BIOLOGICAL CONSERVATION

Tree invasion in naturally treeless environments: Impacts of quinine (*Cinchona pubescens*) trees on native vegetation in Galápagos

Heinke Jäger[a,b,], Alan Tye[b,1], Ingo Kowarik[a]*

[a]*Institute of Ecology, Department of Ecosystem Sciences and Plant Ecology, Technical University Berlin, Rothenburgstr. 12, 12165 Berlin, Germany*
[b]*Department of Botany, Charles Darwin Research Station, Galápagos, Ecuador*

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ABSTRACT

Impacts of plant invasions are largely scale-dependent and responses to the same exotic species may vary among communities. Since impacts caused by individual trees could anticipate consequences of a closed canopy of an invader, we studied the response of Galápagos native plants to quinine (*Cinchona pubescens*) trees in two vegetation zones. Quinine has invaded >11,000 ha of Santa Cruz Island, including the Miconia- and Fern-Sedge-Zones. We analysed species composition and abundance along transects radiating from the trunks of individual quinine trees. Species richness and percentage cover decreased significantly with proximity to individual trees, and these effects were more pronounced in the Fern-Sedge Zone than in the Miconia Zone. Cover of endemic and native herb species and grass species significantly declined by 57–88% in the Fern-Sedge Zone. This was not the case in the Miconia Zone, but here the dominant endemic *Miconia robinsoniana* decreased by 41%. Quinine is a major driver of plant community change in both vegetation zones. The greater susceptibility of species in the Fern-Sedge Zone was ascribed to the presence of a new growth form: quinine trees in a formerly treeless environment. Species of the Miconia Zone appeared to be better pre-adapted to higher shade levels created by the *Miconia* shrubs. Our results emphasize the need for future control of quinine to preserve the diversity of the native Galápagos flora.

1.   Introduction

Biological invasions have increasingly been recognized as one of the greatest threats to biodiversity (Mack et al., 2000; Davis, 2003) especially on islands (Elton, 1958; Loope and Mueller-Dombois, 1989). The understanding of mechanisms and consequences of species invasions is growing (Rejmánek et al., 2005; Sax et al., 2005; Daehler, 2006), but assessing ecological impacts of invasive species is often still speculative or based upon limited quantitative observations (Starfinger et al., 2003; Gurevitch and Padilla, 2004; Thieltges et al., 2006). The level of human impacts on habitats often coincides with the richness of non-native species (e.g., Kowarik, 1995 on urban habitats), but simple correlations between the numbers or dominance of exotic and native species need not indicate causal relationships. Even dominant non-native species may

sometimes evoke only minor biodiversity effects (e.g., Hejda and Pyšek, 2006). Non-native species may be rather 'passengers' than 'drivers' of community change when anthropogenic disturbances directly cause a decline of native species (MacDougall and Turkington, 2005).

As invasion impacts are scale-dependent (Parker et al., 1999; Richardson and Pyšek, 2006; Kühn and Klotz, 2007), data from large sample areas may not be appropriate to capture changes at small spatial scales (Stowe and Wade, 1979). Single trees may significantly alter their immediate surroundings (Zinke, 1962) but such effects might be underestimated by large sample areas (Amiotti et al., 2000). Because early phases of a tree invasion can subsequently develop into a canopy closure of the invader, impacts caused by single trees can be used to predict consequences of later invasion stages. We thus used a single-tree approach to identify impacts of the introduced red quinine tree (Cinchona pubescens Vahl) on the native vegetation in Galápagos.

Cinchona pubescens is one of the most invasive tree species in Galápagos (Macdonald et al., 1988) and has spread over at least 11,000 ha in the highlands of Santa Cruz Island (Buddenhagen and Yánez, 2005). It dominates large parts of the Miconia- and Fern-Sedge Zones (vegetation zones sensu Wiggins and Porter, 1971), both of which are rich in endemic and threatened plant species.

The Galápagos Islands are renowned for their unique biological diversity and as a natural laboratory for evolutionary studies, in part due to their high endemism and late human settlement. The native vascular flora of Galápagos amounts to only about 500 native species, amongst which some 180 are endemic (Lawesson et al., 1987). The unique ecosystems of Galápagos are undergoing profound alterations as a result of plant and animal introductions (Lawesson and Ortiz, 1990; Itow, 2003). The number of alien plant species has risen to more than 800, now making up more than 60% of the Galápagos flora (Tye, 2006, unpubl. data up to 2007). Despite this, very few studies have attempted to determine if and how introduced plant species have affected the Galápagos ecosystem (Adsersen, 1990; Shimizu, 1997).

Invasion patterns vary broadly between regions, habitats and communities (Lonsdale, 1999; Chytrý et al., 2005; Palmer, 2006; Vilá et al., 2006). Within the same region, an introduced species may evoke varying responses in different plant communities, but comparative studies at the community level are surprisingly rare (Alvarez and Cushman, 2002). We compared the impacts of C. pubescens trees in two vegetation zones in Galápagos. As both zones are naturally treeless, the establishment of a non-native tree species presents the native vegetation with a novel growth form. In line with the novel weapons hypothesis (which refers to biochemical traits: Callaway and Ridenour, 2004), species traits that distinguish an introduced species from the resident species are supposed to provide competitive advantages for the invader. Due to assumed changes in resource availability we hypothesise (a) that a C. pubescens tree in a formerly treeless environment exerts significant impacts on the native vegetation, (b) that these impacts decrease with increasing distance from the tree, and (c) that impacts of C. pubescens are higher in the Fern-Sedge Zone than in the Miconia Zone because species in the latter are adapted to higher shade

levels created by Miconia robinsoniana as a dominant endemic shrub.

The main questions addressed by this study were (1) Does plant species composition change with distance from individual C. pubescens trees? (2) Are different species groups, especially locally rare and endemic plant species, more affected by the C. pubescens invasion than others? and (3) Do species in different vegetation zones vary in their susceptibility to the C. pubescens invasion? Our results help to determine management priorities for C. pubescens in Galápagos and provide information for other islands where C. pubescens has been introduced and is becoming invasive, such as the Hawaiian Islands and Tahiti.

2. Materials and methods

2.1. Study area

Field work was carried out from May to October 1998 in the Miconia- and Fern-Sedge Zones in the highlands of Santa Cruz Island (986 km²). The study areas were in the National Park and were not influenced by recent human activities. The Miconia Zone extends from approximately 500 to 680 m above sea level and is dominated by the endemic shrub M. robinsoniana (Melastomataceae) along with many fern species (especially the native bracken Pteridium arachnoideum, Blechnum polypodioides and B. occidentale). Miconia robinsoniana shrubs grow to 3 m in height. The Fern-Sedge Zone reaches from about 570 m to the highest point of the island at 864 m above sea level. Before the arrival of introduced plants, it was dominated by P. arachnoideum, other fern species, and several herbaceous and gramineous species, with scattered groups of the endemic tree fern Cyathea weatherbyana. Average annual precipitation at 620 m above sea level is about 1700 mm (Hamann, 1979). The soils of the Miconia- and Fern-Sedge Zones are ferruginous andosols, consisting of young pyroclastic deposits with a pH (KCl) of about 4.3–5.2 (Laruelle, 1966) and are shallow (Geist, 1996). Nomenclature for plant species follows Jørgensen and León-Yánez (1999).

2.2. Study species

The native range of C. pubescens Vahl (syn. C. succirubra Pavon ex Klotzsch; Rubiaceae) extends from Costa Rica to Venezuela and Bolivia (Andersson, 1998). It has naturalized in Hawai'i and Tahiti, where it is also 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 agricultural zone at middle elevations (Shimizu, 1997) and from there the light, winged seeds were carried to higher altitudes. By 1972, it had started to spread rapidly by seed and vigorous vegetative production (Hamann, 1974). Today it covers over 11,000 ha in the highlands of Santa Cruz Island (Buddenhagen and Yánez, 2005). Cinchona pubescens grows to 10 m in height in Galápagos and now dominates large parts of the Fern-Sedge Zone and is co-dominant with M. robinsoniana in the Miconia Zone. Many species in these vegetation zones are threatened according to IUCN red-list criteria (Valencia et al., 2000).

Despite its widespread occurrence in Galápagos, little is known about the impacts of *C. pubescens* on the plant communities. The effect of *C. pubescens* on the *M. robinsoniana* community was examined by Palacios (1993), but using randomly located rather than fixed plots, and it was not possible to separate effects of location from effects of the invader.

2.3. Vegetation sampling

The standard approach of comparing plots in invaded and non-invaded areas (Pyšek and Pyšek, 1995; Holmes and Cowling, 1997) was inadequate for this study since most parts of the highlands of Santa Cruz were already invaded by *C. pubescens*, although at a wide range of densities. Consequently, a new approach was developed to examine the effect of individual *C. pubescens* trees on the plant communities in immediate proximity to them. Changes in species richness and abundance of understorey species were quantified by comparing measurements under the tree crown with the surrounding areas. The sampling procedure consisted of laying out four 5-m transects in the cardinal directions, radiating from the trunk of tall individual *C. pubescens* trees. Chosen trees were at least 10 m from the nearest neighbouring tree in order to minimise overlap of influence. Trees were also rejected if they were less than 5 m high or were associated with the other invasive tree species in the area, the common guava (*Psidium guajava*). In total, 42 *C. pubescens* trees were selected in the Miconia Zone and 42 in the Fern-Sedge Zone. Crowns of *C. pubescens* trees in the Miconia Zone had an average diameter of 3 m (SE = 0.74 m) and in the Fern-Sedge Zone of 3.5 m (SE = 0.78 m). Each transect was divided into three segments: 1 = inner, 2 = transition, and 3 = outer (Fig. 1). The length of the inner segment was the distance from the tree trunk to the edge of the tree crown. The transition segment was always 1.7 m long. The length of the outer segment was equal to the difference between the sum of the inner and transition segment lengths and 5 m, which was the total transect length. Species presence/absence and percentage cover were

recorded for each of the segments using the line-intercept method (Floyd and Anderson, 1987).

2.4. Statistical analysis

Since the distance from the *C. pubescens* tree was the primary factor distinguishing the three segments of each transect, this species was excluded from the analysis of species richness and abundance. Prior to the analysis, species presence/absence counts and values for percentage cover (subsequently referred to as 'cover') obtained from the four transects of a tree were pooled per segment. Species richness was determined in two ways. First, 'observed number of species' is the mean number of species encountered in a given segment of the four transects per tree. Second, a non-randomized method was used to compute 'estimated number of species' from mean estimated species accumulation curves based on the observed number of species in each of the three segments, using EstimateS software (Colwell, 2005). By this means, the survey data were used to produce a better estimate of species richness extrapolated to a larger sample area. In addition, 'locally rare species' were determined, which were those that occurred only in one of the 42 samples per segment and vegetation zone. For comparison of species cover, cover of each species was averaged over the four transects of a tree for each of the three segments. Data for individual species were subsequently grouped to analyse different species groups (Appendix A). For 'total cover', cover of all species was combined and value may exceed 100%, since several vegetation strata were measured.

To satisfy the assumption of homogeneity of variances, an arcsin transformation was applied to cover data prior to analysis. One-way ANOVAs were conducted for comparisons of species cover between segments in each vegetation zone. Furthermore, a two-way ANOVA for comparisons of observed numbers of species between segments and vegetation zones was carried out, using SPSS (2003). Post hoc tests were conducted using the Tukey HSD test.

To determine whether the distance from the tree trunk influenced species composition and if patterns varied between vegetation zones, observed numbers of species and cover of individual species in the three transect segments were subjected to principal component analysis (PCA) using CANOCO (ter Braak and Šmilauer, 1998). Species data were centred by sample and not standardized prior to analysis.

3. Results

3.1. Species richness

Analysis of species richness clearly demonstrated that both estimated and observed numbers of plant species were affected by the presence of *C. pubescens* (Fig. 2, Table 1). In the Miconia Zone, species accumulation curves showed a clear reduction of the estimated number of species from the outer to inner segments by 33% (Fig. 2A). This trend was less pronounced in the Fern-Sedge Zone but nonetheless 10% fewer species were estimated for the same comparison (Fig. 2B). These results concurred with those of the two-way ANOVA carried out on the observed numbers of species
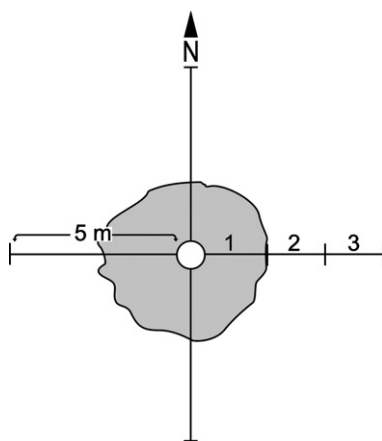

Fig. 1 – Transects laid out in the cardinal directions under individual *C. pubescens* trees; division of transects: 1 = inner segment, 2 = transition segment (always 1.7 m), and 3 = outer segment.
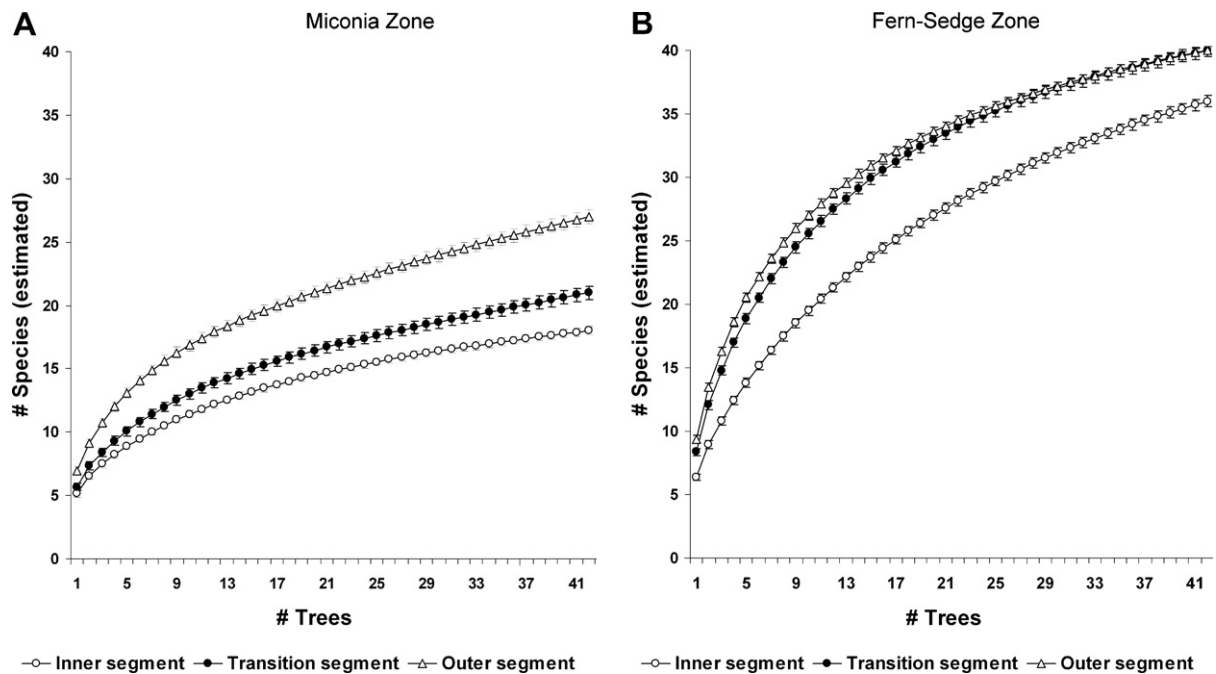
Fig. 2 – Estimated number of species (expected species accumulation curves) in the Miconia Zone (A) and Fern-Sedge Zone (B) for inner, transition, and outer segments of transects under *C. pubescens* trees (values are means ± 1 SE, *n* = 42).

Table 1 – Observed numbers of species in the Miconia- and Fern-Sedge Zones with distance from individual C. pubescens trees (inner segment = closest to the tree and outer segment = furthest away from the tree; see Fig. 1)					
Vegetation zone/segment					Mean ± SE
Fern-Sedge, outer	A				9.45 ± 0.29
Fern-Sedge, transition	A				8.57 ± 0.29
Miconia, outer		B			6.98 ± 0.29
Fern-Sedge, inner		B	C		6.38 ± 0.29
Miconia, transition			C	D	5.67 ± 0.29
Miconia, inner				D	5.14 ± 0.29

Means ± 1 SE are given, *n* = 42. Results of post hoc tests (Tukey HSD), performed following two-way ANOVA with vegetation zone and segment as factors. Levels not connected by same letter are significantly different at *p* < 0.001.

with vegetation zones and segments as factors. The vegetation zone had a significant effect on observed numbers of species, with the Fern-Sedge Zone hosting significantly more species in all segments than the Miconia Zone ($F_{1,246} = 87.3$, $p < 0.001$). Secondly, the segment factor was significant for all comparisons with $F_{1,246} = 41.2$, $p < 0.001$. Post hoc tests indicated that mean observed numbers of species for the inner and transition segments of the transects in the Miconia Zone were significantly lower than for the outer segments (26% reduction from outer to inner segments and 19% from transition to inner segments (Table 1). In the Fern-Sedge Zone, mean observed number of species for the inner segments was significantly lower compared to the transition and outer segments (32% reduction from outer to inner segments and 26% from transition to inner segments, Table 1). There was also a significant interaction detected between vegetation zones and segments ($F_{2,246} = 3.3$, $p < 0.038$), which means that the distance effect (increasing distance from the tree trunk from inner to the outer segment) depends on the vegetation zone.

The number of locally rare species right under the *C. pubescens* canopy varied conspicuously among vegetation zones. In the Miconia zone, only 5 such species occurred in the inner segments (compared to 10 in the outer segments, Appendix B1) and all these species were also found in the transition and/or outer segments except for *Phlebodium pseudoaureum*, which grew as an epiphytic fern on the *C. pubescens* trunk. In contrast, in the Fern-Sedge Zone more locally rare species were found in the inner segments compared to the outer segments (12 versus 8, Appendix B2), five of which (three epiphytic ferns, one epiphytic orchid and a seedling of the introduced *P. guajava*) were unique to the inner segments, with the other seven also occurring in the transition and/or outer segments.

3.2. Species cover

There were significant differences in species cover with distance from the *C. pubescens* tree (Fig. 3). In the Miconia Zone, average total cover of all species grouped (except for *C. pubes-*
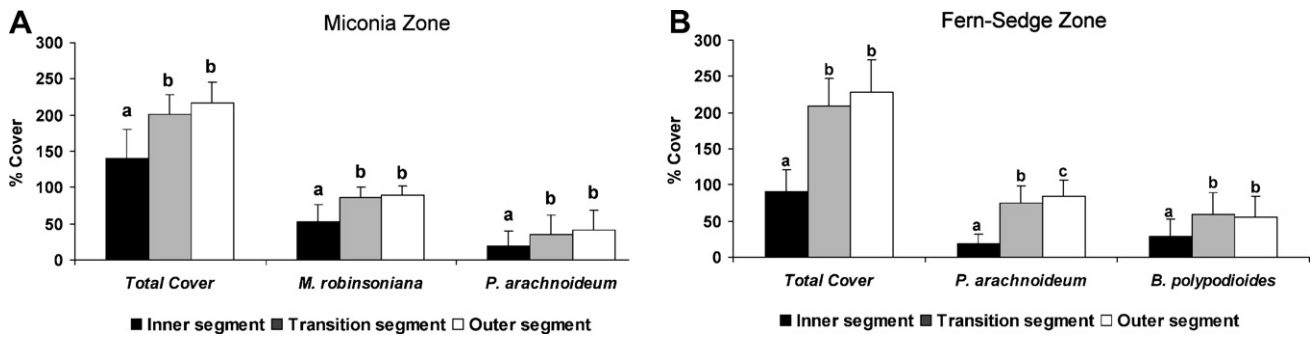
Fig. 3 – Percentage cover in the Miconia Zone (A) and Fern-Sedge Zone (B) of total cover (all species combined) and of selected dominant species, with distance from individual *C. pubescens* trees (values are means + 1 SE, *n* = 42). Levels not connected by same letter were significantly different at *p* < 0.001.

cens) in the inner segments was significantly reduced, by 30% and 35% ($F_{2,123} = 68.2$) compared to the transition and outer segments, respectively. The average cover of the threatened endemic shrub *M. robinsoniana* was also significantly reduced, by 38% and 41% ($F_{2,123} = 50.1$) for the same comparison. *Pteridium arachnoideum* was reduced by 47% and 54% ($F_{2,123} = 8.2$), respectively (Fig. 3A and Table 2, all *p* < 0.001).

In the Fern-Sedge Zone, reductions in species cover were more drastic than in the Miconia Zone. Here, average total cover in the inner segments was significantly reduced, by 46% and 60% ($F_{2,123} = 163.4$) compared to the transition and outer segments, respectively. Cover of *P. arachnoideum* was significantly reduced, by 75% and 77% ($F_{2,123} = 81.7$) for the same comparison and *B. polypodioides* was reduced by 51% and 49% ($F_{2,123} = 12.8$), respectively (Fig. 3B and Table 2, all *p* < 0.001). The species group 'endemic herbs' was significantly reduced in cover, by 68% and 79% ($F_{2,123} = 9.3$) comparing the transition and outer segments with the inner segments, respectively (Table 2). This group included the endemic *Pilea baurii* which, analysed on its own, was reduced by 79% ($F_{2,123} = 10.8$) when comparing both the outer with the inner segments and the outer with the transition segments (Table 2). Similarly, cover of 'native herbs' was reduced by 46% and 57%, respectively, for the same comparison. The group 'doubtfully native herbs' and 'introduced herbs' were reduced by 72% and 77% in cover, respectively, when comparing the outer with the inner segments ($F_{2,123} = 3.8$, *p* < 0.026 and $F_{2,123} = 5.7$, *p* < 0.004, respectively). 'Native grasses and sedges' were reduced by 88% for the same comparison ($F_{2,123} = 4.2$, *p* < 0.018). All results were significant at *p* < 0.001, unless otherwise indicated. For results on other individual species and species groups, see Table 2.

3.3. Species composition

PCA on observed number of species and species cover combined revealed differences in species composition between the two vegetation zones (Fig. 4). In the Miconia Zone, samples taken in the three segments were clustered together, which indicated that they varied only slightly in their species composition (Fig. 4A). In contrast in the Fern-Sedge Zone, samples taken in the inner segments were shifted on the horizontal axis, thus reflecting their proximity to the *C. pubescens* trees (Fig. 4B). Inspection of the data matrix revealed that differences in total number of species and both frequency and

cover of dominant species (mainly fern species) in samples of the inner segments compared to the transition and outer segments in the Miconia Zone were not as pronounced as in the Fern-Sedge Zone. These findings confirmed results obtained from the statistical analysis of cover, showing that reductions of species cover with proximity to the *C. pubescens* trees were greater in the Fern-Sedge Zone (Table 2).

The first PCA axis explained 80% of total variance of the species community in the Miconia Zone and 69% in the Fern-Sedge Zone.

4. Discussion

With reference to the main questions posed by this study, results showed that the number of plant species and their percentage cover decreased significantly with proximity to individual *C. pubescens* trees (Figs. 2 and 3, Tables 1 and 2). Moreover, endemic and locally rare species were proportionally more negatively affected by *C. pubescens* than non-endemic and common ones. Species in the Miconia- and Fern-Sedge Zones differed in their susceptibility to the *C. pubescens* invasion.

Results clearly showed that *C. pubescens* was associated with drastic effects on the local plant communities. These can without doubt be attributed to the novel presence of *C. pubescens* as a tree invading formerly treeless environments. Therefore this species has to be considered a 'driver' rather than a 'passenger' of environmental change (cf. MacDougall and Turkington, 2005). The single-tree approach allows prediction of the impacts that a near-continuous canopy of *C. pubescens* would have on the flora of Santa Cruz Island. In addition, if there were a difference between single trees and a closed canopy, an even more severe impact of *C. pubescens* would be expected in the latter case.

4.1. Impacts on resident plant species

The estimated and observed numbers of species under individual *C. pubescens* trees were reduced when compared to the surrounding areas, the observed numbers significantly so (Fig. 2 and Table 1). Overall, cover of all individual species and of all species groups under the *C. pubescens* canopy in the Miconia- and Fern-Sedge Zones was significantly reduced when compared to the adjacent areas (Fig. 3, Table 2). Among

Table 2 – Species cover and distance from individual *C. pubescens* trees in the Miconia- and Fern-Sedge Zones: percentage reduction of cover of dominant species and of species groups (all comparisons are between the segment furthest from the trunk and that closest to the trunk; explanation of segments see Fig. 1)

		Miconia Zone					Fern-Sedge Zone				
		ANOVA		Segments compared (Tukey HSD) (% reduction of percentage cover)			ANOVA		Segments compared (Tukey HSD) (% reduction of percentage cover)		
		F	P	Transition:Inner	Outer:Inner	Outer:Transition	F	p	Transition:Inner	Outer:Inner	Outer:Transition
Total cover	All species combined (except for *C. pubescens*)	68.2	<0.001	30***	35***	n.s.	162.4	<0.001	46***	60***	n.s.
Dominant species	*Pteridium arachnoideum*	8.2	<0.001	47*	54***	n.s.	81.7	<0.001	75***	77***	10*
	Miconia robinsoniana	50.1	<0.001	38***	41***	n.s.	N/A	N/A	N/A	N/A	N/A
	Blechnun polypodioides	0.4	0.648	n.s.	n.s.	n.s.	12.8	<0.001	51***	49***	n.s.
	Blechnum occidentale	1.7	0.184	n.s.	n.s.	n.s.	3.3	0.04	n.s.	n.s.	n.s.
Endemic herbaceous species	*Pilea baurii*	1.2	0.303	n.s.	n.s.	n.s.	10.8	<0.001	n.s.	79***	79***
	Jaegeria gracilis	N/A	N/A	N/A	N/A	N/A	0.5	0.634	n.s.	n.s.	n.s.
	Justicia galapagana	1.4	0.245	n.s.	n.s.	n.s.	1.8	0.173	n.s.	n.s.	n.s.
	Peperomia galapagensis	1.3	0.291	n.s.	n.s.	n.s.	N/A	N/A	N/A	N/A	N/A
Species groups	Endemic herbs	1.3	0.289	n.s.	n.s.	n.s.	9.3	<0.001	68*	79***	n.s.
	Native herbs	0.2	0.816	n.s.	n.s.	n.s.	6.9	0.001	46*	57***	n.s.
	Doubtfully native herbs	2.2	0.11	n.s.	n.s.	n.s.	3.8	0.026	n.s.	72*	n.s.
	Introduced herbs	0.8	0.536	n.s.	n.s.	n.s.	5.7	0.04	n.s.	77**	n.s.
	Endemic ferns	0.7	0.483	n.s.	n.s.	n.s.	0.3	0.757	n.s.	n.s.	n.s.
	Native ferns	1.2	0.304	n.s.	n.s.	n.s.	3.0	0.054	n.s.	33*	n.s.
	Native grasses and sedges	0.7	0.476	n.s.	n.s.	n.s.	4.2	0.018	n.s.	88*	n.s.
	Endemic shrubs	N/A	N/A	N/A	N/A	N/A	1.8	0.176	n.s.	n.s.	n.s.
	Introduced shrubs	N/A	N/A	N/A	N/A	N/A	0.6	0.558	n.s.	n.s.	n.s.
Lycopodium spp.	*L. cernuum*										
	L. clavatum										
	L. thyoides	2.7	0.071	n.s.	n.s.	n.s.	0.8	0.445	n.s.	n.s.	n.s.

Values based on results of one-way ANOVA and Tukey HSD tests ($n = 42$, * = $p \leqslant 0.05$, ** = $p \leqslant 0.01$, *** = $p \leqslant 0.001$, n.s. = not significant, N/A = species was not present).
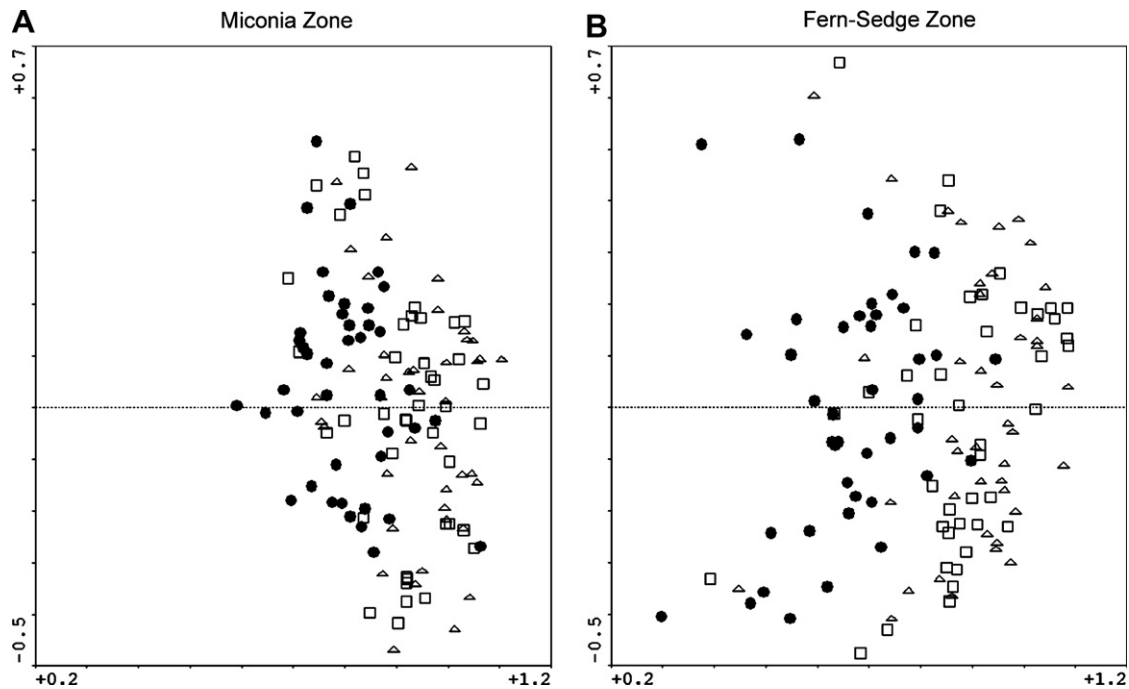
Fig. 4 – Ordination plot of observed number of species and species cover in the Miconia Zone (A) and Fern-Sedge Zone (B) with distance from individual *C. pubescens* trees, based on a sample-centred principal component analysis (PCA), (n = 42, circle = inner, quadrate = transition, and triangle = outer segment).

the species affected were threatened species like *M. robinsoniana* and *P. baurii*. Cover of introduced herbaceous species was also reduced which suggests that it is the herbaceous growth form that reacts to the *C. pubescens* presence rather than that native species are particularly susceptible. The effect of *C. pubescens* on grasses and sedges was especially drastic in the Fern-Sedge Zone (reduction of 88%, Table 2) and even more pronounced than the effect of invasive guava (*P. guajava*) on grasses in Costa Rica where grass cover under the canopy was 49–63% of that in the open area (Somarriba, 1988).

4.2. Community-level impacts

Comparative studies on impacts of invasive species at the community level are surprisingly rare (Alvarez and Cushman, 2002). Before the present study, it was unknown whether plant communities of adjacent vegetation zones in Galápagos vary in their susceptibility to invasion by *C. pubescens*. The results revealed big differences in community-level reactions (Figs. 2 and 3, Tables 1 and 2). In both vegetation zones, species richness significantly decreased under the canopy of *C. pubescens* compared to the surrounding areas (Fig. 2, Table 1). However, a divergent spatial reach of floristic changes with increasing distance from *C. pubescens* trees was detected. In the Miconia Zone, the mean observed number of species in the outer segments was significantly higher than for the transition segments, but there was no difference between the transition and inner segments. In contrast, in the Fern-Sedge-Zone, significant differences existed between inner and transition segments but not between transition and outer segments (Table 1). A possible explanation is that, in the Fern-Sedge Zone, where light levels are generally higher, shading is only significant in the inner segment, while the shade cast in

the transition segment might not have been enough to affect many species. In the Miconia Zone on the other hand, the additional shading in the transition segments (above the naturally higher shade level under dense *M. robinsoniana* canopy) is enough to tip the balance for some species so that they disappeared here.

This hypothesis is supported by the analysis of species cover (Table 2). In the Fern-Sedge Zone, cover of almost all species and species groups analysed was significantly reduced by the presence of *C. pubescens*. In the Miconia Zone, this was only true for the dominant species *M. robinsoniana* and *P. arachnoideum*, and for total cover (all species combined). However, the latter vegetation zone is also under severe threat by *C. pubescens* due to the drastic decrease in the endemic *M. robinsoniana* as a previously dominant species (Fig. 3, Table 2).

These results were confirmed by ordination (PCA), which combined the analysis of number of species and species cover, and supported the theory that species in the Fern-Sedge Zone were more susceptible to the *C. pubescens* invasion than in the Miconia Zone (Fig. 4). Species composition of samples taken in the three tree segments was very similar in the Miconia Zone, with no clear separation of samples. In contrast, samples taken in the inner segments of the Fern-Sedge Zone were shifted away from those of the other two segments. As for species number and species cover, the composition of these inner samples differed much more from the surrounding areas than did those in the Miconia Zone. This is likely another indication that species were less adapted to shade in the Fern-Sedge Zone.

Generally, fewer locally rare species occurred under the canopy of *C. pubescens* trees than in the adjacent vegetation. The numbers of locally rare species in the outer and

transition segments were similar in both vegetation zones, but reduced in the inner segments (Appendices B1 and B2). Significantly, among the species unique to the outer and transition segments in the Miconia Zone is the near-threatened *Justicia galapagana*, and in the Fern-Sedge Zone the endangered endemic tree fern, *Cyathea weatherbyana* (Valencia et al., 2000). One species was unique to the inner segments in the Miconia Zone (Appendix B1) and 5 in the Fern-Sedge Zone (Appendix B2), of which four were epiphytes and the other a seedling of the introduced common guava (*P. guajava*). However, *P. guajava* was not otherwise recorded in the transects because the study trees had been chosen so as not to have this species in their immediate vicinity. The locally rare fern and orchid species encountered are uncommon throughout the Fern-Sedge Zone and usually grow epiphytically as well as on the ground. In this study, they were recorded as epiphytes on mature *C. pubescens* trunks.

We hypothesise that the new resources provided by the introduced tree in a naturally treeless vegetation zone facilitates the establishment of locally rare species as well as other epiphytes associated with older *C. pubescens* trees in the Fern-Sedge Zone. Tree trunks offer suitable habitats for epiphytes and a closed *C. pubescens* canopy may provide favourable conditions for shade tolerant species with higher humidity requirements (see below).

Hence, *C. pubescens* appears to function in several ways as an 'ecosystem engineer', an organism influencing resource availability by altering abiotic or biotic characteristics of an ecosystem (Jones et al., 1994). According to Crooks (2002), non-indigenous ecosystem engineers often evoke cascading effects on resident biota by modifying the physical environment. However, not all species were affected negatively, as exemplified by the occurrence of locally rare species as epiphytes on *C. pubescens* trunks.

4.3. Mechanisms of species displacement

Our results demonstrate that species in the Fern-Sedge Zone are more affected by *C. pubescens* trees than species in the Miconia Zone (Figs. 2 and 3, Tables 1 and 2), supporting our hypothesis that plants in the Miconia Zone were pre-adapted to shading by the dense shrubby *M. robinsoniana* canopy. In the naturally treeless and shrubless Fern-Sedge Zone, the emergence of *C. pubescens* resulted in a reduction of the photosynthetically active radiation (PAR) by 85% ($120\ \mu mol\ m^{-2}\ s^{-1}$ as measured at 13:00 under *C. pubescens* canopy compared to $817\ \mu mol\ m^{-2}\ s^{-1}$ in the adjacent vegetation, unpubl. data). Shade is not qualitatively novel and suppression is a quantitative effect (cf. Reinhart et al., 2006).

Changes in nutrient availability are a further driver of species displacement (Ehrenfeld, 2003; Siemann and Rogers, 2003) and may cause far-reaching impacts on the ecosystem (e.g. Vitousek and Walker, 1989). Volcanic soil naturally has low levels of certain nutrients (especially nitrogen and phosphorus), so native plants are adapted to these conditions (Laruelle, 1966; Smith, 1985). However, *C. pubescens* may benefit from increased nutrient uptake due to its association with vesicular-arbuscular mycorrhizal fungi. As such fungi are mainly lacking in native species (Schmidt and Scow, 1986),

this association may aid *C. pubescens* invasion. This hypothesis is currently being investigated.

Inhibitory mechanisms are likely strongest immediately under *C. pubescens* trees (Figs. 2–4). Soil properties under individual forest trees generally change with distance from the tree trunk, due to changes in the effects of bark litter, leaf litter and the adjacent opening or neighbouring tree (Zinke, 1962). Boettcher and Kalisz (1990) named this phenomenon 'single-tree influence circles' and Amiotti et al., 2000) confirmed its validity by showing that soil properties fell into a distinctive radial pattern around each tree, with systematic and predictable variation. This variation in soil properties is frequently reflected in the spatial differentiation of the ground flora (Zinke, 1962) as in our study. Since a variety of mechanisms might explain the displacement of native and endemic species by *C. pubescens*, experimental manipulations and further quantitative measurements of environmental factors are needed to fully understand the underlying mechanisms (Levine et al., 2003).

5. Implications for conservation

This study showed that single-tree approaches can reveal marked impacts of invasive species on the surrounding vegetation. Such approaches at small scales may be useful in early invasion stages. As early detection of invasion risks enhances the efficiency of control (Rejmánek and Pitcairn, 2002), results from single-tree approaches may also be useful to set management priorities in the early invasion stages.

Our results clearly show that native and endemic species are threatened by the *C. pubescens* invasion in Galápagos and that immediate action is needed to protect both vegetation zones and to conserve the diversity of the Galápagos flora. Effective methods for *C. pubescens* control have recently been developed (Buddenhagen et al., 2004; Buddenhagen and Yánez, 2005). However, since other introduced plants co-occur with *C. pubescens* and the latter may suppress their abundance, special attention has to be paid to the potential spread of other invasive species after *C. pubescens* control (Alvarez and Cushman, 2002).

Appendix A

Species included in 'species groups'. The species occurred in the Miconia Zone (M) and Fern-Sedge Zone (FS), respectively; no abbreviation indicates that the species occurred in both zones.

Endemic Ferns: *Megalastrum pleiosorus* (FS), *Cyathea weatherbyana* (FS), *Polypodium tridens* (M); **Native Ferns**: *Asplenium auritum*, *A. feei*, *A. praemorsum* (FS), *A. pumila* (M), *Asplenium*

serra, Ctenitis sloanei, Diplazium subobtusum (FS), *Doryopteris palmata, Hypolepis hostilis* (FS), *Nephrolepis pectinata, Pityrogramma calomelanos* (FS), *Phlebodium pseudoaureum, Thelypteris grandis, T. oligocarpa*; **Endemic herbs**: *Jaegeria gracilis* (FS), *Justicia galapagana, Peperomia galapagensis* (M), *Pilea baurii*; **Native herbs**: *Blechum pyramidatum* (FS), *Commelina diffusa, Drymaria cordata* (FS), *Habenaria monorrhiza, Hypericum thesiifolium* (FS), *Ipomoea triloba* (M), *Liparis nervosa* (M), *Mecardonia procumbens* (FS), *Phyllanthus caroliniensis* (FS), *Polygonium opelousanum* (FS), *Vigna luteola* (FS); **Doubtfully native herbs**: *Borreria laevis, Ageratum conyzoides*: **Introduced herbs**: *Oxalis corniculata* (M), *Pseudelephantopus spirales, Stachys agraria* (FS); **Native grasses and sedges**: *Digitaria ciliaris* (FS), *D. horizontalis* (FS), *Eleocharis maculosa* (FS), *Kyllinga brevifolia* (FS), *Paspalum conjugatum, Rhynchospora rugosa, Scleria distans* (FS), *S. melaleuca* (FS); **Endemic shrubs**: *Miconia robinsoniana* (FS), *Psychotria rufipes* (FS), *Tournefortia rufo-sericea* (FS), **Introduced tree**: *Psidium guajava* (FS): ***Lycopodium*spp.**: *Lycopodium cernuum* (M), *L. clavatum, L. thyoides* (M).

Appendix B

Locally rare species (species occurring in only one of 42 samples per segment and vegetation zone), i = inner, t = transition, and o = outer segment. [1] = fern or fern ally, [2] = herbaceous species, [3] = grass or sedge, [e] = endemic, [n] = native, [dn] = doubtfully native, [i] = introduced, (for definition of species status see Tye, 2006; 'introduced' corresponds to accidental (Ac) of Tye, 2006); species occurring in more than one sample for a particular segment and therefore not 'locally rare' for that segment per vegetation zone are indicated by an '*' next to the corresponding segment.

1 – Miconia Zone: *Ageratum conyzoides*[2dn] (o), *Asplenium feei*[1n] (t, o), *A. pumila*[1n] (o), *Ctenitis sloanei*[1n] (o), *Doryopteris palmata*[1n] (t), *Habenaria monorrhiza*[2n] (i, t, o), *Justicia galapagana*[2e] (t, o*), *Liparis nervosa*[2n] (i, t, o), *Lycopodium thyoides*[1n] (o), *Nephrolepis pectinata*[1n], (i, o), *Oxalis corniculata*[2i] (o), *Phlebodium pseudoaureum*[1n] (i), *Polypodium tridens*[1e] (t, o), *Pseudelephantopus spiralis*[2i] (i, t, o*), *Rhynchospora rugosa*[3n] (t).

2 – Fern-Sedge Zone: *Asplenium auritum*[1n] (t*, o), *A. feei*[1n] (i, t*, o*), *A. praemorsum*[1n] (i), *Blechum pyramidatum*[2n] (o), *Ctenitis sloanei*[1n] (i, t*, o), *Cyathea weatherbyana*[1e] (t), *Digitaria horizontales*[3n] (t, o), *Diplazium subobtusum*[1n] (i), *Eleocharis maculosa*[3n] (t), *Habenaria monorrhiza*[2n] (i), *Hypolepis hostilis*[1n] (t, o), *Justicia galapagana*[2e] (i, t*), *Mecardonia procumbens*[2n] (o), *Miconia robinsoniana*[4e] (t*, o), *Nephrolepis pectinata*[1n] (t, o*), *Paspalum conjugatum*[3i] (o), *Phyllanthus caroliniensis*[2n] (i, t*, o*), *Phlebodium pseudoaureum*[1n] (i, t), *Polypodium tridens*[1e] (i), *Pseudelephantopus spiralis*[2i] (i, t, o*), *Psidium guajava*[4i] (i), *Rhynchospora rugosa*[3n] (i, t, o*), *Tournefortia rufo-sericea*[4e] (t, o*).

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