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RESEARCH ARTICLE

Resilience of Native Plant Community Following Manual Control of Invasive *Cinchona pubescens* in Galápagos

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Abstract

As invasive plant species are a major driver of change on oceanic islands, their control is an important challenge for restoration ecology. The post-control recovery of native vegetation is crucial for the treatments to be considered successful, but few studies have evaluated the effects of control measures on both target and non-target species. To investigate the efficiency of manual control of *Cinchona pubescens* and its impacts on the sub-tropical highland vegetation of Santa Cruz Island, Galápagos, vegetation was sampled before and up to two years after control was carried out in permanent sampling plots. Manual control significantly reduced *Cinchona* density. Due to regeneration from the seed or bud bank, follow-up control is required, however, for long-term success. Despite heavy disturbance from tree uprooting, herbaceous angiosperms were little affected by the control actions, whereas dominant fern species declined in cover initially. Most native, endemic, and other introduced species regained their pre-control levels of cover 2 years after control; some species even exceeded them. The total number of species significantly increased over the study period, as did species diversity. The native highland vegetation appeared to be resilient, recovering to a level probably more characteristic of the pre-invasion state without human intervention after *Cinchona* control. However, some introduced species seemed to have been facilitated by the control actions, namely *Stachys agraria* and *Rubus niveus*. Further monitoring is needed to confirm the long-term nature of vegetation change in the area.

Key words: **conservation, disturbance, facilitation, national park, oceanic island, red quinine tree, restoration, Santa Cruz Island.**

Introduction

Restoration efforts include a broad array of approaches (Perrow & Davy 2002; SER 2004), and one of them is the control of invasive species to restore degraded ecosystems or to conserve threatened species (D'Antonio & Meyerson 2002; Clewell & Aronson 2006). The control or eradication of invasive species has become an important conservation issue (United Nations CBD 1993; Hulme 2006), particularly on islands (Dulloo et al. 2002), where invasive introduced species are major agents of environmental change (Reaser et al. 2007).

Even though management of invasive species is now commonly carried out, few studies have evaluated the success of the programs and the recovery of native vegetation (Flory 2008), especially in the long term (Blossey 1999; Erskine Ogden & Rejmánek 2005). Ideally, successful management should result in the re-establishment of a community similar to that of a pre-defined reference community (SER 2004; Willis et al. 2007). However, data describing the pre-invasion ecosystem are often unavailable (Parker et al. 1999), the state of the invaded ecosystem is often not assessed prior to control measures (Zavaleta et al. 2001), and the response of the resident biota to these measures is only studied over short periods (Erskine Ogden & Rejmánek 2005).

When invasive woody plants become dominant, they may represent a challenge for the recovery of the native vegetation (Loh & Daehler 2008). Further, control actions inevitably create disturbances that may change resource availability (Davis et al. 2000), produce new microhabitats, or influence dispersal processes (Byers 2002). Species removal can be as damaging to a site as the invader itself (Ogle et al. 2000). Such changes can increase the vulnerability of plant communities to invasion (Rejmánek 1989) and control actions might facilitate other introduced species (Alvarez & Cushman 2002; Mason & French 2007). These alterations can also result in unexpected changes to other ecosystem processes, e.g. when the invader has changed the habitat to such a degree that native species cannot establish any more (Zavaleta et al. 2001). In these cases, thresholds may have been surpassed and further human intervention is required for full restoration, e.g. replanting of

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Figure 1. Permanent sampling plot in the Fern-Sedge vegetation zone before (left) and within 2 weeks after manual *Cinchona pubescens control* in 2005 (right) on Santa Cruz Island. Height of plot PVC tube: 2 m (photos: H. Jäger).

native species (Lugo 1988; Aronson et al. 1993). Paying closer attention to the invaded ecosystem and its management as a whole is likely to be more effective (Hobbs & Humphries 1995). Because control measures usually affect both target and non-target species, it is important to evaluate the impacts on the entire plant community.

Like many oceanic archipelagos, the Galápagos Islands have been invaded by several introduced species which severely affect the natural ecosystems (Bensted-Smith 2002). *Cinchona pubescens* (henceforth referred to as *Cinchona*) is one of the most invasive tree species in the humid zone of Santa Cruz Island (Macdonald et al. 1988), where it reduces indigenous plant species cover and diversity (Jäger et al. 2007, 2009). *Cinchona* was introduced to Galápagos in the 1940s (Hamann 1974; Lundh 2006) and began spreading in 1972 (Hamann 1974), and now covers more than 11,000 ha in the highlands of Santa Cruz Island. Actions have been carried out by the Galápagos National Park Service (GNPS) to control *Cinchona* manually and chemically (Buddenhagen et al. 2004).

In this study we documented the pre-control state of invaded highland vegetation in Galápagos and analyzed the response of both invader and resident species to control, during control and in the two subsequent years. We investigated (1) the effectiveness of manual control measures carried out by the GNPS to reduce the abundance of *Cinchona*, (2) the impacts of manual *Cinchona* control on the resident vegetation, (3) whether other introduced plant species were facilitated by the control actions, and (4) whether the native vegetation was able to recover over a 2-year-post-control period.

Materials and Methods

Study Site

Field work was carried out in the Fern-Sedge zone in the highlands of Santa Cruz Island, within the Galápagos National Park. The Fern-Sedge zone extends from about 570 m to the highest point of the island (Mount Crocker) at approximately 864 m.a.s.l. See Jäger et al. (2009) for a description of this vegetation zone. The approximate coordinates for sampling locations were between S 00° 38′ 56.3″ W 90° 19′ 42.0″ and S 00° 39′ 13.6″ W 90° 19′ 44.9″ in an area of approximately 0.3 km^2. Plant species nomenclature follows Jørgensen and León-Yánez (1999). Definition of species status follows Tye (2006a) and Leeuwen et al. (2008); the term “native species” is defined as not including endemic species (i.e. non-endemic native species).

Focal Species

The native range of *Cinchona pubescens* Vahl (syn. *C. succirubra* Pav. ex Klotzsch, red quinine tree, Rubiaceae, Fig. 1) extends from Costa Rica to Bolivia (Andersson 1998). It has been introduced to several countries and is considered invasive in Hawaii and Tahiti (Weber 2003; Meyer 2004). *Cinchona* grows to 15 m in height in Galápagos (Shimizu 1997) and resprouts by underground stems and also by opportunistic vertical sprouts, coming out of fallen stems (see definitions of sprouting by Del Tredici 2001). This way, *Cinchona* trees take on a multi-stemmed growth form that is difficult to control.

Manual *Cinchona* Control

During the past 25 years, various manual and chemical control techniques have been used by the Galápagos National Park Service (GNPS) and Charles Darwin Foundation staff to control *Cinchona* (Buddenhagen et al. 2004). Experimental manual control was carried out by the GNPS in January 2005 in the Fern-Sedge zone in an area of approximately 33 ha. Control measures consisted of uprooting large *Cinchona* trees by cutting the stems and digging up the underground stems and rootstocks with picks and machetes. Great care has been taken to remove all root fragments from the soil to prevent resprouting (Macdonald et al. 1988) and young seedlings were removed by hand-pulling. Follow-up removal of seedlings and resprouting saplings from stem and root fragments was carried out by the GNPS approximately 1 year after control actions were carried out.

Sampling

Vegetation was sampled in 20 *P*ermanent *S*ample *P*lots (PSPs) during the rainy season (January–March) of 2005 (before and approximately 2 weeks after control actions were carried out), 2006, and 2007 (Fig. 1). All PSPs were 20 × 20 m^2. Five parallel 20 m transects were set through each plot, each transect 5 m apart. Vegetation measurements along the transects were carried out by the line-intercept method and percentage vegetation cover estimated for each species. To account for rare species, the spaces between transects were searched for additional species. All *Cinchona* individuals were counted and divided into the categories <0.2 m and >0.2 m. Before control was carried out, the latter category also contained tall trees of up to 10 m in height; after control, it mainly comprised individuals between 0.2 and 1 m in height.

Data Analysis

All data for temporal comparisons are presented as the means of twenty 20 × 20 m^2 PSPs. Since *Cinchona* was the focal species, its cover was analyzed separately and excluded from the analysis of the total cover. Prior to analysis, values for percentage cover (subsequently referred to as "cover") obtained from the five 20 m transects in a PSP were pooled. Species richness was determined as "mean number of species," which is the average number of species in the 20 PSPs and second, as "total number of species," which is the number of all species in the 20 PSPs. Cover data for dominant species were analyzed individually, while data for less dominant species were grouped into a number of "species groups," for analysis (Appendix S1). Since cover data include several vegetation strata, total cover may exceed 100%.

Cover of all species and "species groups" and *Cinchona* stem counts were analyzed by repeated measures ANOVA with year of monitoring (2005 before control, 2005 after control, 2006, and 2007) as a within-subjects factor. In cases where the sphericity assumption was not met, 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. The assumption of normality 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 and counts of *Cinchona* individuals $\log_{10}$-transformed to achieve normality. Linear regression analysis was used to asses the relationship between *Cinchona* cover and bare ground area. All analyses were conducted using SPSS Version 14.0 for Windows.

The Shannon diversity index (H′) was used to measure the diversity of each sample using EstimateS software (Colwell 2005) and the Shannon evenness index was calculated using the formula H′/ln *S* (where *S* is the total number of species in the sample).

Results

Response of *Cinchona* to Manual Control

Monitoring carried out within 2 weeks after the control actions were applied revealed that on average more than 100 *Cinchona* stems ha^{-1} > 0.2 m height (mostly 0.2–1 m tall, $F_{2,38.8} = 46.0$, $p < 0.001$) and over 300 stems ha^{-1} < 0.2 m (termed *Cinchona* seedlings, $F_{3,57} = 9.1$, $p < 0.001$) were still present in the PSPs (Fig. 2). The number of stems >0.2 m tall increased 10-fold to over 1,000 stems ha^{-1} before the follow-up control took place in 2006, whereas the number of *Cinchona* seedlings remained almost unchanged (Fig. 2). Along with the increase in the number of *Cinchona* stems, there was also a significant fivefold increase in *Cinchona* cover within a year after control ($F_{3,57} = 154.0$, $p < 0.001$, Fig. 3). Shortly after the 2006 monitoring, *Cinchona* stems were manually pulled out again by the GNPS. Consequently, both the numbers of stems ha^{-1} > 0.2 m and *Cinchona* cover decreased again, as shown by the 2007 data, but remained higher than their levels immediately after the 2005 control (Figs. 2 & 3).

Response in Species Cover

Manual control consisted of uprooting large *Cinchona* trees, which damaged surrounding vegetation and created openings in the ground up to 3 m in diameter (Fig. 4). The area of bare ground increased fourfold after control compared to the pre-control level (Fig. 3). Figure 5 shows that 73% of the

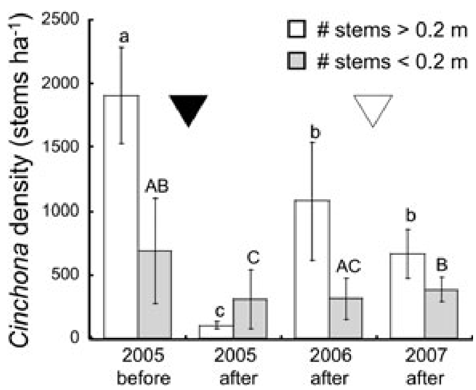

Figure 2. Density of *Cinchona* (stems ha^{-1}) before and after control in 2005 in 400 m^2 PSPs in the Fern-Sedge zone (solid triangle indicates major and open triangle minor control event). Values are means ± SE, levels within the same variable not connected by the same letter were significantly different in post-hoc pairwise comparisons using Bonferroni adjustment after repeated measures ANOVA at $p < 0.05$ (numbers of stems >0.2 m: lower case letters; numbers of stems <0.2 m: upper case letters), $n = 20$. Note: number of stems >0.2 m in 2005 before control also included *Cinchona* stems of up to 10 m in height, after control mainly stems of 0.2–1 m.

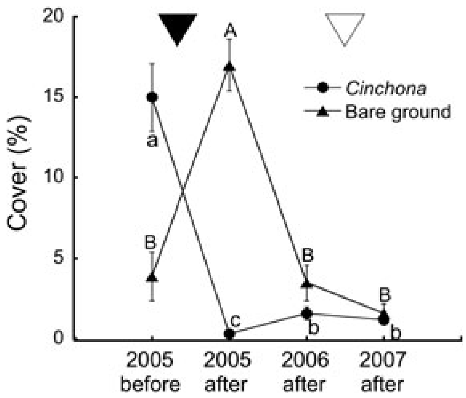

Figure 3. Change in *Cinchona* cover and bare ground before and up to 2 years after manual *Cinchona* control in 2005 in 400 m^2 PSPs in the Fern-Sedge zone (solid triangle indicates major and open triangle minor control event). Values are means +SE, levels within the same variable not connected by the same letter were significantly different in post-hoc pairwise comparisons using Bonferroni adjustment after univariate repeated measures ANOVA (*Cinchona* cover: lower case letters; bare ground: upper case letters), $n = 20$.

Figure 4. Impacts of manual *Cinchona pubescens* control in the Fern-Sedge vegetation zone in 2005 on Santa Cruz Island, Galápagos. Note bare ground patch in the foreground (Photo: H. Jäger).

bare ground in 2005 was explained by *Cinchona* cover before control and even 2 years later, it still explained 26% of bare ground.

Comparisons of total cover (cover of all species, except *Cinchona*) revealed a significant decrease by 18% between the monitoring before and after control in 2005 ($F_{1.7,31.5} = 23.5$, $p < 0.001$; Fig. 6). Species most directly affected were the fern species group ($F_{2,38.7} = 23.8$, $p < 0.001$), which was mainly composed of *Pteridium arachnoideum*, *Blechnum polypodioides*, and *Thelypteris oligocarpa*. In contrast, cover of herbaceous species was not affected by control measures and significantly increased within 2 years after control (Fig. 6). Cover of native herbaceous species increased by 26% ($F_{2.1,39.6} = 19.1$, $p < 0.001$), with the cover of endemic and introduced herbaceous species increasing by 67 and 56%, respectively ($F_{2,37.3} = 9.8$, $p < 0.001$ and $F_{2.4,44.8} = 43.3$, $p < 0.001$). The only rare species directly affected by control was the endemic herb *Justicia galapagana*, whose cover significantly decreased right after control actions were carried out ($F_{2.3,44.2} = 7.6$, $p = 0.001$), but then recovered again toward the second year of monitoring. The increase in cover of the introduced species was mainly caused by the herb *Stachys agraria*. *Rubus niveus* (blackberry) increased in cover from approximately 0% pre-control to 0.1% in 2007, which represents an area of approximately 0.4 m^2 in a PSP of 400 m^2.

The other species and species groups analyzed were also reduced in cover after control but these changes were not statistically significant (Fig. S1).

Response in Species Richness and Diversity

The total number of species encountered in all 20 PSPs continuously increased from 49 pre-control to 62 at the end of the study period in 2007 (Table 1). During the same period, the mean number of species per PSP significantly increased from 19.5 to 23.6 ($F_{3,57} = 21.5$, $p < 0.001$).

The total number of native species continuously increased from 33 pre-control to 41 at the end of the study period in 2007 and the mean number significantly increased by 1.8 species ($F_{3,57} = 8.5$, $p < 0.001$; Table 1). However, the proportion of native species to the total number of species did not change over the monitoring period (Fig. S2). During the same time, the mean number of endemic species also increased ($F_{3,57} = 12.6$, $p < 0.001$; Table 1) but the total number of endemic species remained almost constant, while the proportion of endemic species to total number of species decreased by over 20% (Fig. S2).

The total number of introduced species increased from 7 pre-control to 12 at the end of the study period in 2007, while the mean number of introduced species only increased from 3.1 to 3.7 ($F_{3,57} = 5.5$, $p = 0.002$; Table 1). This represents an increase in the proportion of introduced species by 26% (Fig. S2).

Species diversity (represented by the Shannon–Wiener diversity index and the Shannon evenness index) did not significantly change right after manual control (Fig. 7), but a year later these indices had steeply and significantly increased (Shannon–Wiener diversity index: $F_{1.1,20.3} = 110.1$, $p < 0.001$ and Shannon evenness index: $F_{3,57} = 12.5$, $p < 0.001$); they then decreased again toward the end of the study.

Discussion

Control Effects on *Cinchona pubescens*

Our study of the efficacy of manual *Cinchona* control showed that despite a thorough uprooting of large *Cinchona* trees, many smaller individuals (up to 1 m) were overlooked, resulting in an increase in stem density one year after control (Fig. 2). Despite subsequent hand-pulling, the number of *Cinchona* seedlings did not vary largely over the 2-year monitoring period, revealing the high regeneration potential of *Cinchona*, which is typical of many introduced species (Lonsdale et al. 1988). Our findings also suggest that combining

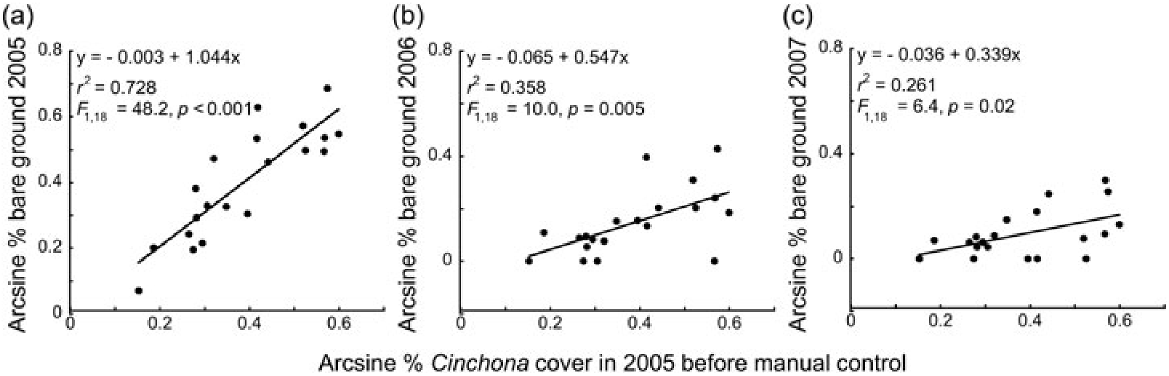

Figure 5. Positive relationships between arcsine square-root transformed data for cover of *Cinchona pubescens* in 2005 before manual control and bare ground after manual control in 2005 (A), 2006 (B), and 2007 (C) in 400 m^2 PSPs in the Fern-Sedge zone (n = 20). Line is the best-fit linear regression line.

Table 1. Comparison of mean number of species and total number of species (in parentheses) before and up to 2 years after manual *Cinchona* control in 2005 in 400 m^2 PSPs in the Fern-Sedge zone. Values of mean number of species are means +SE, levels within the same variable not connected by the same letter were significantly different in post-hoc pairwise comparisons using Bonferroni adjustment after univariate repeated measures ANOVA, n = 20. Note: see also Fig. S2 for the proportion of native, endemic, and introduced species in the total number of species in all PSPs.

	2005 before	*2005 after*	*2006 after*	*2007 after*
All species	**19.5 ± 0.7^b (49)**	**18.6 ± 0.8^b (50)**	**22.3 ± 0.9^a (56)**	**23.6 ± 1.0^a (62)**
Native species	14.0 ± 0.5^{ab} (33)	13.1 ± 0.6^b (35)	15.4 ± 0.8^a (35)	15.8 ± 0.7^a (41)
Endemic species	2.9 ± 0.3^b (9)	2.6 ± 0.3^b (8)	3.6 ± 0.4^{ab} (10)	4.1 ± 0.3^a (9)
Introduced species	3.1 ± 0.2^{ab} (7)	2.9 ± 0.2^b (7)	3.4 ± 0.2^{ab} (11)	3.7 ± 0.2^a (12)

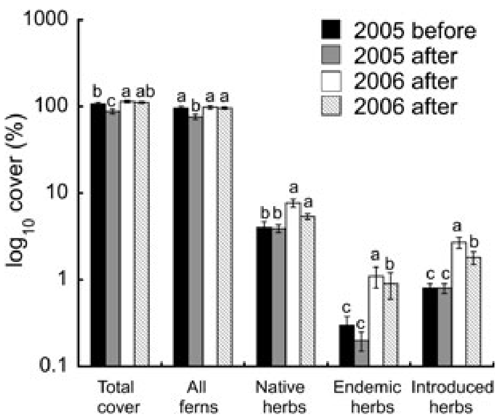

Figure 6. Change in total cover (all species except for *Cinchona pubescens*), cover of all fern species, and cover of native, endemic and introduced herbaceous species before and up to 2 years after manual control in 2005 in 400 m^2 PSPs in the Fern-Sedge zone (for species in species groups see Appendix S1). Values are means +SE, levels within the same variable not connected by the same letter were significantly different in post-hoc pairwise comparisons using Bonferroni adjustment after univariate repeated measures ANOVA, n = 20.

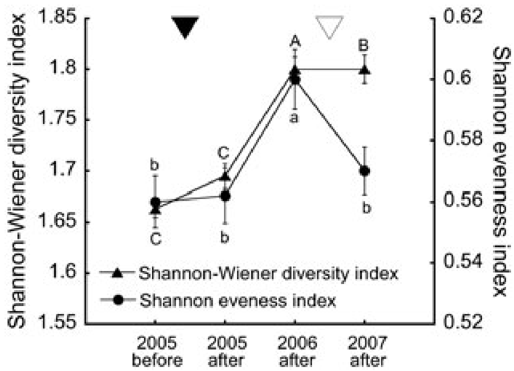

Figure 7. Shannon–Wiener diversity and Shannon evenness index in 400 m^2 PSPs before and after manual *Cinchona* control in 2005 in the Fern-Sedge zone (solid triangle indicates major and open triangle minor control event). Values are means ± SE, n = 20, levels within the same index not connected by the same letter were significantly different in post-hoc pairwise comparisons using Bonferroni adjustment after repeated measures ANOVA (Shannon–Wiener diversity index: upper case letters; Shannon evenness index: lower case letters).

uprooting of tall trees and hand-pulling of small seedlings can result in a loss of efficiency, with seedlings being overlooked.

Manual control measures are often insufficient to control or eradicate introduced species (Kowarik & Schepker 1998; Meloche & Murphy 2006). Our results add evidence to the insight that vegetative regeneration of invasive woody species may counteract control efforts, as shown, e.g. for *Ailanthus altissima* (Kowarik & Säumel 2007). However, our results also indicated that subsequent hand-pulling of small *Cinchona* plants 1 year after initial control reduced the number of small stems significantly. If repeated hand-pulling were applied regularly, it seems likely that *Cinchona* density could be further reduced. The same was shown for *Rosa rugosa* management, where uprooting of plants produced rather unsatisfactory results, but could be more successful if combined with subsequent hand-pulling as well as other measures (Kollmann et al. 2009). Thus, successful control depends more on continuing commitment and resources than on the efficiency of specific control techniques (Mack et al. 2000).

Control Effects on Native Vegetation

The removal of a dominant species is expected to lead to an increase in native species richness and abundance due to reduction of competition (Hobbs & Huenneke 1992; Brudvig 2008). On the other hand, radical measures, such as uprooting, could also damage non-target species. In our study, the total and mean numbers of species consistently increased over the 2-year monitoring period after control (Table 1). Apparently, dispersal ability and the existence of safe sites for germination from the seed bank were sufficient for the recovery of species, which is not always the case (Posada et al. 2000). There was a steeper increase in the total than in the mean number of species, which indicates that new species entered the study area but were not recorded frequently. This was especially true for native species. For endemic species, in contrast, the total number of species remained almost constant while the mean number increased over the monitoring period. This suggests that the same species were encountered more frequently in the PSPs after control. While the proportion of native species to total species did not change, the proportion of endemic species decreased by over 20% (Fig. S2). The overall increase in species richness may be a consequence of the creation of bare ground which stimulated the soil seed bank and permitted colonization of additional species (Bakker et al. 1996; Chytrý et al. 2001).

Manual control of *Cinchona* initially reduced the cover of all species (Fig. 6), particularly of *Pteridium arachnoideum* and other dominant native ferns. Only a year after control, however, ferns had regained their pre-control cover. In contrast, herbaceous species cover was not significantly affected by the physical impact, except for the endemic herb *Justicia galapagana*, and all species subsequently even surpassed their pre-control cover. The relative rapid recovery of native and endemic species may be a result of the secondary nature of the fern-sedge vegetation, because we assume that at least some parts of our study area had been burned during occasional fires in the highlands between the 1930s and the 1960s (van der Werff 1978; Kastdalen 1982). On the first recorded ascent of Mount Crocker in 1932, Howell noted that from an altitude of 616 m.a.s.l. on the vegetation consisted entirely of fern species (Howell 1942; Howell [1942] mistakenly reported the maximum elevation of Santa Cruz Island as 1700 ft [518 m], instead of the actual elevation at 864 m, so we adjusted the altitude accordingly in the citation quoted here). Because our sampling plots were located at an altitude of 600–660 m.a.s.l., they approximately overlapped with the lower part of the original Fern-Sedge zone. Therefore, it is possible that species that had survived or recovered well from the fires are now also the ones that recovered well from the disturbance caused by the *Cinchona* control. Two years after control, cover of almost all species and species groups slightly diminished again, but in most cases cover was still higher than pre-control. The reason for this late reduction in cover is not clear but is probably not due to climatic changes, since precipitation and mean temperature were fairly constant over the study period (Fig. S1). However, it could indicate that the plant community has not reached a stable state yet after the disturbance caused by manual control.

Concurrent with the significant increase in cover and number of species in 2006, both diversity indices also increased 1 year after control (Fig. 7). This suggests either that there were more species present and these species were also more abundant, or that the abundance of rare species had increased while that of common species had decreased. Even though the number of species further increased the subsequent year, both diversity indices had significantly decreased again by 2007, suggesting that species had become less abundant again. It appears that mainly the common species had spread and become more common, therefore causing a decrease in the diversity indices via a decrease in evenness. These results stress the need for long-term monitoring of control measures as "snapshot-studies" could produce misleading results (Blossey 1999).

Control Effects on Other Introduced Species

The removal of invasive species can facilitate the establishment of other introduced species (Alvarez & Cushman 2002; Mason & French 2007). In our study, the cover of introduced herbs, which mainly consisted of the species *Stachys agraria*, significantly increased after manual control (Fig. 6). The total number of introduced species increased more steeply than the average number of species, which means that the newly arrived species were rarely recorded in the plots (Table 1). This represents an increase in the proportion of introduced species to the total number of species by 26% (Figure S2). These findings indicate that new introduced species either entered the study area or emerged from the seed bank as has also been shown for woody encroachment removal from oak savannas (Brudvig 2008). Introduced pioneer species may thus have been favored by the disturbance (e.g. *Conyza bonairiensis*, Asteraceae) as in other studies (Hobbs & Huenneke 1992; Sakai et al. 2001). In addition, people performing the control and monitoring activities could also have involuntarily contributed to the dispersal of both introduced and native species by attachment of seeds to footwear, clothes, and tools (Wichmann et al. 2009).

Further monitoring will be necessary to determine whether introduced species that were newly recorded in the study area toward the end of the study are only ephemeral members of the community after anthropogenic disturbance (MacDougall & Turkington 2005) or permanent. If the latter, they could be drivers of further change. The peak in cover of introduced species 1 year after control (Fig. 6) might suggest an ephemeral element. Seedlings of the introduced herb *Stachys agraria* were immediately very abundant in the bare ground after control and consequently its cover more than tripled within 1 year after control. Although *Stachys* appears to be "integrating" without causing obvious ecological damage ("integrating" *sensu* Tye 2001), the potential spread of this species should be monitored in the future as *Stachys* also increased in cover due to disturbance caused by the *Cinchona* invasion (Jäger et al. 2009). Results suggest that *Cinchona* control created a "point of entry" for the highly invasive *Rubus niveus*, which was not present at the beginning of the study. Even though its total cover was still low at the end of the study (0.1%), this is of concern, since this species is a "transformer" species (*sensu* Richardson et al. 2000), highly invasive on Santa Cruz Island (Buddenhagen 2006) and elsewhere (Randall 2002). However, due to logistic constraints, this study lacks true control plots monitoring vegetation that did not undergo the disturbance of manual control actions. Therefore, we are not able to distinguish the general increase of *Rubus* in the area adjacent to the study area from that in the PSPs. Results from a vegetation sampling nearby suggest that the increase in *Rubus* cover is lower outside the PSPs (H. Jäger, unpublished data) but a thorough analysis still remains to be done. The lack of control plots is a limitation of our study and should be considered when interpreting the results. Nevertheless, control of *Rubus* in areas of *Cinchona* control should be given high priority (cf Loh & Daehler 2008). Other invasive woody species in the Fern-Sedge zone, *Psidium guajava*, was also recorded in the study area. However, cover of *Psidium* did not change significantly with time since it was simultaneously controlled by the GNPS.

Restoration of the Native Vegetation

Here we define restoration as the "return of an ecosystem to a close approximation of its condition prior to disturbance" (National Research Council 1992). Restoration efforts in tropical regions have mainly focused on the removal of stressors, such as invasive species, in anticipation that natural recuperation will occur (Aronson et al. 1993; Posada et al. 2000) but the restoration process can be complex and lengthy (D'Antonio & Meyerson 2002; Flory 2008). As shown by this study, regeneration of the sub-tropical highland vegetation after control was rapid, despite the heavy disturbance associated with uprooting *Cinchona* trees. Results suggest that in the absence of major climatic events at the time of control (i.e. a dry La Niña year, see Itow 2003; Erskine Ogden & Rejmánek 2005), the vegetation in the area investigated has the potential to recover from manual control impacts without further restoration aid, in contrast to experiences in other regions (Kueffer & Vos 2004; Vidra et al. 2007). Hence, human intervention in form of planting of native plant species after manual *Cinchona* control seems unnecessary.

Our results parallel the findings of rapid vegetation regeneration in Galápagos following the removal of introduced herbivores (Hamann 1979; Hamann 1993), thus confirming the general resilience of Galápagos vegetation to disturbances (Tye 2006b). However, the Santa Cruz highland plant communities have faced several disturbances in the past. First, extensive fires in the middle of the 20th century, then the establishment of invasive *Cinchona* over the past 30 years, and now the disturbance caused by manual *Cinchona* control measures in 2005. Early botanical surveys of the Fern-Sedge zone mention only the most dominant plant species (Wiggins & Porter 1971; Hamann 1981). Hence, the composition of the pre-invasion state of the vegetation in our study area is not exactly known, as is true of most plant communities in Galápagos (Tye 2006b) and elsewhere (Parker et al. 1999; SER 2004). As it was the primary aim of this study to elucidate the impact of manual control on the native vegetation, we regard the fern-sedge vegetation as nearly natural vegetation although it might diverge, at least in part, from the primary, pre-fire disturbed vegetation. Previous studies showed that even single *Cinchona* trees as well as a continuous *Cinchona* invasion over 7 years severely reduced the abundance and diversity of resident plant species in the Fern-Sedge zone (Jäger et al. 2007, 2009). Therefore, it is likely that the state of recovery of the resident vegetation documented in this study is not equivalent to its pre-invasion state. In the survey of the Galápagos vegetation, 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 PSPs. Some of the species listed in this work were not found in our study area, some are found in other areas of the Fern-Sedge zone (Jäger et al. 2007, 2009; H. Jäger, unpublished data), and others were not found in either of the authors' studies. It seems likely that the species composition had already partly changed after the fires and before van der Werff carried out his study. Because there is no positive evidence for an irreversible change in the original species composition by the *Cinchona* invasion, it is hoped that the fern-sedge communities will revert to a near-original state once the invader is removed, if permanent control of regenerating *Cinchona* plants can be carried out. In the absence of information on the pre-invasion state of species in the plant community, native species richness determined in this and other studies (van der Werff 1978; Hamann 1981; Jäger et al. 2007, 2009) can count as a proxy for the original species diversity.

There are other specialized plant communities in the higher parts of the Fern-Sedge zone, such as those of the fens and *Sphagnum* bogs (Itow & Weber 1974; Hamann 1981), which are likewise invaded by *Cinchona*. Whether these are as resilient as the communities we studied is unknown. Therefore, a restoration model for the Galápagos highland plant communities is needed, to address ecological and management issues across the vegetation mosaic, as has been developed for the *Scalesia* forest (Wilkinson et al. 2005).

Conclusions

The goal of restoration is often to return ecosystems to a state containing characteristic species assemblages that occur in a reference system and that are resilient to natural disturbances. This study clearly showed that the fern-sedge vegetation is resilient and can recover even after heavy physical disturbance caused by manual *Cinchona* control. Despite the fact that the pre-*Cinchona* invasion state of the highland vegetation is not completely known, we expect the plant community to revert to a stage similar to its pre-invasion state, if *Cinchona* management continues to be effective. However, management goals for the future *Cinchona* control have to be set to be able to decide whether and where a nearly pre-invasion state is desired and financially feasible. If so, the question arises whether *Cinchona* control should be carried out in priority areas (as currently applied by the Galápagos National Park Service) or on a broader scale up to a pre-defined threshold density. A third possibility would be to view the presently invaded Fern-Sedge zone, or parts outside a defined priority area, as a "novel ecosystem" (*sensu* Hobbs et al. 2006) and to accept the changes in the plant (and possibly animal) communities.

Post-control monitoring of other introduced species that appeared to be facilitated by manual control of *Cinchona* is indispensable to anticipate future invasion. Although our results suggest a high potential for the recovery of the highland vegetation in Galápagos, not all factors investigated showed clear unidirectional trends over the study period. Hence, the outcome of this study stresses the need for long-term monitoring following control to reveal whether recovery is transient or long lasting.

Implications for Practice

- Sub-tropical highland vegetation can be resilient and recover quickly after heavy physical disturbance caused by uprooting of tall trees, like *Cinchona pubescens*, without human intervention (e.g. planting native species).
- When manually controlling large trees, which spread by abundant seed production and suckering, a continuous follow-up control is necessary for long-term management.
- Manual control methods can cause a significant disturbance to the system, often facilitating the establishment and spread of other introduced species in the area. Their post-control monitoring and removal should be given high priority.
- Pre- and post-evaluation of the target species and recovery of native community over a longer period (at least 2 years) should be included into the management plan to determine if restoration criteria have been met.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of species included in "species groups."

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

Figure S2. Proportion of the number of native, endemic, and introduced species.