

# Destruction without extinction: long-term impacts of an invasive tree species on Galápagos highland vegetation

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## Summary

**1.** A common belief in invasion ecology is that invasive species are a major threat to biodiversity, but there is little evidence yet that competition from an exotic plant species has led to the extinction of any native plant species at the landscape scale. However, effects of invasive species at community and ecosystem levels can severely compromise conservation goals.

**2.** Our model species, the red quinine tree (*Cinchona pubescens*), was introduced to the Galápagos Islands in the 1940s and today extends over at least 11 000 ha in the highlands of Santa Cruz Island. It is also invasive on other oceanic islands.

**3.** We adopted a long-term approach, analysing permanent plots in the Fern-Sedge vegetation zone over 7 years, to test for impacts of *C. pubescens* density on resident plant species composition and on microclimate variables. We also tested whether the *C. pubescens* invasion facilitated the invasion of other species.

**4.** The rapid pace of the *C. pubescens* invasion was indicated by a more than doubling of percentage cover, a 4.6-fold increase in mean stand basal area and a 4-fold increase in the number of stems ha<sup>-1</sup> in 7 years.

**5.** Photosynthetically active radiation was reduced by 87% under the *C. pubescens* canopy while precipitation increased because of enhanced fog interception.

**6.** *Cinchona pubescens* significantly decreased species diversity and the cover of most species by at least 50%. Endemic herbaceous species were more adversely affected than non-endemic native species. *Stachys agraria*, another invasive species, colonized bare ground that developed under the *C. pubescens* canopy.

**7.** The numbers of native, endemic and introduced species in the study area remained constant throughout the 7-year period.

**8. Synthesis.** This study clearly established *C. pubescens* as a habitat transformer, although its average cover did not exceed 20%. Despite the fact that no plant species has been lost completely from the study area so far, the introduction of the novel tree life form to a formerly treeless environment led to significant changes in stand structure and environmental conditions and to decreases in species diversity and cover. Such changes clearly conflict with conservation goals as set by the Convention on Biological Diversity.

**Key-words:** biodiversity loss, *Cinchona pubescens*, ecosystem engineer, ecosystem impacts, facilitation, habitat transformer, introduced species, oceanic islands, plant invasion, threatened species

## Introduction

A common belief in invasion ecology and nature conservation is that invasive species are a major threat to biodiversity and a particular risk to isolated island ecosystems (Brockie *et al.*

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1988; Loope, Hamann & Stone 1988). In this context, the statement by Wilcove *et al.* (1998) is often cited, that about 57% of the endangered plant species in the US, which are mostly species of the Hawaiian archipelago, are negatively affected by alien species. Not specified, however, is whether these threats stem from alien plant or animal species. Other authors advise caution in making generalizations about invasive species effects, pointing out that, so far, there is little evidence that competition from an exotic plant species has led to the extinction of a native plant species (Sax & Gaines 2008). However, for the evaluation of impacts of invasive species it is important to know not only whether or not a species goes extinct but also what changes were generated at the population genetic, community and habitat levels, and the scale of the changes which are highly relevant for nature conservation (cf. United Nations CBD 1993).

Drastic negative impacts of invaders are particularly expected on isolated oceanic islands, which are commonly regarded as more susceptible to invasion by alien species than mainland areas because of their depauperate floras and faunas, with fewer highly competitive species (Elton 1958; Carlquist 1974). Although the Galápagos Islands are comparatively pristine relative to other tropical oceanic archipelagos, this unique ecosystem is undergoing profound alterations as a result of plant and animal introductions (Hamann 1984; Lawesson 1990; Itow 2003). For example, over 800 plant species have been introduced, now making up more than 60% of the total flora (Tye, Atkinson & Carrión 2008).

Furthermore, strong adverse effects of invasive species on the structure and composition of resident plant and animal communities are especially anticipated for certain species, termed 'habitat transformers' (Richardson *et al.* 2000) or 'ecosystem engineers' (Jones, Lawton & Shachak 1994; Crooks 2002). These are species that directly or indirectly change the availability of resources for other species by causing physical state changes in biotic or abiotic materials (Jones, Lawton & Shachak 1994). In this regard, far-reaching effects are expected from the *Cinchona pubescens* invasion in the Galápagos highland vegetation, since its introduction represents the establishment of a novel growth form – 'tree' – in formerly treeless vegetation zones. Even the presence of single *C. pubescens* trees severely reduces the cover and diversity of resident plant species (Jäger, Tye & Kowarik 2007).

Finally, changes in nutrient cycling caused by invasive species may lead to drastic changes in communities and ecosystems (Vitousek & Walker 1989; Ehrenfeld 2003). Investigations of changes in soil characteristics provoked by *C. pubescens* indicate that it alters nutrient turnover (H. Jäger, unpubl. data).

Impacts of an invading species vary spatially as well as temporally (Parker *et al.* 1999; Richardson & Pyšek 2006). Similarly, the relationship between the richness of native and introduced species is variable and complex. Observational, theoretical and experimental studies investigating the role of diversity in the resistance of species communities to invasions have produced different results (Fridley *et al.* 2007). To generalize these results, there is often a positive correlation between native and introduced species on a larger scale, while there is a

negative correlation on a smaller scale (Shea & Chesson 2002; Stohlgren *et al.* 2006; but see Sax 2002).

Adverse effects of invasive species may only become apparent over the course of an invasion, and are often not documented by impact studies, many of which are short-duration 'snapshots' and rarely sample multiple times (Blossey 1999; Strayer *et al.* 2006). Because of changes in the invader, the invaded community and interactions between them, the ecological consequences of invasions likely vary through time. In the case of *C. pubescens*, we tested a range of impacts of an invasion process that had begun about 40 years earlier and since the 1990s has resulted in the dominance of *C. pubescens* over about 11 000 ha in the highlands of Santa Cruz Island, Galápagos. About 5000 ha of this invaded area are situated in the Galápagos National Park, the remainder in the agricultural zone (Buddenhagen *et al.* 2004). Comparisons of vegetation measurements underneath and around tall individual *C. pubescens* trees in the National Park area revealed significant decreases in species richness and percentage species cover with proximity to the tree trunks (Jäger, Tye & Kowarik 2007). This approach simulated a *C. pubescens* cover of up to 100%, and it remained unclear whether the effects encountered would scale up for larger sampling units and how the resident vegetation would be affected by changes in the *C. pubescens* population over time. By analysing permanent plots established in dense *C. pubescens* stands, over 7 years, we address both the dynamics of the invasive species and changes in species richness, diversity and cover. With a continuously increasing *C. pubescens* invasion, we predicted adverse effects on the native vegetation, even to the point of the extinction of native species, considering the frequently cited generalizations about severe invasion impacts.

We differentiated impacts on endemic, non-endemic native plants and introduced plants, and were thus able to test whether these species groups responded differently to the invasion, in particular whether *C. pubescens* facilitated the establishment of other invasive species (Simberloff & Von Holle 1999). As the emergence of the novel growth form 'tree' is expected to change environmental conditions significantly (Vitousek 1986; Mack 2003; Jäger, Tye & Kowarik 2007), we also analysed the differences between microclimate variables measured under a *C. pubescens* canopy and those measured in the open vegetation.

Hence, we addressed the following questions: (i) Does *C. pubescens*, over time, alter the species richness, diversity and cover of the invaded plant community, and are these changes related to the varying abundance of the invader? (ii) What were the impacts of *C. pubescens* on the microclimate? (iii) Did the *C. pubescens* invasion (a) facilitate invasion by other species, (b) affect endemic species more severely than non-endemic native species and (c) lead to extinction of plant species?

## Materials and methods

### STUDY AREA

The area of the National Park invaded by *C. pubescens* on Santa Cruz Island comprises about 5000 ha (Buddenhagen *et al.* 2004), spanning

the Scalesia-, Miconia- and Fern-Sedge zones. Sampling was carried out in the Fern-Sedge zone, which extends from about 570 m a.s.l. to the highest point of the island, Mount Crocker, at 864 m a.s.l. Before the arrival of *C. pubescens*, this vegetation zone was dominated by native bracken (*Pteridium arachnoideum*), other fern species and several herbaceous and gramineous species, with scattered aggregations of the endemic tree fern *Cyathea weatherbyana*. It is not clear whether this type of Fern-Sedge zone vegetation is a secondary formation that developed or increased after several fires in the highlands in the 1950s and 1960s. The fires partly destroyed the former shrubby vegetation dominated by the endemic shrub *Miconia robinsoniana* (Van der Werff 1978; Kastdalen 1982), which occurs below the Fern-Sedge zone, but their impact higher up is unknown. However, on the first recorded ascent of Mount Crocker in 1932, Howell noted that at an altitude of 616 m a.s.l. the *Miconia* vegetation zone became entirely replaced by Ferns (Howell 1942)<sup>1</sup>. Since our sampling plots were located at an altitude of 600–660 m a.s.l., they approximately coincided with the lower part of the Fern-Sedge zone. The fires were the only known significant physical disturbances to the study area before 1967, apart from patchy grazing by livestock. After this, no further large-scale disturbances have been documented (Hamann 1975; Kastdalen 1982), although sporadic cattle grazing has been permitted in drought years. Within the Fern-Sedge zone, an area of about 1000 ha was identified on the SW-slope of the island within which physical parameters (aspect, slope and altitude) were fairly constant. Plots were established within c. 32 ha of this area, between 00°39'24.8" S, 90°19'52.5" W and 00°39'11.7" S, 90°19'57.7" W. The average percentage inclination (slope) for the study area was 24%, mainly in an SSW direction. Average annual precipitation at the altitude of the study sites (610–660 m a.s.l.) was 1694 mm (Hamann 1979a) while the annual temperatures varied between 17 and 33 °C (mean minimum and maximum temperature; H. Jäger, unpubl. data) from July 2004 to May 2006. The soils of the Fern-Sedge zone are ferruginous Andosols, consisting of young pyroclastic deposits with a pH<sub>KCl</sub> ranging from 4.3 to 5.2 (Laruelle 1966). Field work was carried out during the rainy season (January to March) of 1998, 2003 and 2005.

Plant species nomenclature follows Jørgensen & León-Yáñez (1999). Definition of species status follow Tye (2006) and Leeuwen *et al.* (2008), the term for the species group 'native species' is defined as not including endemic species (i.e. non-endemic native species).

#### STUDY SPECIES

The native range of *Cinchona pubescens* Vahl (syn. *Cinchona succirubra* Pav. ex Klotzsch, red quinine tree, Rubiaceae) extends from Costa Rica to Venezuela and Bolivia (Andersson 1998). It has become naturalized in Hawaii and Tahiti (Cronk & Fuller 1995) where it has also become invasive (Weber 2003; Meyer 2004). *Cinchona pubescens* was introduced to the Galápagos Islands in the 1940s (Hamann 1974; Lundh 2006). It was planted in the upland agricultural zone, below our present study site, and from there the light, winged seeds were carried to higher altitudes by the wind. By 1972, it had begun to spread rapidly by seed and vigorous suckering (Hamann 1974; Macdonald *et al.* 1988). *Cinchona pubescens* grows to 15 m in height in Galápagos (Shimizu 1997) and now dominates large parts of the Fern-Sedge zone (Fig. 1).

<sup>1</sup>Howell (1942) mistakenly reported the maximum elevation of Santa Cruz Island as 1700 ft (518 m), instead of the actual elevation of 864 m, so we adjusted the altitude accordingly in the citation quoted here.

#### SAMPLING

Vascular plants were sampled in 14 randomly placed permanent plots with a range of different *C. pubescens* densities in the Fern-Sedge zone. All plots were 20 × 20 m with the NE-corner marked by a PVC tube. The plots comprised 0.56 ha in a sampling area of 32 ha within an overall area of about 1000 ha with similar physical characteristics. This way, 1.8% of the study area was sampled, which in turn represents about 3.2% of the invaded Fern-Sedge area. Five parallel 20-m transects were set through each plot 5 m apart from each other. Vegetation measurements were carried out along the transects and percentage vegetation cover was estimated for each species by the line-intercept method in 1998, 2003 and 2005, always by the same investigator (H. Jäger). To account for rare species, the spaces between transects were searched, and species not recorded along the transects were noted. Soil depth was measured every 5 m along each transect by hammering an iron bar into the ground. All *C. pubescens* individuals in each plot were counted and those exceeding 1.5 m in height were marked with an aluminium tag and the d.b.h. at c. 1.3 m was measured. The percentage slope of each plot was measured with a clinometer (Suunto, Vantaa, Finland).

#### MICROCLIMATE MEASUREMENTS

Microclimate variables (air temperature, relative humidity, soil temperature, precipitation and light) were measured in the Fern-Sedge zone (00°38'56.3" S, 90°19'48.2" W). Measurements were taken every hour from July 2004 to May 2006 at approximately 1.5 m above the ground with paired sensors (underneath the *C. pubescens* canopy and in the open intact native vegetation), which were 8 m apart and connected to a waterproof data logger (DataHog2, Skye Instruments, Llandrindod Wells, UK). Soil temperature was measured at approximately 15 cm depth.

#### DATA ANALYSIS

All data for temporal comparisons are presented as the means of fourteen 20 × 20 m plots. Since *C. pubescens* cover was the potential driver of change in the rest of the plant community, it was excluded from the analysis of percentage total cover of the plant community. Prior to analysis, species presence/absence counts and values for percentage cover (subsequently referred to as 'cover') obtained from the five 20-m transects in a plot were pooled. Species richness was determined in two ways: first, as 'mean number of species', which is the average number of species in the fourteen plots; second, as 'total number of species', which is the number of all species in the 14 plots. Cover data for dominant species (other than *C. pubescens*) were analysed separately, while data for less common species were grouped into a set of 'species groups' prior to analysis (see Appendix S1 in Supporting Information). Since cover was combined across several vegetation strata, total cover may exceed 100%.

The assumption of normality of the data was checked with the Kolmogorov–Smirnov test and that of homogeneity of variances with Levene's test. Percentage cover data were arcsine-square root-transformed to achieve normality and *C. pubescens* density data were log<sub>10</sub>-transformed. Cover of all species combined (except for *C. pubescens*), dominant species, species groups and species of special interest (endemic and introduced species) was analysed by repeated-measures ANOVA with year of monitoring (1998, 2003 and 2005) as a within-subjects factor. In cases where the sphericity assumption was not met (all except for *C. pubescens*).





**Fig. 1.** *Cinchona pubescens* invasion in permanent sample plot 20 in 1998 (above) and 2005 (below). *Cinchona pubescens* trees are in the background and on the left, natural vegetation is in the foreground (mainly *Pteridium arachnoideum*). Note the growth of *C. pubescens* trees on the far left and right of the photos and the encroachment of *C. pubescens* in the centre. Height of plot PVC tube: 2 m (Photos: H. Jäger).

*cens*, *P. arachnoideum*, *S. agraria* and bare ground), the Huynh–Feldt correction was applied. *Post hoc* pairwise comparisons were performed at the 0.05 significance level on estimated marginal means using the Bonferroni adjustment for multiple comparisons. In addition, the comparison of differences in the reductions of cover of all pooled fern species and herbaceous species over the 7-year study period was carried out by a one-way ANOVA. *Post hoc* tests were conducted using the Tukey’s HSD test. Linear regression analysis was used to assess the relationship between *C. pubescens* cover and the cover of other species and was carried out on the means of each plot, separately for each year (1998, 2003 and 2005). All analyses were conducted using spss version 14.0 for Windows (SPSS Inc., Chicago, IL, USA).

The Shannon diversity index ( $H'$ ) was used to measure the diversity of each sample using ESTIMATE S software (Colwell 2005). This index was chosen because it is more sensitive towards rare species than for example the Simpson index (Magurran 1988). The Shannon evenness index was calculated using the formula  $H'/\ln S$  (where  $S$  is the total number of species in the sample).

Stand basal area ( $G$ ) was calculated as the sum of the basal area of each individual tree in the plot, determined as  $G$  (in  $m^2$ ) =  $0.0000785398 \times d^2$  (where  $d$  is d.b.h. in cm).

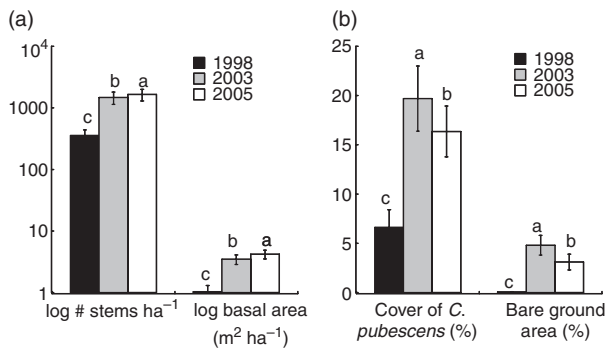
Microclimate data from underneath the *C. pubescens* canopy and the surrounding area were  $\log_{10}$ -transformed prior to analysis to achieve normality and a paired *t*-test was applied. Results are shown as the ratios of each microclimate variable measured under the *C. pubescens* canopy compared with the open canopy.

Results were interpreted on two spatial scales: local and landscape. The local scale refers to the plant community within a  $400\text{-m}^2$  ( $=0.04$  ha) plot and the landscape scale refers to the vegetation within the entire study site in an area of about 32 ha.

## Results

### INVASION DYNAMICS

There was a significant increase in *C. pubescens* abundance in the study plots from 1998 to 2005. The mean stand basal area increased 4.6-fold ( $F_{1,2,15.6} = 174.8$ ,  $P < 0.001$ , Fig. 2a) and the number of *C. pubescens* stems  $\text{ha}^{-1}$  increased 4-fold ( $F_{1,03,13.3} = 18.7$ ,  $P = 0.001$ , Fig. 2a). The mean *C. pubescens* cover increased significantly in all plots from 1998 to 2003 by 70% and from 1998 to 2005 by 65%,



**Fig. 2.** Change in (a) *Cinchona pubescens* density [number of stems ha<sup>-1</sup> and stand basal area (m<sup>2</sup> ha<sup>-1</sup>)] and (b) *C. pubescens* cover (%) and bare ground area (%) in 14 permanent plots in the Fern-Sedge zone from 1998 to 2005. Values are mean + SE, levels within the same variable not connected by the same letter were significantly different in *post hoc* pairwise comparisons using Bonferroni adjustment after repeated-measures ANOVA at  $P \leq 0.05$ .

but decreased from 2003 to 2005 by 20% ( $F_{2,26} = 89.3$ ,  $P < 0.001$ , Fig. 2b). Cover of *C. pubescens* in individual plots varied from 0 to 21% in 1998, 3 to 42% in 2003 and from 2 to 29% in 2005 (data not shown).

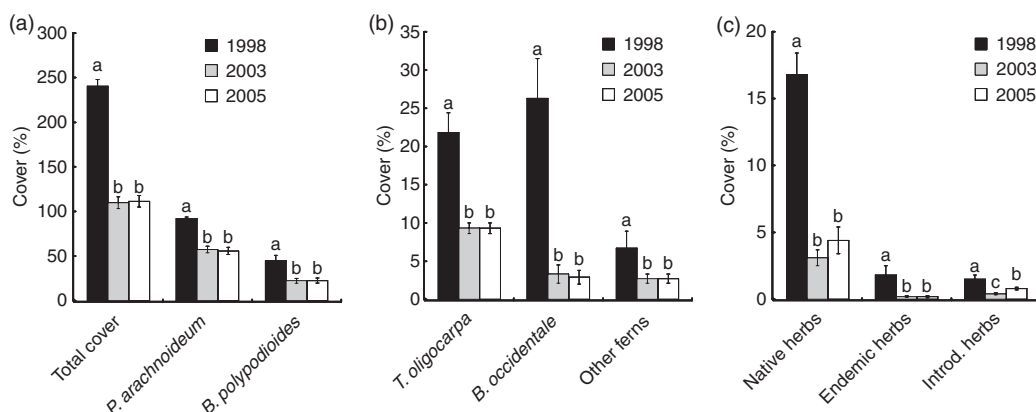
#### SPECIES COVER

There were profound changes in the cover of species between 1998, 2003 and 2005 (Fig. 3). The average cover of all species (except for *C. pubescens*) grouped together (= total cover), was significantly reduced by 50% from 1998 to 2003 and from 1998 to 2005 ( $F_{1,4,18.5} = 285.2$ ,  $P < 0.001$ , Fig. 3a). Cover of the following species groups and dominant species was also significantly reduced (by at least 30% for both comparisons) from 1998 to 2003 and from 1998 to 2005:  $F_{2,26} = 211$ ,  $P < 0.001$  for *P. arachnoideum*,  $F_{1,3,16.7} = 15.7$ ,  $P = 0.001$  for *Blechnum polypodioides*,  $F_{1,1,14.7} = 82.8$ ,  $P < 0.001$  for *B. occidentale*,

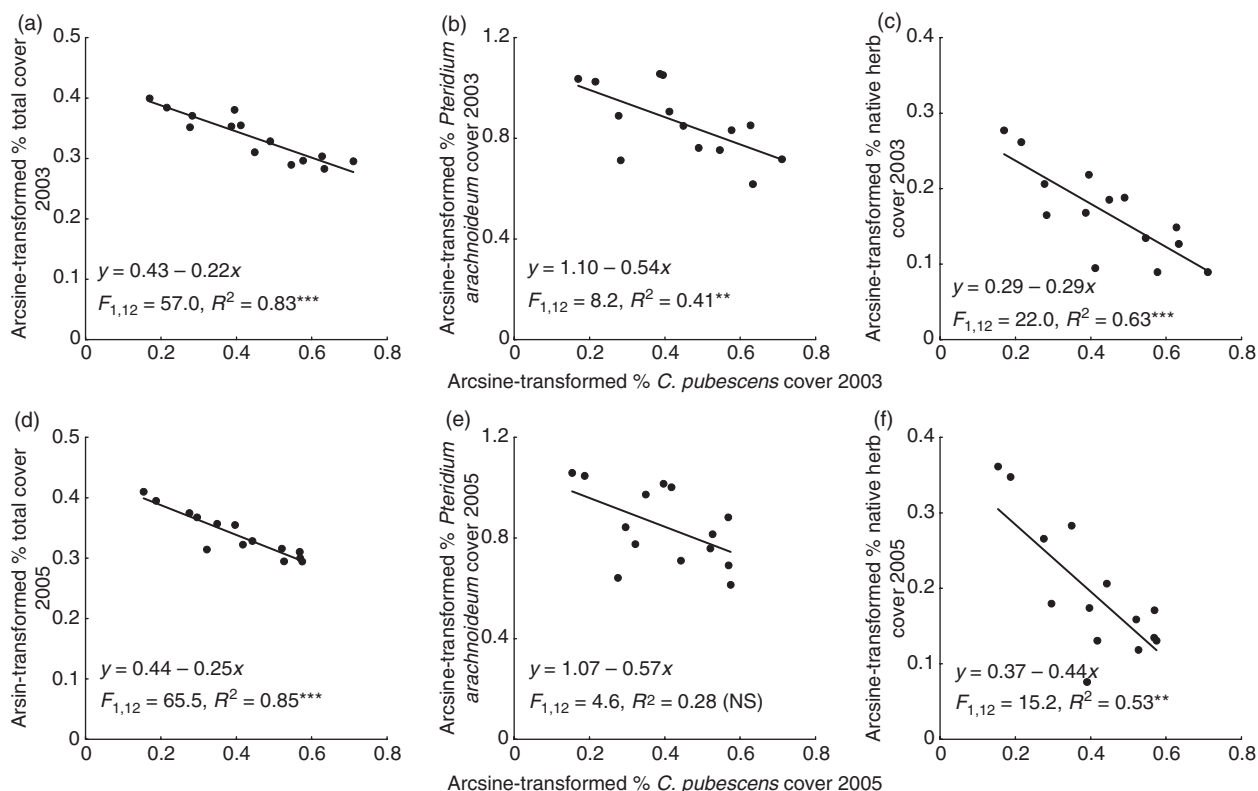
$F_{1,3,17.5} = 35.7$ ,  $P < 0.001$  for *Thelypteris oligocarpa* and  $F_{1,2,15.2} = 6.9$ ,  $P = 0.016$  for 'other ferns' (Fig. 3a,b). In addition, the reduction in cover was especially pronounced for herbaceous species, which were reduced by 89% for endemic, by 82% for native and by 73% for introduced species from 1998 to 2003 ( $F_{1,2,14.9} = 16.3$ ,  $P = 0.001$ ,  $F_{1,3,17.3} = 72.7$ ,  $P < 0.001$ ,  $F_{2,26} = 11.4$ ,  $P < 0.001$ , respectively, Fig. 3c). Among the endemic herbaceous species, *Pilea baurii* was reduced by 99% from 1998 to 2003 and by 98% from 1998 to 2005 ( $F_{1,2,15.4} = 28.9$ ,  $P < 0.001$ ). The percentage decrease in cover was significantly higher for overall herbaceous species (mean decrease of 81% from 1998 to 2003 and of 73% from 1998 to 2005) than for overall fern species (mean decrease of 50% for both comparisons,  $F_{2,39} = 31.3$ ,  $P < 0.001$  for comparison from 1998 to 2003 and  $F_{2,39} = 10.5$ ,  $P < 0.001$  for comparison from 1998 to 2005). When the very dominant fern *P. arachnoideum* was taken out of the analysis, the percentage decrease in cover of the remaining fern species was greater but still significantly lower than that of herbaceous species (mean decrease of 62% from 1998 to 2003 and of 60% from 1998 to 2005).

Native and endemic species cover did not significantly change between 2003 and 2005, while the cover of introduced herbs doubled during this period. This was mainly caused by an increase in *S. agraria* ( $F_{2,26} = 9.1$ ,  $P = 0.001$ , Fig. 3c). The only species increasing in cover over the 7 years of monitoring was the introduced shrub or tree common guava (*Psidium guajava*). Its cover increased 5.7-fold from 1998 to 2003 but then did not increase further towards the end of the study ( $F_{1,2,15.6} = 6.2$ ,  $P = 0.02$ , data not shown).

Negative relationships between arcsine-transformed percentage *C. pubescens* cover and the arcsine-transformed percentage cover of almost all other species and species groups emerged as the prevailing result of the regression analyses (Fig. 4). For example, there were significant negative relationships between *C. pubescens* cover and total cover, cover of *P. arachnoideum* and cover of native herbs. In 2003, *C. pubes-*



**Fig. 3.** Change in cover of different species and species groups in 14 permanent sample plots in the Fern-Sedge zone from 1998 to 2005: (a) total cover, cover of *Pteridium arachnoideum* and *Blechnum polypodioides*; (b) cover of *Thelypteris oligocarpa*, *Blechnum occidentale* and of all other fern species combined; (c) cover of species groups (native, endemic and introduced herbaceous species). Values are mean  $\pm$  SE, levels within the same variable not connected by the same letter were significantly different in *post hoc* pairwise comparisons using Bonferroni adjustment after repeated-measures ANOVA at  $P \leq 0.05$ . For species in 'species groups' see Appendix S1.



**Fig. 4.** Negative relationships between means of arcsine-transformed cover of *Cinchona pubescens* and of native species in 14 permanent sampling plots in the Fern-Sedge zone within years. Line is the best-fit linear regression line (NS = not significant; \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$ ): (a) total cover in 2003, (b) total cover in 2005, (c) cover of *Pteridium arachnoideum* in 2003, (d) cover of *P. arachnoideum* in 2005, (e) cover of native herbs in 2003 and (f) cover of native herbs in 2005. Note: minimum *C. pubescens* cover: 2.8% = 0.17; maximum *C. pubescens* cover: 42% = 0.71).

**Table 1.** Negative relationships between means of *Cinchona pubescens* density ( $x$ , stand basal area and stems  $\text{ha}^{-1}$ ) and the dependent variables ( $y$ ) of cover of all species combined (= total cover) and cover of native herbaceous species in 14 permanent sample plots in the Fern-Sedge zone in different years (only significant results shown)

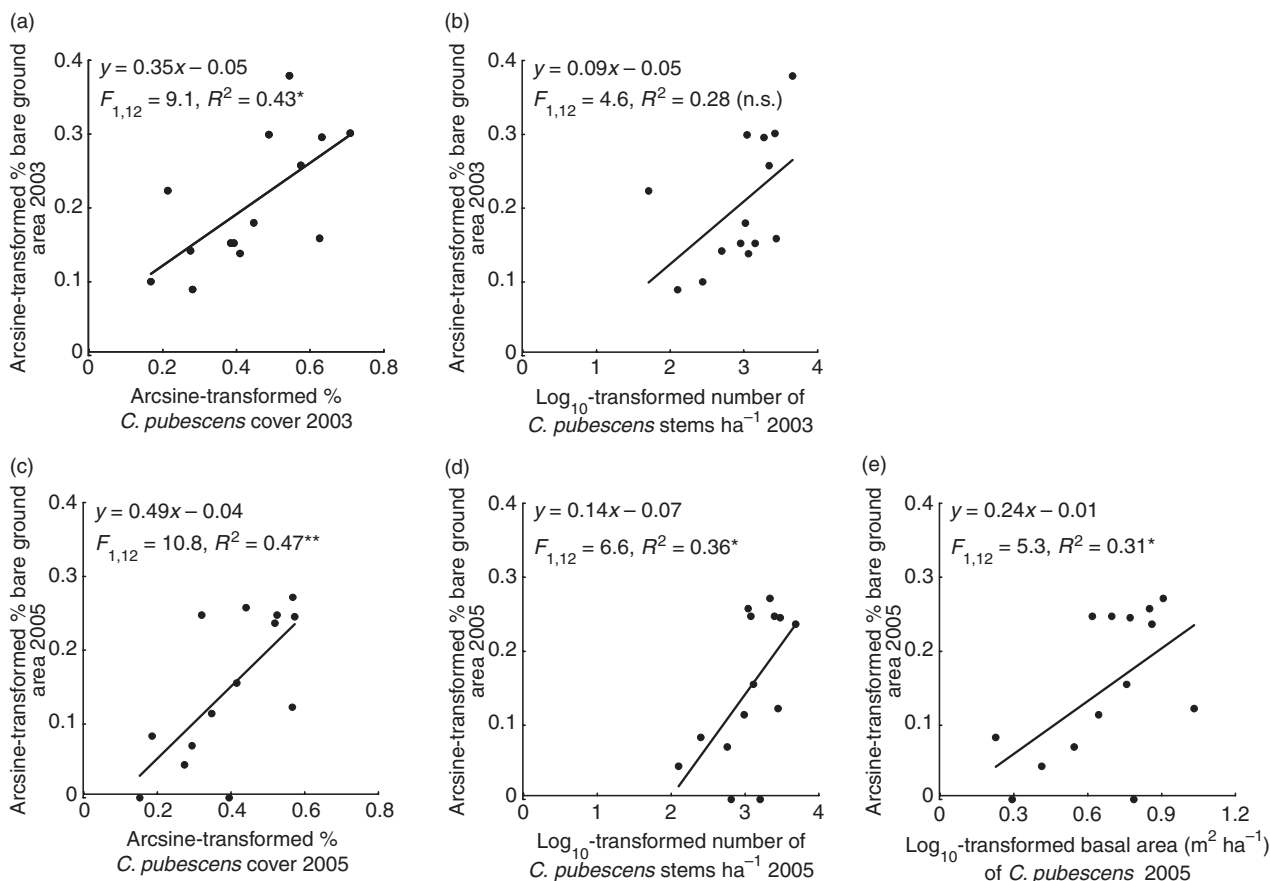
	Equations	$R^2$	$F$	$P$
<i>Cinchona pubescens</i> stand basal area ( $\text{m}^2 \text{ha}^{-1}$ ) and:				
Total cover (%) 1998	$y = 0.549 - 0.128x$	0.52	13.1	0.004
Total cover (%) 2003	$y = 0.413 - 0.129x$	0.64	21.0	< 0.001
Total cover (%) 2005	$y = 0.428 - 0.133x$	0.68	25.0	< 0.001
Native herb cover (%) 2003	$y = 0.243 - 0.137x$	0.35	6.4	0.027
Native herb cover (%) 2005	$y = 0.377 - 0.269x$	0.53	13.5	0.003
<i>Cinchona pubescens</i> stems $\text{ha}^{-1}$ and:				
Total cover (%) 2003	$y = 0.505 - 0.057x$	0.63	20.4	< 0.001
Total cover (%) 2005	$y = 0.548 - 0.068x$	0.61	19.1	< 0.001
Native herb cover (%) 2003	$y = 0.395 - 0.077x$	0.50	11.8	0.005
Native herb cover (%) 2005	$y = 0.603 - 0.133x$	0.44	9.5	0.009

*pubescens* cover explained 83, 41 and 63% of the total cover and cover of *P. arachnoideum* and native herbs, respectively. In 2005, the percentage variation explained by *C. pubescens* cover was 85, 28 and 56% for total cover, cover of *P. arachnoideum* and cover of native herbs, respectively. *Cinchona pubescens* cover explained 41% of the cover of the introduced herb *S. agraria* ( $F_{1,12} = 8.2$ ,  $P = 0.014$ ) in 1998 and 29% in 2003 ( $F_{1,12} = 4.9$ ,  $P = 0.047$ ; results not shown).

The total cover and cover of native herbs were also significantly negatively correlated with the stand basal area and stem density of *C. pubescens* in 2003 and 2005 (Table 1). In addition, there was a significant negative relationship between *C. pubescens* stand basal area and total plant cover in 1998.

With an increase in *C. pubescens* cover from 1998 to 2003 and a subsequent decrease from 2003 to 2005, the percentage of bare ground simultaneously increased and then decreased





**Fig. 5.** Positive relationships between means of percentage bare ground area and *Cinchona pubescens* cover (both arcsine-transformed) and means of *C. pubescens* density ( $\log_{10}$ -transformed) in 14 permanent sample plots in the Fern-Sedge zone within years. Line is the best-fit linear regression line (NS = not significant; \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ): (a) *C. pubescens* cover in 2003, (b) *C. pubescens* cover in 2005, (c) *C. pubescens* stems  $\text{ha}^{-1}$  in 2003, (d) *C. pubescens* stems  $\text{ha}^{-1}$  in 2005 and (e) *C. pubescens* stand basal area ( $\text{m}^2 \text{ha}^{-1}$ ) in 2005.

during the same periods ( $F_{2,26} = 39.1$ ,  $P < 0.001$ , Fig. 2b). There were several significant positive relationships between *C. pubescens* abundance and bare ground (Fig. 5). For instance, *C. pubescens* cover was positively related to bare ground in 2003 and 2005 (43% and 47%, respectively), as were *C. pubescens* stand basal area and bare ground in 2005 (31%). Furthermore, *C. pubescens* stem density was positively related to bare ground in 2003 and 2005 (28% and 36%, respectively).

#### SPECIES RICHNESS AND DIVERSITY

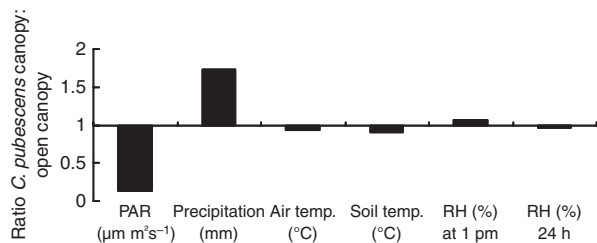
Surprisingly, species richness did not vary significantly between 1998, 2003 and 2005, neither in the mean number of species per plot nor in the total number of species in all 14 plots (see Table S1 and Appendix S2). There was a striking constancy in the absolute numbers as well as relative proportions of native, endemic and introduced species over the 7-year monitoring period (see Table S1). At the level of all 14 plots, two species recorded in 1998 were not recorded in 2005 (see Appendix S1). Considering the individual plots, 23 species were recorded in one or more plots in 1998 but not again in the same plots in 2003 or 2005 (Appendix S3). These were mainly fern and herbaceous species, with the native herb *Drymaria cordifolia* recorded in six

and the endemic herb *Pilea baurii* recorded in eight of the 14 plots. There was no relationship between the number of plots in which species occurred only in 1998 and not in 2003 or 2005, and the level of *C. pubescens* invasion in these particular plots (data not shown). In addition, no relationship was detected between the number of indigenous (native and endemic) species and the number of introduced species in each plot during any of the three sampling periods (see Appendix S2).

In contrast, species diversity (represented by the Shannon–Wiener diversity and evenness index) significantly declined from 1998 to 2003 but then remained unchanged towards the end of the study in 2005 ( $F_{1,1, 13.9} = 3872$ ,  $P < 0.001$  for the Shannon–Wiener diversity index and  $F_{2, 26} = 134$ ,  $P < 0.001$  for the Shannon evenness index, data not shown). This analysis confirmed the results for species cover and showed that these effects are linked, even though species richness was not changed by the *C. pubescens* invasion (see Table S1).

#### MICROCLIMATE

Results of a paired *t*-test on different microclimate variables showed that the photosynthetically active radiation (PAR) measured at 1 pm daily was significantly reduced by 87% under



**Fig. 6.** Ratio of microclimate variables measured under the *Cinchona pubescens* canopy compared with the open canopy for daily means for the period of July 2004 to May 2006 (ratio 1 = no change; ratio > 1 = increase; factor < 1 = decrease). Results of paired *t*-test of microclimatic variables measured simultaneously by paired sensors (8 m apart) at 1.5 m height at 1 pm daily in the Fern-Sedge zone (PAR = photosynthetically active radiation,  $n = 359$  for PAR,  $n = 350$  for precipitation,  $n = 260$  for air temperature,  $n = 350$  for soil temperature,  $n = 218$  for relative humidity (RH) measured daily at 1 pm and  $n = 5235$  for relative humidity measured hourly for 24 h; all comparisons significant at  $P < 0.001$ ).

the *C. pubescens* canopy [ $99.4 \pm 3.3$  vs.  $755.5 \pm 27.0$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); d.f. = 349,  $t = 80.6$ ,  $P < 0.001$ ; Fig. 6]. Air and soil temperatures were also significantly reduced by about 6% and 9%, respectively [ $22.1 \pm 0.2$  vs.  $23.6 \pm 0.2$  ( $^{\circ}\text{C}$ ); d.f. = 259,  $t = 18.4$ ,  $P < 0.001$  for air temperature and  $20.0 \pm 0.1$  vs.  $22.0 \pm 0.15$  ( $^{\circ}\text{C}$ ); d.f. = 349,  $t = 35.7$ ,  $P < 0.001$  for soil temperature; Fig. 6]. Mean precipitation under the canopy measured at 1 pm was 42% higher [ $0.59 \pm 0.17$  vs.  $0.34 \pm 0.11$  (mm); d.f. = 349,  $t = 4.2$ ,  $P < 0.001$ ; Fig. 6]. When only considering measurements at 1 pm, relative humidity was 6% higher under *C. pubescens* than in the surroundings [ $75.1 \pm 1.1$  vs.  $70.9 \pm 1.1$  (%); d.f. = 217,  $t = 10.4$ ,  $P < 0.001$ ; Fig. 6], but taking all hourly measurements into the analysis revealed a 3% lower relative humidity under the canopy compared with the open canopy [ $86.5 \pm 9.4$  vs.  $89.4 \pm 13.4$  (%); d.f. = 5234,  $t = 15.8$ ,  $P < 0.001$ ; Fig. 6].

## Discussion

### INVASION DYNAMICS

Since its introduction to the Galápagos Islands, *C. pubescens* has gradually invaded the highlands of Santa Cruz and has virtually converted the formerly treeless Fern-Sedge zone into a forest. Even though *C. pubescens* was already abundant at the beginning of this study, the continued rapid increase in *C. pubescens* stem density and stand basal area over the 7-year study period (Fig. 2a) suggested that no saturation point had been reached and that no self-thinning of the *C. pubescens* stand had occurred (cf. Yoda *et al.* 1963). However, despite the increases in stems and stand basal area over the 7-year period, *C. pubescens* cover decreased by 20% from 2003 to 2005 (Fig. 2b). This is probably related to the fact that in 2005 precipitation at the study site was lower than in previous years (H. Jäger, unpubl. data), which is not reflected by annual precipitation data recorded at a metrological station lower in elevation (194 m a.s.l., see Fig. S1). Therefore, *C. pubescens* trees had

fewer and smaller leaves in 2005 than in 2003, which resulted in a reduced cover.

### COMMUNITY-LEVEL EFFECTS OF *C. PUBESCENS*

Our results showed clear changes in plant community structure in the Fern-Sedge zone during the 7-year monitoring period. While native sedges and grasses showed no response to *C. pubescens*, individual dominant fern species did, and herbaceous species suffered a decline in cover of up to 90%. Herbaceous species as a group were more affected than overall fern species, which presented a lesser reduction in cover. The cover reduction of herbaceous species included introduced species, like *S. agraria*. These findings suggest that it is the herbaceous growth form that reacts to the *C. pubescens* presence rather than native species being more susceptible, which cause these changes in plant community structure. This was also suggested by the results of our previous study on the impact of individual *C. pubescens* trees (Jäger, Tye & Kowarik 2007). Strong relationships were detected between increasing *C. pubescens* abundance (cover, stand basal area, stem density) and declining cover of almost all dominant and individual plant species and species groups (Fig. 4, Table 1).

The first year of monitoring (1998) was an 'El Niño' year with exceptionally high rainfall (see Fig. S1), so vegetation growth was generally enhanced. Therefore, the reduction in vegetation cover might have been especially pronounced post-El Niño from 1998 to 2003, although this might have been offset by the minor El Niño that occurred in 2002 (see Fig. S1). However, no significant reduction in vegetation cover was observed during the following sampling period (2003–2005), which was a period when *C. pubescens* cover decreased (Fig. 2b).

Potential explanations for the negative relationships between *C. pubescens* abundance and the cover of associated plant species include competition for space, light and nutrients. *Cinchona pubescens* trees sucker by specialized underground stems and by layering, so that new stems emerge a short distance away from the primary trunk (cf. Del Tredici 2001). This way, *C. pubescens* trees take on a multi-stemmed growth form (Shimizu 1997), which occupies large areas. Thus, some of the impacts were likely caused by competitive displacement of other plant species by the emerging *C. pubescens* stems.

Another impact of the *C. pubescens* invasion was the depression of plant species diversity between 1998 and 2003. The *C. pubescens* invasion likely decreased the abundance of rare species and enhanced the abundance of common species during this period. No effects on species diversity were recorded during the last 2 years of the study, when *C. pubescens* cover was decreasing. As for vegetation cover measurements in 1998, the elevated El Niño rainfall might have also enhanced the emergence of rare species in the plots in 1998. This might partly explain the sharp drop in species diversity between 1998 and 2003. On the other hand, both the average number of species per plot and the total number of species in all plots did not change over the 7-year monitoring period (see Table S1), which was surprising considering that the cover of *C. pubescens* had significantly increased by up to 70% (Fig. 2b).



We had expected to find significant reductions in native plant species richness, possibly because of species extinctions associated with the increase of *C. pubescens* and the reduction in the cover of native plant species. However, our data indicated that no species disappeared from the overall species pool in the 14 study plots. Of the two species of plant only recorded in 1998, one, *Diplazium subobtusum*, a fern, is otherwise common in the Fern-Sedge zone and has been sampled outside the plots after 1998 (H. Jäger, unpubl. data). The other species, the native grass *Panicum hirticaule*, is not common in the highlands of Santa Cruz and the record from 1998 is now thought to be a probable misidentification (see Appendix S1). However, when considering the species pool of the individual plots, 23 species were recorded only in 1998 in more than one of the 14 plots and were not recorded again in 2003 or 2005 in the same plots. These were mainly fern and herbaceous species, with the endemic herb *Pilea baurii* found in eight plots in 1998 but only in one plot in 2003 and two in 2005, respectively (see Appendix S3). As already discussed, the heavy rainfall in 1998 might have contributed to the enhanced appearance of rare species in that year. However, all of the 25 species were still present in the Fern-Sedge plant community in a similar habitat around the plots in 2005 (H. Jäger, unpubl. data). It was also surprising that no relationship was detected between the number of indigenous (native and endemic) species and the number of introduced species (see Appendix S2), such as has been reported elsewhere (Stohlgren *et al.* 1999; Sax 2002; McDougall *et al.* 2005).

#### ECOSYSTEM-LEVEL EFFECTS OF *C. PUBESCENS*

The 87% reduction of PAR under the dense *C. pubescens* canopy (compared with the open vegetation), exceeded our initial expectations of *C. pubescens*-induced alterations to local environmental conditions (Fig. 6). A major reason for the impacts of *C. pubescens* on the native vegetation is therefore likely to be a change in the light regime, reducing light availability to other plant species. This is supported by the fact that the largest reductions in cover of species and species groups occurred between 1998 and 2003 when *C. pubescens* cover was at its peak (Fig. 2b). Correspondingly, species diversity significantly decreased from 1998 to 2003. The cover of herbaceous species was in general more reduced by the *C. pubescens* invasion than the cover of ferns, which are usually more shade-adapted.

The effects of shading were assumed to be the underlying mechanism for reductions in vegetation cover under individual *C. pubescens* trees compared with the surrounding Fern-Sedge vegetation (Jäger, Tye & Kowarik 2007). These impacts were stronger there than in the lower-altitude Miconia zone, probably because of the shade pre-adaptation of species that normally grow under the dense *Miconia robinsoniana* shrub cover, compared with the more open Fern-Sedge zone (Jäger, Tye & Kowarik 2007). All these findings suggest that *C. pubescens* creates shade atypical of the light-exposed highland plant communities, which leads to further dominance of the invader and strong inhibition of native species (Reinhart *et al.* 2006). This

is the consequence of an addition of a life form novel to the native vegetation community, in this case a tree species (Vitousek 1986; Mack 2003).

The increased 'precipitation' under the *C. pubescens* canopy (Fig. 6) was probably occult precipitation, because of leaves trapping moisture from the regular highland mist. Intercepted drops are larger than normal raindrops and can reach terminal velocity when falling from trees taller than 8 m (Satterlund & Adams 1992). As a likely consequence, water-filled depressions in the ground were created under *C. pubescens* trees, which remained bare: few species seemed able to grow in these conditions. These observations probably explain the significant increase of bare ground with increases in *C. pubescens* cover and abundance (Figs 2b and 5). Allelochemical effects are an alternative explanation for these bare patches and should be tested by experiments.

#### FACILITATION OF INTRODUCED SPECIES BY *C. PUBESCENS*

Invasive species are well known for modifying and disturbing their physical environment, thereby sometimes facilitating the spread of other species (Rejmánek 1989). *Cinchona pubescens* may do this by creating bare ground patches available for colonization. From 2003 to 2005, bare ground decreased significantly, corresponding to the decrease in *C. pubescens* cover. This may have been caused by enhanced light penetration through the more open canopy of trees in 2005, the drying out of depressions under them and consequent re-colonization by vegetation. By 2005, this re-colonization included other introduced species (mainly the herb *S. agraria*), which explained the significant increase of the introduced herbaceous species group from 2003 to 2005 (Fig. 3c) and the concurrent decrease of bare ground (Fig. 2b). However, separate linear regression analysis of the cover of introduced species and bare ground did not reveal any significant relationships. *Stachys agraria* was already abundant at the outset of the study and its cover had significantly decreased by 2003. In addition, cover of *S. agraria* in 1998 and 2003 was significantly inversely related to the *C. pubescens* cover in the same year. But *S. agraria* was the only species that increased again from 2003 to 2005 with a concurrent decrease in *C. pubescens* cover (Figs 2b and 3c). This pattern shows that even though *S. agraria* was negatively affected by the *C. pubescens* invasion, as were other species, it might have been indirectly facilitated by the creation of bare ground under *C. pubescens*. These findings also suggest that the system is still unstable and highlights the importance of long-term monitoring of invader impacts.

Further studies should investigate whether *S. agraria* continues to spread, as well as whether *C. pubescens* facilitates invasion by common guava *Psidium guajava*, which was the only species whose cover increased significantly up to 2003, as *C. pubescens* cover also increased. Investigation of the role that *C. pubescens* plays in nutrient cycling may shed light on this, since elevated phosphorus and nitrogen concentrations were found in leaf litter and soils in *C. pubescens*-invaded areas in the highlands of Santa Cruz (H. Jäger, unpubl. data). This

was ascribed to the enhanced nutrient uptake of *C. pubescens* because of its association with vesicular–arbuscular mycorrhiza fungi (Schmidt & Scow 1986). *Cinchona pubescens* itself, as well as other introduced species adapted to higher nutrient levels, might flourish on the enhanced nutrient supply provided (Allison & Vitousek 2004), thereby exacerbating introduced plant problems in the highlands (Simberloff & Von Holle 1999).

#### FACILITATION OF NATIVE SPECIES BY *C. PUBESCENS*

Invasive species can facilitate native species, although this is often overlooked in invasion studies (Rodríguez 2006). The changes in physical variables measured in this study (more water available and lower soil and air temperatures) could ameliorate the habitat and facilitate plant species that might otherwise find it difficult to establish, as documented elsewhere (Bertness & Callaway 1994; Bruno, Stachowicz & Bertness 2003; Crain & Bertness 2006). Indeed, we found that these conditions favoured a few hygrophilous, shade-adapted species, including fern species that were rare in the study area, which grew as epiphytes on moss-covered old *C. pubescens* trunks (Jäger, Tye & Kowarik 2007). A study on the impact of two *C. pubescens* species on forest plantations and a near-natural *Acacia* forest on Maui, Hawaii, showed that the *C. pubescens* invasion had similar effects, i.e. reducing vegetation cover but at the same time significantly enhancing the number of endemic species (Fischer, von der Lippe & Kowarik 2009). In Hawaiian forests, structurally simplified by forest management, this process might have resulted in the functional replacement of parts of the previous natural vegetation structure that had been destroyed (substitutive facilitation *sensu* Rodríguez 2006). In Galápagos, however, *C. pubescens* invasions established novel vegetation structures, which adversely affected the majority of resident species while only a few species of epiphytes colonized *C. pubescens* trunks.

#### *CINCHONA PUBESCENS* AS A HABITAT TRANSFORMER

The results of this study clearly showed that *C. pubescens* is a habitat transformer *sensu* Richardson *et al.* (2000), changing the character and conditions of the Fern-Sedge zone, and an ecosystem engineer according to the criteria of Jones, Lawton & Shachak (1994, 1997). Ecosystem engineering can have both positive and negative effects on species richness and abundance, both of which are scale-dependent (Jones, Lawton & Shachak 1997; Wright & Jones 2006). In the case of *C. pubescens*, most of the changes were clearly negative. It altered the architectural characteristics of the resident vegetation with consequent changes to the microclimate and vegetation. *Cinchona pubescens* trees had large per capita effects on PAR, have been present in the highlands of Santa Cruz for a long time, occur at high densities over large areas, and live for decades. This has resulted in pronounced negative impacts on the abundance of resident plant populations and on species diversity (Table 1, Figs 3, 4 and 6). Spatial distribution patterns were also modified by *C. pubescens*, as indicated by changes in plant cover in relation to the canopy of individual trees (Jäger,

Tye & Kowarik 2007). *Cinchona pubescens* likely influenced resource availability to other plant species as suggested by significantly higher phosphorus and nitrogen concentrations in soils under *C. pubescens* (H. Jäger, unpubl. data) and also via alterations to the microclimate (Fig. 6).

#### MISSING PROOF OF SPECIES EXTINCTION

The most remarkable outcome of this research is that the powerful negative effects of the *C. pubescens* invasion on species cover and diversity detected at the local (plot) scale did not translate into species extinctions at a landscape scale. Given that *C. pubescens* cover had only reached an average of 20% in the plots, this seems less surprising. However, given also that our previous study (Jäger, Tye & Kowarik 2007) found significant decreases in species cover and richness under the canopy of individual *C. pubescens* trees, it seems quite possible that local extinctions could be expected in the future if *C. pubescens* cover continues to increase.

Also, the possibility that sensitive species had already disappeared before the beginning of this study in 1998 cannot be excluded. In his survey of the Galápagos flora, van der Werff (1978) also sampled in the Fern-Sedge zone, but it is not certain how much of his sample area overlapped with our plots. Some of the species listed in this work were not found in our study area but are found in other parts of the Fern-Sedge zone (H. Jäger, unpubl. data). So the question remains whether these species have disappeared from the study area prior to our investigation or whether sampling for the two studies was conducted in different parts of the highlands. It is also conceivable that our sampling area was not large enough to detect the disappearance of species that were never recorded in our plots. For the 23 species recorded in more than one plot in 1998 but not again in the same plots in 2003 or 2005 (Appendix S3), there was no relationship between the disappearance of species from an individual plot and the *C. pubescens* cover in the same plot.

As discussed already, the enhanced frequency of individual species in the study area at the start of the study could be due to the El Niño rainfall. Still, the question remains why all the species that were present in 1998 endured in the study area, despite the significant changes over 7 years. The answer seems to be that the current *C. pubescens* cover still leaves enough open areas for all the resident species to survive, at least at low densities. Even though total *C. pubescens* cover in individual plots reached 42% (Fig. 4), the average cover for all plots did not exceed 20%. Nevertheless, there is a clear negative relationship between the cover of resident species and the cover of *C. pubescens* (Fig. 4). So it seems that, at the current density, *C. pubescens* only limits the establishment of other species, resulting in a significant decrease of species diversity (Yurkonis, Meiners & Wachholder 2005). There is strong evidence that this would change if *C. pubescens* were to develop cover approaching 100%, since few species occur under a *C. pubescens* canopy (Jäger, Tye & Kowarik 2007). These results, in combination with the PAR measurements of this study, indicate that shading is the main agent by which *C. pubescens* affects the vegetation. It remains to be seen how the vegetation

will respond to a continuing increase in *C. pubescens* cover. Herbaceous species were generally more negatively affected by *C. pubescens* than were shade-adapted ferns, and endemic herbaceous species were more affected than native species (e.g. *Pilea baurii* up to 99%). Therefore, there is still a risk that with an increasing *C. pubescens* cover species might disappear at a landscape scale in the future.

#### SYNTHESIS: DESTRUCTION WITHOUT EXTINCTION

Previous studies suggested that some introduced ecosystem engineers, those which increase habitat complexity, may cause species abundance and richness to rise (Crooks 2002). This was not the case in this study even though *C. pubescens* increased structural complexity by adding an extra vegetation layer to the habitat. Our results clearly showed that the negative impacts of *C. pubescens* scale up from individual trees (Jäger, Tye & Kowarik 2007) to community level (this study). But the most surprising outcome was that, despite the significant transformation of the Fern-Sedge vegetation zone, no plant species, including threatened endemic species (Valencia *et al.* 2000), went extinct on the landscape scale. These findings add to the evidence that native species extinctions have not so far been caused solely by competition with introduced plants (Davis 2003; Sax & Gaines 2008). However, our results strongly suggest that the outcome will be different if *C. pubescens* cover approaches 100% (Jäger, Tye & Kowarik 2007). It seems to be that so far the species pool is still largely complete, which holds promise for future restoration. With effective *C. pubescens* management, the native vegetation may be expected to recover again relatively quickly, as has been shown when other introduced species have been removed from native vegetation communities in Galápagos (e.g. Hamann 1979b).

Our findings of changing invader characteristics and varying invader effects over time clearly demonstrate the need for long-term studies (Strayer *et al.* 2006). Longer monitoring would show how the species pool will react to continued *C. pubescens* invasion. Furthermore, the example of *S. agraria* showed that an introduced species can be overall negatively affected but then indirectly facilitated again by the disturbance caused by the invader. The reaction of other introduced species to the invader should be studied over the course of an invasion to make accurate predictions about final outcomes. It is clear that better understanding of the temporal progress of invasions is important to predict and evaluate their ecological consequences.

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## Supporting Information

The following Supporting Information is available for this article:

**Appendix S1.** List of species included in ‘species groups’ from 1998–2005.

**Appendix S2.** List of non-significant results.

**Appendix S3.** List of species, which were recorded only in 1998 and not again in 2003 or 2005 in the same plot.

**Table S1.** Species richness in permanent plots from 1998–2005.

**Figure S1.** Annual precipitation and temperature on Santa Cruz Island.

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