Fire modulates the effects of introduced ungulates on plant–insect interactions in a Patagonian temperate forest

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Abstract Disturbances like biological invasions and fire may affect in unexpected ways plant-animal interactions. In northwestern Patagonia, introduced ungulates (cattle, horses and deers) are widespread and very common occupying more than 50% of forests and shrublands, widely affecting these habitats. In addition, fire play a major role in creating landscape patterns in this region. We evaluated whether fire modify the impacts of introduced ungulates on plant-animal interactions. In a mature forest (unburnt) and in an early post-fire area (burnt) we used structural equation modeling (SEM) to analyzed the impacts of introduced ungulates on insect herbivory, pollination and pre-dispersal seed predation on *Berberis darwinii*, one of the most common understory shrub of temperate forests. We found that the effects of cattle on pollination and fruit set depended on the habitat condition (i.e. unburnt or burnt). Introduced ungulates in unburnt forest decreased fruit set through a reduction on pollinator visits. Conversely, introduced ungulates in burnt forest increased pollinator visits and flower production without affecting fruit set. On the other hand, damage patterns (herbivory and fruit/seed predation) were unaffected by cattle in both forests types. Either, low browsing pressure or induction of plant defences may explain our results. This study illustrates how modifications on biotic and abiotic conditions produced by fire may affect in complex ways the effect of introduced ungulates on plant-animal interactions.

Keywords *Berberis darwinii* · Cattle · Patagonian forest · Plant-animal interactions · Post-fire

Introduction

Grazing, browsing and trampling by introduced ungulates are a common component of ecosystems throughout the world (Belsky 1986; Nuñez et al. 2010; Vázquez 2002). These animals modify primary productivity, nutrient cycles, soil properties and fire regimes, which all have an impact on the ecology of other organisms (Hobbs 1996; Stritar et al. 2010; Vázquez and Simberloff 2003). Introduced ungulates might disrupt plant-animal interactions affecting both animals and plants through direct and indirect ways (Rodriguez-Cabal et al. 2013; Rooney and Waller 2003; Vázquez and Simberloff 2004). On plants, introduced ungulates can directly affect plant growth, architecture, chemistry and phenology (Smith et al. 2015) and/or indirectly by modify plant–plant interactions through selective foraging and/or modification of floral traits (Mothershead and Marquis 2000; Smith

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Y. Sasal (✉) · A. Farji-Brener · E. Raffaele
Laboratorio Ecotono, Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Universidad Nacional del Comahue-CONICET, Pasaje Gutiérrez 1125, 8400 S. C. de Bariloche, Río Negro, Argentina
e-mail: sasal.yamila@gmail.com

et al. 2015). On animals, introduced ungulates affect insects directly by accidental predation (Gómez and González-Megías 2002) or nests damage (Gómez and González-Megías 2007; Kearns et al. 1998), and/or indirectly through removal of food resources (i.e. leaves, flowers, fruits, seeds) (Bolker et al. 2003; de Paz and Raffaele 2013; Kearns and Inouye 1997). Plant–insect interactions are crucial for maintaining the structure and biodiversity of ecosystems (Fisher 1998; Traveset and Richardson 2006; Valiente-Banuet et al. 2015), but the effects of introduced ungulates on biotic interactions are less documented than those focused on community structure. Despite this, some studies showed relevant impacts, both on plant-animal mutualisms (Rodriguez-Cabal et al. 2013; Vázquez and Simberloff 2003, 2004), and on antagonistic interactions like herbivory (Gómez and González-Megías 2007). Moreover, the sign and magnitude of the effect of introduced ungulates on plant-animal interactions may depend on the biotic or abiotic context (Chamberlain et al. 2014).

Local biotic and abiotic conditions affect the abundance, behavior and foraging selectivity of non-native species, so the magnitud and even the direction of impacts of the same species may differ across heterogeneous sites (D'Antonio et al. 2000; Kestrup and Ricciardi 2009; Randall and Walters 2011). Episodic disturbance agents, such as fire, interact with introduce ungulates across time and space (Wisdom et al. 2006). In particular, if the disturbance includes directional change such as a shift in abiotic conditions, the environment may become less hospitable for natives but not necessary for non-natives, and could modify the tempo and magnitude of invasive species impacts (Byers 2002; Didham et al. 2007). However, when and how disturbance acts as modulator of non-native species impacts has been poorly explored (Ricciardi et al. 2013).

In northwestern Patagonia Argentina, herbivory by natives animals are less relevant than those produced by non-natives (Iranzo et al. 2013; Merino et al. 2009). Natives ungulates such as huemul (*Hippocamelus bisulcus*) and pudu pudu (*Pudu pudu*) are present in low population densities and their impact has always been limited to ecotones zones (Vázquez 2002). On the other hand, introduced ungulates like cattle (*Bos taurus*), horses (*Equus caballus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), sheep (*Ovis aries*) and goats (*Capra hircus*) arrived by Europeans by the late eighteenth century (Jaksic et al. 2002; Veblen et al. 1992) and now show high density and impact. Currently, introduced ungulates are widespread occupying more than 50% of Patagonian forests and shrublands (Jaksic 1998; Jaksic et al. 2002; Merino et al. 2009; Navas 1987). Introduced ungulates have greatly affected the vegetation of the region, preventing regeneration of some tree species, shifting dominance towards spiny shrubs, favoring exotic plants, and in some circumstances shifting the structure of forests from tall trees to shrublands (Martín et al. 1985; Piazza et al. 2016; Relva et al. 2010; Relva and Veblen 1998; Vázquez 2002; Veblen et al. 1989, 1992). In addition, disturbances like fire, both natural and human-set, had played historically a major role in creating landscape patterns in this region along the precipitation gradient from dry steppe to wet Andean rain forests (Kitzberger and Veblen 1999; Veblen et al. 2003, 2011). Hight severity fire events created a mosaic of patches of different structure, age and species composition (Mermoz et al. 2005). Some studies shown that introduced ungulates, particularly cattle, affected post-fire plant regeneration in temperate forest modifying vegetation structure and composition, retarding plant succession and growth (Blackhall et al. 2008; Raffaele and Veblen 2001; Raffaele et al. 2011; Tercero-Bucardo et al. 2007) and facilitating the introduction of non-native species (Nuñez et al. 2008). Although in this region introduced ungulates and fire have been present togheter since late eighteenth century, their effects on plant-animal interaction have been studied separately.

The goal of this study was to evaluate whether fire modify the impacts of introduced ungulates on plant-animal interactions, using structural equation modeling (SEM). Particularly, we studied cattle browsing effects in a burnt and unburnt areas on insect herbivory, pollination and pre-dispersal seed predation on *Berberis darwinii* Hook. (Berberidaceae), an abundant native understory shrub of Patagonian temperate forests.

Materials and methods

Study area

We conducted the study in the Andean forest located on the eastern side of "Lago Espejo", in Nahuel Huapi

National Park, Patagonia Argentina (40°38′S–71°42′W; 850 m above sea level). In this region, the mean annual temperature is 8 °C and it ranges from a minimum of 2 °C (July) to a maximum of 23 °C (January). Precipitation is concentrated mainly in autumn and winter as snow with an annual rainfall of 2000 mm (Barros et al. 1983). Native forest vegetation in the area belongs to the Subantartic biogeographical region (Cabrera 1994). Dominant trees are the evergreen south-beech *Nothofagus dombeyi* and the conifer *Austrocedrus chilensis*. The understory is dominated by Valdivian temperate rain forest species like bamboos, ferns, and evergreen shrubs (Cabrera 1994).

In January 1999, approximately nine ha of a mixed *Nothofagus-Austrocedrus* forest were affected by an intense wildfire that was quickly suppressed (Administración de Parques Nacionales 1999). The fire severity was high and it consumed all forest litter and killed the above-ground vegetation, leaving all standing trees dead ("Appendix 1"). Because *Nothofagus* and *Austrocedrus* forests are characterized by obligate seed reproduction, post-fire stands are replaced, early in the succession by shrub species with vigorous post-fire resprouting capabilities (Kitzberger and Veblen 1999; Veblen et al. 2003). Hence, this burnt area is characterized by dead tree trunks standing or fallen with an understory dominated by shrubs, herbaceous and bamboos.

The near unburnt forest was dominated by *N. dombeyi* and *A. chilensis,* reaching heights of 40 and 35 m, respectively ("Appendix 1"). Dominant individuals of both species are 1–1.2 m diameter-at-breast height (DBH). Probably this forest was originated after severe fires in the early part of the nineteenth century (Veblen 1989), however is considered as unburnt site because was unaffected by fire for more than 50 years (Suarez and Kitzberger 2010). Both forests (unburnt and burnt) have similar understory composition, dominated by shrubs such as *Ribes magellanicum*, *Aristotelia chilensis*, *Berberis darwinii*, *Azara lanceolata*, *Desfontainia spinosa,* tall bamboo *Chusquea culeou*, the climber *Vicia nigricans* and a variety of herbaceous species like *Acaena pinnatifida*, *Oxalis valdiviensis*, *Ozmorhiza chilensis*, *Adenocaulon chilense* and *Viola* sp.

The unburnt and burnt areas were both affected by browsing and trampling of cattle belonging to local people who are allowed to freely range over extensive areas. The distance between burnt and unburnt study areas was of 500 m, and they slightly differed in altitude; burnt area was at 890 m a. s. l. and unburnt at 840 m a. s. l. Cattle move freely among burnt and unburnt sites.

Study plant species

Berberis darwinii Hook. (Berberidaceae) called "Michay" is a native evergreen spiny shrub that reaches 1–3 m. This shrub is distributed in Chile between 37° and 43°S and inhabits the Argentinean Patagonian Andes between 37° and 45° (from Neuquén to Tierra del Fuego) (Correa 1988). It is a shadow tolerant (Allen 1991) and very common understory species at different forest types and shrublands. Their leaves are simple but grow in fascicles of up to 10 folliates, dark green with a clear underside, and a dentate-spiny edge of 1–2 cm. The stems have five spines at the base of the fascicles (Correa 1988). The orange-yellow flowers cluster in racemes made up of 8–14 hermaphrodite flowers that are produced from October to November (Paritsis et al. 2006) ("Appendix 2"). Pollination is entomophily, being the most common pollinators bees, bumblebees and flies (Morales and Aizen 2002), the reproductive system is auto-incompatible and present a high pollinators dependence for reproduction (Vázquez and Simberloff 2004). The fruit is a bluish black berry, 0.5 cm across, containing 3–6 seeds (Brion et al. 1988) and their seeds are dispersed by birds. *B. darwinii*, fruits mature between November and January (Paritsis et al. 2006). After fire it colonize the understory by resprouting or being dispersed by birds. Once other more palatable species become rare, it is slightly preferred by cattle (Blackhall et al. 2008). Yet, it seems tolerant to browsing since in areas under ungulates pressure *B. darwinii* increase their abundance (De Pietri 1992; Veblen et al. 1989). We could not find information about herbivorous insects or seed/fruit predators that feed on *B. darwinii*.

Sampling design

In 2002, we placed eight 25 × 25 m plots; four plots were installed in unburnt and four in burnt areas, all with equal cattle presence ("Appendix 3"). Cattle move freely among burnt and unburnt sites. These plots are part of a network of long term experiments which were installed since 2001 and located in different forest types in the Nahuel Huapi and Lanín National Parks, Argentina. In each plot, we placed 20 permanent subplots of 2 m^2 located across two lines of 10 subplots each, were we measured cattle browsing and some vegetation variables described below. In addition, in these plots we randomly selected a total of 56 *B. darwinii*, plants of similar size (mean = 91.5 cm tall), 28 in the unburnt forest area and 28 plants in the adjacent burnt forest, to measure plant–insect interactions ("Appendix 4").

Environmental and site variables

To characterize unburnt and burnt forests we recorded six variables per plot: light availability, air temperature, air humidity, cattle browsing, understory vegetation cover, plant species richness and *B. darwinii* cover. Light availability was estimated by taking hemispherical photographs on each *B. darwinii* selected. Photographs were taken at a height of 1 m above the ground using a leveled digital camera (CoolPix 995 digital camera, Nikon, Japan) aimed at the zenith, using a fish-eye lens with a 180° field of view (FCE8, Nikon). All photographs were taken in overcast weather to ensure homogeneous illuminator and adequate canopy-sky contrast. Photographs were analyzed using software WinSCANOPY^{TM} for hemispherical image analysis, estimating the parameter direct site factor (DSF) which is defined as the proportion of direct radiation received below the canopy as a fraction of that received above the canopy (Gómez et al. 2004). Air temperature (C°) and air relative humidity were recorded with 6 thermal and relative humidity sensors (HOBO ® TMC6-HA) installed from November 2006 to May 2007. The sampling period was climatically an average year, neither very dry nor very hot with an annual mean temperature of 8.1 °C and mean annual precipitation of 1890 mm (Clima Bariloche Aerodrome, climatic data: 1957–2017 (Tutiempo Network 2017)). Three sensors were located in burnt forest and the other three in unburnt forest, near a *B. darwinii* plants 1 m above the ground in shaded areas and measurements were taken at 2-h intervals. Daily temperature and relative humidity were averaged per hour.

The degree of cattle browsing, understory vegetation cover, plant species richness and *B. darwinii* cover were estimated in the 20 subplots of 2 m^2 described before. In each subplot, we estimated the degree of cattle browsing by observing the number of browsed branches on each woody and climber species. Each species was assigned a browsing rating, ranging from 0 to 3, following Veblen et al. (1992) methodology (3 = heavy, most of the branches browsed, 2 = moderate, more than two branches browsed, 1 = light, one or two branches browsed and 0 = none, no evidence of browsing). Browsing rates per subplot were used to compute the mean browsing index (MBI) per plot, which indicates the intensity of browsing on all species in the area sampled. MBI = Σ BI for all species/N, where BI is the estimation of the total amount of browsing on each species in the area sampled, BI = Σ browse ratings, and N is the total number of subplots in the area. We recorded percentage cover and species identity of all vascular plant species in each subplot. The total mean cover was estimated as the sum of each species cover; hence it could be greater than 100% due to the presence of different layers.

To evaluate differences in the environmental and site variables between unburnt and burnt forest we performed one way ANOVA for each variable: solar radiation, air temperature, air relative humidity, cattle browsing index, total vegetation cover, plant species richness and *B. darwinii* cover. Each variable was estimated for each plot, four unburnt plots and four burnt plots. "Fire" was considered a fixed factor with two levels (unburnt and burnt). The variables were tested to meet assumptions of normality and homoscedasticity (Sokal and Rohlf 1999). The analyses were done with the function aov in the stats package of R statistical software (R Development Core Team 2015).

Plan–insect interactions

To determine the effects of cattle browsing on plant-animal interactions for unburnt and burnt forests, we quantified levels of insect herbivory, pollination and pre-dispersal seed predation during 2007 field season for each of the 56 *B. darwinii* selected. All the response variables listed below were assessed on the same selected plants. We measured the height (cm) of each plant and the total number of leaves produced per branch. Two or three new branches on each plant (depending on plant size) were marked at the beginning of the growing season (October), to avoid measuring herbivory on leaves of different ages. At the end of the growing season

(March–April), we measured the leaf area removed by insects. For each leaf, herbivory was quantified as leaf area removed or damaged by insects using categories depending on the percentage (%) of leaf area affected: 0: without herbivory, 1: 1–5%, 2: 6–12%, 3: 13–25%, 4: 26–50% y 5: 51–100%. We calculated the herbivory index (HI) for each branch as $HI = \sum(n_i * i)/N$; where n_i is leaves frequency per herbivory category, i is the herbivory category and N is the number of leaves per branch (Dirzo and Domínguez 1995). This method for evaluating herbivory is non-destructive, allowing for the assessment of the herbivory magnitude for a large number of leaves over a short period of time. Furthermore, this method renders herbivory values as accurate as other putatively more precise methods, such as image processing, which are more time demanding and often require detaching the leaf from the plant (Rodríguez-Auad and Simonetti 2001). This index has been used in several studies and is widely accepted as an accurate estimator of plant damage (Nuñez-Farfán and Dirzo 1991; Simonetti et al. 2007; Vásquez et al. 2007). Then, we averaged the herbivory index per plant. Damage levels represent cumulative herbivory within the whole growing season, which is considered as a direct evidence of insect consumption. Flower production was estimated by counting the total number of flowers three times along the reproductive season, which then were averaged per plant. The frequency of pollinator visits was estimated via direct observations in 10-min periods between 11:00 and 17:00 h, coinciding with peak activity of pollinator insects. On each census we registered the number of flowers observed and the number of visited flowers. Pollinator visit frequency per plant was calculated as the average of flower visited/flower observed during each 10′ census. We made between 2 and 4 censuses per plant during the flowering period, with a total of 201 census. The reproductive success was estimated as fruit set, measured with tagging flowers in 3 branches and calculating the rate of fruits per flowers. Finally, to estimate fruit and seed predation we collected 20 ripe fruits per plant before dispersion. Each fruit was classified as healthy or predated, and then all the seeds per fruit were counted and classified as damaged or healthy. Fruit or seed were considered as predated when we found larvae inside or predation signals as holes ("Appendix 2"). We estimated the percentage of predated fruits and the percentage of predated seeds per fruit for each plant.

Structural equation analysis

We developed structural equation modeling (SEM) to analyze the effect of cattle browsing on *B. darwinii*-animal interactions in unburnt and burnt forests. SEM is a useful framework for investigating the effects of habitat modifications due to its capacity to evaluate complex systems composed of non-independent variables with direct and indirect relationships (Grace 2006). We parameterized models using average values for each plant. The path coefficients are standardized regression coefficient, estimated by maximum likelihood and represent the magnitude effect (Grace 2006). The indirect effects values were obtained multiplying the respective path coefficient from the pathway proposed, and the total effect value were obtained adding direct and indirect effects. We also calculated the proportion of variance explained (Mitchell 2001). We developed meta-models described the causal relationships among variables allowing the partition of the direct and indirect effects (Shipley 2000). Our meta-models included nine variables of interest: cattle browsing, plant height, leaves production, flower production, predated fruits, predated seeds, insect herbivory, pollinator visits and fruit set ("Appendix 5"). The overall goodness of fit is commonly evaluated using a model χ^2- statistic. A p value less than 0.05 indicates a significant mismatch between model and data, suggesting model respecification (usually involving additional linkages between variables). We also used the comparative fit index (CFI) as an indicator of model fit. CFI values range from 0 to 1 with values approximating 0.95 indicating a well-fitting model; this measure is more robust to small sample sizes than others commonly used measures of model fit (Grace 2006). Prior to SEM analyses, all variable were examined for distributional properties and linearity of relationships and transformed when was needed. Because we transfored our variables to increased linearity of relationship among variables and decreased skewness and kurtosis, we also asses model fit using the Bollen-Stine bootstrapping procedure, which is robust to data that are not multivariate normal (Bollen and Stine 1992). The final 'best' model was determined when the fit of the resulting model was adecuate (χ^2- statistic $p > 0.05$ and CFI approximating 0.95) ("Appendix 6"). On the best model we applied multigroup analysis that permit the evaluation of subsets of the data (for example, burnt and unburnt) to a common model (Grace 2006). First, we estimated models for unburnt and burnt sites separately to ensure that the basic model structure was consistent with the data. Then, we conducted a multigroup analysis in which all path coeficients, covariances, and variances were constrained to be equal across groups to ensure that models differs between groups. Subsequent analyses were used to determine which parameters are equal among groups and which ones differ employing single degree of freedom χ^2 tests. The analyses was done with lavaan and semTools packages using R statistical software (R Development Core Team 2015).

The biology behind the paths: The 'best' model

Our 'best' meta-model included nine variables. In this hypothetical model (Fig. 1), the insect herbivory was modeled indirectly, with cattle browsing affecting plant height and leaf production via direct consumption of branches and photosynthetic tissues (Huntly 1991), or via affecting the environment and the resource availability. Besides the known negative effect of defolation on plant performance, sometimes herbivory produce new branches and leaves (pruning effect) via over-compensation growth (Price 1991). Also, foliar damage by insects can affect the attraction for pollinators; plants with high leaf damage may be less attractive and receive fewer visits (Fig. 1).

Pollination may also be affected by cattle browsing. Cattle may affect flower density directly by consuming flowers or indirectly through the consumption of photosynthetic tissues affecting the attractiveness of flowering plants (Mothershead and Marquis 2000). Eventually, flower production might increase under certain level of consumption of vegetative tissues by pruning effect (McNaughton 1983; Paige and Whitham 1987). Further, cattle browsing can affect pollinator visits by reducing plant attraction or may increase attraction if they compensate the damage by producing more nectar (Aizen and Feisinger 2003; Traveset and Richardson 2006) and affecting

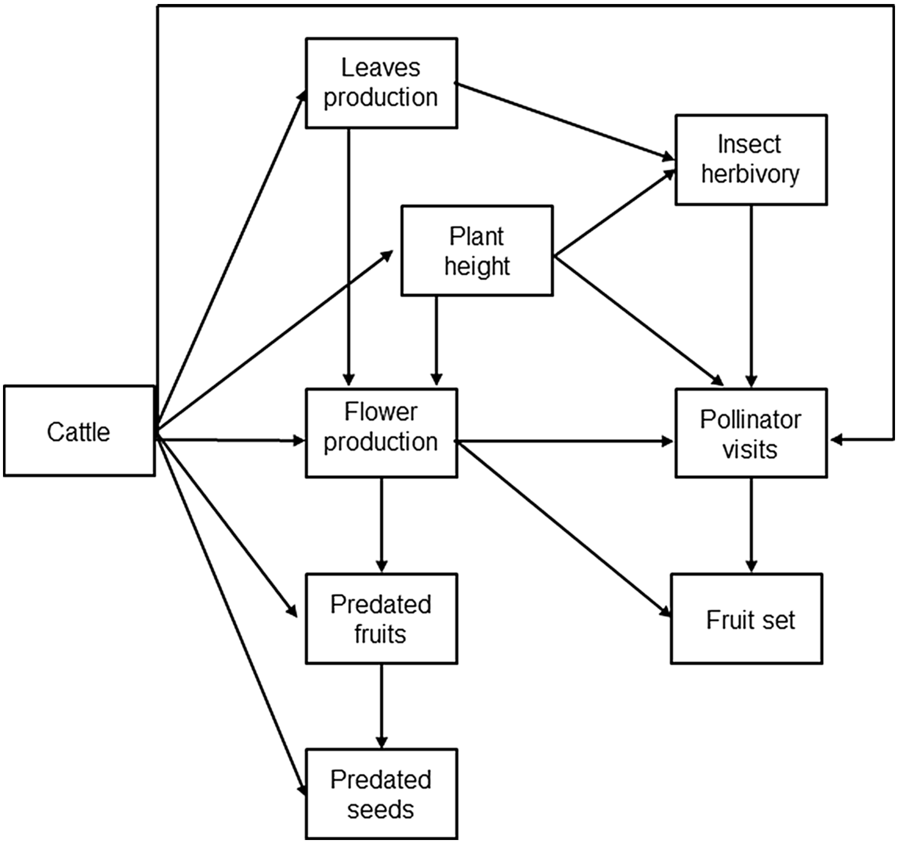

Fig. 1 Meta-model depicting hypothesized causal relationships among cattle browsing and plant-animal interactions (insect herbivory, pollination and seed predation). Variables included are: cattle browsing (mean browsing index), plant height (cm), leaves production (mean leaves produced branch^{-1}plant^{-1}), flower production (mean total flowers plant^{-1}), predated fruits (mean number of fruits predated 20 fruits^{-1} plant^{-1}), predated seed (mean predated seeds 20 fruit^{-1}plant^{-1}), insect herbivory (total herbivory index plant^{-1}), pollinator visits (mean number of visits plant^{-1}) and fruit set (mean number of fruits flower^{-1} plant^{-1})

pollinator populations by trampling of nests or generate favorable or unfavorable conditions for pollinator visits. Indirectly, cattle browsing can affect the reproductive success measured as fruit set by three ways: (1) affecting the frequency of pollinator visits, (2) affecting the production of flowers, or (3) first affecting the production of flowers which in turn affects the frequency of visits (Fig. 1). In addition, plant height can affect pollinator attraction that could increase or decrease visits.

Pre dispersal seed predation was modeled by cattle browsing affecting flower production as described above, and flower production affecting the rate of oviposition of insects whose larvae feed on fruit. In addition, cattle can affect fruit predation of fruits due to changes in production, phenology or chemistry of the fruits that affect the plant attraction for insects (Freeman et al. 2003; Juenger and Bergelson 1998; Lehtilä and Strauss 1997) or by effects on populations of fruit-eating insects (Gómez and González-Megías 2007). The direct effect of cattle on seed predation involves effects that are not mediated by the production of flowers or by fruit predation, such as insect mortality caused by trampling or browsing, or the habitat changes that affects population insects that feed on seeds. Indirectly, cattle can affect seed predation by changes in leaf production that affect the flowers production, which in turn, may affect the rate of oviposition of the fruit predators insect. The pulp consumption can facilitate seed consumption or reduce consumption because the fruit being predated decrease the attraction for seed consumers, assuming pulp and seed consumers are different (Fig. 1).

Results

Environmental and site variables

Both sites, unburnt and burnt differed in most of the variables measured such as light availability, cattle browsing, vegetation cover, plant species richness and *B. darwinii* cover (Table 1). In particular, unburnt forest had 49% higher cattle browsing and 74% more cover of the focal species *B. darwinii* (Table 1). On the other hand, burnt forest had 50% higher light availability, 23% higher vegetation cover, and 23% more plant species richness than unburnt forest (Table 1). Fire did not modify air temperature and air humidity, being similar in both forest types (Table 1).

Plant–insect interactions

The best overall model fitted well with the data ($\chi^2 = 17.53$, df = 18, $P = 0.49$, Fig. 2). Separate analyses for unburnt and burnt showed that the data for both groups fit to the 'best model' well (Unburnt forest,. $\chi^2 = 16.49$, df = 36, $P = 0.49$, Bentler–Bonett = 0.99; and burnt forest $\chi^2 = 10.27$, df = 36, $P = 0.70$, Bentler–Bonett = 0.997; Fig. 2). Both the low χ^2 and the high fit values indicate a good concordance between data and models. The complete constraint analysis suggests that models for unburnt and burnt sites differed between them in the relative importance of pathways (χ^2 difference test, $\chi^2 = 216$, df = 34, $P < 0.001$; these differences were indicated with asterisks in Fig. 2). In unburnt forest cattle browsing and plant height did not affect flower

Table 1 Means ± SE and ANOVA results of habitat parameters for fire effects on unburnt and burnt forests

	Unburnt			Burnt			*F*	*P*
Light availability (DSF)	**0.31**	**±**	**0.02**	**0.62**	**±**	**0.04**	**42.47**	**0.00001**
Air temperature (°C)	10.30	±	0.89	11.47	±	1.42	0.48	0.50
Air humidity (%)	82.12	±	3.38	75.29	±	5.85	1.02	0.32
Cattle browsing (MBI)	**3.44**	**±**	**0.70**	**1.74**	**±**	**0.40**	**4.72**	**0.04**
Vegetation cover (%)	**88.8**	**±**	**4.52**	**115.9**	**±**	**7.05**	**6.63**	**0.04**
Plant species richness (n°)	**23.00**	**±**	**1.12**	**30.00**	**±**	**1.69**	**7.44**	**0.03**
B. darwinii cover (%)	**2.73**	**±**	**0.73**	**0.70**	**±**	**0.35**	**6.36**	**0.02**

Significant effects are shown in bold type ($P < 0.05$)

DSF direct site factor; *MBI* mean browsing index; *N* 8, 4 burned and 4 unburned

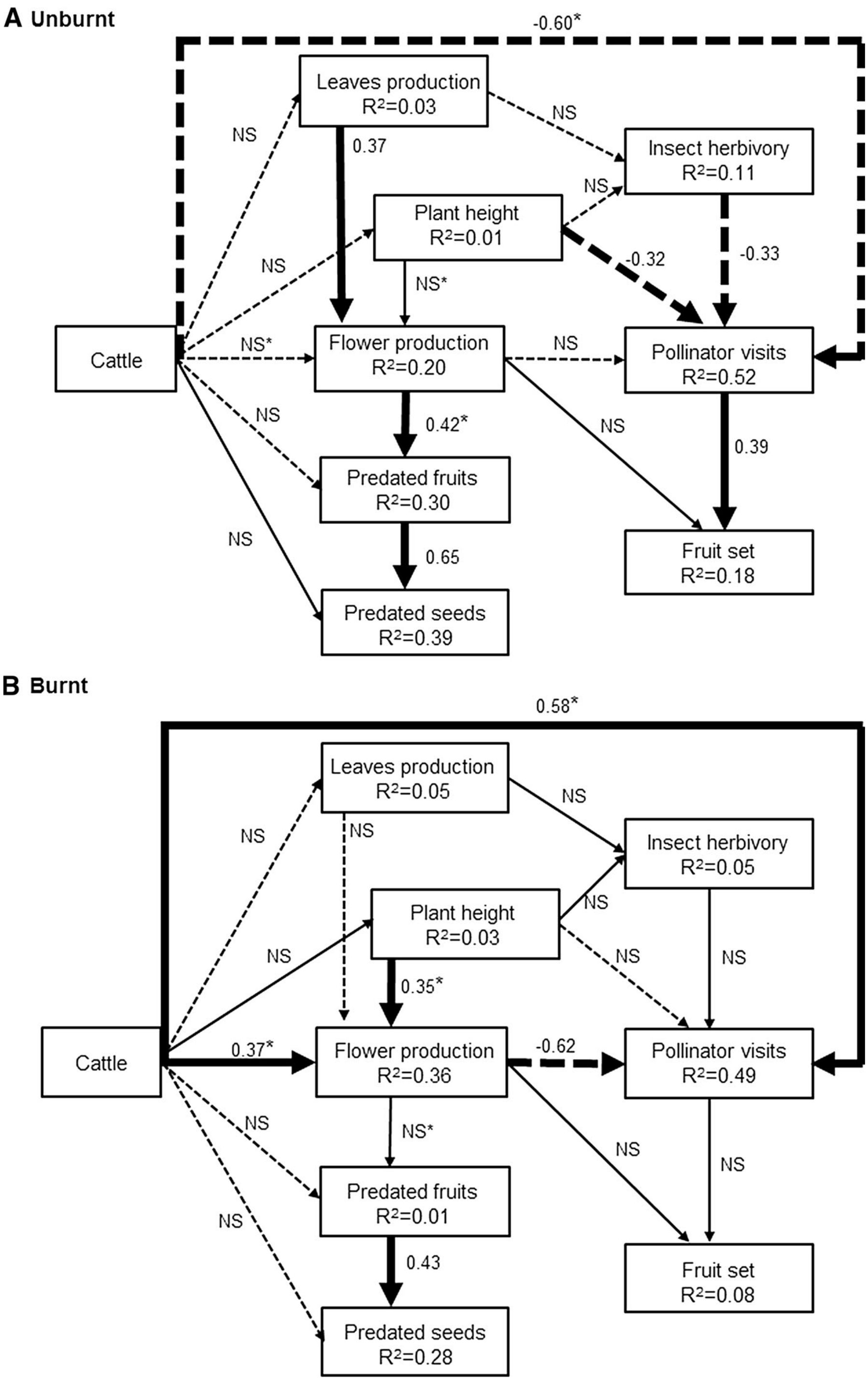

Fig. 2 Structural equation model (SEM) for *Berberis darwinii* in **A** unburnt forest and **B** burnt forest. Standardized path coefficients are significant ($P < 0.05$) and shown in *black thick arrows*. Paths indicated with *asterisk* are statistically different between groups. *Solid lines* indicate positive effects and *dashed lines* indicate negative effects. Path indicated by "*NS*" represent non-significant relationships R^2 is the proportion of variance explained by the model for each variable

production being both paths nonsignificative, also cattle browsing decreased significatively pollinator visits, and flower production increased significatively predated fruits (Fig. 2a). Conversely, in burnt forest cattle browsing and plant height increased flower production, also cattle browsing increased significatively pollinator visits and flower production without affecting predated fruits (Fig. 2b).

Some path did not differ across unburnt and burnt, but were significant on each model (parameters on the paths without asterisks, Fig. 2a y b). In unburnt forest, pollinator visits were affected negatively by insect herbivory, by plant height and cattle browsing, and thus indirectly cattle browsing decreased reproductive success measured as fruit set (Total effect: $-0.60 \times 0.39 = -0.23$, Fig. 2a). In addition, leaves production increased flower production (Fig. 2a). Conversely, in burnt forest althought cattle browsing directly increased flower production and pollinator visits they did not affect fruit set (Fig. 2b). Hence, in burnt sites cattle browsing decreased pollinator visits via flower production ($0.37 \times -0.62 = -0.23$, Fig. 2b). Finally, in both forest types, predated fruits increased predated seeds (Fig. 2a y b).

Discussion

Our results suggest that the effect of introduced ungulates on *B. darwinii*-insect interactions are partially modulated by past fires (Fig. 2). The multigroup analysis showed that the impact of introduced ungulates on plant-animal interactions was different between unburnt and burnt forests. The most conspicuous difference was related with the effect of cattle browsing on pollination. In the unburnt forest, cattle browsing directly decreased pollinator visits without a detectable effect on flower production. Conversely, in burnt forest cattle browsing increased pollinator visits and flower production (Fig. 2). Also, in the unburnt forest cattle browsing indirectly decreased fruit set, but the opposite happens in the burnt forest where cattle browsing increased flower production and pollinator visits without translating this positive effect into fruit set (Fig. 2). Therefore cattle browsing in unburnt forest could be detrimental for the plant if fruit set was an important step on the population dynamic of *B. darwinii*. Hence, our results suggest that the negative effect of cattle on pollinator visits could be neutralized or overcame in the post-fire forest. In addition, the effect of cattle browsing on pollinator visits was opposite in sign (negative in unburnt and positive in burnt) but similar in magnitude (Fig. 2). This opposite effect is difficult to explain because we did not test the mechanisms involved. In some way, cattle browsing could affect pollinator visits via their abundance, richness and behavior. The disturbance level in each forest type could affect pollinator visits, for example, butterflies are abundant with low or moderate disturbance level in their habitat compared to no disturbance (Hamer et al. 2003). Furthermore, we measured flower visitors activity not their identity, so pollinator assemblage could be different in unburnt or burnt sites independently of cattle effect (Campbell et al. 2007; Ne'eman et al. 2000; Tadey 2015). In sum, disturbance like fire increased habitat heterogeneity where cattle feed and move, affecting floral dynamics and concomitant pollinator visits in burnt forest.

In burnt forest, enhanced flower production decreased pollinator visits, a result against expectations (Fig. 2b). In general, a larger flower supply is associated with more pollinator visits, because flower quantity is an attraction cue for pollinators (Strauss et al. 1996). However, a larger flower production could reduce nectar and pollen availability per flower, and eventually reduce pollinator attraction and visits frequency known as "resource dilution effect"(Cohen and Shmida 1993; Veddeler et al. 2006).

Another difference between unburnt and burnt forests was the relationship between flower production and predated fruits, positive in unburnt forest and non-significant in burnt forest. The flower production in unburnt forest was 86% lower than in burnt forest but the percentage of predated fruits were similar across forests ("Appendix 4"), so the low number of flowers could be more attacked by fruit predators because its low availability. However, in burnt forest, where the flower production is higher this relationship was non-significant. Also, forests differed in the plant characteristics that may affect flower production such as plant height (unburnt forest) and leaves production (burnt forest, see Fig. 2). Abiotic conditions like light availability and vegetation cover greatly also differed between unburnt and burnt forests (Table 1). All these variations may influence the way in which flower production interact with plant performace.

In terms of antagonistic interactions, past fires did not influence the effect of introduced ungulates on insect herbivory, predated fruits and predated seeds (Fig. 2). Although both forests differed in several habitat conditions and in cattle browsing intensity, damage patterns in *B. darwinii* were not affected. In unburnt forest, where cattle browsing intensity was higher, plants could increased their anti-herbivore defenses (Shimazaki and Miyashita 2002). In burnt forest, cattle grazing pressure could be too low to affect this antagonistic interactions, despite the number of cattle was likely the same at both sites. Also, in both forests cattle could eliminate accidentally insect fruit/seed predators and their nests, or affecting insect plant attractions changing fruit production, reproductive phenology and/or chemistry (Freeman et al. 2003; Juenger and Bergelson 1998; Lehtilä and Strauss 1997).

We also did not found differences between both forest sites in the positive relationship between fruit predation ans seed predations. Fire did not affect this relationship, suggesting that fruit and seed predators could be the same specialist species, or if there were different species they interact positively. If predators were the same, when the larval stadia came out of the fruit produced damage in the fruit pulp, like occur in *Berberis hispanica* (Herrera 1984). Conversely, if predators were different species, the pulp predator could facilitate the activity of seed predators. So, to identify the mechanism of fruit predation on seed predation we need to know the insect's identity and their natural history.

In sum, our results indicate that fire and cattle affect pollination interaction in *B. darwinii* mainly through floral dynamics and pollinator visits and slightly via fruit set but not in burnt forest. Despite we don't know the mechanisms involved, the patterns found in this study are the necessary first step to propose mechanistic hypotheses to test in the future. Moreover, our results illustrates how modifications on biotic and abiotic conditions, produced in this case by fire, may affect in complex ways the effect of introduced ungulates on plant-animal interactions.

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Appendix 1

See Fig. 3.

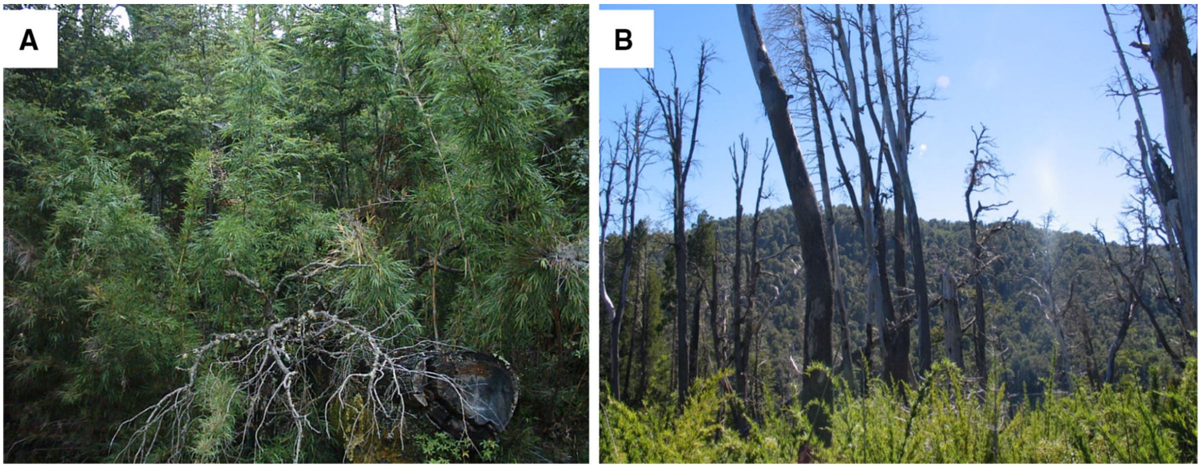


Fig. 3 Forest types, **A** unburnt and **B** burnt

Appendix 2

See Fig. 4.

Fig. 4 Details of *Berberis darwinii*: **A** shrub with flowers in racemes, **B** flowers, **C** ripe fruits, and **D** predated seeds

Appendix 3

See Fig. 5.

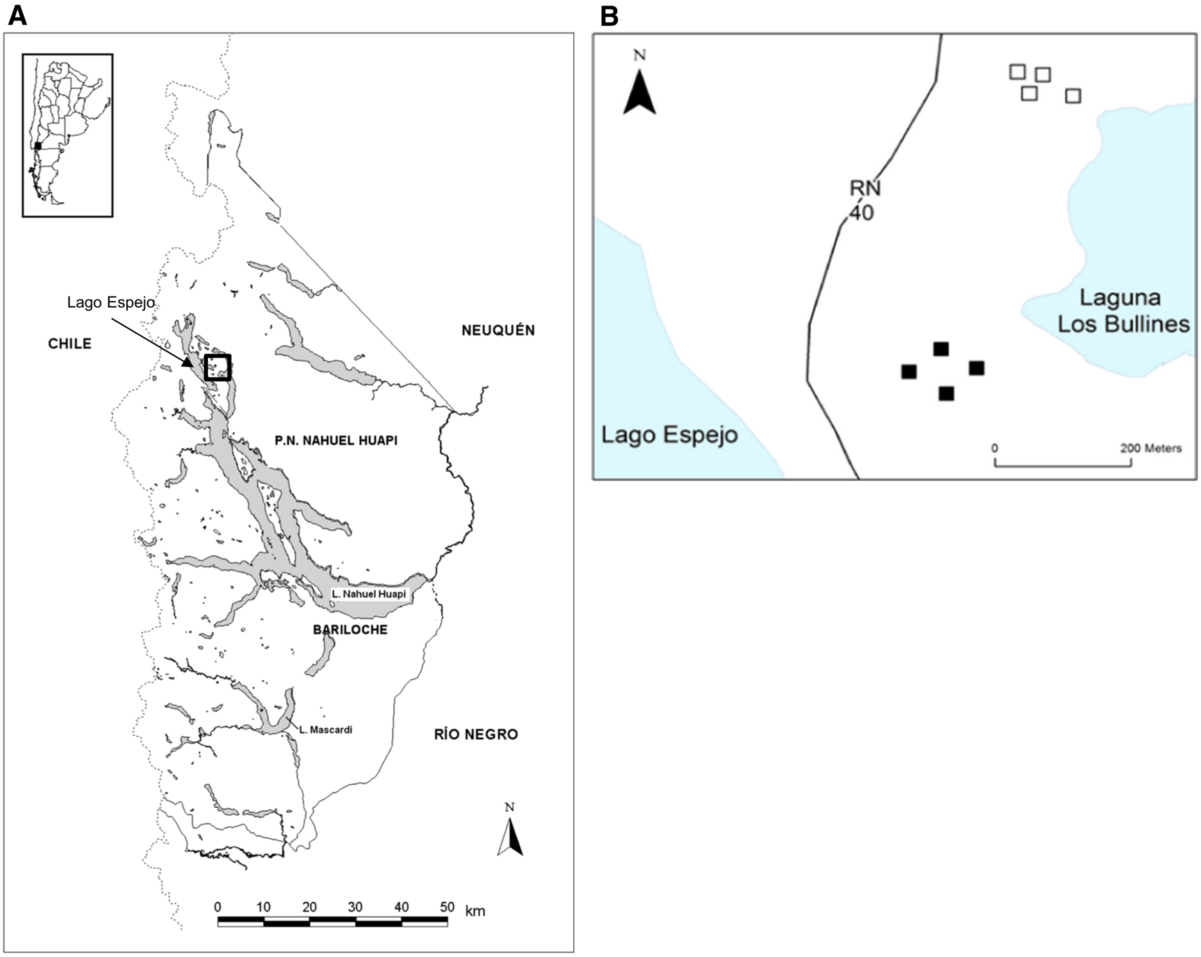


Fig. 5 Map showing the study area **A** Nahuel Huapi National Park, Argentina. **B** position of the sampling plots (*square* unburnt plots and *filled square* burnt plots)

Appendix 4

See Table 2.

Table 2 Means ± SE and ANOVA results of plants characteristics of *Berberis darwinii* in unburnt and burnt forests

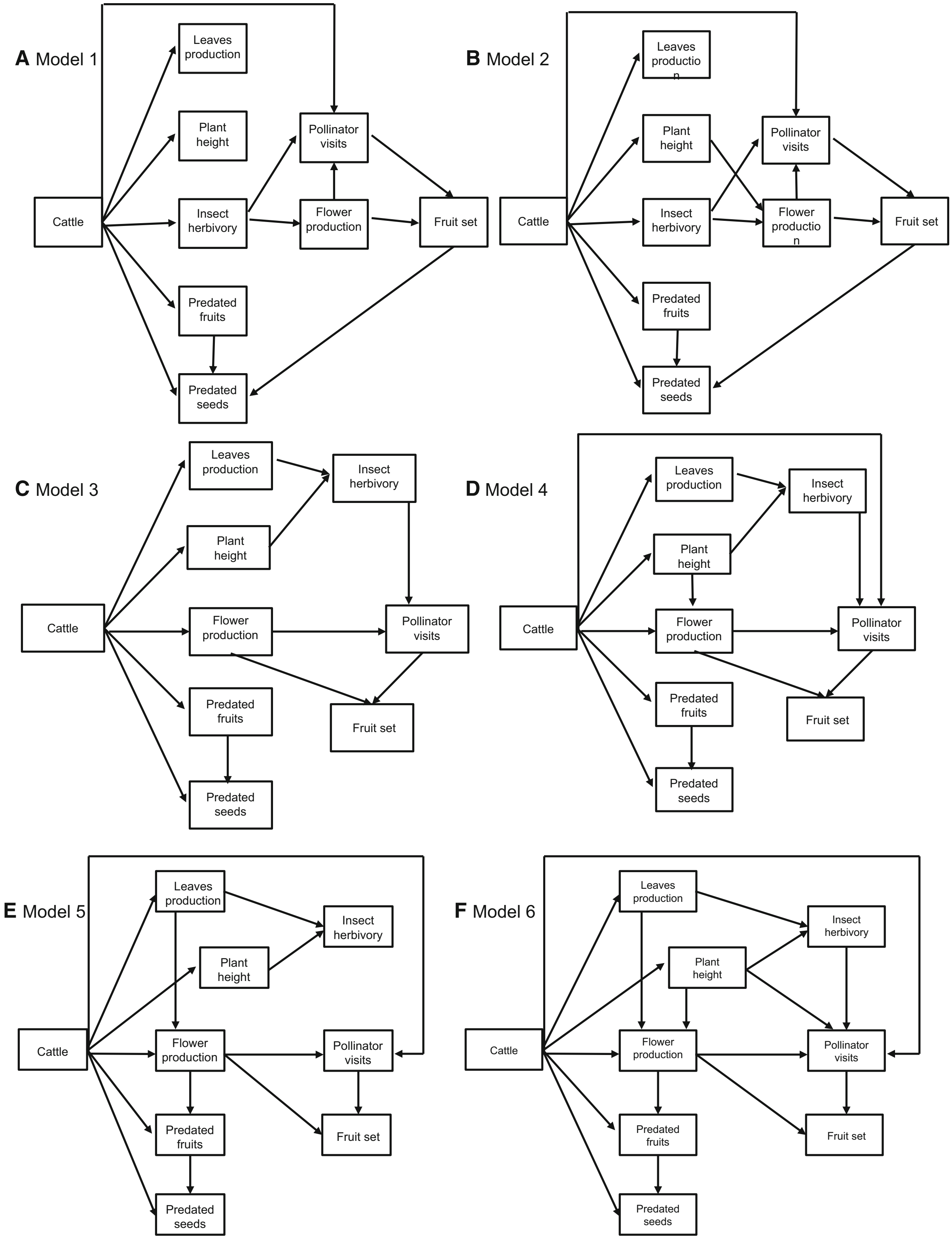
	Unburnt			Burnt			*F*	*P*
Plant height (m)	88.35	±	6.45	101.29	±	6.76	1.91	0.17
Leaves production	31.34	±	3.09	35.86	±	4.61	0.66	0.42
Flower production	**112.07**	**±**	**19.4**	**812.14**	**±**	**155.57**	**19.94**	**>0.0001**
Predated fruits	51.71	±	7.06	51.14	±	6.32	0.004	0.95
Predated seeds	12.25	±	3.24	10.84	±	3.04	0.1	0.75
Insect herbivory (HI)	1.06	±	0.09	0.94	±	0.15	0.48	0.49
Pollinator visits	**0.66**	**±**	**0.16**	**2.67**	**±**	**0.35**	**26.68**	**>0.0001**
Fruit set	0.58	±	0.06	0.62	±	0.05	0.34	0.60

Significant effects are shown in bold type ($P < 0.05$)

HI herbivory index. *N* 56, 28 unburnt and 28 burnt

Appendix 5

See Fig. 6.


A Model 1
Cattle
Leaves production
Plant height
Insect herbivory
Predated fruits
Predated seeds
Pollinator visits
Flower production
Fruit set
B Model 2
Cattle
Leaves productio n
Plant height
Insect herbivory
Predated fruits
Predated seeds
Pollinator visits
Flower productio n
Fruit set
C Model 3
Cattle
Leaves production
Plant height
Flower production
Predated fruits
Predated seeds
Insect herbivory
Pollinator visits
Fruit set
D Model 4
Cattle
Leaves production
Plant height
Flower production
Predated fruits
Predated seeds
Insect herbivory
Pollinator visits
Fruit set
E Model 5
Cattle
Leaves production
Plant height
Insect herbivory
Flower production
Pollinator visits
Predated fruits
Fruit set
Predated seeds
F Model 6
Cattle
Leaves production
Plant height
Insect herbivory
Flower production
Pollinator visits
Predated fruits
Fruit set
Predated seeds

◀**Fig. 6** Six candidate models that relate the nine variables of interest: cattle browsing, plant height, leaves production, flower production, predated fruits, predated seeds, insect herbivory, pollinator visits and fruit set. They were based on theory and experience in the study system

Appendix 6

See Table 3.

Table 3 Model rankings and goodness of fit for alternative models of the effects of cattle browsing on plant–insect interactions of *B. darwinii*

Model	χ^2	DF	CFI	χ^2Bollen	AICc
1	0.54	20	1.00	0.64	1504
2	0.89	21	1.00	0.88	1499
3	0.19	22	0.73	0.34	1505
4	0.83	20	1.00	0.87	1489
5	0.44	21	0.98	0.6	1503
6	0.90	20	1.00	0.97	1493

χ^2 Chi squares; *DF* degrees of freedom; *CFI* comparative fit index; χ^2 *Bollen* Bollen–Stine bootstrapping procedure; *AICc* small-sample-size corrected version of Akaike information criterion

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