functional response of beetles to local seedling availability (Holt & Kotler 1987). That herbivory reduced survivorship at a fixed rate implies that tree seedling recruitment would increase with initial emergence success (Kitzberger, Steinaker & Veblen 2000).

Although 1-week-old seedlings were highly vulnerable to predation, insect damage decreased rapidly with seedling age. It thus appeared that, within just a few weeks of emergence, tree seedlings would have grown into a kind of ontogenetic refuge, which narrowed their 'window of susceptibility' to beetle predation. Such ontogenetic shifts in resistance to herbivory could reflect changes in tissue quality or accessibility to insects (Boege & Marquis 2005). More generally, prey-size refugia are known to play a major role in stabilizing predator-prey interactions (Chase 1999; Berryman & Hawkins 2006). While in non-choice trials 3- to 6-week-old plants experienced little damage (Fig. 5), in the field, age effects could interact in complex ways with other time-dependent factors such as seasonal weather conditions, beetle abundance-activity levels, seedling patch depletion and spatial location. Nevertheless, results suggested that seedling transition to a less vulnerable stage likely helped to reduce the total impact of apparent competition, influencing the balance of positive vs. negative interactions under nurse shrubs. Similar life-stage specific effects have been found to modulate the balance between facilitation and resource competition in arid communities (Callaway & Walker 1997; Escudero *et al.* 1999; Rousset & Lepart 2000; Maestre *et al.* 2003b).

THE BALANCE OF FACILITATION VS. APPARENT COMPETITION

First-summer survival constitutes a major bottleneck for tree establishment in the study system as well as in other xeric environments (Kitzberger, Steinaker & Veblen 2000; Gómez-Aparicio *et al.* 2004). We knew that severe drought years offset shrub facilitation. Yet we had only circumstantial evidence that insects could alter recruitment. Our results indicate that apparent competition via insect herbivory can be a significant force altering the net balance of nurse-plant effects on tree seedling establishment. Importantly, several factors appeared to prevent seedlings from being wiped out by herbivory, including low beetle activity, density-independent herbivory, seedling growth into an age or size refuge, and the fact that tenebrionid beetles act as facultative herbivores. Thus, facilitation was found to be the prevalent interaction during early tree recruitment under shrubs (see also Callaway 1992; Ibañez & Schupp 2001). These findings, however, may apply chiefly to moderately stressful years, when facilitative shrub effects should prevail (Kitzberger, Steinaker & Veblen 2000). We hypothesize that the net outcome of habitat facilitation and apparent competition may be regulated by the severity of environmental stress, as shown before for the facilitation-competition balance (Callaway & Walker 1997; Brooker *et al.* 2008). In very dry years, abiotic stress offers little opportunity for seedling survival regardless of microsite cover. By contrast, in wetter and cooler years, when facilitation is reduced by improved conditions in bare soil areas, apparent competition might become the dominant force under nurse plants, leading to higher recruitment in open microsites. The latter would mirror the impact of indirect effects mediated by seedling consumers in mesic systems (Gill & Marks 1991; Reader 1992; Lambrinos 2006; Caccia, Chaneton & Kitzberger 2009). Inter-

annual variability in the balance of facilitation vs. apparent competition, coupled with small-scale heterogeneity in insect activity, could influence the spatio-temporal dynamics of the study shrub steppe–woodland ecotone.

Recent claims for a more pluralistic theory have prompted research on how positive interactions contribute to community structuring along gradients of abiotic stress and consumer pressure (Bertness & Callaway 1994; Bruno, Stachowicz & Bertness 2003; Michalet *et al.* 2006; Graff, Aguiar & Chaneton 2007; Smit *et al.* 2007; Smit, Rietkerk & Wassen 2009). Associational defences from herbivory have been proposed to increase in importance with increasing consumer pressure towards benign habitats (but see Craine 2008; Smit, Rietkerk & Wassen 2009). Contrary to these predictions, the net balance of neighbourhood interactions may shift with herbivore pressure from positive to neutral, or even negative, if consumers perceive nurse plants as physical refugia and tend to aggregate in otherwise suitable recruitment microsites (cf. Bruno, Stachowicz & Bertness 2003; this study). Further, in less harsh physical environments, the negative indirect effect of apparent competition could outweigh the positive effect of direct facilitation. These considerations imply that the nature of consumer-mediated indirect interactions along stress gradients will depend on how dominant herbivores utilize local plant mosaics (see Agrawal, Lau & Hämbäck. 2006). We argue that a comprehensive theory of the relative importance of positive and negative interactions along environmental gradients should explicitly consider the role of apparent competition elicited by habitat-forming plants.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. A description of field methods for sampling beetle abundance-activity levels using pitfall traps placed in sheltered and open microsites.

Figure S1. Photographs showing the tenebrionid *Nyctelia rotundipennis* feeding on a newly emerged seedling of *Austrocedrus chilensis*.

Table S1. Abundance-activity levels of major tenebrionid beetle species measured during each of the experiments, and results of statistical analyses of microsite effects on beetle activity.

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