

Effects of herbivory and patch size on tree seedling survivorship in a fog-dependent coastal rainforest in semiarid Chile

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Abstract The landscape (matrix) surrounding habitat fragments critically affects the biodiversity of those fragments due to biotic interchange and physical effects. However, to date, there have been only a limited number of studies on plant–animal interactions in fragmented landscapes, particularly on how tree seedling herbivory is affected by fragmentation. We have examined this question in a fog-dependent mosaic of rainforest fragments located on coastal mountaintops of semiarid Chile (30°S), where the effects of the surrounding semiarid matrix and forest patch size (0.1–22 ha) on tree seedling survival were simultaneously addressed. The rainforest is

strongly dominated by the endemic evergreen tree species *Aextoxicon punctatum* (Olivillo, approx. 80% of basal area). To assess the magnitudes and causes of Olivillo seedling mortality, we set up a field experiment where 512 tree seedlings of known age were transplanted into four forest fragments of different sizes in four 1.5 × 3-m plots per patch; one-half of each plot was fenced off with chicken wire to exclude small mammals. The plots were monitored for 22 months. Overall, 50% of the plants died during the experiment. The exclusion of small mammals from the plots increased seedling survival by 25%, with the effect being greater in smaller patches where matrix-dwelling herbivores are more abundant. This experiment highlights the important role of the surrounding matrix in affecting the persistence of trees in forest fragments. Because herbivores from the matrix cause greater tree seedling mortality in small patches, their effects must be taken into account in forest conservation–restoration plans.

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Introduction

Habitat fragmentation is known to alter regional biodiversity and species distribution patterns due to species loss from small habitat patches (Saunders et al. 1991). In forests, habitat loss and fragmentation increase isolation and physical and biotic edge effects and, therefore, may alter tree regeneration and biotic interactions inside the fragments (Janzen 1983; Benítez-Malvido and Lemus-Albor 2005; McEuen and Curran 2006). The nature of the surrounding landscape (external matrix) often has the largest effect on tree regeneration (Alverson et al. 1988; Saunders et al. 1991) because of the increased biotic and physical

interchanges (Paton 1994; Curran et al. 1999; Laurance 2000; Laurance et al. 2002). For example, Alverson et al. (1988) found that the presence of large mammalian herbivores in the surrounding matrix decreased tree sapling survival inside the fragmented forests, while Janzen (1986) found that increased wind blow at the edges of patches prevents the regeneration of tree species that require persistent humid conditions.

A limited number of herbivory studies in remnant habitat patches have found that mammal (Benítez-Malvido 1998) and insect herbivory (Arnold and Asquith 2002) are reduced in small fragments compared to larger fragments and that herbivorous mammals have less impact on seedlings in fragmented habitats than in a continuous forest (Dirzo 2001). However, Rao et al. (2001) showed higher levels of herbivory by *Atta* ants in smaller forest fragments in Lago Guri, Venezuela. When edge effects are considered, herbivory can be affected in different ways – not changed by edges (Benítez-Malvido and Lemus-Albor 2005), higher at edges (Cadenasso and Pickett 2000; Lienert and Fischer 2003) or reduced with respect to the forest interior (Cadenasso and Pickett 2000). Altered herbivore abundances in habitat fragments may respond to changes in food quality/food availability, changes in predator and/or disease abundances, changes in temperature and humidity (particularly for invertebrates) and changes to direct defaunation by human interference (Dirzo 2001). Generalizations require that we pay particular attention to whether herbivores are matrix (e.g. leaf-cutter ants) or fragment dwellers (e.g. small mammals in Panama islands)

In the semiarid region of Chile (30°S), where annual precipitation is <150 mm (López-Cortés and López 2004), a mosaic of temperate rainforest patches occurs on coastal mountaintops. These are surrounded by a floristically distinct matrix of xerophytic vegetation (Squeo et al. 2004). Despite their improbable location, these forests bear a striking resemblance in their tree, fern and epiphyte species composition to Valdivian temperate rainforests found more than 1000 km to the south (Villagrán and Armesto 1980) where rainfall far exceeds 2000 mm per year. These rainforest patches are strongly dominated by the endemic evergreen tree *Aextoxicon punctatum* (Olivillo). Olivillo forests are distributed continuously along the ocean-facing slopes and deep ravines of the Chilean Coastal Range, from about 33 to 43°S, but isolated remnant patches occur in the semiarid region at 30°S on coastal mountaintops where fogs are a constant input of moisture (del-Val et al. 2006).

The semiarid vegetation matrix surrounding the forest patches represents a barrier for the dispersal of several groups of forest-dwelling animals: 33.3% of bird species present in the landscape are restricted to forest patches (Cornelius et al. 2000) and 14.3% of beetles do not extend their presence outside of the forest patches (Barbosa and Marquet 2001). These studies also found that most species

of birds and beetles present in the landscape are associated with the semiarid matrix, suggesting a possible displacement of forest species by shrubland species (Cornelius et al. 2000; Barbosa and Marquet 2001).

Among Chilean small mammals, 52% of the species are herbivores (Silva 2005). For the semiarid matrix of Fray Jorge National Park, our study area, four species of highly mobile herbivorous rodents exhibit high densities and rates of dispersal (Meserve 1981a, b). Information on herbivory in coastal Olivillo forests is essentially lacking even though small mammals from the matrix are frequently found inside the forest patches. In the only investigation available, Murúa (1996) reported that 63.4% of Olivillo seeds were consumed from the forest floor by birds and/or mammals in Valdivian rainforests.

Earlier studies in Fray Jorge indicated that regeneration in Olivillo forests is largely restricted to forest patch edges facing the ocean and thus directly receiving the incoming fog (del-Val et al. 2006) and that it is abundant in larger (>20 ha) than in smaller (<1 ha) forest patches (Barbosa, unpublished results). One possible explanation for the differences in regeneration among patch sizes is differential moisture availability, as larger patches could intercept more of the incoming fog per unit area. However, the same pattern could be due, at least in part, to a larger impact of matrix herbivores on smaller patches due to increased edge effects.

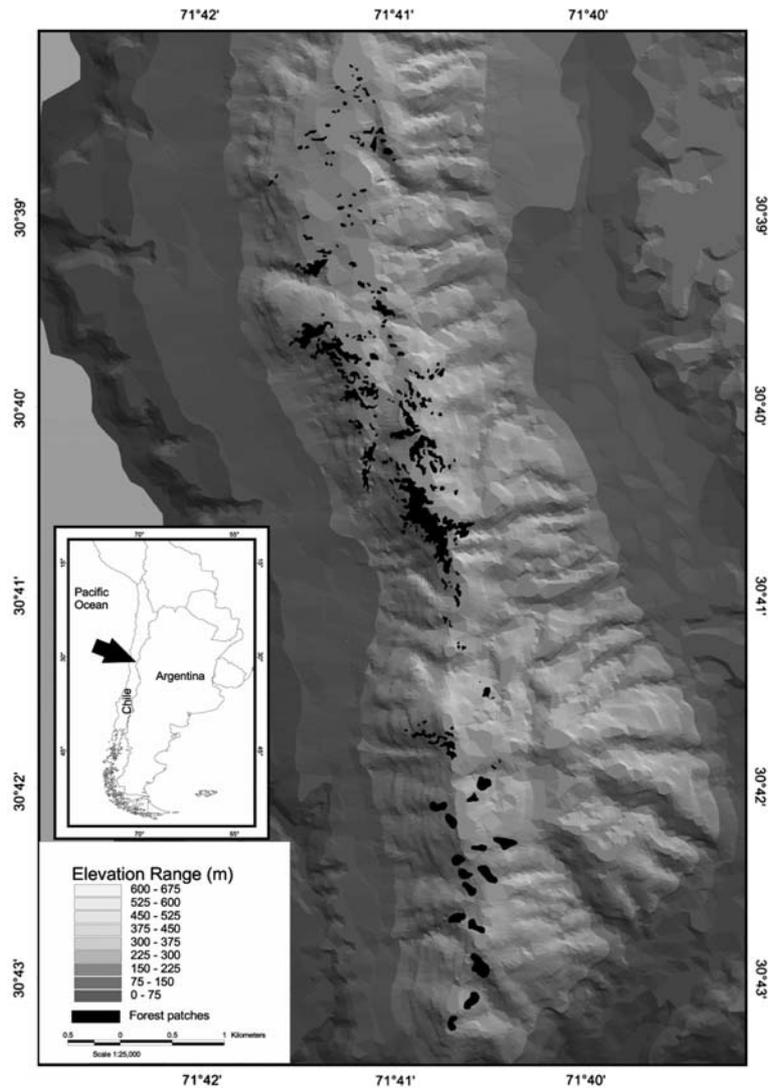
We report here our investigation of the magnitude and causes of Olivillo seedling mortality in rainforest patches located in the Fray Jorge National Park. We addressed the following specific questions: (1) to what extent is Olivillo seedling mortality in remnant forest patches due to herbivory by small mammals and (2) what are the causes of patch size effects, if present, upon seedling survival? Such questions are relevant to any assessment of whether tree regeneration differs between large and small patches and to the designing of conservation programmes that will assure the future continuity of regeneration and the conservation prospects of fog-dependent rainforest relicts in the semiarid environment.

Methods

Study site

The study was carried out in Fray Jorge National Park (FJNP; 30°40'S, 71°30'W), the northernmost outpost of the Olivillo forest (Fig. 1). This area contains a mosaic of 180 rainforest patches, ranging in size from 0.1 to 22 ha, located on the summits of coastal mountains surrounded by a matrix of semiarid scrub vegetation (Novoa-Jerez et al. 2004). The regional climate is Mediterranean-arid, with a

Fig. 1 Location of the study site showing the rainforest patch mosaic in Fray Jorge National Park (FJNP). Modified from Novoa-Jerez et al. (2004)



mean annual rainfall of 147 mm (from 21-year records, 1983–2003) concentrated during the cool winter months from May to August (Di Castri and Hajek 1976). The mean annual temperature is 13.6°C. Precipitation shows large inter-annual variability [coefficient of variance (CV): 81%] because of the wetter winters associated with the positive phases of the El Niño–Southern Oscillation (ENSO) and dry winters associated with negative phases (Jaksic 2001; Montecinos and Aceituno 2003; López-Cortés and López 2004). These temperate rainforest relicts persist under semiarid conditions because of constant fog inputs rolling in from the Pacific Ocean. It has been estimated that fog contributes about 200–400 mm of additional precipitation per year (O. Barbosa, unpublished results). The isolation of these northern forests outposts of Valdivian rainforests has been attributed to a pronounced aridization in northern Chile that developed during the Quaternary (Pérez and Villagrán 1994). Due to the long isolation, current populations of Olivillo forest in FJNP are genetically distinct from all

the other populations along the coast of Chile (Núñez-Avila and Armesto 2006). The present fragmentation of this system is the result of natural processes linked to spatial heterogeneity in fog direction and water content and to a lesser degree to human impacts that occurred before Fray Jorge was declared a National Park in 1941 (Barbosa and Marquet 2001).

Rainforest patches are dominated (approx. 80% of basal area) by the evergreen, broad-leaved tree *Aextoxicon punctatum* (Olivillo), the only member of the endemic family Aextoxicaceae. In addition to Olivillo, rainforest patches contain other broad-leaved evergreen trees, such as *Myrceugenia correifolia* (Myrtaceae), *Drimys winteri* (Winteraceae), and the less common *Rhaphithamnus spinosus* (Verbenaceae) and *Azara microphylla* (Flacourtiaceae). Woody vines such as *Griselinia scandens* (Cornaceae), *Sarmienta repens* and *Mitraria coccinea* (both Gesneriaceae), and epiphytic ferns (e.g., *Polypodium feullei*) and bryophytes are frequent components of the forest canopy

(Muñoz and Pisano 1947; Squeo et al. 2004; Villagrán et al. 2004). The dense coat of mosses, lichens and liverworts reflects the humid microclimate inside the patches.

Experimental design

We selected four forest patches in the FJNP as the experimental locations. These patches varied in size from 0.2 to 22 ha and represented the two extremes of the range of patch sizes available in the landscape (Table 1). Forest patches have similar tree species composition, with the exception of the most hygrophilous species (*Drymis winteri*) that only occurs in large patches (>10 ha) (del-Val et al. 2006). In each patch, we set up four plots of 1.5 × 3 m, with one-half of each plot fenced off entirely with chicken wire, with a mesh opening of 4 cm, to exclude small mammals (primarily rodents and introduced rabbits). The other half of the plot was left open as a control. The wire fence was buried 10 cm into the forest floor to prevent animal tunnelling. Experimental plots were dispersed throughout the forest patches under the canopy shade, and they were separated by at least 200 m from other small patches as well as being located at least 200 m away from the edge. In each half of the plots we planted 16 seedlings of Olivillo, for a total of 512 plants (four patches × four plots/patch × 32 seedlings/plot = 512). The seedlings were germinated from Olivillo seeds collected in the same study site 1 year earlier. The plants were kept in a shade-house inside individual jiffypots (biodegradable pots made out of peat), with acidic compost from grape soil, and watered regularly. Once the seedlings had one or two true-leaves (approx. 3 months old), they were simultaneously transplanted to the field without disturbing their roots. Seedlings inside individual jiffypots were planted directly in the forest floor in December 2003. Every 4–8 months and for a period of 22 months after planting (October 2005), we recorded seedling growth (leaf production per plant) and mortality.

Because water can be a limiting factor for plant growth in the semiarid landscape, and water in forest patches derives from fog interception by the trees, we used fog water interception and soil water availability estimates for different patch sizes (O. Barbosa, unpublished results) to assess their correlation with tree seedling survival. We estimated the water inputs per patch (in millilitres) for 1 year by adding up mean monthly measures per patch (September 2003 and 2004) obtained from six through-fall and six stem-flow water collectors located inside the same four forest patches used in this study. We also estimated mean soil water moisture content per patch using monthly measures derived from six 15-cm-deep soil samples in the same patches.

The small mammal community in same forest patches was assessed using a trapping grid consisting of five 75-m-long transects with five trapping stations per transect, covering an area of 0.56 ha (75 × 75 m). Each station had two Sherman live traps (8 × 9 × 23 cm; H. B. Sherman Traps, Tallahassee, Fla.). A total of 50 traps were set up per forest patch for 4 consecutive nights; oat was used as bait. Trapping was conducted at 3-month interval, starting in the spring of 2002 ending in the summer of 2006. Trapped animals were identified, measured, sexed, marked with numbered aluminium ear-tags and then released at the same point. Species were classified as herbivorous or non-herbivorous according to Silva (2005). In the two smallest patches (0.2 and 0.3 ha), the grid also included a section of matrix vegetation. Animals trapped in the matrix are reported separately and are not included in the statistical analyses.

Statistical analyses

To determine tree seedling survival, we calculated the percentage of the initial number of seedlings planted that were still alive per subplot ($n = 32$) in the fenced and control halves. We examined the causal effect of herbivore exclusion, fog water input and soil gravimetric content on seedling

Table 1 Physical and biotic characteristics of forest patches studied in Fray Jorge National Park (FJNP) situated in semiarid Chile (*SE* standard error)

Patch	Area (ha)	Mean annual fog-water capture (mm)	Mean soil water gravimetric content (g H ₂ O/g soil)	Total small mammal abundance in a 3-year period ^a	Total herbivore abundance in a 3-year period ^a	Seedling survival ^b (% ± SE)		Number of leaves per seedling ^b (±SE)	
						Control	Fenced	Control	Fenced
1	0.2	692.9	0.299	220 (90)	114 (28)	28.1 ± 13.1	67.2 ± 5.9	3.7 ± 0.8	4.7 ± 0.3
2	0.3	420.5	0.267	197 (165)	128 (115)	14.1 ± 12.1	26.3 ± 10.3	3.3 ± 0.3	3.9 ± 0.5
3	14.1	417.3	1.166	56	8	23.4 ± 8.6	50.0 ± 12.0	2.3 ± 0.5	3.0 ± 0.3
4	21.9	512.2	0.836	96	42	28.1 ± 8.3	48.4 ± 10.3	3.1 ± 0.3	2.5 ± 0.3

^a For small mammal abundance and herbivore abundance inside the forest, the numbers in parenthesis refer to the number of animals trapped in the matrix grid section

^b Mean seedling survival and number of leaves per surviving seedling were recorded after 22 months in the field in control and fenced plots

survival per patch. The statistical model was built up as a split-plot design that included different sampling dates, forest patch sizes and herbivore exclusions treatment in the error terms in order to obtain the correct degrees of freedom and avoid pseudoreplication (spatial and temporal). The response variable, percentage seedling survival per subplot, was arcsine-transformed. The explanatory variables were herbivore exclusion log patch area and the interaction of herbivore exclusion \times log patch area. The effects of fog water input and soil moisture content per patch were analysed using the same split-plot model structure, but in two different models, since we did not have enough degrees of freedom at the patch level (only four patches were used). We also analysed the effect of herbivore exclusion on final seedling growth (leaf production) with an ANOVA; the response variable was final number of leaves and the explanatory variables were herbivore exclusion, log patch area, the interactions between herbivore exclusion and log patch area and initial leaf number as a covariate. Due to seedling mortality, we could not build a split-plot model for seedling growth; therefore, we have interpreted the results on seedling growth with caution. We analysed total small mammal abundance and herbivore abundance inside different size fragments with a linear regression using log (patch area) as the explanatory variable and abundance as the response variable. Due to the small size of the forest patches, it was not possible to have replicated trapping in the same patches and, therefore, regression analysis was assessed to provide the best statistical approximation. All analyses were performed in R (Mathsoft Inc).

Results

Seedling survival and growth

Overall survival of current-year seedlings of Olivillo in remnant rainforest patches after 22 months ranged from $23.5 \pm 5\%$ (mean ± 1 SE) in open, control subplots to $48 \pm 5.7\%$ in fenced subplots. Herbivore exclusions increased seedling survival by approximately 25% ($F_{(1,14)} = 59.2$, $P < 0.001$; Fig. 2) in all patches. The rate of seedling mortality was greatest during the first 8 months of the experiment and declined afterwards.

Forest patch size (measured as the log patch area) did not have a significant effect on tree seedling survival ($F_{(1,2)} = 0.15$, $P = 0.7$); however, the interaction between herbivore exclusion and patch area was marginally significant ($F_{(1,14)} = 4.23$, $P = 0.058$), indicating a differential impact of herbivores depending on forest patch area. The difference in seedling survival between fenced and control plots decreased as forest patch area increased, from a 39%

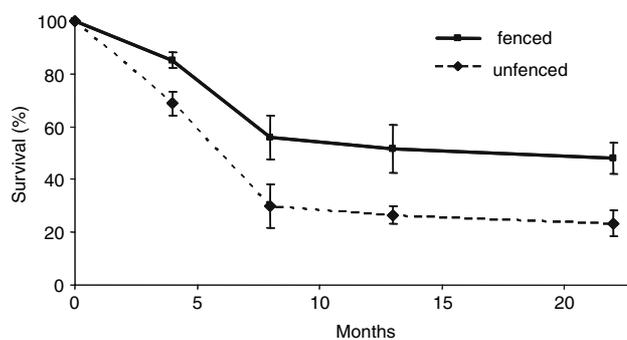


Fig. 2 Survival of *Aextoxicon punctatum* seedlings inside fenced (exclusion of small mammal herbivores) and unfenced plots during the 22-month study period ($F_{(1,14)} = 59.2$, $P < 0.001$) in forest patches of Fray Jorge National Park

difference in the smallest forest patch sampled to a 20% difference in the largest forest patch (Fig. 3), suggesting that herbivores consuming tree seedlings have a greater influence on mortality in smaller patches.

In addition to differences in area, humidity and water drip inside forest patches varied markedly (Table 1). Patch 1 (the smallest) captured the greatest amount of water from fog, but the humidity level in the soil was the lowest of all patches. In general, soil humidity tended to increase with forest patch size, probably correlated with less evapotranspiration, but water capture was not related with patch size.

Tree seedling survival at the end of the experiment (22 months) was not significantly affected by mean annual fog water capture per patch ($F_{(1,2)} = 4.06$, $P = 0.18$) nor by mean soil moisture content per patch ($F_{(1,2)} = 0.01$, $P = 0.9$). However, the interaction between patch mean annual fog water capture and herbivore exclusion was significant ($F_{(1,14)} = 19.0$, $P < 0.001$), since seedlings growing in fenced plots inside the patch with the greatest fog water capture (patch 1) had a disproportionately greater survival (67%).

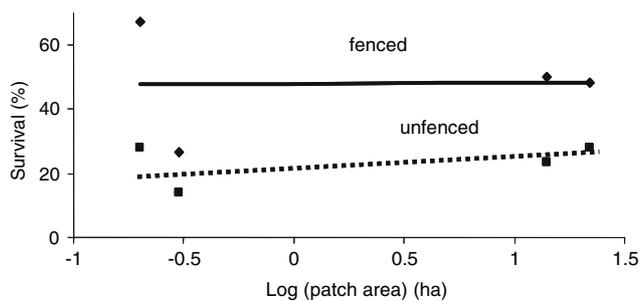


Fig. 3 Relationship between survival of *Aextoxicon punctatum* seedlings and forest patch area (log area) inside fenced (herbivore excluded) and unfenced plots in semiarid Fray Jorge National Park. Values shown are mean survival after 22 months per forest patch. Note the positive relationship between seedling survival and patch area in unfenced plots, and the interaction between patch area and herbivore exclusion. Lines represent regression models

Seedling growth, measured as the production of new leaves, was marginally affected by the herbivore exclusion treatment ($F_{(1,139)} = 3.28$, $P = 0.07$), and leaf production of tree seedlings was significantly affected by forest patch area ($F_{(1,139)} = 26.3$, $P < 0.001$). Tree seedlings produced more leaves in the smaller patches, and the interaction between herbivore exclusion \times patch area was not significant. The initial number of leaves on the seedlings when they were planted did not affect the final number of leaves ($F_{(1,139)} = 0.004$, $P = 0.9$). Fog water input or soil water content per patch did not significantly affect leaf production of the seedlings ($F_{(1,139)} = 2.16$, $P = 0.14$; $F_{(1,139)} = 0.12$, $P = 0.72$, respectively). Tree seedlings in smaller patches (1 and 2) produced 1.5- and 1.3-fold more leaves than in those in larger patches (3 and 4); this result is probably related with plants in the smaller patches having both enough water to grow and better light conditions.

Small mammals in patches

Overall, we found a total of 569 individuals of eight small mammal species in the forest patches and 255 in the matrix section. These mammals belonged to the families Abrocomidae: *Abrocoma bennetti*; Muridae: *Abrothrix longipilis*, *Abrothrix olivaceus*, *Chelemys megalonyx*, *Oligoryzomys longicaudatus*, *Phyllotis darwini*; Octodontidae: *Octodon degus*, *O. lunatus*; Didelphidae: *Thylamys elegans*. Small mammal abundance was significantly affected by forest patch size ($R^2 = 0.92$, $F_{(1,2)} = 22.9$, $P = 0.04$). The density of small mammals was higher in small forest patches (Table 1). The same pattern held true for the five known herbivorous species (*Abrocoma bennetti*, *Abrothrix longipilis*, *Octodon degus*, *Octodon lunatus* and *Phyllotis darwini*) examined separately, although in this case the effect of patch area was marginally significant ($R^2 = 0.88$, $F_{(1,2)} = 14.18$, $P = 0.06$). The herbivorous individuals added up to a total of 292 mammals inside forest patches and 143 in the matrix section.

Discussion

Tree seedling mortality inside forest patches of FJNP was important, as half of the seedlings initially planted died during the following 22 months. Compared with Olivillo trees growing at wet-temperate latitudes in Valdivian rainforests in Chile, where no mortality occurred during a 14-month study (Lusk 2002), seedling survival was much lower in the relict rainforest patches in the semiarid region, highlighting the harsher physical and biotic environment for Olivillo in its northern distributional limit (Kummerow 1966; del-Val et al. 2006).

Mortality due to herbivory

Although tree seedling growth was unaffected by herbivore exclusion, Olivillo seedling survival increased by approximately 25% when plants were protected against small mammals. Consequently, herbivores, especially rodents, had a statistically significant and negative impact on the regeneration of Olivillo in all forest patches in FJNP, but especially in smaller ones. Herbivores have been found to significantly affect tree seedling survival in other studies in temperate and tropical forests. Weltzin et al. (1998) found a 50% increase in the survival of *Prosopis* seedlings when small mammal herbivores were excluded. Dirzo (2001) and Asquith and Mejia-Chang (2005) showed that tree seedlings formed a dense carpet in the forest understory in patches where mammals have been extirpated by humans. Apart from the population consequences, the reported mortality of Olivillo seedlings in forest patches, driven by herbivores derived from the surrounding semiarid vegetation, may have important ecosystem consequences. Because the persistence of forest patches depends upon the interception of fog water by adult Olivillos (del-Val et al. 2006), lower regeneration in the long run may affect the water inputs necessary for patch persistence.

Seedling mortality related to forest patch size and water availability

Tree seedling survival was not significantly affected by forest patch area per se, but when the interaction with herbivore exclusion is taken into consideration, mortality was higher in the control plots inside small forest patches (Figs. 2 and 3). We also found that small mammals were more abundant in smaller patches. These findings provide insights on the factors explaining the patch area effect (Janzen 1983; Saunders et al. 1991; Laurance et al. 2002; Benítez-Malvido and Lemus-Albor 2005) that account for the differences in Olivillo regeneration found in this and other studies (O. Barbosa, unpublished results; del-Val et al. 2006). We propose that small mammal herbivores are largely responsible for greater tree seedling mortality in small patches, accounting at least in part for the higher number of Olivillo seedlings found in larger rainforest patches.

Asquith et al. (1997) studied fragmented forest patches on small and large islands of Panama and in mainland Panama. These researchers reported a greater seedling mortality due to herbivorous mammals on the smaller islands than on the larger islands and in mainland Panama and attributed this difference to the absence of vertebrate predators on the small islands, where seedling survival increased sixfold when protected from the herbivores. In a hardwood North American forest, McEuen and Curran (2006) also found greater levels of herbivory in isolated fragments. However,

in landscapes where small mammals have been decimated by habitat fragmentation, there is less herbivory in small fragments (Benítez-Malvido 1998; Dirzo 2001).

In addition to our evidence showing that the greater presence of small mammals in small forest patches negatively affects tree seedling survival, we have corroborated earlier findings that small mammal activity is greater in small forest patches of sand arenas (E. del-Val unpublished results). As has been found for some forests of southern UK (Crawley 1990) and in North America (Alverson 1988), our results indicate that when forests are surrounded by a matrix suitable for herbivores, habitat fragmentation can disrupt tree regeneration. Consequently, in these systems, tree population dynamics inside forest patches may be externally driven because herbivores coming from the surrounding matrix are negatively affecting tree seedling survival (Saunders et al. 1991). Just how pervasive the herbivores are as external drivers in other forest ecosystems warrants further investigation.

Seedling growth, as estimated by the number of new leaves produced during the 22-month study period, was enhanced in small forest patches, probably because light can be a more limiting factor for seedling growth in the shaded understory of larger patches. However, even though seedling growth was promoted in small patches, plants may not reach the adult stage because both the high herbivore pressure and the greater evapotranspiration demand limiting survival (Janzen 1983). Most mammals trapped in forest patches are probably derived from the semiarid matrix where their populations are high (Meserve 1981a; Jaksic et al. 2004). These matrix species are more abundant in small patches where physical conditions (i.e. temperature, light availability, etc.) are closer to those found in the semiarid vegetation. The impact of herbivores is likely to change in intensity in response to climatic variability that modulates the contrast between forest patches and the semiarid matrix habitat. Studies of native small mammal communities in the semiarid matrix surrounding the forest patches in FJNP have documented high fluctuations in population abundances associated with different phases of the ENSO (Meserve 1981b; Gutiérrez and Meserve 2000; Holmgren et al. 2001). Because plant productivity usually crashes in the semiarid scrub during dry “La Niña” years, when annual rainfall is 0–40 mm, populations of small mammal herbivores may survive by moving inside forest patches. The productivity of forest patches is less influenced by ENSO fluctuations because most of their water derives from fog rather than rain (del-Val et al. 2006). Since herbivores are feeding on tree seedlings in forest patches, these patches may be acting as a “rescue system” during periods of low food supply in the matrix. These hypotheses warrant further investigation.

Water interception from fog in conjunction with herbivore exclusion benefitted the survival of Olivillo seedlings

in forest patches. Greater water drip inside the forest patch was beneficial for tree seedling survival during the study period. This result is consistent with a tree regeneration survey in forest patches of FJNP showing that regeneration was strongly associated with patch locations where fog interception increased (del-Val et al. 2006). The lack of relationship between seedling survival and soil moisture content may be due to the heterogeneity of soil moisture and/or inadequate sampling. This point warrants further study.

If we consider the magnitude of seedling mortality due to herbivory and water limitation as well as seed predation (which for Olivillo may be up to 63% according to Murúa 1996), only a very small proportion of the annual seed produced is likely to reach sapling size in forest patches of FJNP. Field surveys have shown that Olivillo saplings are rare in rainforest patches of FJNP (approx. 0.08 saplings/m²; del-Val et al. 2006). This emphasizes the importance of examining different stages of tree regeneration for managing and conserving these rainforest relicts. In our study, the regeneration of Olivillo was strongly constrained by herbivory, primarily by rodents (biotic factor), and by fog water inputs (abiotic factor) in remnant patches of FJNP, and both factors explain the relationship between forest patch area and tree regeneration. To these causes of mortality, we must add the availability of seed producers in each patch and the probable limitations of seed dispersal among patches (M. Nuñez-Avila, personal communication). In order to ensure tree regeneration in all forest patches and conserve this forest patch mosaic, it may be advisable to control small mammals in small patches.

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