

Acacia caven nurses endemic sclerophyllous trees along a successional pathway from silvopastoral savanna to forest

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Abstract. The successional pathways linking the *Acacia caven*-dominated savanna habitat “espinal” and the closed sclerophyllous forest of central Chile have long been debated. Previously, espinal was considered an invasive degradation of closed forest that tended toward desertification, could not be restored to forest, and had little ecological value. Recent GIS (Geographical Information System) research on land-use change has, however, detected apparent regeneration of sclerophyllous forest from espinal. This suggests that there is a successional path linking espinal and sclerophyllous forest. Here, we used surveys of transects in espinals and espinal–sclerophyllous forest transitions to ask whether (1) *A. caven* is an invasive species or a pioneer species, (2) forest regenerates by sclerophyllous trees “filling in” spaces between *A. caven* individuals, and then shading them out (plant–plant competition), or (3) forest regenerates by plant–plant facilitation between *A. caven* and other species, and (4) how current and historical management and condition affect these potential successional mechanisms. We find that *A. caven* establishes primarily in full sunlight and is unlikely to degrade forests via invasion. We also find, for the first time, evidence that *A. caven* is a nurse tree to several sclerophyllous forest tree-beneficiary species. Measurements of the under-canopy microhabitat of *A. caven*, compared to *Lithraea caustica*, another possible nurse species, suggest that it provides a balance between shade and soil moisture retention, making it a regeneration site not only for directed bird-dispersed seeds but also for undirected wind-dispersed ones. Conservation and restoration of espinals, especially in drier areas, could provide capacity for future dynamic successional pathways in central Chile.

Key words: *Acacia caven*; Chile; conservation; degradation; disturbance; espinal; land-use; *Lithraea caustica*; restoration; sclerophyllous forest; succession.

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INTRODUCTION

The historical and successional trajectories of open woodlands have been a source of ecological debate for decades. Discussion has surrounded ancient deforestation and degradation in the

Mediterranean Basin (Tomaselli 1977, Williams 2000, Butzer 2005). The degree of openness in northern European forests, and the role of large herbivores in driving dynamic mosaics of open and closed woodland, has more recently been a source of debate (Vera 2000, Svenning 2002,

Mitchell 2005). Interest in the roles of herbivory, fire, and grass-tree competition in African and South American savanna cyclical succession has also been strong (Staver et al. 2011, Hoffmann et al. 2012, Veldman et al. 2015). These strands of research focus on the interactions between disturbance regimes and plant-plant competition. Other recent developments in understanding woodland composition have focused on plant-plant facilitation (e.g., Soliveres et al. 2012, Schob et al. 2013, Synodinos et al. 2015, Xu et al. 2015), including beneficiary and nurse tree species pairings (Valiente-Banuet et al. 2006, Valiente-Banuet and Verdú 2007, Verdú et al. 2009). Here, we examine the impact of plant-plant interactions and historical and current land management on successional trajectories in two semi-arid woodland types in South America.

Two main vegetation types of central Chile, in its semi-arid mediterranean-climate plant endemicity hotspot (Armesto et al. 2007), are the sclerophyllous woodland or forest and the “espinal,” a silvopastoral savanna found in drier and human-dominated mosaics (Donoso 1982, CONAF 2011, Moreira-Muñoz 2011). Sclerophyllous woodlands and forests are dominated by evergreen, dry-adapted trees endemic to central Chile (Donoso 1982, Bambach et al. 2013). Endemic sclerophyllous tree diversification has been linked to the uplifting of the Andes, ensuing fragmentation of the southern South American biota, and the subsequent drying of the west coast of South America as a consequence of the Andean uplift and cooling of the Pacific Humboldt current, which began in the Miocene–Pleistocene (Arroyo et al. 1988, Hinojosa et al. 2006, Armesto et al. 2007, Antonelli et al. 2009, Moreira-Muñoz 2011, Le Roux 2012). Closed-canopy sclerophyllous forest is now found in remnants primarily on steep slopes and deep ravines of the Coastal Mountain Range and the Andes (Schulz et al. 2010, van de Wouw et al. 2011). Researchers often assume a primordial continuous forest, heavily fragmented and degraded by early colonists and modern agriculture (Aronson et al. 1993b, Torrejón and Cisternas 2002, Armesto et al. 2010). The possible roles of indigenous peoples who lived in and cultivated southern and central Chile in maintaining open woodlands or mosaics through silvopastoralism and swidden farming are still poorly known (Otero 2006, Armesto et al. 2010).

The espinal is an open woodland or savanna, also referred to as a “steppe” when its woody species are all classified as shrubs (Donoso 1982, Olivares 2006a, Armesto et al. 2007, Moreira-Muñoz 2011). Espinal is described as dominated by *Acacia caven* (*Vachellia caven*), a Fabaceae tree presumably native to the chaco, a seasonally dry forest of central South America (Ovalle et al. 1990, Olivares 2006a). The phylogenetic origin of *A. caven* has been dated to around 10 mya (Miocene) in open habitats of South America (Bouchenak-Khelladi et al. 2010). The expansion of dry formations in the mid-Holocene in central and southern Chile may coincide with the development of Fabaceae savannas (Villagrán and Varela 1990, Armesto et al. 2007), which since the mid-20th century are dominated by *A. caven* due to its resilience to anthropogenic pressures (Fuentes et al. 1989). At least since the colonial period if not before, espinal or Fabaceae savanna has been used for silvopastoralism (Olivares 2006b, Otero 2006). The espinal is widely considered to be a desertified anthropogenic degradation of sclerophyllous forest (Ovalle et al. 1990, 1999, Aronson et al. 1993a, 1998). Espinal has also been described as an invasive formation because it replaces sclerophyllous forests (Aronson et al. 1993b, van de Wouw et al. 2011). According to some research, espinal represents the last stage of degradation, crossing an irreversible ecological threshold (Ovalle et al. 1990, 1999). However, more recent research suggests that espinals can be restored to higher productivity and biodiversity (Holmgren et al. 2006, Westley et al. 2010, Newton et al. 2011, Ovalle et al. 2015, Root-Bernstein and Jaksic 2015, Hernández et al. 2016).

Recent research on land-cover change suggests that both sclerophyllous forest and espinal lose area through conversion to agriculture, and gain area under agricultural abandonment (Schulz et al. 2010, 2011, Newton et al. 2011, 2012, van de Wouw et al. 2011, Fuentes-Castillo et al. 2012, Hernández et al. 2015, 2016). The studies disagree markedly on the magnitude and direction of woodland land-cover class changes, and cannot provide successional mechanisms due to their resolution and scale. However, they agree that sclerophyllous forest regenerates from its own fragments (Schulz et al. 2010, van de Wouw et al. 2011, Fuentes-Castillo et al. 2012). Hernández et al. (2015, 2016), also using a remote-sensing

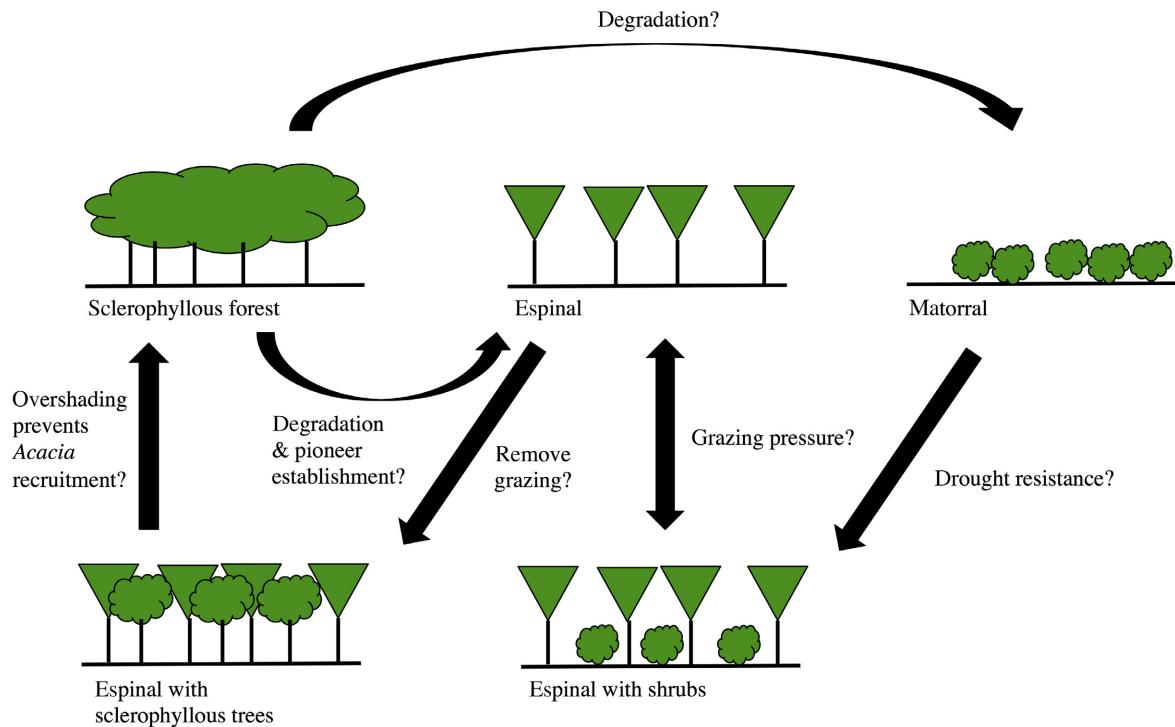


Fig. 1. Successional model of principal central Chilean habitats. The grazer and its type of grazing may affect whether shrubs are favored or not in espinals; this is not well understood. Drought resistance varies between woody species, and selection for drought resistance is important under variation in precipitation due to ENSO (El Niño Southern Oscillation).

approach, have detected sclerophyllous forest regenerating from dense espinal woodlands or via “arborescent shrubland” that itself can form from espinal. By analogy to experiments with three sclerophyllous woody species (Fuentes et al. 1989), some researchers have suggested that *A. caven* could act as a nurse tree (Holmgren et al. 2000, Fleury et al. 2015). To date, the natural occurrence of nurse–beneficiary interactions in central Chilean woodlands has not been demonstrated. However, a section of Río Clarillo National Park that was formerly an espinal has subsequently spontaneously “filled in” with sclerophyllous trees, forming a dense, intermediate forest type (L. Peña, *personal communication* 2013; M. Root-Bernstein, *personal observation*). *A. caven* has also been described as a pioneer species that establishes in open areas (Armesto and Pickett 1985, Fuentes et al. 1989), although its establishment rate appears to be low and sporadic (Holmgren et al. 2006; Root-Bernstein and Jaksic, *in press*; M. Root-Bernstein, *personal observation*).

These observations suggest a different successional model to the degradation trajectory described above.

We hypothesize that espinal is not the end-point of an anthropogenic/ invasive degradation process that has crossed an irreversible threshold, but rather the first successional stage after degradation or disturbance (Armesto and Pickett 1985, Root-Bernstein and Jaksic 2015). Under this model, some succession trajectories can lead to sclerophyllous forest formation (Fig. 1). Here, we seek additional evidence for this successional model. We ask (1) Is the pattern of *A. caven* establishment consistent with *A. caven* invading sclerophyllous forests or with *A. caven* as a pioneer species in open habitats? (2) Is there evidence for in-filling of the gaps in espinals with sclerophyllous trees? In this case, we would expect to see a pattern of increasing species richness, from *A. caven* domination, first adding light-tolerant species (e.g., *Lithraea caustica*, *Maytenus boaria*, *Quillaja saponaria*) and finally adding shade-tolerant and moisture-requiring species

(e.g., *Luma apiculata*, *Cryptocarya alba*, *Persea lingue*) (Hoffmann 2012). Does this lead to over-shadowing and death of *A. caven* and formation of closed sclerophyllous forests (plant–plant competition hypothesis)? (3) Is there evidence that the under-canopy microhabitat of *A. caven* facilitates sclerophyllous tree establishment leading to higher density via nucleation and nurse–beneficiary species pairs (plant–plant facilitation hypothesis)? Since we also found evidence for possible facilitation by *L. caustica*, a less abundant species also associated with post-disturbance landscapes, we further examined the role of the under-canopy microclimate in facilitation by sampling soil and light characteristics under canopies and in the open in order to assess whether *A. caven* and *L. caustica* canopies provided functionally differentiated microsites for establishment. (4) Does current espinal density or land-use history better explain sclerophyllous forest regeneration? Remote-sensing GIS (Geographic Information System) analyses (Hernández et al. 2015, 2016) find that sclerophyllous forest regeneration depends on espinal density in a northeastern area of central Chile. However, there may be other trajectories of woodland succession in central Chile. Another common explanation for the presence of particular regeneration processes and species assemblages in forests is their history of disturbance or degradation (e.g., Abrams et al. 1985, Chazdon 2003). Specifically, we propose sclerophyllous forest trees may, at least in some sites, establish independently of the density of *A. caven*. Sclerophyllous forest establishment may instead be related to the history of specific disturbances in areas with *A. caven*. What are the roles of past degradation, current successional state, and historicity? We answered these four questions through field surveys across espinals and espinal–sclerophyllous forest transitions.

METHODS

Sites and transects

We set up transects at seven sites in central Chile, including La Rinconada, an experimental station of the Universidad de Chile, Río Clarillo National Reserve (now National Park), the privately owned Fundo Fontaine, Altos de Cantillana private Nature Reserve, San Carlos de Apoquindo private Nature Reserve, the privately owned Fundo Los Alpes, and Lago de Peñuelas National

Reserve (for locations, see Fig. 2). These represent sites to the east, west, and center of the mediterranean-climate area of central Chile, while not including sites at the extreme north or south of this area. At each site, we determined the main formations and tree–species associations in which we observed *Acacia caven* individuals. We then set up representative transects across those habitats. The initial points for transects were selected to start at an arbitrary tree and the direction was chosen in order to cross the habitat we wished to sample while avoiding roads, rivers, ravines, and other barriers, and using available landmarks to ensure that the transect was straight. Transect length was defined as including 30 trees, although we also made some half-length transects (around 15 trees) and some double-length transects (around 70 trees) depending on the area of the habitat formation being sampled and local tree density. Transects were 4 m wide. We did not intend to have our transects represent random samples at each site because this would have resulted in sampling habitat formations without *A. caven*, which was outside the scope of the study. There were at least three transects at each site except Fundo los Alpes where we had one double-length transect, for a total of 27 transects in all. We consider $N = 27$; that is, each transect is treated as an independent sample. We justify this with the assertion that while the species pool varies slightly at a regional scale, successional trajectories respond to local and patch-scale circumstances, and the mechanisms of interest (tree–tree competition or facilitation) occur at an individual tree scale.

In each transect, we counted all trees >40 cm high and with their main trunk within the transect boundary. We numbered trees in order. For each tree, we recorded species, GPS (Geographic Positioning System) location, height, canopy radius, number of stems at 10 cm from the ground, and the diameter of the base of the tree at ground level, including all detectable live and dead stems. We used base diameter rather than diameter at breast height (1.37 m) since a large proportion of trees were multi-stemmed from the base. Additionally, we recorded when one individual was found growing under the canopy of another, and whether its own trunk was under or outside the canopy it was under. Within the same count, we recorded trees growing under the entire canopy even when the canopy extended outside the

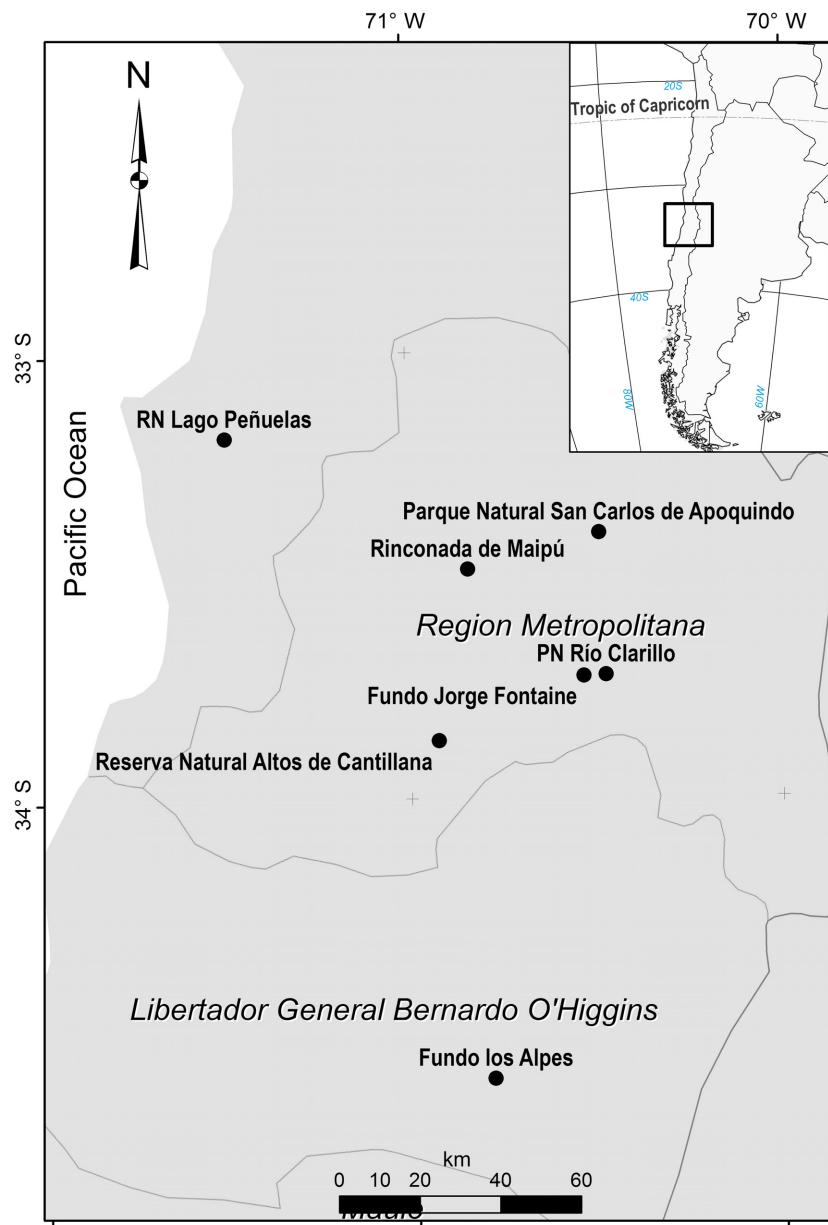


Fig. 2. The locations of the seven research sites in central Chile.

transect. We also noted the existence of seedlings <40 cm when we detected them, but they were not numbered for inclusion in the dataset; we counted approximately 85 seedlings of several species. In total, we included 859 individual trees >40 cm in 27 transects.

At each site and transect, we recorded evidence of the presence of livestock, camelids, and rabbits (the non-native *Oryctolagus cuniculus*) and other

past and present anthropogenic uses of the landscape. We also interviewed park rangers and landowners to obtain oral histories of how each site had been managed and exploited over the past 100 yr. Land managers and owners had a general knowledge of the history of their sites over this period.

We calculated the area in which trees were counted (transect area plus canopy area extending

outside the transect) using GIS. We calculated the transect size with the “minimum bounding geography” around the GIS points for the trees in each transect. We then dissolved the union between the transects and the canopy areas, represented with a buffer function.

*Data on the under-canopy microhabitat space of *A. caven* and *L. caustica**

In order to better understand the potential role of plant–plant facilitation, we sampled the under-canopy microhabitat of the two tree species, *A. caven* and *L. caustica*, which based on preliminary data analysis from the transects were potential nurse species. We collected data characterizing under-canopy microhabitats on two different days during the germination season (spring). As winter is the rainy season in central Chile and the winter of 2015 was dry, this provides an indication of the species’ canopy microhabitats under relatively extreme conditions. In order to assess each microhabitat’s capacity to maintain soil moisture, we collected samples at 2 d after rain (11 September 2015) and 6 d after rain (30 September 2015). According to the geographically closest available records, on 9 September it rained 0.1 mm, and on 24 September it rained 10.1 mm (Los Tilos station, agromet.inia.cl). Each day, we sampled at two sites in RN Río Clarillo, next to the river (“River”) and in an area several hundred meters from the river (“Station”). At each site, we sampled 15 *A. caven* trees in an espinal, and 15 *L. caustica* trees in a *L. caustica*-dominated woodland. Trees were selected on a convenience basis. Combining all conditions (days after rain and site), this gave a sample size of 120 trees, 60 of each species. In addition, on 30 September 2015, we collected control data at five arbitrarily selected open areas in each site (River and Station), not under tree canopies. For each tree, we recorded the canopy diameter, the height, the number of trunks, and the base diameter at ground level (as before). For each tree, we also measured four variables representing dimensions of the under-canopy microhabitat space, representing key variables expected to affect seed establishment. Moisture availability may be critical for establishment under nurse plants in semi-arid habitats (Badano et al. 2009), and light, temperature, and nutrient levels will affect which seeds are favored (Solivares et al. 2011). The four variables measured under each sampled tree

included light reaching through the canopy, soil moisture under the canopy, soil conductivity under the canopy, and soil temperature. Soil conductivity depends on nutrients (ions), water, and temperature and is used as a measure of soil quality. We measured light using a convex spherical crown densiometer from Forestry Suppliers. We measured soil moisture using a Lutron Professional Soil Moisture Meter PMS 714 (Taiwan), and conductivity and temperature using a Hanna Soil Conductivity Temperature Pocket Meter HI98331 (Padova, Italy). We additionally collected two soil samples at 10 cm depth on each day, at both sites, under the canopies of each tree species, as well as five samples in open areas (not under canopy) at the River and Station sites 6 d after rain. This gave a total of 26 soil samples. These samples were sent to the Soil Laboratory of the University of Chillán, where they were analyzed for available N, percent organic matter, C/N ratio, and pH. For statistical analysis of under-canopy microhabitat differentiation (see *Statistical analysis*), we assigned the mean available N, percent organic matter, C/N ratio, and pH to all trees of the same species, condition, and day. These data are shown in the Results.

Statistical analysis

To answer question (1), if *A. caven* is invading sclerophyllous forest or acting as a pioneer, we first sought to characterize the habitats in our transects by (1) habitat structure, in terms of the spatial ordering of species along the transects, and (2) habitat types, in terms of the species composition. These analyses would allow us to classify the situations in which *A. caven* co-occurs with other species, and in a subsequent step to assess whether the growth patterns of *A. caven* vary across habitat structures or species composition clusters. To determine habitat structure, we used the Wald–Wolfowitz test, implemented with the abe package in R. This is a non-parametric categorical test that assesses the significance of “runs” or series of the same category. Each species was treated as a category, and tree number along the transect was treated as series order. Thus, we consider structure only along the long axis of the transect, ignoring any variation along the narrow 4 m width of the transect. Significance occurs when a given species of tree is more likely to be followed by a tree of the same species than by a tree of another

species. When the structure was non-random, we inspected the data and compared with our field notes to distinguish between patchy habitats and gradients. We defined "patchy" as runs of trees where the species were mixed in small clusters or alternating. Note that patchiness here only refers to species distribution along the transect and not to the existence of open spaces between groups of trees, which was not considered. We defined "gradients" as runs of trees that switched from one species at the beginning of the transect to another species at the end. We thus sorted transects into three habitat structures: random or "unstructured" series of tree species (including transects of only *A. caven*), patchy habitats, and gradients between espinal and sclerophyllous forest. To determine whether the transects could be categorized into different habitat types in terms of species composition, we used NMDS (Non-metric Multi Dimensional Scaling) analysis. We used the Dist, metaMDS, Tree, and Group commands in the vegan package in R version 3.1.0. We used Jaccard distances since they are suitable for analysis of species composition, and the "average" command for forming clusters. We chose a height cutoff for the cluster dendrogram based on visual analysis of the tree. We then assessed whether spatial structure (unstructured, patchy, or gradient) is related to species composition clusters using a χ^2 test implemented in R version 3.1.0. We used the outcomes of these analyses to structure the remainder of analyses throughout the paper.

Next, we sought to understand the growth and reproductive dynamics of *A. caven* in different habitat structures (unstructured, patchy, or gradients). We thus analyzed the distributions of height and trunk base diameter of *A. caven*, and where *A. caven* seedlings and saplings (<1 m) were observed. If *A. caven* is an invasive species, then we would expect to find a disproportionate and/or high level of *A. caven* seedlings and small trees (<1 m) in sclerophyllous forest—espinal gradients, as this species establishes and crosses the forest edge. Alternatively, if *A. caven* seeds can penetrate deep into forests, we might find young *A. caven* growing either in the shade of or within clusters of older sclerophyllous trees that do not show evidence of disturbance. If *A. caven* is a pioneer but not an invasive species, we should see young trees established primarily in open areas

and in areas with evidence of prior disturbance. Due to the very low number of *A. caven* seedlings and saplings observed, we report only descriptive results. For all trees >0.4 m, we looked separately at single-stemmed and multi-stemmed trees, and sorted them by habitat structure. We then fit linear models to relate height to the log of trunk base area. We also compared the height of trees across habitat structures (unstructured, patchy, gradient) using the Kolmogorov-Smirnov test (a non-parametric test that detects differences in distributions) implemented in R version 3.1.0. Height, trunk base area, and stem number can be interpreted to understand relative tree age, disturbance history, and whether *A. caven* grows more frequently or rapidly in certain habitat types. This was an exploratory analysis to determine whether the behavior of *A. caven* might vary across habitats. For example, if *A. caven* is taller in some habitat structures or species composition clusters than others, this could provide a suggestion about possible conditions under which *A. caven* is invasive or most competitive.

To answer question (2), testing the plant–plant competition hypothesis, we distinguished between *A. caven* overshadowing by filling-in and potential nurse–beneficiary relationships according to three criteria: the position of the trunks relative to the canopies, the relative sizes of the trees, and the growth form of the trees. We included all observed species pairs in this analysis. Filling-in can be assumed when the *A. caven* is under another tree's canopy, shorter, suppressed, or dead, and the other tree's trunk is outside the canopy of the *A. caven*. A potential nurse–beneficiary relationship can be assumed when the other tree's trunk is under the canopy of the *A. caven*; the relative sizes are not necessarily indicative since *A. caven* grows very slowly. When the *A. caven* showed signs of suppressed growth, and the other tree's trunk was under its canopy, we interpreted this as a potential nurse–beneficiary relationship where the beneficiary grew more quickly. We interpreted cases of *A. caven* <1 m under larger trees with the *A. caven* trunk under the other species' canopy, and showing no signs of suppression, as potential nurse–beneficiary relationships, with the *A. caven* as the beneficiary.

We intended to analyze the relative frequency of finding *A. caven* >0.4 m under different species' canopies in different habitat structures,

considering cases of overshadowing of *A. caven* by in-filling with sclerophyllous forest tree species. However, the number of observations of overshadowed live or dead *A. caven* was too small for statistical analysis and so is reported descriptively. We also intended to look at the relationship between species composition, and the position of different species under or outside of canopies. We expected to find that light-tolerant species would fill in outside of canopies first, followed by shade-tolerant and moisture-requiring species at a later stage. However, this analysis was not supported by the results of the species composition cluster analysis (see above, *Habitat structures and species composition*), which showed no evidence of the additive accumulation of tree species to species clusters on the basis of species characteristics.

To answer question (3), whether nurse–beneficiary relationships drove habitat succession, we analyzed the occurrence of all other species under *A. caven* canopies, corrected for canopy area relative to transect area. Each individual tree was classed as found under *A. caven* canopy, under another tree species canopy, or in the remaining open sampled space. We included all trees >0.4 m. We then sorted the data by habitat structure. For each habitat structure, we compared the observed frequencies in each category to the percent space in each category with χ^2 tests. Since we also observed various tree species growing under the canopies of *L. caustica* individuals, we also assessed *L. caustica* as a potential nurse species by counting the number of individual trees of each species growing under *L. caustica* canopies. However, due to the low number of observations of potential beneficiary trees under *L. caustica*, we did not conduct an analysis of their distribution corrected for canopy and transect area.

Additionally, to assess whether the germination microhabitats under *A. caven* and *L. caustica* canopies could account for the higher number of beneficiary trees under *A. caven* canopies, we assessed whether *A. caven* under-canopy microsites were significantly different from *L. caustica* under-canopy and open microsites. We used NMDS ordination analysis, as above, and linear models, as above, as complementary methods to analyze the data on the under-canopy microhabitats of *A. caven* and *L. caustica*. We asked whether the microhabitat dimensions measured (light reaching through the canopy, soil moisture under the

canopy, soil conductivity under the canopy, and soil temperature, available N, percent organic matter, C/N ratio, and pH) assorted into clusters by tree species, and also whether tree species, days after rain, and site were significant variables in explaining the variation in each dimension.

Finally, we addressed question (4), whether current condition (tree density) or historical conditions (disturbance history) better explain successional mechanisms, through two different analyses. We focused on explaining the frequency of individual beneficiary trees in nurse–beneficiary relationships, since this was the main mechanism of succession for which we obtained evidence. Previous work from remote-sensing data (Hernández et al. 2015, 2016) has claimed that establishment of sclerophyllous forest is dependent on the formation of increasingly dense espinal and mixed formations. Other explanations for forest regeneration and successional processes suggest that rather than succession responding deterministically to a biotic condition (e.g., tree density), disturbance or degradation histories affect the prevalence and efficacy of successional mechanisms and thus successional trajectories (e.g., Abrams et al. 1985, Chazdon 2003). In this case, dense espinal might be just one of many possible conditions leading to sclerophyllous forest. To test the dense espinal claim, we first assessed whether tree density predicted the number of trees growing from under other trees' canopies encountered in each transect. For this analysis, under-canopy trees were not counted toward tree density regardless of their size. We considered the variables site, percent *A. caven* canopy cover, percent other tree species canopy cover, total canopy cover, and habitat structure, and ran a linear model analysis in R version 3.1.0. Second, we ran a linear model to explain the number of beneficiary trees in transects, including the variables site, presence of horses, camelids, rabbits, cattle, sheep, water within 100 m, dry arroyo within 100 m, irrigation in the past 50 yr, woodcutting in the past 30 yr, woodcutting in the past 100 yr, animal pasturage in the past 100 yr, conversion to crops within the past 100 yr, fire within the past 10 yr, and altitude, also in R version 3.1.0. These variables were derived and coded from observations noted during tree measurement collection on the transects and the oral history interview data.

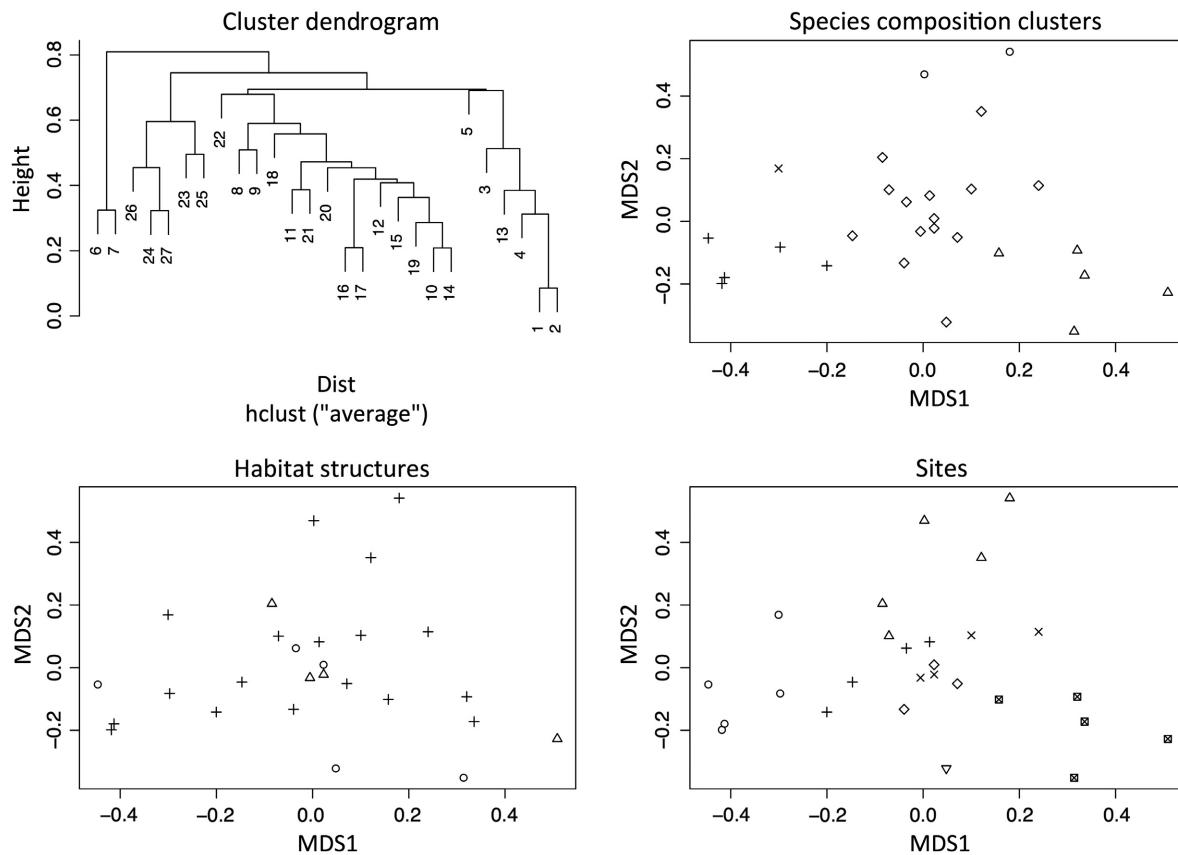


Fig. 3. NMDS analysis of species composition clusters by transect. Top left: cluster dendrogram of transects by species composition. Sites 6 and 7, on the left, correspond to sites at later stages of succession closer to sclerophyllous forest in form, while on the right, the cluster of 3, 13, 4, 1, and 2 represents *Acacia caven*-dominated early-successional areas. The other clusters are intermediate in form. Top right: plot of NMDS clusters, using a height cutoff from the dendrogram (top left) at 0.68. Each shape represents a different species composition cluster. Bottom left: the same clusters, with the point shapes representing the unstructured, gradient-structured, and patchy-structured habitats. Bottom right: the same clusters, with the point shapes representing the sites.

RESULTS

Habitat structures and species composition

An overview of the data collected in the transects is presented in the Appendix S1. By applying the Wald–Wolfowitz test to each transect, we identified 18 unstructured habitats, four patchy-structured habitats, and five espinal-sclerophyllous forest gradients. We noted that patchy structures were all found near to flowing water or in areas with evidence of intermittent natural water flow or dry irrigation channels.

We also assessed an NMDS ordination analysis to understand whether the transects should be considered one or many habitat types in terms

of species composition. For two dimensions, stress was 0.1173, indicating an accurate representation of the data in two dimensions. The cluster dendrogram and NMDS clustering are shown in Fig. 3.

We observed no relationship between spatial structuring of trees (unstructured, patchy, and gradients) and habitat type (species composition clusters) ($\chi^2 = 5.0357$, $df = 8$, $P = 0.7538$). Rather, the main species composition clusters corresponded well with the research sites ($\chi^2 = 58.0693$, $df = 24$, $P = 0.000119$ (reject null hypothesis of independence)). Specifically, the group consisting of transects 1–4 and 13 corresponded to La Rinconada, in the area dominated

by *Acacia caven* (transects 1–4), in the center of the geographical distribution of the sites. Transect 5 was also in La Rinconada. Transects 6 and 7 were both found in RN Río Clarillo at the eastern edge of the distribution, and represent nearly closed-canopy woodland dominated by large sclerophyllous trees. Finally, the cluster of transects 23–27 corresponded exactly to RN Lago Peñuelas, our western-most site.

Recruitment and growth of A. caven

In unstructured habitats, young *A. caven* were rare and we observed that they were usually distributed in small groups. We observed only two transects with groups of *A. caven* saplings <40 cm, and only three transects with groups of *A. caven* <1 m. Across all of our transects, we recorded 12 *A. caven*, including seedlings <0.4 cm high not included in the dataset, growing under the canopies of other *A. caven*. Many of these may have been vegetative reproduction from the roots of the adult tree.

Disturbed *A. caven* regrow from multiple trunks. In both the unstructured habitat and forest–espinal gradients, the proportion of single stem and multiple stem *A. caven* was close to half and half. In patchy-structured habitats, due to the presence of seedlings, there were almost twice as many single- as multiple-stemmed *A. caven*. Fig. 4 shows the relationship between the log area of the base of the trunk and tree height, for single-stemmed and multiple-stemmed *A. caven* in each habitat structure. In the patchy-structured habitat, which as noted above may be related to the presence of water, both single- and multiple-stemmed trees appear to be taller than those in other habitat structures for a given base area, and single-stemmed trees appear to have a higher height per log base area than multiple-stemmed trees. However, the distribution of tree heights did not differ significantly between habitat structures for either single- or multiple-stemmed *A. caven*, nor within habitat structures comparing single- to multiple-stemmed *A. caven* (multiple Kolmogorov–Smirnov tests, all $P > 0.05$).

We found little evidence that *A. caven* establishes under sclerophyllous canopies. We observed eight *A. caven* trees (>0.4 m) growing under two *L. caustica* individuals, three growing under one *Quillaja saponaria* individual, and one growing under a *Talguenia quinquinervia*. Thus, *A. caven*

grows directly under only 0.4% of the trees sampled. Due to the low numbers of *A. caven* under-canopy trees (12), we did not carry out a statistical analysis to quantify the potential overshading relationship between each of these potential nurse species and *A. caven*, or the relationship between overshaded *A. caven* height and canopy size or density.

Overshading of A. caven by in-filling of sclerophyllous trees

We did not find any cases of live or dead *A. caven* under canopies of sclerophyllous trees where it appeared that the *A. caven* had established prior to the sclerophyllous tree, and the sclerophyllous tree's trunk was outside the canopy of the *A. caven*. Note, however, that we did find overshaded *A. caven*, including those discussed in the previous section, as well as many others that were overshaded by other tree species growing out from under their own canopies—consistent with a nurse tree mechanism but not with an in-filling mechanism. We did not find clear evidence for stepwise community assemblage corresponding to sclerophyllous trees establishing in light followed by other species of sclerophyllous trees establishing in shade, as expected (see above, *Habitat structures and species composition*). To check this, we asked whether tree species richness was explained by the abundance of the two shade- and moisture-requiring trees observed in our sample (*Cryptocarya alba* and *Luma apiculata*). As seen in Fig. 5, these tree species appear when there are >3 species present in a transect (the first species is always *A. caven*). The best linear model relating abundance of shade- and moisture-requiring trees to tree species richness excluded the abundance of *C. alba*, the more abundant species, and included only the abundance of *L. apiculata*, of which three individuals were found at a single site, the site with highest species richness (overall model $P = 0.0327$, $F = 5.1_{1,25}$, adjusted $R^2 = 0.1365$).

Overshaded sclerophyllous forest trees

We observed all of the following sclerophyllous forest trees growing under the canopy of *A. caven*: *L. caustica*, *Q. saponaria*, *Maytenus boaria*, *Peumus boldus*, *Cryptocarya alba*, *Schinus latifolius*, *Azara serrata*, *Kageneckia oblonga*, and *Luma chequen*. Other species observed under *A. caven* were *Cassia*

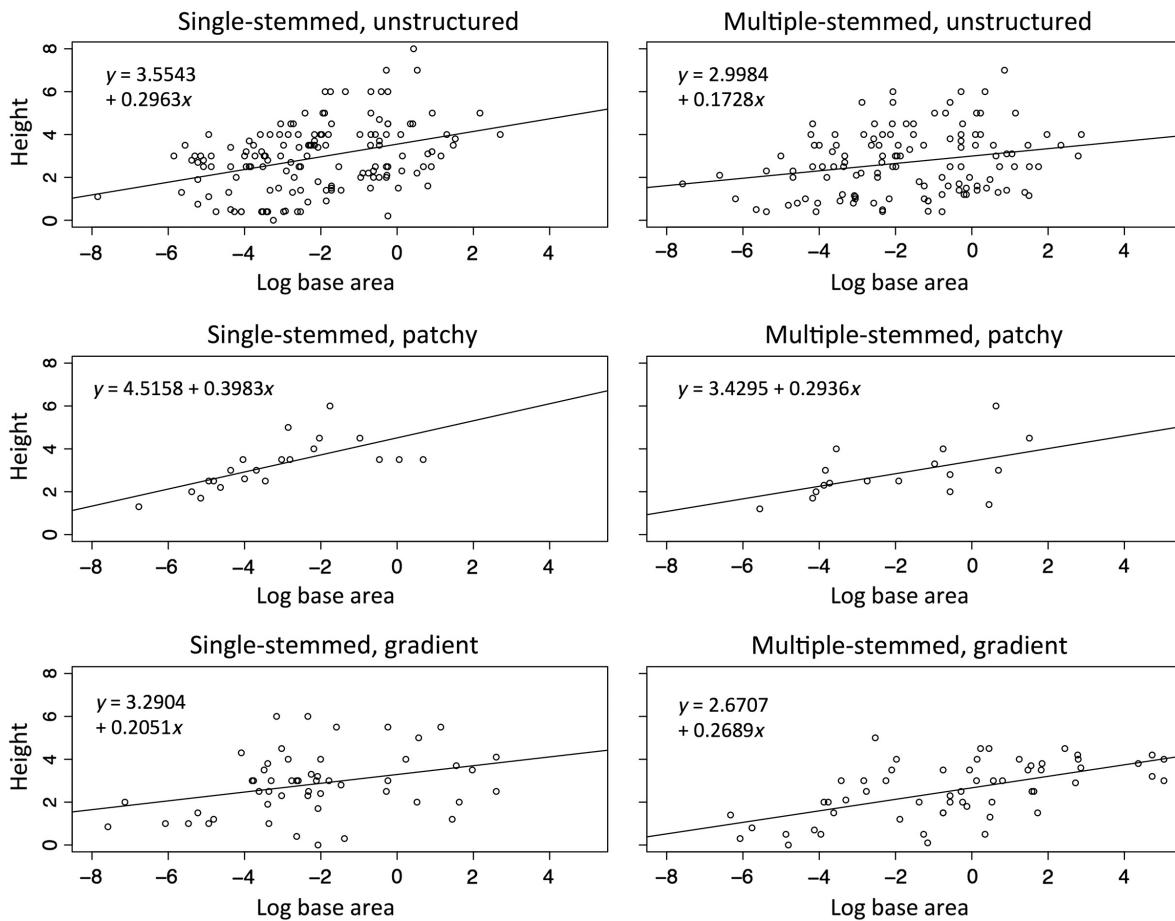


Fig. 4. Relationships between *Acacia caven* height (m) and log of trunk base area (m²), across habitat structures.

sp., the cactus *Echinopsis chiloensis*, and various shrubs. Other tree species observed in transects but not under *A. caven* canopies were *Talguenea quinquinervis*, *Schinus polygamus*, *Porlieria chilensis*, and *Azara dentata*. A total of 54 *A. caven* potential nurse trees were observed in transects.

In unstructured habitats, *Q. saponaria*, *M. boaria*, *S. latifolius*, and *Cryptocarya alba* grew under the canopy of *A. caven* more than expected given the canopy area of *A. caven* and avoided open space more than expected, given the area of open space ($\chi^2 = 25.456$, $df = 2$, $n = 38$, $P = 2.968 \times 10^{-6}$; $\chi^2 = 49.639$, $df = 2$, $n = 31$, $P = 1.664 \times 10^{-11}$; $\chi^2 = 22.924$, $df = 2$, $n = 8$, $P = 1.052 \times 10^{-5}$; $\chi^2 = 13.859$, $df = 2$, $n = 50$, $P = 0.0009787$). *Lithraea caustica* and *Peumus boldus* were distributed randomly over canopy and open spaces ($\chi^2 = 5.5698$, $df = 2$, $n = 52$, $P = 0.06173$; $\chi^2 = 2.0592$, $df = 2$, $n = 9$, $P = 0.3572$). We also

observed *Azara serrata* and *Schinus oblongus* growing under *A. caven*, but sample sizes for those species were too small for statistical analysis. At least one under-canopy tree was observed in 12 out of the 18 sampled unstructured habitats.

In patchy-structured habitats, *Cryptocarya alba* grew more frequently under *A. caven* canopy and less frequently in open space than expected ($\chi^2 = 27.421$, $df = 2$, $n = 6$, $P = 1.11 \times 10^{-6}$). *M. boaria* grew both more in open areas and under *A. caven* than expected, but never under the canopies of species other than *A. caven* ($\chi^2 = 7.5429$, $df = 2$, $n = 32$, $P = 0.02302$). In the patchy-structured habitats, we also observed between one and three individuals each of *Azara serrata*, *Q. saponaria*, *Peumus boldus*, and *Kageneckia oblonga* growing under an *A. caven* or other tree species, and none in the open. In addition, we

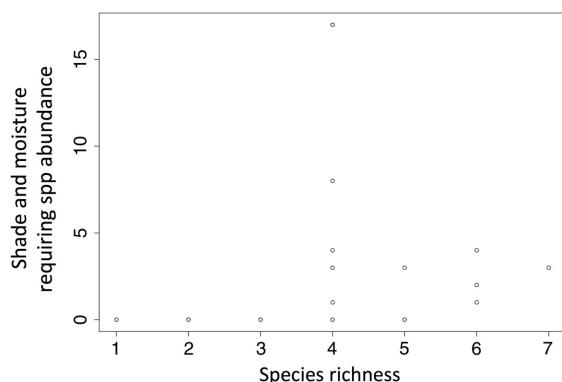


Fig. 5. Abundance of shade- and moisture-requiring species relative to the total tree species richness, per transect. The first species present is always *Acacia caven*.

observed two individuals of *Luma apiculata* growing under *A. caven* and one growing in the open. Trees growing under the canopies of other trees were observed in all patchy-structured habitats sampled.

In espinal to forest gradients, *M. boaria* grew more under *A. caven* and in the open, and less under other tree species, than expected ($\chi^2 = 7.7747$, df = 2, $n = 75$, $P = 0.0205$). *Lithraea caustica* and *Q. saponaria* were distributed across canopy and open spaces randomly ($\chi^2 = 4.2152$, df = 2, $n = 21$, $P = 0.1215$; $\chi^2 = 1.112$, df = 2,

$n = 8$, $P = 0.5735$). *Peumus boldus* and *Cryptocarya alba* also appeared to be distributed randomly across the gradient, but there were insufficient data to test. All gradients had at least one example of an under-canopy tree.

After *A. caven*, the second most common species observed with trees growing under its canopy was *L. caustica*, but as we observed only eight potential nurse trees of this species across all of our transects, we did not have a sufficient sample size to perform statistics on its associations with potential beneficiary tree species.

Under-canopy microhabitats of *A. caven* and *L. caustica*

The data from soil samples are shown in Table 1. We analyzed the microhabitat space data separately for 2 d after rain and 6 d after rain for *A. caven* and the other potential nurse species, *L. caustica*. All of the orditurf models were significant ($P < 0.001$, statistical details not shown) for all microhabitat dimensions (light reaching through the canopy, soil moisture under the canopy, soil conductivity under the canopy, and soil temperature, available N, percent organic matter, C/N ratio, and pH) for 2 d after rain as well as 6 d after rain. Two days after rain, two clusters of *L. caustica* emerged as distinct from the other weakly differentiated clusters (N clusters = 5, data not shown). Six days after rain, the

Table 1. Data included in the microhabitat dimension model.

Species	Site	Date	N	pH	Organic material	Available N	C/N
<i>Acacia caven</i>	Station	11 September	2	5.74	4.365	25.75	2.05
<i>A. caven</i>	Station	30 September	2	5.57	5.75	20.7	1.8
<i>A. caven</i>	River	11 September	2	6.035	3.365	11.55	2.55
<i>A. caven</i>	River	30 September	2	5.425	7.175	58.95	2.3
<i>A. caven</i> total mean			8	5.693	5.164	29.238	2.175
SE			8	0.093	0.722	10.321	0.188
<i>Lithraea caustica</i>	Station	11 September	2	6.655	9.015	19.8	2.75
<i>L. caustica</i>	Station	30 September	2	6.825	10.355	35.15	2.65
<i>L. caustica</i>	River	11 September	2	6.65	13.505	23.9	2.9
<i>L. caustica</i>	River	30 September	2	6.505	8.325	16.3	2.4
<i>L. caustica</i> total mean			8	6.659	10.3	23.787	2.675
SE			8	0.227	2.039	6.107	0.243
None	Station	30 September	5	6.416	4.648	16.52	1.98
None	River	30 September	5	6.018	3.772	14	1.8
Total mean			10	6.334	4.21	15.26	1.89
SE			10	0.203	0.746	2.308	0.131

Notes: Each combination of species, site, and date was represented by two samples, and the mean of those two samples is shown here. Total means and SE are shown for illustrative purposes only.

clusters were also not strongly differentiated (N clusters = 6, data not shown). However, in both cases, the clusters almost completely split *A. caven* from *L. caustica*. In Fig. 6a, b, we show the ordisurf models with the highest effect sizes (for space reasons). Both 2 and 6 d after rain, it can readily be observed that *L. caustica* microhabitat samples had less light, a lower temperature, and a higher C/N ratio than *A. caven* microsite samples, with the difference in soil moisture less clear-cut.

There was significant variation between conditions (the combination of site, day, and species) for all microhabitat dimension variables (ANOVA, $P < 0.001$ all tests, details not shown, Bonferroni correction accepting $P < 0.00625$ as significant). We show only the four variables with the highest effect sizes in the ordisurf models (Fig. 7). We tried to explain differences in microhabitats across the conditions with linear models using the data on tree species, number of stems, trunk diameter at the base, canopy radius, tree height, site, and day. We highlight that tree species was a significant variable included in best models for microhabitat dimensions soil moisture, light, pH, organic material, available nitrogen, and carbon-to-nitrogen ratio (Table 2). We use a Bonferroni correction for eight comparisons, accepting $P < 0.00625$ as significant for the overall P value.

Effect on nurse–beneficiary pairs of current condition and historical condition

As there was little evidence of in-filling and tree–tree competition, we focused this analysis on explaining the remaining mechanism of succession, nurse–beneficiary pair formation. We found that no variables related to tree density or habitat structure explained the number of under-canopy trees observed in transects, since high numbers of under-canopy trees were observed for the entire range of total canopy cover (including sclerophyllous trees) as well as *A. caven* canopy cover. The best model (highest overall R^2 , lowest P value) is shown in Table 3. We thus tested the alternative prediction that current and historical landscape and land-use context is more important to determining the number of beneficiary trees found in transects. We found that historical land-uses and most current land-uses were not included in significant models. In the best model, the presence of horses, and high elevation, reduced the number of observed beneficiary trees (Table 4).

DISCUSSION

We discuss our four research questions in order and then consider emergent issues.

If *Acacia caven* were an invasive species that contributed to sclerophyllous forest degradation, then we would expect to find a disproportionate and/or high level of *A. caven* seedlings and saplings (<1 m) in sclerophyllous forest–espalinal gradients or within closed forests. We did not find this pattern. Sapling *A. caven* individuals (<1 m) were always either in full sunlight or growing away from the shade of a parent tree from which they appeared to be a vegetative offshoot. We conclude that *A. caven* does not invade closed-canopy forest, but does act as a heliophyte pioneer species (Armesto et al. 1995). We found that *A. caven* seedlings and saplings were rare in all habitats. One explanation for its low establishment rate might be that trees recovering from disturbance are investing a large proportion of their resources in slow multi-stemmed regrowth, and relatively fewer resources in sexual reproduction (e.g., Nzunda and Lawes 2011). Thus, the perception that espinal tends to degrade rather than to recover could be a result of growth vs. reproductive tradeoffs following severe disturbance.

The presence of approximately equal proportions of multi-stemmed and single-stemmed *A. caven* in all habitat types suggests a high level of past disturbance from livestock herbivory, fire, and/or woodcutting, as well as subsequent (re)-growth. This observation is in accordance with the oral histories of management practices that we collected for each site, which generally indicated a peak in woodcutting, mainly for charcoal, between the 1950s and the 1970s, followed by a decline or abandonment of woodcutting and live-stock-raising. A similar use pattern has been observed in northern Chile (Dubroeucq and Livenais 2004).

We found little support for succession to sclerophyllous forest by tree–tree competition and filling-in of the spaces between *A. caven* individuals with sclerophyllous trees. If filling-in were a common mechanism, then *Maytenus boaria*, *Talguenia quinquervia*, and *L. caustica*, which showed evidence of recruitment into open spaces, should be highly abundant at an intermediate stage of succession. Next we would expect to see shade-loving species appear, followed by the death by

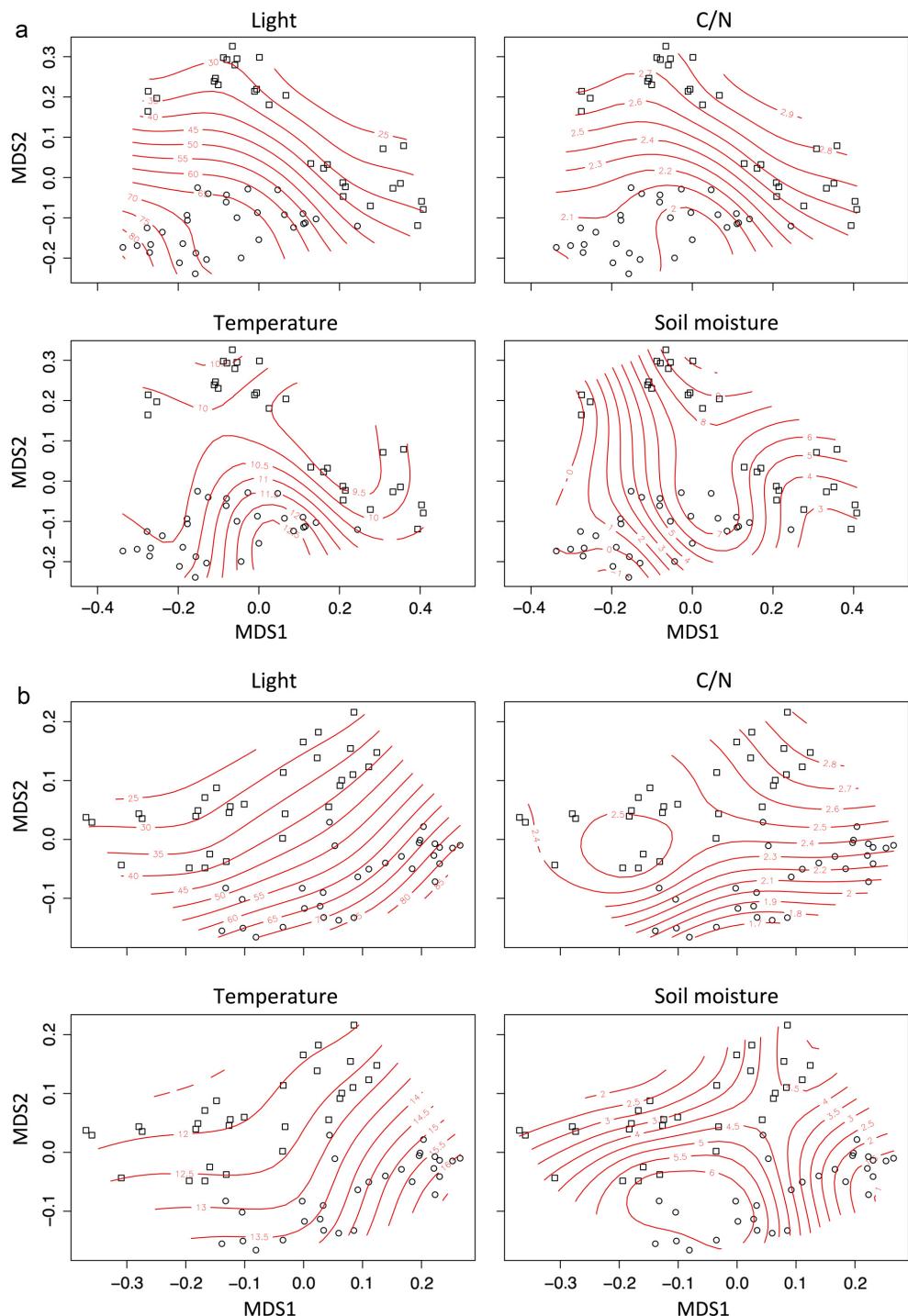


Fig. 6. (a) Two and (b) six days after rain, ordisurf models showing the distribution of temperature, light, C/N ratio, and soil moisture over the NMDS clusters for the sampled under-canopy tree microhabitats. *Lithraea caustica* are shown in squares, and *Acacia caven* in circles.

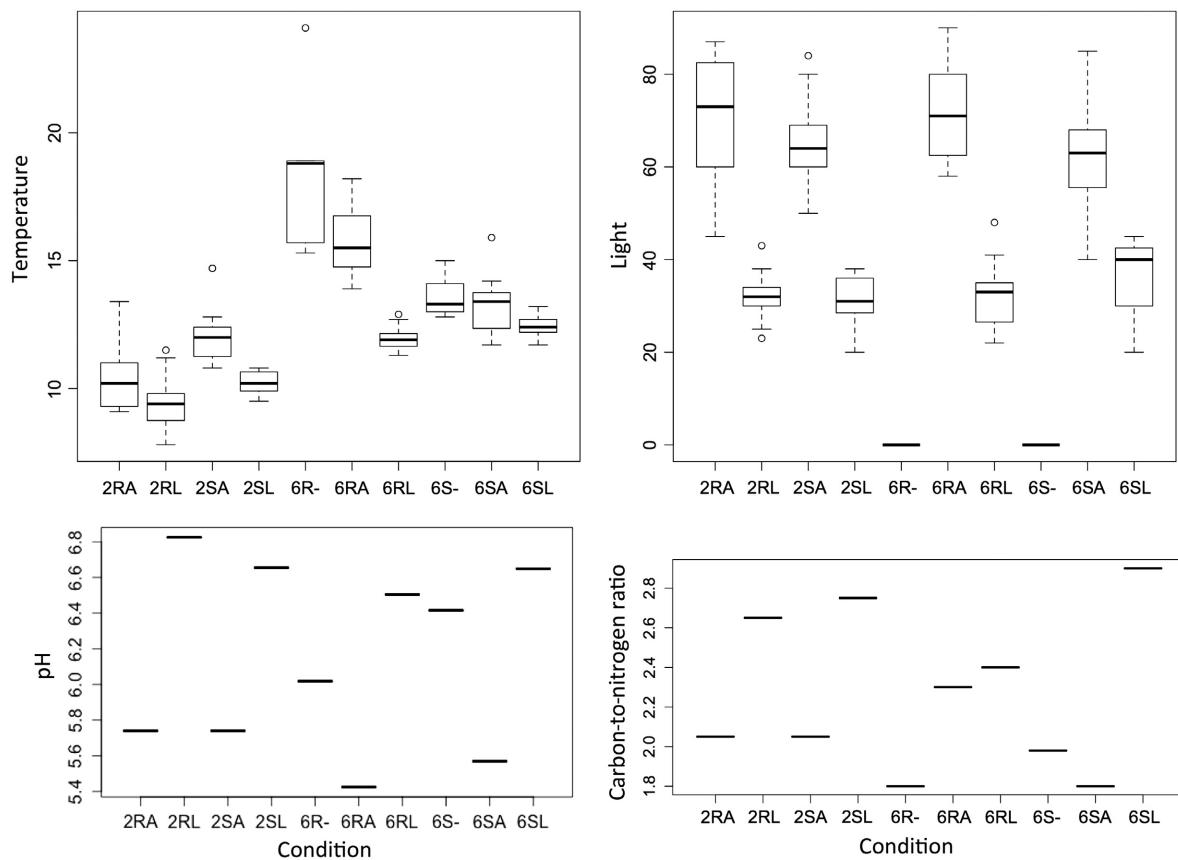


Fig. 7. Four key dimensions of the under-canopy microhabitats assorted by condition. Within condition acronyms, the number indicates days after rain, R = River site, S = Station site, A = under *Acacia caven*, L = under *Lithraea caustica*, — = control site in a clearing. Condition explains significant differences between values for each dimension. Temperature is measured in °C, light is measured in % transmission through the canopy (hence there is no measure for the control sites), and C and N are measured in mg/kg.

overshading of *A. caven* in dense woodlands. We found no clear support for such a pattern. Of the two shade- and moisture-requiring species observed, the rare *Luma apiculata* appeared only in the most species-rich site, supporting the filling-in prediction that these species should arrive in habitats last, but the far more abundant *Cryptocarya alba* was most abundant at intermediate species richness. Hoffmann (2012) describes *C. alba* as requiring moisture rather than shade. Thus, contrary to our assumption, a possible filling-in of the spaces between *A. caven* canopies with other tree species' canopies would not appear to affect habitat availability of soil moisture in a way relevant to *C. alba*. Species such as *Peumus boldus*, *Q. saponaria*, and *C. alba* were more likely to be found under *A. caven* canopies in unstructured

and patchy-structured habitats, but were distributed randomly in gradients. This suggests that successional pathways are partly controlled by place-based biophysical conditions, such as water availability, or spatial proximity to other woodlands. We were also unable to detect any dead *A. caven* under canopies of younger trees that had grown in the spaces between them and subsequently closed above them. However, this might reflect that closed sclerophyllous forests are likely to predate the extensive anthropogenic disturbances of the past 100 yr, and dead *A. caven* might have already decomposed or been harvested for firewood. We did, however, observe some *A. caven* that were overshadowed by sclerophyllous species. These include the 12 examples of *A. caven* that had recruited under other tree

Table 2. Under-canopy microhabitat dimensions and best linear models explaining each one.

Microhabitat dimension	Temperature	Soil moisture	Conductivity	Light	pH	Organic material	Available N	C/N
Intercept								
t value	19.9	2.9	2.1	28.6	287.1	19.9	23.1	48.0
P value	<2 × 10 ^{-16***}	0.004737**	0.0350*	<2 × 10 ^{-16***}	<2 × 10 ^{-16***}			
V1	Canopy diameter	Location: station	Location: station	<i>Lithraea caustica</i>	<i>Lithraea caustica</i>	<i>Lithraea caustica</i>	<i>Lithraea caustica</i>	<i>Lithraea caustica</i>
t value	-3.6	14.6	5.6	-18.1	46.1	16.5	-4.7	19.2
P value	0.000401***	<2 × 10 ^{-16***}	1.52 × 10 ^{-07***}	<2 × 10 ^{-16***}	<2 × 10 ^{-16***}	<2 × 10 ^{-16***}	7.85 × 10 ^{-06***}	<2 × 10 ^{-16***}
V2	Days since rain	<i>Lithraea caustica</i>	<i>Lithraea caustica</i>	Canopy diameter	Location: station	Location: station	Location: station	Canopy diameter
t value	9.6	3.9	1.7	-1.9	2.4	2.0	-5.9	-2.5
P value	<2 × 10 ^{-16***}	0.000136***	0.09	0.058	0.019	0.0437*	<2 × 10 ^{-16***}	0.0157*
V3					Days			
t value					-16.1			
P value					<2 × 10 ^{-16***}			
Adjusted R ²	0.46	0.66	0.21	0.75	0.98	0.69	0.32	0.76
F	55 on 2 and 126 DF	114.8 on 2 and 117 DF	17.1 on 2 and 117 DF	180.6 on 2 and 116 DF	2356 on 3 and 116 DF	138.3 on 2 and 117 DF	28.8 on 2 and 117	186.5 on 2 and 116
P	<2 × 10 ⁻¹⁶	<2 × 10 ⁻¹⁶	3.124 × 10 ⁻⁰⁷	<2 × 10 ⁻¹⁶	<2 × 10 ⁻¹⁶	<2 × 10 ⁻¹⁶	6.7 × 10 ⁻¹¹	<2 × 10 ⁻¹⁶

Notes: Each column represents a different linear model, with the variables (V1, V2, and V3) and their t and P values shown, as well as the overall adjusted R², F, and P for each model. *Lithraea caustica* increases soil moisture and decreases under-canopy light relative to *Acacia caven*. Asterisks and bold type indicate significance.

species (see *Recruitment and growth of A. caven*), as well as many examples in which the sclerophyllous forest tree was growing out from under the canopy of the *A. caven* and was taller. These, however, are examples of nurse–beneficiary relationships, not of filling-in and tree–tree competition (noting that overshading by the beneficiary tree may eventually switch to being a competitive interaction [Valiente-Banuet and Verdú 2008]). At best, the evidence for filling-in and tree–tree competition is equivocal and may require a more extensive dataset to assess thoroughly.

Table 3. Effect of tree density on beneficiary species.

Variables	Estimate	SE	t value	P value
Intercept	5.208117	4.455772	1.169	0.2556
<i>Acacia caven</i> density	0.191855	0.099630	1.926	0.0678
Other tree density	0.137871	0.080305	1.717	0.1007
Patchy habitat	-3.549816	5.838110	-0.608	0.54927
Unstructured habitat	-2.700057	4.435243	-0.609	0.5492
<i>A. caven</i> density × Other tree density	-0.007813	0.005280	-1.480	0.1538

Notes: Density is measured as percent cover of the total area of the transect. The adjusted R² is 0.01734. The F-statistic is 0.9113_{5,21} DF. The P value is 0.4926.

We record, for the first time, evidence of naturally occurring tree–tree facilitation in the form of sclerophyllous-tree beneficiary species nursed by *A. caven*. Under experimental conditions, facilitation occurs between various central Chilean trees (see *Introduction*), but this is the first time it has been demonstrated that one species grows under the canopy of the other more than expected by chance according to area, under natural conditions (compare, e.g., Valiente-Banuet et al. 1991, López et al. 2007). *Acacia caven* acts as a nurse species to at least four endemic sclerophyllous tree species: *Quillaja saponaria*, *M. boaria*, *Schinus latifolius*, and *Cryptocarya alba*. Other species that we observed may be nursed by *A. caven*, but were too rare in our relatively small transects to assess whether they grew under *A. caven* canopies beyond chance levels. Similarly, *L. caustica* appeared to facilitate other sclerophyllous species at times, but we were not able to demonstrate a significant nurse–beneficiary relationship.

This partially supports the nucleation hypothesis (Armesto and Pickett 1985) according to which sclerophyllous species fill in espinals by seed dispersal by birds mainly to under-canopy spaces (Holmgren et al. 2000, Reid and Armesto 2011). However, the issue is more complex

Table 4. Best model of contextual and historical factors affecting the number of individual beneficiary trees in nurse–beneficiary relationships.

Variables	Estimate	SE	t value	P value
Intercept	30.06635	5.28587	5.688	0.000202
Horses	-12.78141	3.83034	-3.337	0.007530
Near water	-11.91032	7.28662	-1.635	0.133191
Altitude	-0.01625	0.00665	-2.444	0.034601
Horses × Near water	20.35211	9.91186	2.053	0.067135

Notes: P values in boldface are significant. The adjusted R^2 is 0.5273. The F-statistic is 4.905_{4,10} DF. The P value is 0.01892.

because we observed wind-dispersed beneficiary trees (*Q. saponaria*), as well as many bird- and mammal-dispersed trees that were not significant beneficiaries or actually avoided the under-canopy space (e.g., *Talguenia quinquinervia*, *M. boaria*, *L. caustica*).

The under-canopy microhabitat space of *A. caven* formed a gradient with that of *L. caustica*, the other species that we found most often as a nurse tree to other sclerophyllous species. Although water availability may be an important factor in promoting beneficiary survival under nurse canopies (Badano et al. 2009), we observed no gallery forest effect (compare Azihou et al. 2013a). *Lithraea caustica* seemed better able to retain soil moisture under its own canopy up to a week after rain, which might favor the germination of seeds requiring higher soil moisture to grow deeper root systems, or might be advantageous in particularly dry areas such as rain shadows or the northern limit of espinal distribution, if the increased shade is tolerated (compare Badano et al. 2009). Holmgren et al. (2000) show experimentally that for *Q. saponaria* and *Cryptocarya alba* seeds in mesic matorral habitats, more seeds survived in open habitats than under sclerophyllous forest canopy (the canopy tree species and percent cover are not specified). They suggest that the opposite pattern would be found in more arid sites. Indeed, we found that both *Q. saponaria* and *C. alba* were beneficiaries of *A. caven*, showing that they survive under nurse tree canopies in semi-arid habitats and under the attenuated shade of espinal open woodland canopy. Responses to nurse canopy microsites are expected to vary across beneficiary species, habitat types, and abiotic and biotic conditions (Solivares et al. 2012, Torres and Renison 2015).

Acacia caven under-canopy microhabitats had relatively higher N and lower organic material, compared to *L. caustica*, resulting in the higher C/N ratio of *L. caustica*, and both were higher than outside the canopy. This is in line with the literature, which shows that soil organic carbon increases with canopy density (and potentially litter accumulation which appears to be correlated) in espinals and mixed woodlands (Muñoz et al. 2007, 2008, Nangari Piña 2012, Soto et al. 2015). *Acacia caven* is also, unlike *L. caustica*, a nitrogen fixer (Aronson et al. 2002), although the effect on soil N content varies with soil depth (Muñoz et al. 2008). We predict that the distinct microhabitat clusters observed translate into differential survival of beneficiary seedlings, and may thus explain the nurse function of *A. caven* and why it is by far the most common nurse species in this ecosystem. *Acacia caven* spines are rarely found near ground level (only if the tree has collapsed or is a shrub, which was rare in our dataset); thus, we doubt physical protection from herbivory favors the survival of woody seedlings (Gómez-Aparicio et al. 2008). We discuss the possible role of herbivory below.

The nurse function of *A. caven*, and espinal more generally, allows both early- and later-successional sclerophyllous species to establish outside of sclerophyllous forest nuclei. Unlike Hernández et al. (2015), we found that sclerophyllous forest tree establishment was not dependent on *A. caven* or all-tree density. This was due to isolated *A. caven* in low tree density areas, with large numbers of beneficiary trees under their canopies. Isolated trees are known to attract birds, act as islands of suitable establishment conditions for other plants, and provide connectivity (Galindo-González et al. 2000, Manning et al. 2006). An expanding nucleus of connectivity and seed attraction might eventually lead from a very low-density espinal to a mixed woodland formation, by expanding outward rather than filling in.

Based on our site oral histories and our model of nursed species frequency, it appears that the history of disturbances including historically intensive woodcutting, pasturing, and conversion to cropland has little or no effect on current espinal successional trajectories. Presence of horses, but not other livestock, had a small negative effect on beneficiary tree frequency, and nursed species also decreased with altitude and

closeness of water. The last two factors presumably reflect a lesser benefit of under-canopy niches at higher (colder, less disturbed) altitudes and areas with higher soil moisture (although as our under-canopy microhabitat data showed, closeness to water does not guarantee higher soil moisture). Thus, our prediction that the history of disturbances may explain successional mechanisms is only partially supported and depends on the role of horse pasturing.

The issue of livestock grazing and other disturbances in espinal management is complex and understudied. Although horses appeared to have a negative effect on the number of beneficiary trees in sites away from water, we did not have data on changes in horse (or other animal) density over time, or on the time of year when livestock are present. The negative effect of horses is also puzzling since horses are known as primarily grass grazers (Rook et al. 2004), and would thus be predicted to open microhabitats and reduce tree–grass competition experienced by tree seedlings. However, since they bite very close to the ground, they might also eat small seedlings missed by cattle or sheep (Rook et al. 2004). Horses, as well as cattle and camelids, may also contribute to the dispersal of *A. caven* seeds via endozoochory (Gutiérrez and Armesto 1981, Fuentes et al. 1989). Livestock may thus be critical for the successional process at the early stages of espinal development after agricultural abandonment, fire, or severe woodcutting. Large herbivores can interact in complex ways with other disturbance factors such as fire to affect the overall balance between tree–tree and tree–grass competition and facilitation mechanisms (e.g., Holmgren et al. 2000, Van Langevelde et al. 2003, Armesto et al. 2009, Staver et al. 2009, Soliveres et al. 2012, Azihou et al. 2013b, Doughty et al. 2015). A key take-away message, in any case, is that most large herbivores had no effect on sclerophyllous tree presence under *A. caven*. While we doubt that *A. caven* primarily provides physical protection to nursed seedlings, the rate of large herbivore foraging might be lower under the canopy of these trees compared to open areas, not because of the spines but due to the absence of an herbaceous understory in many cases after early spring. Relatedly, the time of year and stocking density at which horses and cattle are allowed to graze in espinals may

determine whether seedlings are able to establish. Horses and cattle may also facilitate European rabbit (*Oryctolagus cuniculus*) herbivory by keeping herbaceous vegetation low, lowering the rabbits' predation risk (Bakker et al. 2009). European rabbits are generally found to reduce tree establishment in Chile (e.g., Fleury et al. 2015). Our data did not suggest that rabbits directly affect nurse–beneficiary interactions, although the negative effect of horses could potentially be due to a non-detected interaction with rabbits. Experimental work on this subject could reveal the effect of facilitation between herbivores on facilitation between trees.

CONCLUSION

Plant–plant facilitation occurs between *Acacia caven* and endemic Chilean sclerophyllous forest trees and may provide successional mechanisms linking espinals and sclerophyllous forests. Considering the variation we observed in the composition of sclerophyllous species across our seven sites, we expect that more intensive sampling would increase the number of endemic tree species found nursed by *A. caven*. These findings suggest that the biodiversity value of espinals should be re-examined or acknowledged. Mixed habitats of *A. caven* and endemic sclerophyllous species should be classed as intermediate espinal–sclerophyllous forest successional habitats. We also propose that floristically diverse espinal sites should be protected for conservation as potential sclerophyllous forest areas and restored whenever possible, without necessarily preventing their management for silvopastoralism and related uses. This opens new scenarios for central Chilean woodland conservation (Rey Benayas et al. 2008, Newton et al. 2011). Some rare endemic central Chilean tree species with poor dispersal, including *Jubaea chilensis* (Fleury et al. 2015) and *Beilschmiedia miersii* (Becerra et al. 2004), may be restricted in their ability to access suitable regeneration microsites under nurse trees, suggesting an avenue for further research on their conservation. We propose that further research on espinal and sclerophyllous forest restoration and conservation should examine their ecological linkages within a framework of dynamic successional exchange under anthropogenic disturbance and climate stress.

Our results partially support the findings of related work on plant–plant facilitation in semi-arid habitats. As in similar habitats, we found evidence of important effects of open woodland or savanna tree canopies on other plant species (Belsky et al. 1989, Hoffmann 2000, Azihou et al. 2013b, Bufford and Gaoue 2015, Stahlheber et al. 2015). However, our results do not reflect the fleshy fruit/Tertiary and dry fruit/Quaternary syndromes reported for nurse and beneficiary pairs in other mediterranean-climate habitats (Verdú et al. 2003, Soliveres et al. 2012). Rather, all species are thought to be of Miocene/early Pleistocene origin (see *Introduction*) corresponding to the Tertiary, and *A. caven* has a fleshy bean pod, while beneficiary trees have wind-dispersed seeds (*Quillaja saponaria*), dry fruits (*Maytenus boaria* and *Schinus latifolius*), and fleshy fruits (*Crypocarya alba*). Our results emphasize that tree–tree facilitation may emerge under many conditions.

Previous conclusions that espinal had crossed a threshold and was a degradation endpoint are likely due to the stage of early succession following extensive wood-cutting, characterizing many espinals in the 1990s (see Newton 2007). A key conclusion is thus that the combination of a particular successional/ degradation framework and observations at a particular point in time can strongly influence inferences about restoration potential and ecological trajectories (e.g., Veldman et al. 2015).

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