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# Challenges for the management of the invasive blackberry (*Rubus niveus*) in the restoration of the Scalesia forest in the Galapagos Islands

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## Abstract

Strong competitive ability of introduced plant species has been frequently stated as a key factor promoting successful invasion. The dynamics of invasive species may depend on their abilities to compete for resources and exploit disturbances relative to native species. This study compares the growth performance of the invasive blackberry (*Rubus niveus* Thunb.) with four of the most common woody native species of the Scalesia forest in the Galapagos Islands. Using a series of greenhouse and field studies, the growth rate and biomass production of native species alone and in competition with *R. niveus* was compared under different water and light stress conditions. *Rubus niveus* showed a faster growth rate and biomass production than the native species as well as a broad tolerance to light and water stress conditions. Competitive ability was also assessed by looking at the seedbank and regeneration processes after herbicide control in the field. Although the number of *R. niveus* seedlings that germinated from the soil samples was considerably larger than that of native species, recruitment of the invasive on the experimental plots was limited. Overall, *R. niveus* showed superior competitive ability over native species with comparable growth forms, suggesting a possible mechanism that enables *R. niveus* to successfully invade a wide range of habitats in the Galapagos Islands. Implementing an integrated management strategy including biological control, seedbank reduction, and active revegetation, should improve the efficiency of *R. niveus* management, enabling the restoration of degraded vegetation in the Galapagos.

## Introduction

Establishment and impacts of invasive species depend on their biological attributes, their biotic interactions with the native community, and the environmental characteristics of the invaded ecosystem (Keane and Crawley 2002; Lloret et al. 2005; Pysek et al. 1995). Introduced plants may become aggressive invaders outside their home ranges for a number of reasons, including release from natural enemies, higher performance in a new site, direct chemical (allelopathic) interference with native plant performance, and variability in the responses and resistance of native systems to invasion (Blossey and Nötzold 1995; Callaway and Aschehoug 2000). Introduced plant species might be released from constraints present in native environments, allowing individuals of a species in an alien environment to be taller and more vigorous and to produce more seeds (Blossey 1999; Schmidt et al. 2008).

Another major explanation for the success of invading species is that the invader possesses individual traits or a combination of traits that are unique or underrepresented in the recipient community, allowing the invader to exploit resources or opportunities not exploited by the native community (Fargione et al. 2003; Vitousek et al. 1987). Studies have generally found that invasive plant species have higher relative growth rates, greater leaf-area ratios, and maximal photosynthetic rates compared with natives plant species (Grotkopp et al. 2002; McDowell 2002).

One mechanism that may facilitate invasion by introduced plant species is increased resource availability resulting from disturbance or low resource uptake by the native plant community. Habitats with increased light and nutrients tend to be more productive for invasives (which are often disturbance specialists), which leads to higher growth rates and higher rates of spread (Meekins et al. 2001). Phenotypic plasticity may help invasive plants to exploit a wider range of environmental conditions than native species (Hulme 2008; Lande 2009; Sultan 2000). Invasive plant species often have more efficient water use, better nitrogen uptake, and higher

## Management Implications

*Rubus niveus* (blackberry) is commonly controlled in the Galapagos using chemicals to kill adult plants. While effective in the short term, this creates gaps that may stimulate the reinvasion of *R. niveus* from the seedbank. Moreover, the long-term effects of herbicide use on non-target species may slow down the regeneration of native plant communities, giving a competitive advantage to *R. niveus*. This study provides evidence of the need of two management actions in addition to chemical control of adult plants to allow native Scalesia forest to recuperate. First, a mechanism to reduce the size of the *R. niveus* seedbank is critical to reduce reinvasion after chemical control of adult plants, and second, active high-density planting using young plants of fast-growing species such as *Scalesia pedunculata* and *Tournefortia rufo-sericea* can help by shading bare soil, reducing the germination rate of *R. niveus* from the seedbank.

biomass and can produce seeds that are more likely to germinate compared with natives (DeFalco et al. 2003). There is evidence that some invasive *Rubus* are able to rapidly and efficiently exploit a wide range of soil moisture conditions (Caplan and Yeakley 2010).

Finally, the success of many plant species as invaders is increased by their capacity to maintain persistent stores of seeds in the soil (Passos et al. 2017; Richardson and Kluge 2008). The ability to produce a large number of seeds together with high germination rates increases invasion success (Greenberg et al. 1997; Rejmánek and Richardson 1996). The more propagules an organism produces, the greater its chances of becoming established (Williamson 1996). However, while the importance of traits to attributes of invasive success is recognized, it is now generally accepted that many other factors, such as the biological and ecological interactions with other species in the new environment, play an equally important role (Dunbar and Facelli 1999).

Invasive blackberry (*Rubus niveus* Thunb.) is a thorny, perennial shrub native to India, southeastern Asia, the Philippines, and Indonesia (Morton 1987). This species has a wide climatic range, from near sea level to montane environments at 3,000 m. However, *R. niveus* is not resistant to drought or frost (Morton 1987; Wagner et al. 1999). In places with harsh winters, the species behaves as an annual plant growing back each spring from the seedbank or roots, while in most tropical areas it can grow all year round (Morton 1987). The plant is cultivated throughout the world for its heavy production of sweet fruit. *Rubus niveus* has been introduced into Central America, South America, the United States, South Africa, and Australia (Morton 1987; St. Quinton et al. 2011).

In the Galapagos, *R. niveus* has invaded grass- and farmlands, shrublands, and forest alike. It forms dense thickets, replacing native vegetation and threatening several native communities, including the Scalesia [*Scalesia pedunculata* Hook.f. (Asteraceae)] forest (Itow 2003; Renteria and Buddenhagen 2006; Wilkinson et al. 2005). On Santa Cruz Island, the Scalesia forest is situated within the humid zone (600 m asl) and receives a mean annual precipitation of approximately 1,845 mm (Itow and Mueller Dombois 1992). Soils are up to 1-m deep, of basaltic origin, well weathered, and sandy loam in texture (Laruelle 1966; Stoops 2014). The humid zone comprises a number of subzones that vary between islands and include the Scalesia Zone, Miconia Zone, and Fern-Sedge Zone (Stoops 2014; Tye 2006). The Scalesia Zone is the most fertile habitat in the archipelago, where agricultural settlements were established (Moll 1990). In Santa Cruz Island, this zone was

historically dominated by the endemic tree *S. pedunculata*; however, land-use change has severely reduced the original vegetation, leaving small and sparse fragments (Mauchamp and Atkinson 2011; Moll 1990; Watson et al. 2010). The Scalesia forest at Los Gemelos on Santa Cruz Island is one of the best remnants of this humid vegetation type. This forest is still dominated by *S. pedunculata* and constitutes the habitat of many endemic and native species (Hamann 2001; Itow 1995). The Scalesia forest has been invaded by a number of introduced plant species, including *R. niveus* (Renteria and Buddenhagen 2006).

Several life-history traits may contribute to *R. niveus* invasiveness in the Scalesia forest. As is the case for other invasive *Rubus* spp., rapid growth of the shoot and root, ability to reproduce vegetatively, early flowering, self-compatibility, and high rate of seed production may contribute to its success in the Galapagos Islands (Baret et al. 2008; Gerrish et al. 1992). A possible mechanism that may enable *R. niveus* and other invasive species to successfully invade and persist in a wide range of habitats is superior competitive ability over native species as measured by its rapid growth, early maturity, large quantities of seeds and fruit, effective seed dispersal, vegetative reproduction, and generation of dense shade (Atkinson et al. 2008; Bellingham et al. 2004; Landázuri 2002; Rejmánek and Richardson 1996).

Because invasive species represent a threat to native biota and contribute to the decrease of native biological diversity (Levine et al. 2003; Mooney and Cleland 2001), it is fundamental to identify the mechanisms, traits, or external factors that contribute to successful invasion (Lake and Leishman 2004; Pyšek et al. 2004). Understanding interactions between invaders and residents and the mechanisms by which invasive species outperform native species is essential to efficient management and restoration of native-dominated habitats (Richardson and Kluge 2008). Management of invasive plants in natural areas should aim at a self-sustaining ecosystem with desired species composition and ecosystem functions (D'Antonio et al. 2016).

This study examines the growth performance of *R. niveus* relative to the four most common native plant species from the Scalesia forest in Santa Cruz Island in the Galapagos Islands: the tree *S. pedunculata*, the woody vine-shrub *Chiococca alba* (L.) Hitchc. (Rubiaceae), and the shrubs *Psychotria rufipes* Hook.f. (Rubiaceae) and *Tournefortia rufo-sericea* Hook.f. (Boraginaceae). We used greenhouse experiments to compare: (1) the relative growth rate of *R. niveus* and these native species and (2) the tolerance and performance of both native species and *R. niveus* under different stress conditions. Additionally, experimental plots were established in the Scalesia forest to assess interspecific competition in infested areas, as well as seedbanks and seedling recruitment from *R. niveus*.

## Material and Methods

### Relative Growth Rate

To assess the relative growth rate of *R. niveus* and the four native species, seedlings of each species were collected from the Scalesia forest (approximately 2- to 3-wk old, 5 cm average height) and grown in individual plastic pots (1,500 $cm^3$) containing soil from the highland farms (agricultural areas adjacent to the Scalesia forest) under a shade house (70% of natural sunlight, with a 12-h daylight regime, average annual temperature of 22.2 C). Fifteen seedlings of each species were randomly positioned in the shade house and watered as required. Seedlings dying within

2 wk after potting were replaced. Initial and final stem length and cover area index (represented by the product of minimum and maximum length) of each plant were measured. After 8 mo, all plants were harvested and samples were dried at 45 C and weighed to determine foliar and root biomass. We use linear models (multivariate analysis of variance [MANOVA]) with species as fixed effects to determine significant differences in relative growth and biomass production between species; values of each response variable were log transformed. The statistical analysis for the whole study was performed using the computing environment R (R Core Team 2018), an open-access software environment.

## Stress Tolerance

To determine the response of *R. niveus* and the four native species to different light and water conditions, seedlings of the different species were planted in individual plastic pots (1,500 $cm^3$) containing soil from the highland farms and grown under two different light levels (90% and ~10% of ambient sunlight). These represent an approximation for "open ground" and "closed canopy" sunlight conditions at the Scalesia forest; the low-sunlight treatment was provided using wooden frames covered with shade cloth. Two different watering regimens were used (500 ml and 250 ml as proxies of 100% and 50% volume saturation, respectively), water was applied manually twice a week. A two-way factorial design was used with 12 replicates per treatment (each plant as a replicate). Initial and final stem diameter and length per plant were measured. After 5 mo, the experiment was stopped; plants were harvested, dried at 45 C, and weighed to determine foliar and root biomass. We used a linear model (MANOVA) to assess the influence of light and water treatments as fixed effects on the variation in relative growth and biomass production of the different species; values of each response variable were log transformed.

## Seedbank and Competition between Recruits

To assess the seedbank contribution to the regeneration process of the Scalesia forest, a set of 20 paired plots (4 by 4 m) were set up along the Scalesia forest. Each pair consisted of heavily invaded ("invaded areas," with at least 90% *R. niveus* cover) and a nearby uninvaded plot ("uninvaded vegetation"). The uninvaded plots were selected to represent as closely as possible the same habitat conditions as the corresponding invaded plots. The vegetation of heavily invaded plots was cleared completely (using a machete and spraying *R. niveus* stems with glyphosate (Roundup 2%, Roundup Custom, Bayer CropScience LLC, Research Triangle Park, NC, USA), as suggested by Renteria et al. [2006]) to assess competition recruits. In each plot, five soil samples were taken within centrally located 1-$m^2$ subplots using a metal core (4.5-cm diameter by 5-cm deep). Soil cores from each plot were mixed together and spread out into plastic trays containing a layer of sterile vermiculite; trays were watered regularly and kept in a shade house to monitor germination over 5 mo. Seedling emergence was recorded as counts per species and then removed after identification to avoid double counting. Regeneration of vegetation in the invaded plots 9 mo after clearing was assessed by estimating the species cover percentage within the 1-$m^2$ subplots. Generalized linear models (GLM) with Poisson distribution were used to compare variation of seedbank composition among "invaded" and "uninvaded" treatments, with these treatments as fixed factors; germination values were log transformed.

## Results and Discussion

### Relative Growth Rate

The percentage of survivorship of most of the species was 100%, except for *S. pedunculata* (87%). Growth parameters differed significantly among species, expressed both as increased length and cover (Figure 1A) and final foliar and root dry biomass (Figure 1B). *Rubus niveus* showed greater increase in length than other species ($F(4, 68) = 69.3$, P < 0.001). *Scalesia pedunculata* had the greatest incremental growth for stem length among the native species. *Scalesia pedunculata*, *T. rufo-sericea*, and *R. niveus* showed a significantly higher foliar cover increase than the woody vine *C. alba* and the endemic shrub *P. rufipes* ($F(4, 68) = 18.8$, P < 0.001). *Rubus niveus* showed greater production of foliar biomass compared with all native species tested, ($F(4, 68) = 7.7$, P < 0.001). *Rubus niveus* and *T. rufo-sericea* produced greater root biomass ($F(4, 68) = 28.6$, P < 0.001).

Overall, *R. niveus* grew faster relative to the native species. After 8 mo, *R. niveus* showed greater increase in size and biomass production than native species for each of the four growth parameters. Among the native species, *S. pedunculata* and *T. rufo-sericea* showed greater growth, whereas *C. alba* and *P. rufipes* showed the lowest values of growth rate and biomass production. On average, *R. niveus* increase was: 8.5- and 3.5-fold greater than *P. rufipes* and *T. rufo-sericea* in stem length; 4- and 2.5-fold greater than *C. alba* and *P. rufipes* in foliar cover; 1.7- and 1.6-fold greater than *T. rufo-sericea* and *S. pedunculata* in foliar biomass; and 2.3- and 1.7-fold greater in root biomass.

*Rubus niveus* showed higher growth rates than the native species, supporting the hypothesis that invasive plant species generally have a performance advantage over native species (Daehler 2003; Milberg et al. 1999; Rejmánek and Richardson 1996). Under the same environmental conditions, *R. niveus* showed faster growth rates for stem length and cover area and higher production of foliar and root biomass compared with the four native species. Rapid growth may enable *R. niveus* to quickly occupy free space and therefore outgrow associated native shrub and tree species (McDowell and Turner 2002; Pysek et al. 1995; Williamson and Fitter 1996); however, it is not known whether this differential growth rate continues through to maturity. In general, native woody species allocate resources to develop stems and branches (Grime 2001); the high production of foliar and root biomass may give *R. niveus* an advantage over native ecologically similar species when accessing resources such as water, nutrients, and light (Grotkopp et al. 2002; Kolar and Lodge 2001).

### Stress Tolerance

Survivorship was greater than 90% for most species within all treatment types. However, the endemic tree *S. pedunculata* exhibited 100% mortality within the shaded treatment; therefore, this species was removed from the analysis. Light availability significantly affected the growth parameters (stem diameter, stem length, and foliar and root biomass) of both *R. niveus* and the three native species, whereas watering regimens only affected the foliar and root biomass of all species. The interaction of light and water treatment did not significantly affect growth parameters (Figure 2; Table 1).

All species in the stress experiment, except for *S. pedunculata*, showed high survival (>90%) under the different light and water treatments. Almost all *S. pedunculata* plants died in shaded treatments, showing a limited tolerance to low light conditions. *Scalesia pedunculata* is an heliophytic successional tree whose regeneration
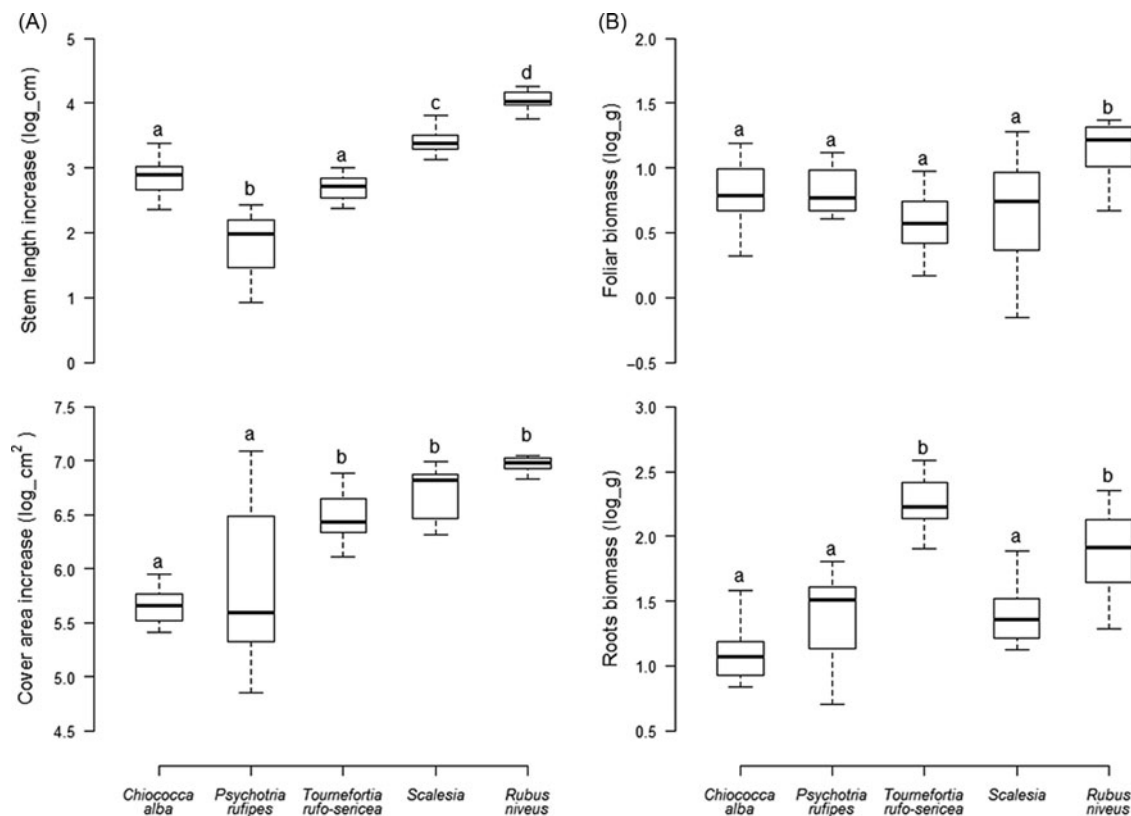
**Figure 1.** Final (A) stem length and foliar cover increase and (B) foliar and root dry biomass values of *Rubus niveus* and four native species of the Scalesia forest. Median value of the growth parameters; letters denote significant differences among species (P < 0.05).

depends on canopy openings (Hamann 1979). Light was the major cause of variation in growth and biomass production of both *R. niveus* and native species. Because the humid highland vegetation of the Galapagos Island has evolved with highly variable rainfall conditions—high precipitation during extreme El Niño events often followed by marked droughts (La Niña) (Hamann 1985; Wilkinson et al. 2005)—native species are adapted to survive prolonged hot-season droughts. Conversely, *R. niveus* was the only species clearly affected by water stress. Studies have shown that abundant light (Baret et al. 2008) and water access are fundamental factors for the successful invasion of other *Rubus* spp. (Caplan and Yeakley 2010). *Rubus niveus* experienced higher sensitivity than native species to light and water conditions expressed by higher variation in growth and biomass production. This trait may help *R. niveus* to more readily access resources than slower growing native species (Vasquez et al. 2010), especially once resources become available after disturbance (Funk and Vitousek 2007; King and Grace 2000). Natural disturbance is a critical element for the regeneration of Scalesia forest in Galapagos (Itow and Mueller Dombois 1992; Wilkinson et al. 2005); disturbance caused by tree fall leads to openings in the forest canopy, allowing *S. pedunculata* recruitment (Vasquez et al. 2010; Wilkinson et al. 2005). However, *R. niveus* is now filling these gaps and is more competitive than *S. pedunculata* (Renteria et al. 2021).

In communities with seasonally fluctuating resource regimes such as the Scalesia forest, an invasive plant could potentially have an advantage by exploiting surplus resources during periods of high availability (Caplan and Yeakley 2010; Funk and Vitousek 2007). This may be the case for *R. niveus*, which showed more sensitivity to light and water availability; this particular trait may allow

*R. niveus* to more effectively exploit resources or opportunities not utilized by the native species (Davis and Thompson 2000; Meiners 2007). Although all habitats are vulnerable to invasion (Williamson 1996), the results from this experiment indicate water availability is a limiting factor for the distribution of *R. niveus*. The species has only been reported from the humid zone of the Galapagos highlands, unlike the four native species, which are more widespread (Atkinson et al. 2008; Renteria and Buddenhagen 2006). *Rubus niveus* distribution seems to be limited to the humid and very humid zones, where edaphic conditions (especially depth, moisture-holding capacity, and fertility) may be more suitable (Atkinson et al. 2008; Hamann 2001; Itow 1995).

## Seedbank and Competition between Recruits

A total of 1,171 seedlings of *R. niveus*, 960 seedlings of native species, and 41 seedlings of other introduced species emerged from soil samples within invaded areas, whereas 1,648 seedlings of native species, 57 seedlings of *R. niveus*, and 12 seedlings of other introduced species emerged from soil samples from the uninvaded areas. A total of 22 vascular plant species were recorded, comprising 17 native and 5 introduced species. Species consisted of 15 herbs (3 introduced), 1 vine, 3 shrubs (1 introduced), and 3 trees (1 introduced); 82% of the total species occurred within uninvaded areas, while 64 % of the species occurred in invaded areas, but this difference was not significant.

There was a significant difference between the number of *R. niveus* seedlings and the number of native species seedlings that emerged from soil samples collected within invaded areas (GLM, quasi-Poisson error distribution: df = 38, $t = -3.622$, P < 0.001).

**Table 1.** Multivariate analysis of variance (MANOVA) results for the growth parameters (stem diameter, stem length, and foliar and root biomass) of *Rubus niveus* and three native species of the Scalesia forest under different light and water availability.

| Species | Source of variation | MANOVA results | | |
| | | df | F | P (>F) |
| --- | --- | --- | --- | --- |
| *Chiococca alba* | Light | 38 | 48.03 | <0.001 |
| | Water | 38 | 2.451 | 0.06253 |
| | Light:Water | 38 | 2.17 | 0.09091 |
| *Psychotria rufipes* | Light | 39 | 32.168 | <0.001 |
| | Water | 39 | 3.196 | 0.02308 |
| | Light:Water | 39 | 1.273 | 0.29709 |
| *Tournefortia rufo-sericea* | Light | 36 | 32.168 | <0.001 |
| | Water | 36 | 3.196 | 0.1452 |
| | Light:Water | 36 | 1.273 | 0.467 |
| *Rubus niveus* | Light | 40 | 92.315 | <0.001 |
| | Water | 40 | 4.511 | 0.004212 |
| | Light:Water | 40 | 0.371 | 0.827913 |
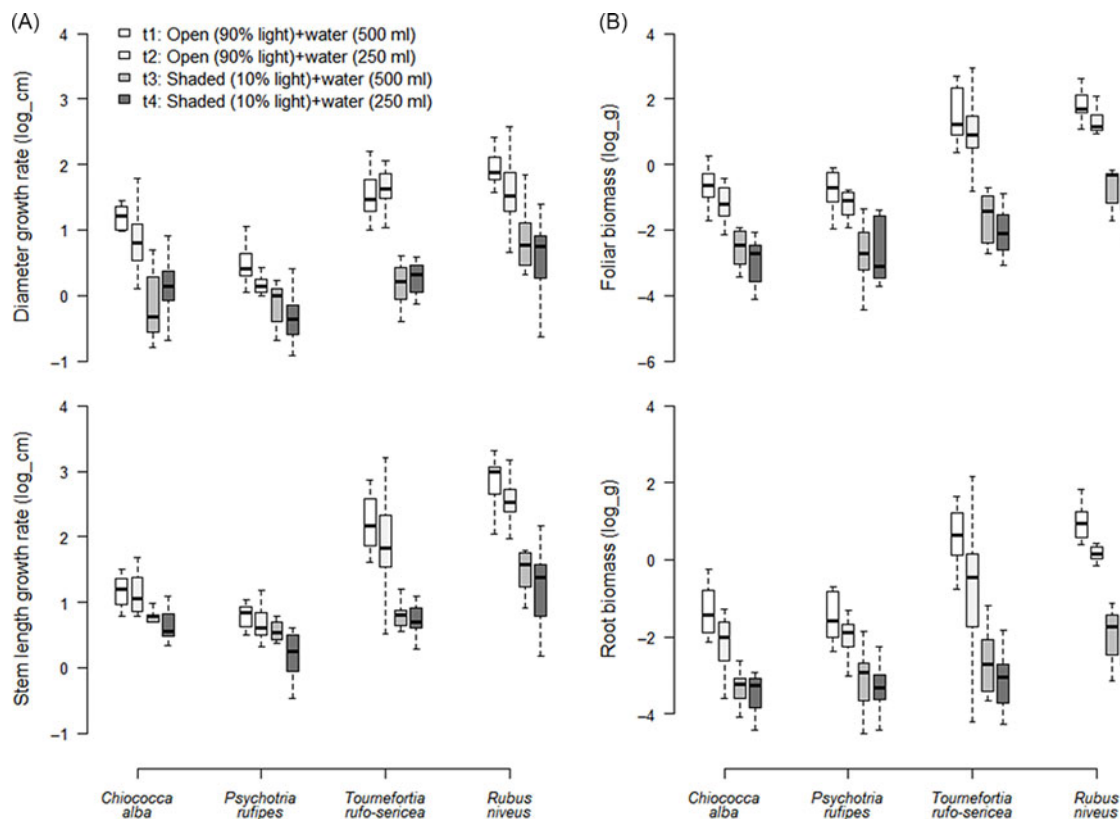


**Figure 2.** Effects of light and water availability on (A) the relative diameter and length growth and (B) final foliar and root biomass of *Rubus niveus* and three native species of the Scalesia forest. Median value of the growth parameters.

Seedlings of *R. niveus* also emerged from soil samples collected from uninvaded areas; however, the number was significantly lower compared with the number of seedlings of native species (GLM, quasi-Poisson error distribution: df = 38, $t$ = 4.178, P < 0.001) (Figure 3).

Herbaceous species strongly dominated the soil seedbank in both invaded and uninvaded areas, making up about 76% and 85% of the total number of seedlings, whereas shrubs and trees made up only 15% and 24%, respectively. Seed germination from soil samples from invaded areas (Figure 3) is expressed as number of seedlings per square meter and is summarized as follows: *R. niveus* = 1,200 ± 378.7, herbs = 266.2 ± 63.2, shrubs = 42.5 ± 15.5, and tree species = 43.7 ± 11.3. The number of *R. niveus*

seedlings per square meter that germinated from soil seedbank in invaded areas was 4.5-, 28.2-, and 27.5-fold greater than the number of native herbs, shrubs, and trees, respectively. *Rubus niveus* seedlings emerged more rapidly than native species seedlings. Within the 5 wk, more than 70% of the total seedlings of *R. niveus* had emerged compared with only 40% of the native species seedlings.

In invaded areas, the total number of emerged seedlings of *R. niveus* was greater than for native species, particularly when compared with the number of seedlings from woody shrubs and trees species. This may result in a competitive advantage for *R. niveus* during the regeneration process; therefore, managed sites can be
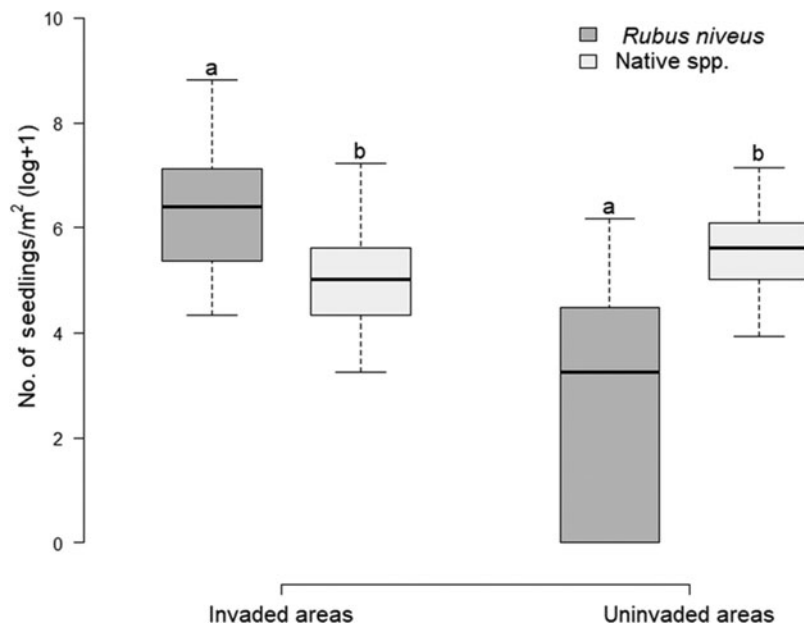
**Figure 3.** Density (median values) of emerged seedlings of *Rubus niveus* and native species geminated from the soil samples in invaded and uninvaded areas. Letters denote significant differences between *R. niveus* and native species (P < 0.05).



**Figure 4.** Relationship between the density of seedlings per square meter and the aboveground cover after *Rubus niveus* control in invaded areas. Values represent the averages of number of seedlings geminated from soil samples and averages of vegetation cover within 1-m² subplots. Bar heights represent mean values, and error bars represent ±SE.

reinvaded easily after control is carried out (Bekker et al. 1997; D'Antonio and Meyerson 2002; Oke et al. 2009; Renteria et al. 2012b; Vilà and Gimeno 2007). Invasive plant species often produce an abundance of seeds and have very large persistent seedbanks (Lonsdale 1988; Oke et al. 2009). In the Galapagos Islands, *R. niveus* fruits all year round, producing copious quantities of seed and forming a large seedbank with up to 7,000 seeds $m^{-2}$ (Landázuri 2002). In addition to its large seedbank, more rapid germination compared with native species delivers a competitive advantage for *R. niveus* in terms of resources and space occupancy (Perez et al. 2000).

As expected, shrubs and trees of native species were poorly represented, whereas herbaceous species were the most predominant group; similar results were found by Wilkinson (2002) when comparing the soil seedbank of the Scalesia forest with an abandoned pasture. Although the stand vegetation is dominated by the endemic tree *S. pedunculata* and shrubs species such as *T. rufo-sericea* and *C. alba* (Shimizu 1997), presence of these species was not evident in the seedbank. Invaded areas and uninvaded areas showed similar native species seedbank; this indicates that native species are not yet limited in invaded areas, offering potential for regeneration if the invader can be controlled or even eliminated (Dunbar and Facelli 1999; Panetta 1982; Richardson et al. 1989; Turner et al. 2008).

The seedbank and standing vegetation after control of *R. niveus* had 16 species in common. These represented 73% of all species in the seedbank and 52% of the species in the standing vegetation.

This variation was the result of a difference in the number of species: 22 species in the seedbank compared with 31 species in the standing vegetation. There was no consistent relationship between the number seedlings per square meter available in the soil seedbank and the aboveground cover regenerated after control of *R. niveus* (Figure 4). Although the number of *R. niveus* seeds available in the soil was considerably greater than the seed counts for all other growth forms, at 9 mo after control, herb and tree layer showed greater values in ground cover than *R. niveus*.

There was a low correspondence between the available seedbank and the regenerated vegetation after control of *R. niveus*. Although there was a large quantity of *R. niveus* seedlings germinating from the soil samples, at 9 mo after control, the regeneration of *R. niveus* on the experimental plots was very low. The lack of soil moisture due to a severe drought that affected the archipelago during 2009 may have affected the regeneration of *R. niveus*. This might be the reason why the seedbank did not reflect the standing vegetation cover. As demonstrated with the soil sample germination experiment, *R. niveus* seeds have the ability to germinate faster than native species under ideal soil moisture conditions. This has been evident in areas under intensive management where reinvasion from the seedbank has occurred right after adult plants have been controlled (Landázuri 2002; Renteria et al. 2012b). On the other hand, regeneration of native species, particularly herbs and trees, demonstrated the greater tolerance of native species to water stress conditions (Hamann 1981; Shimizu 1997).

*Rubus niveus* and natives showed tolerance to changes in light and water conditions; however, *R. niveus* performed better than native species when both moisture and light were in ample supply. The soil seedbank data demonstrated that native species may not be seed limited in the invaded areas; however, the enormous seedbank of *R. niveus* suggests this could constrain the restoration of the native diversity from the native soil seedbank alone. This study is based upon work carried out on seedlings under controlled conditions for a limited period of time. As such, it cannot address the total complexity of the *R. niveus* invasion within the Scalesia forest, although the findings tend to conform to established invasive plant theories.

Management actions for the restoration of native communities should encourage resistance to reinvasion of *R. niveus* in order to favor the persistence or recovery of desirable species (D'Antonio et al. 2016). Chemical control can be an effective short-term management intervention to reduce *R. niveus* invasion; however, there is always a risk of reinvasion from the seedbank resulting in the need for ongoing treatment. Complementary activities should be considered for integrated management and restoration of the Scalesia forest, such as the reduction of the prolific seedbank and active establishment of native canopy species. Certain native species could act as a natural barrier to stop colonization and expansion of undesirable plant species (Kettenring and Adams 2011; Shafroth et al. 2005). The use of fast-growing native species with a high reproductive rates and adapted to the site conditions should be considered; young plants of *S. pedunculata* and *T. rufo-sericea* planted at high densities could provide a rapid source of shade early in the season and limit resources to reduce the reestablishment of *R. niveus* from the seedbank.

The use of biological control could be a cost-effective long-term control strategy to reduce the density of *R. niveus* to below a threshold of impact (Renteria et al. 2012a). While there are some risks involved with the introduction and release of any new exotic organism to the archipelago, these risks are almost negligible if the protocols to develop a biological agent are strictly followed.

Furthermore, there are no *Rubus* or Rosaceae native to the Galapagos. In addition, *R. niveus* is part of a tribe of *Rubus* species from the Old World, so it is very unlikely that a biological control agent would affect the New World *Rubus* species native to mainland Ecuador.

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