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Plant community composition and structural characteristics of an invaded forest in the Galápagos

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Abstract Non-native species have invaded habitats worldwide, greatly impacting the structure and function of native communities and ecosystems. To better understand mechanisms of invasion impacts and how to restore highly impacted and transformed ecosystems, studies are needed that evaluate invader effects on both biotic communities and structural characteristics. On Santa Cruz Island in Galápagos we compared biotic (plant species richness, diversity, and community composition) and structural (canopy openness, forest height, and leaf litter) characteristics of a relic forest dominated by an endemic and highly threatened tree and a forest dominated by an invasive tree. The forests are located within the historical distribution of the endemic tree, which now occupies only

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1% of its original extent. We found that the invaded forest had 42% lower native plant species richness and 17% less plant diversity than the endemic tree dominated forest. Additionally, with the invader there was 36% greater non-native plant species richness, 37% higher non-native plant diversity, and highly dissimilar plant composition when compared to the endemic-dominated forest. Additionally, the invaded forest had a more open and taller tree canopy and greater leaf litter cover than native forest. The presence of the invasive tree and the associated forest structural changes were the primary factors in models that best explained higher non-native diversity in the invaded forest. Our correlational results suggest that an invasive tree has significantly altered plant assemblage and forest structural characteristics in this unique ecosystem. Experiments that remove the invader and evaluate native plant community responses are needed to identify thresholds for practical restoration of this threatened and biologically unique native forest.

Introduction

Invasive plant species can have significant impacts, including changes to ecosystem processes and alteration of community properties such as species richness and composition (Butchart et al. 2010; Dornelas et al. 2014; Ellis and Ramankutty 2008; Ellis et al. 2010; Hejda et al. 2009). Areas that have been extensively altered by invasive species beyond a threshold where they can be restored to historic conditions of native dominance (Hobbs et al. 2009) have been described as "novel ecosystems" (Hobbs et al. 2006, 2009, 2013; Mascaro et al. 2012). Although hundreds of studies have evaluated invasion impacts (Stricker et al. 2015), relatively few studies have focused on comparing abiotic and biotic conditions of native-dominated and novel ecosystems (Lugo 2004; Martínez 2010; Mascaro et al. 2008; Mascaro 2011). Studies that evaluate diversity and species composition and structural conditions of native and heavily invaded habitats provide a baseline for understanding if and how ecosystems are experiencing novel conditions and the potential for restoration of highly-impacted regions (Miller and Beltesmeyer 2016).

Oceanic islands often have especially high numbers of non-native species, depauperate native floras, dense human populations, and extensive land degradation (Ewel et al. 2013; Martinuzzi et al. 2013), the combination of which has promoted changes in plant communities and their structural characteristics on islands worldwide (Denslow 2003; Denslow et al. 2009). For example, the Galápagos archipelago has 97 percent of its land under protection but harbors more non-native ($\sim$ 891) than native ($\sim$ 599) plant species (Guézou et al. 2017), and 15 percent of non-native species are categorized as invasive (Atkinson et al. 2011). Most invasion impacts are on the inhabited highlands where extensive human activities, primarily agriculture, have degraded native ecosystems (Mauchamp and Atkinson 2010; Snell et al. 2002). Some "transformer" invaders (Richardson et al. 2000) can create new plant assemblages that might be particularly difficult to restore (Trueman et al. 2014a) compared to other invaded sites within the archipelago (Jaeger et al. 2007; Restrepo et al. 2012; Rivas-Torres and Adams 2017). Although studies have measured the impacts of invaders in the terrestrial zone of the Galápagos (Jaeger et al. 2007; Rentería 2012), additional studies that determine if and how the species diversity and composition, and structural characteristics of these newly formed ecosystems differ significantly from historic ecosystems are needed (Trueman el al. 2014b). Such information will help determine if restoration efforts can revert invaded

habitats back to native dominated communities, and the amount of economic and managerial resources that will be required to accomplish such goals.

To provide baseline data on native and invaded forests in the Galápagos, we evaluated plant communities and structural characteristics of a relic forest dominated by the endemic tree *Scalesia pedunculata* Hook. f. ("*Scalesia*") compared to a nearby forest that was historically *Scalesia* dominated (P. Jaramillo pers. comm.; Itow 1995; Hamann 2001; Trueman 2014) and is now characterized by the non-native tree *Cedrela odorata* L. ("*Cedrela*"). Specifically, we quantified native (including endemic), and non-native plant species richness, diversity, and composition, and canopy openness, leaf litter, forest height, and average tree size across replicate plots in the *Scalesia* and *Cedrela* forests. Then, we used modeling to explore how the presence of the invader and associated changes in forest structure might affect native and non-native plant diversity and abundance. Quantifying transformer species impacts and the factors that may explain novel trajectories of invaded ecosystems has significant conservation and management implications, particularly on tropical islands with threatened endemic species.

Methods

Study sites

Our study occurred in forests of the highlands of Santa Cruz Island, one of the four inhabited islands in the Galápagos Archipelago (Fig. 1). Santa Cruz is comprised of 98,555 hectares of protected forests and a central agricultural area, and hosts the highest number of non-native plant species ($\sim$ 670) among the Galápagos islands, of which $\sim$ 35% are naturalized (Guézou et al. 2010). The two forests we sampled are in the protected area of the Galápagos National Park (GNP). The native forest is a relic of $\sim$ 100 hectares of "*Scalesia* forest" (Rentería and Buddenhagen 2006) near the "Los Gemelos" tourist area that is dominated by the endemic tree *Scalesia* (more information on *Scalesia* in Online Resource 1). *Scalesia* is considered a key component of Galápagos forests, because it creates particular conditions (see Online Resource 1) which help to maintain native and endemic plant populations and assemblages in sites dominated by this tree (Itow and Mueller Dombois 1988).

The extent of this *Scalesia* forest is now only 1% of its historical area due to land use change and invasions of non-native plant species (Mauchamp and Atkinson 2010). Non-native plants were introduced to Santa Cruz as early as late 1800s (Lundh 2006) and introduction rates increased exponentially when the island was opened for permanent human colonization in the early 1900s (Trueman 2014). Agricultural practices in the inhabited highlands of Isabela, San Cristobal, Floreana and Santa Cruz islands resulted in significant land cover transformation and increased incidence of plant invasions (Gardener et al. 2013).

A primary species threatening *Scalesia* forests is the non-native tree *Cedrela,* one of the most conspicuous plant invaders in the highlands of Santa Cruz (Rentería and Buddenhagen 2006; Online Resource 1). *Cedrela* has been described as a transformer and harmful invasive species in Galápagos (Gardener et al. 2013; Rentería and Buddenhagen 2006; Rivas-Torres and Rivas 2017; Trueman 2014), yet no studies have investigated the mechanisms underlying its ability to be a successful colonizer in this archipelago. It was introduced to the agricultural zone of Santa Cruz in the 1940 s for its valuable timber
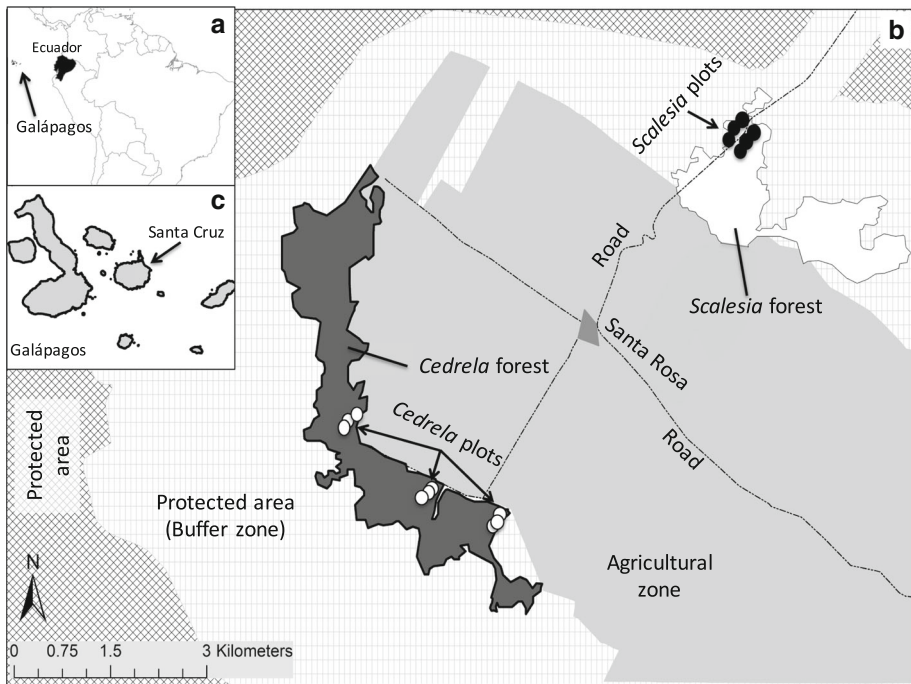
Fig. 1 Location of the Galápagos archipelago approximately 1000 km west of the coast of Ecuador (**a**); location of Santa Cruz Island relative to the other islands in the archipelago (**b**); and Santa Cruz land use in the areas surrounding the study area (i.e., Protected area, Buffer zone, and Agricultural zone) including the *Scalesia* and *Cedrela* forests (**c**). Within the Buffer zone, which is also protected by the GNP, control activities are conducted to contain potential invasive species recorded in the Agricultural zone. *Cedrela* forest located at "El Chato" area and *Scalesia* forest located close to "Los Gemelos" are within the protected boundaries

(Lundh 2006) and is now ranked as the most important wood source for the archipelago (Rivas-Torres and Adams 2017). *Cedrela* dominates the forest canopy of nearly 1600 hectares on Santa Cruz (including the "*Cedrela* forest" within "El Chato" site; Fig. 1) in areas that were historically dominated by *Scalesia* and other native and endemic tree species (Hamann 2001; Itow 1995; Trueman 2014). Some *Scalesia* adult individuals were located near the *Cedrela*-invaded forest used for this investigation, and *Cedrela* adults occurred within the *Scalesia*-dominated forest (Rentería and Buddenhagen 2006). Thus, for our study we sampled replicate plots in the one large "*Scalesia*" dominated forest and the one large "*Cedrela*" dominated forest on Santa Cruz Island. Both forests are situated within the humid highlands ecotone of Santa Cruz between 250 and 600 m.a.s.l. (Itow 2003), have similar third generation lava leaks as their main soil source (INGALA 1987), and experience similar levels of annual average precipitation (*Cedrela*-dominated forest = 65.5 mm and *Scalesia*-dominated forest = 88 mm; http://www.worldclim.org/version1). Given that no other patches of these two forest types exist, we were unable to conduct sampling on replicate *Scalesia* and *Cedrela* forests. Our invaded and native forests were relatively near each other (∼ 6 km), and *Scalesia* was previously recorded in the *Cedrela* forest we sampled. However, the historical species composition of the invaded forest is not well known; thus we interpret our results with caution.

The GNP manages invasive plants in most of their native forest remnants but no control efforts occurred for at least the previous 4 years in the native forest used in this study. Before then the area was managed to reduce invasive species and thus, it likely represents one of the few areas in Galápagos' highlands with ecological attributes similar to what can be considered a historic "pristine" forest. The *Scalesia* and *Cedrela*-dominated sites used in this study represent the two extremes of the historical-novel continuum of forests in the highlands of Santa Cruz (Trueman et al. 2014b). Thus, results from this study fill the gap to inform the extent to which *Cedrela* presence has impacted native, endemic, and non-native flora and structural characteristics compared to historical conditions (i.e., "novelty degree"; Hobbs et al. 2006).

Experimental design and data collection

To compare plant community and forest structural characteristics associated with *Scalesia* and *Cedrela* as canopy dominant species, we randomly chose 48 trees (i.e. ≥ 10 cm DBH) in the *Cedrela* forest and 40 trees in the *Scalesia* forest as centers of 2 m × 2 m plots. We chose a random starting point at each forest edge to place transects heading SW, where the nearest trees to the transects (within 5 m) located at intervals of at least 12 m in the *Scalesia* forest and 20 m in the *Cedrela* forest, were randomly selected as plot centers. Our randomization process could have resulted in selection of *Cedrela* in the *Scalesia* forest or vice versa as plot centers, but because each species heavily dominates each forest type, all plots happened to be centered on *Scalesia* or *Cedrela* in the forests where they dominate. Adult individuals of *Scalesia* had average DBH of 14.7 cm (SE ± 0.63) and *Cedrela* had average DBH of 33.7 cm (SE ± 1.07). No spatial autocorrelation was detected at these distances (correspondence analyses, Sect. 2.3).

To compare plant species abundance, richness, diversity, and composition associated with the dominant species in each forest type, we counted and identified all angiosperm plant species ≥ 20 cm tall in each plot. When species could not be identified in the field, we took photographs and later consulted local experts and herbarium collections. Plant species origin (native, endemic, or non-native) and plant distribution ranges were defined according to plant databases (e.g., Galápagos Species Checklist: Guézou et al. 2017; Jaramillo Díaz and Guézou 2013, last accessed August 2016) and expert opinion (Jaeger H. and Jaramillo P. pers. comm.). "Questionable native" species (after Jaramillo Díaz and Guézou 2013) were designated non-native. Prostrate herbs were counted as one individual when it was not possible to assign unconnected stems to separate plants.

To evaluate forest structural characteristics, we measured canopy openness, forest height, leaf litter, diameter at breast height (DBH), and herbaceous cover in each plot. For canopy openness, hemispherical images were taken early in the morning using a Nikon D40 and a Nikon 8 mm f/2.8 Fisheye lens (Nikon Corporation, Japan) installed over a tripod at 1.30 m height at the center of each plot, leveled, and oriented to magnetic north. Canopy openness, the percentage of forest canopy not covered by leaves (used as a proxy for light transmission into the understory), was then calculated with Gap Light Analyzer 2.0 (Frazer et al. 1999). Forest height was measured in each plot using a Nikon 1200S Range Finder (Nikon Corporation, Japan). Each plot was divided into four 1 m × 1 m subplots and then the spatial extent of leaf litter and herbs in each subplot was quantified. Most of leaf litter in the *Cedrela*-dominated plots was from that same species. Subplot values were then averaged to obtain the mean proportion coverage for each plot. Finally, tree diameter was measured for all individuals ≥ 2 cm DBH.

Data analysis

Species richness and plant diversity (Shannon-H index) were calculated per plot and species origin. To compare plant abundance (i.e., counts of stems per plot), richness, and diversity associated with *Scalesia* and *Cedrela*, we individually analyzed each parameter with non-parametric Mann–Whitney tests (using JMP® software v.10.0, SAS Institute, US, 2012).

To determine if species composition differed based on the forest dominant species we used a multivariate Canonical Correspondence Analysis (CCA). The CCA generates a triplot that allows for visual interpretation of where species are located in the multivariate space in response to particular characteristics such as leaf litter and canopy openness, thereby providing information about how species and community assemblages are influenced by the dominant tree species. To quantitatively interpret the ordination plots from CCA we also used one way-Analysis of Similarities (ANOSIM) with a Bray–Curtis distance measure. ANOSIM values can range from 0 to 1, where 1 signifies complete dissimilarity between communities. Shannon-H, ANOSIM, and CCA calculations were performed using PAST® software (v. 3.01, Norway, 2013). Forest height was highly correlated with leaf litter (Spearman correlation $r > 0.7$) and was not used in the CCA. Because plots were centered on *Scalesia* and *Cedrela* trees, the presence of these species was expected to contribute to differences in species composition in the two forests. Thus, we conducted the CCA and ANOSIM analyses, both including and excluding these canopy dominant species. Likewise, to evaluate differences in canopy openness, forest height, leaf litter, DBH, and herbaceous cover between the two forests we performed independent *t* tests or 2-group Mann–Whitney tests after evaluating data parameters such as normality.

Finally, to better understand how native and non-native plant diversity were linked to either *Cedrela* or *Scalesia* (forest dominant species) presence and associated structural differences, we performed model selection using Generalized Linear Models (GLMs). Prior to using GLMs, we tested for spatial autocorrelation among forest plots using spline correlograms (Zuur et al. 2009). No significant spatial autocorrelation was found among plots at each site. Canopy openness was the only structural characteristic used in the models because forest height and leaf litter were each highly correlated (Spearman correlation r > 0.7) with the variable "forest dominant species" that was maintained as the main independent factor. DBH and herbaceous cover were also not included in the models because they were either not biologically significant (i.e., we did not expect DBH to explain plant diversity) or not significantly different based on dominant species. In the GLMs, forest dominant species was included as a fixed factor to explore the effects of relevant interactions (e.g., forest dominant species × canopy openness) on species diversity patterns. Additionally, we included native richness and non-native richness as additional factors that might help predict native and non-native diversity. All factors were transformed and centered to allow comparisons of estimates. Akaike Information Criterion (AIC) was used as a goodness of fit measure to evaluate all candidate models. GLMs were performed in R software (CRAN v. 3.1.2., Austria, 2013) using the lme4 package (Bates et al. 2011).

Results

We identified 865 individual plants including 500 native and 365 non-native stems in the 88 plots. Abundance was similar among forests, with 449 stems in the *Scalesia* forest and 416 stems in the *Cedrela* forest. However, when abundances among forests were analyzed by origin, the *Scalesia* forest had 111 non-native and 338 native stems while the *Cedrela* forest had 254 non-native and 162 native individuals (Mann–Whitney test natives = 42.20, $P = 0.0001$; non-natives = 22.78, $P = 0.0001$; Fig. 2a). Our results suggest that this pattern was driven by the presence of *Scalesia* and *Cedrela* in their respective forest types, as removing the canopy dominants from the analyses resulted in no differences in stem density of native and non-native species.

We recorded a total of 33 plant species. *Cedrela* forest contained 14 non-native, five native, and three endemic plants (22 species in total), while *Scalesia* forest contained eight non-native, six native, and eight endemic species (also 22 species in total). *Cedrela* forest had lower native plant richness (Mann–Whitney = 6.02, $P = 0.0001$; Fig. 2b) and higher non-native richness (Mann–Whitney = -4.82, $P = 0.0001$) compared to *Scalesia* forest. Forests did not differ in total plant richness, *i.e.* species/m^2 (Mann–Whitney = 1.16, $P = 0.2$). Altogether, more than half of the total species recorded (58%; 19/33) were non-native. *Scalesia* and *Cedrela* forests also had significant differences in both native (Mann–Whitney = 4.93, $P = 0.0001$) and non-native species diversity (Mann–Whitney = -4.28, $P = 0.0001$). For instance, *Cedrela* forest had higher non-native species diversity and lower native species diversity than *Scalesia* forest (Fig. 2c). Total diversity was not significantly different between forests (Mann–Whitney = 1.05, $P = 0.29$). Of the 33 plant species recorded in the two forests combined, 11 were shared between forests; shared species included five native, three endemic, and three non-native plants species (Fig. 3 inset). See Online Resource 2 (Table S1) for a full list of species, their origin, and presence in each forest type.

We found that the origin of the dominant species differed between *Scalesia* and *Cedrela* forest. In *Scalesia* forest, we found more native species, including endemic *Scalesia*, *Solanum cheesmaniae,* and *Psychotria rufipes*. The invasive shrub *Rubus niveus* was the second most common plant in the *Scalesia* forest. In the *Cedrela* forest, three non-native species, *Cedrela*, *R. niveus*, and *Cestrum auriculatum* were the most abundant followed by the native sub-canopy tree *Zanthoxylum fagara* (Fig. 3).

We recorded 22 plant species (11 per forest type) that were found in only *Scalesia* or *Cedrela* plots (Fig. 3 inset). Of these restricted species, six native species (endemics included) and five non-native species were found only in the native *Scalesia* forest. In contrast, all of the restricted species in *Cedrela* forest were non-native species. No individuals of *Scalesia* were found in *Cedrela* forest, nor were any *Cedrela* found in the *Scalesia* forest. Altogether, the two canopy dominant species accounted for 270 of the 387 stems recorded for the 22 restricted taxa.

When *Scalesia* and *Cedrela* species were excluded from the CCA analysis, plots of both forests were different in their species composition (Online Resource 2 Fig. S1, and S2-for results including both species). This difference was also supported by the ANOSIM analysis ($r = 0.32$, $P = 0.0001$). The CCA triplot showed how species such as *Cedrela* were strongly correlated with high leaf litter, while *Scalesia* and other native species were negatively correlated (Online Resource 2 Fig. S2b, and Table S2-for CCA scores excluding and including both tree species).

Fig. 2 Native (including endemics) and non-native plant species abundance (**a**), species richness (**b**), and species diversity (Shannon-H, **c**) in the *Scalesia* and *Cedrela* forests. Values are mean ± SE at plot levels (40 and 48 plots in *Scalesia* and *Cedrela* forests, respectively). All comparisons were significant at $P < 0.001$ for the Shannon-H analysis
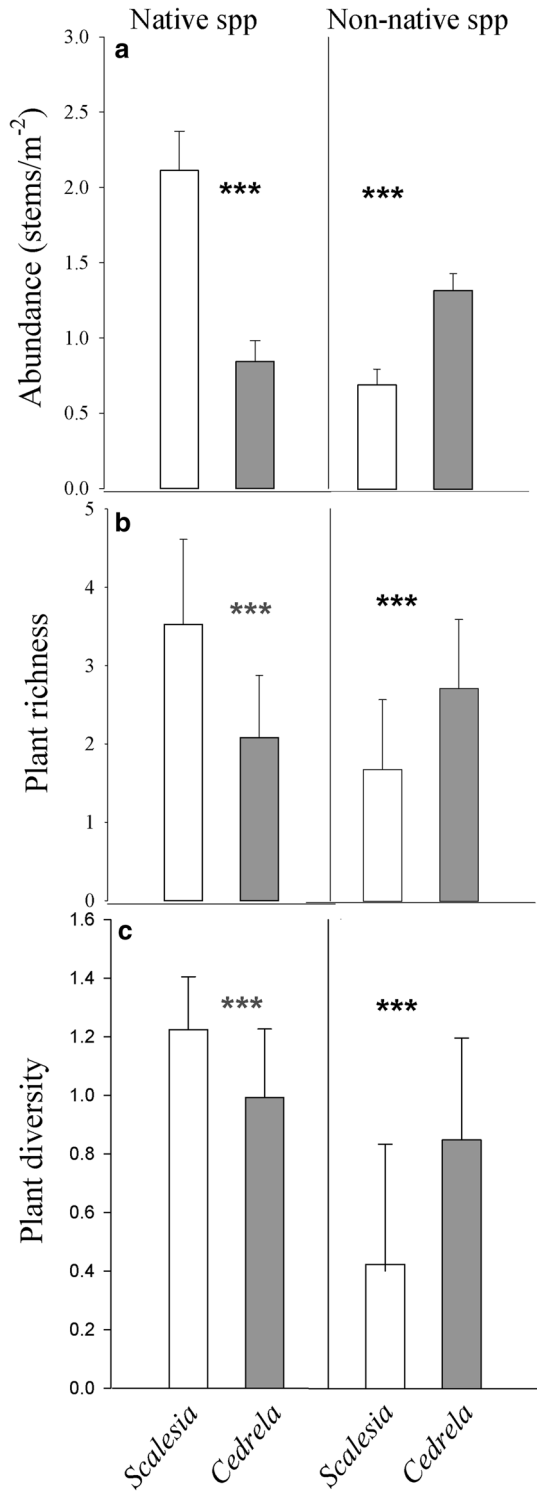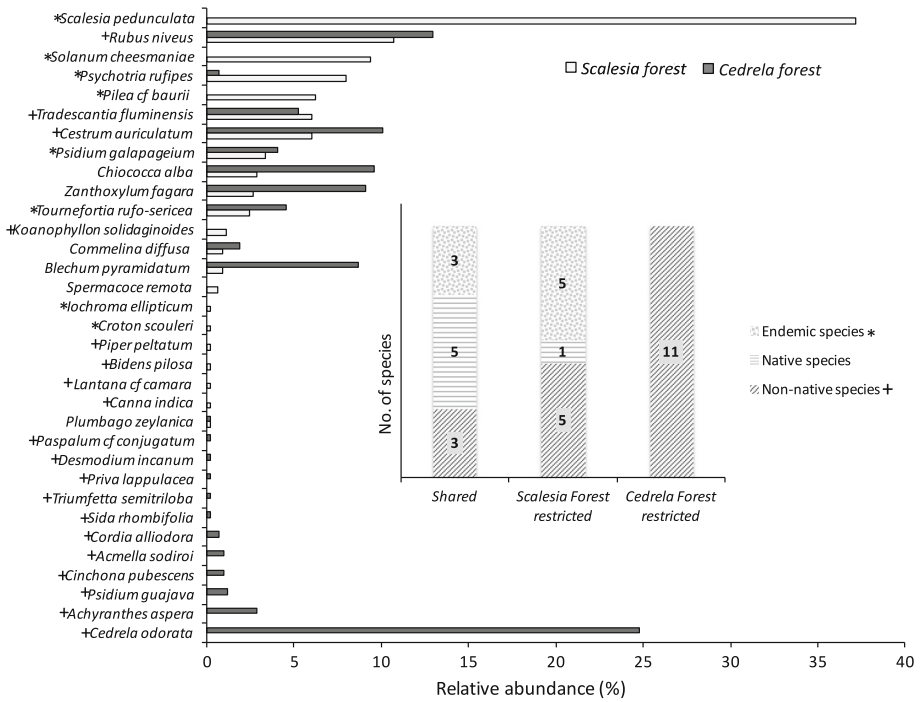
Fig. 3 Relative abundance of the 33 plant species found in the *Scalesia* and *Cedrela* forests. Endemic (asterisks) and non-native species (crosses) are denoted. All other species are native. Species found in only one forest type were designated as "restricted" (11 total for each forest). Inset figure shows the total number of species found in both forest types ("shared"), and restricted species based on origin (non-native, native, or endemic)

Cedrela-dominated forest had distinctly different structural characteristics compared to *Scalesia*-dominated forest. *Cedrela* forest had a more open ($t = -2.55$, $P = 0.01$), and taller (Mann–Whitney $= -8.06$, $P = 0.0001$) canopy, more leaf litter (*Mann–Whitney* $= -7.01$, $P = 0.0001$), and larger diameter trees (DBH; $t = -2.26$, $P = 0.02$) than did *Scalesia* forest (Fig. 4). The amount of herbaceous species cover was similar between forest types (*Mann–Whitney* $= 0.05$, $P = 0.81$).

The best predictors of native species diversity were forest dominant species (*Cedrela*, *Scalesia*) and forest species combined with the number of non-native species. These two models were selected based on their AIC values; models that included canopy openness or other combinations of these variables had less support. In general, native plant diversity was higher in *Scalesia* plots with fewer non-native species (Table 1). On the other hand, we found that forest dominant species (namely *Cedrela*), or forest dominant combined with canopy openness, best explained non-native plant species diversity (Table 2). Other models that included native species, canopy openness, or a combination of these variables, except as noted above had less support.
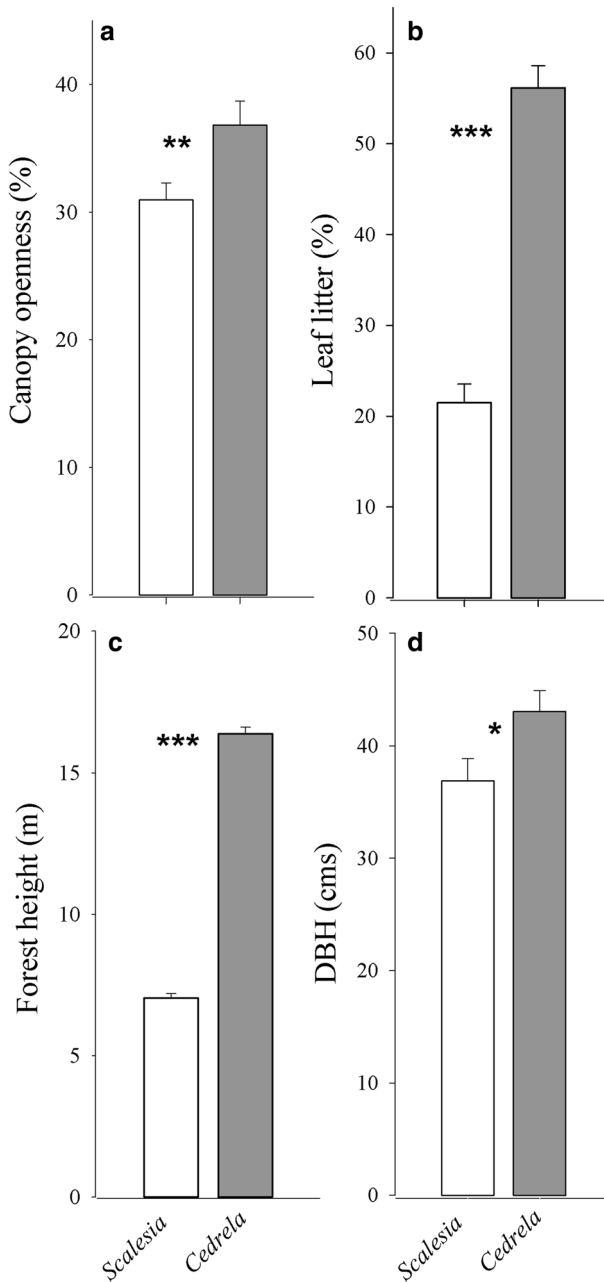
Fig. 4 Canopy openness (**a**), leaf litter (**b**), forest height (**c**), and diameter at breast height (DBH, D; that includes the focal trees) in *Scalesia* and *Cedrela* forest (values are means ± SD). Number of asterisks denotes statistical significance: one asterisk = $P < 0.05$; two asterisks = $P < 0.01$; and three asterisks = $P < 0.001$ for performed Mann–Whitney tests

Table 1 Contrasting GLMs predicting native species diversity for all plots (calculated using the Shannon-H index) arranged from low to high AIC

Model	Estimate	AIC	ΔAIC
Forest dominant species[a]	−0.964	231.33	0
Forest dominant species × non-native species[a]	−0.296	233.31	1.98
Forest dominant species × CO	0.227	233.93	2.6
Forest dominant species × CO × non-native species	−0.502	236.57	5.24
Non-native species	−0.275	247.77	16.44
CO × non-native species	−0.0755	250.16	18.83
CO	−1.747e−01	252	20.67

[a]These models were the best estimators of native diversity according to the lower ΔAIC values. Models with a ΔAIC ≤ 2 are also considered good predictors (Burnham and Anderson 1998). Estimate column presents the strength and sign of the interaction. All estimates values are comparable because factors were centered. CO (canopy openness), "native species" = total number of native species per plot, non-native species = total number of non-native species per plot

Table 2 Contrasting GLMs predicting non-native species diversity for all plots (calculated using the Shannon-H index) ordered from low to high AIC

Model	Estimate	AIC	ΔAIC
Forest dominant species[a]	0.984	230.26	0
Forest dominant species × CO[a]	0.154	231.39	1.13
Forest dominant species × native species	−0.166	233.3	3.04
Forest dominant species × CO × native species	−0.520	235.64	5.38
CO × native species	0.059	247.38	17.12
CO	2.634e−01	248.4	18.14
Native species	−2.509e−01	249.01	18.75

[a]These models were the best estimators of non-native richness according to the lower ΔAIC values. For details on ΔAIC calculation, model prediction, estimates interpretation and factors abbreviations and meaning refer to Online Resource 2 Table S1. Forest height and leaf litter variables were not included because they were highly correlated with the variable "forest dominant species"

Discussion

Our results demonstrate that a forest in the Galápagos dominated by the non-native invasive tree *Cedrela* was associated with greater non-native plant species richness and diversity, lower native species diversity, and significantly different plant communities and structural characteristics compared to forest dominated by the endemic and highly threatened *Scalesia* tree. The higher non-native richness and diversity under the invasive *Cedrela* is congruent not only with investigations in oceanic islands (Mascaro et al. 2008; Mascaro 2011) where invasive species impacts are often prevalent, but also with findings from continental ecosystems (Peltzer and MacLeod 2014). For example, native plant assemblages and forest structure have been modified by invasion of non-native *Pinus* and *Schizolobium parahyba* tree species in native forests in Brazil (de Abreu et al. 2014; de Abreu and Durigan 2011). Similar to other invasive trees, *Cedrela* has traits often

associated with successful invaders (Cervera and Parra-Tabla 2009; Daehler 2003), such as wind dispersed and relatively large seeds and it is a canopy tree up to 30 m in height, which is much taller than the 15 m maximum height of *Scalesia*. Furthermore, *Cedrela's* deciduous nature, and high and open canopy, may allow greater light in the understory and more colonization by non-native species, including *Cedrela*. Finally, the close proximity of the *Cedrela* forest to agricultural land suggests high propagule pressure from non-native plant species that grow densely in such managed areas.

Non-native species introductions and the extent of invaded ecosystems are expected to increase over time across biomes on islands and continents, and in oceans and estuaries (Morse et al. 2014). Our results, together with other similar investigations in the region (Trueman et al. 2014b) suggest this pattern may hold for the Galápagos where seven decades after *Cedrela* was introduced it is now dominating and apparently altering characteristics of native forests. Dissimilarities in both plant community and structural characteristics between the two forest types indicate that the *Cedrela* forest may occupy distinct biotic and abiotic spaces in the historical-altered continuum (*cf.* Hobbs et al. 2006) when compared to native-dominated forests. For example, from the 19 non-native and invasive species found in the *Scalesia* and *Cedrela* forests together, which is ∼ 10% of the total number of naturalized species in Santa Cruz (∼ 200 species, Guézou et al. 2010), eleven were recorded in the *Cedrela*-dominated site alone, suggesting these invader-dominated forests are a significant repository of non-native plants in the region.

Additionally, other studies support the idea that such differences between invaded and native-dominated plant communities will become greater over time, especially where the underlying processes that generate these dissimilarities (e.g., shifts in structural characteristics due to the invader) are maintained (Mascaro et al. 2008). Moreover, *Cedrela* may eventually dominate the *Scalesia* forest without consistent management (Hamann 2001). However, here we did not find any *Cedrela* seedlings colonizing the *Scalesia* forest plots but research has shown *Cedrela* is establishing in other nearby native sites within the same relic on Santa Cruz (Rentería and Buddenhagen 2006). Results presented here show the potential of *Cedrela* to change abiotic and biotic conditions. Further, the patterns of invasion by *Cedrela* suggest vigilant surveys and management actions are needed to prevent *Scalesia* forest from being colonized and altered by *Cedrela*. In addition, experiments to test if the invaded forests are experiencing irreversible conditions (i.e. beyond the novel ecosystem threshold, Hobbs et al. 2009) or if extraction of *Cedrela* trees will help to restore native species dominance and historical structural conditions are needed. Furthermore, given the economic importance of *Cedrela* in the Galápagos, restoration efforts also must include socio-economic considerations, such as impacts of extraction on lumber availability (Rivas-Torres and Adams 2017).

Although native species richness was lower than non-native species richness in *Cedrela* forest (and was also lower when compared with native richness in the *Scalesia* forest plots), native and endemic plants were recorded in the invasive-dominated forest plots. Studies in other oceanic islands have also found that some native plant species can be found in forests dominated by non-native species (Ewel et al. 1999; Lugo 1992, 2004; Lugo and Helmer 2004; Zavaleta et al. 2001). Whether or not these invasive-dominated forests can act as reservoirs for native species in the Galápagos is not known. Conversely, over time, native species may disappear if they fail to recruit under the invader-dominated canopy. Thus, experimental approaches in this site may also help to elucidate if native species can recruit and persist under *Cedrela* forests. Already, three endemic plant species currently found in the *Cedrela* forest (*Psidium galapageium, P. rufipes* and *Tournefortia rufo-sericea*) are categorized as threatened (and Vulnerable according to IUCN status 2014

http://www.iucnredlist.org/; Guézou et al. 2017) for the archipelago. No information is available on their ability to establish in *Cedrela* forest. Hence, an important topic for future investigations is to determine if the presence of the few native and endemic species found in the *Cedrela* forest is a result of persistence under the new habitat conditions below *Cedrela* or recruitment from surrounding habitats.

Our findings provide the foundation for establishment of long-term studies and experiments to better understand the role of *Cedrela* in transforming native forests, including invader effects on both native and non-native plant populations (Flory and D'Antonio 2015; Castro et al. 2010; McKinney and Lockwood 1999; McKinney 2008). In addition, long-term studies can also help to evaluate the potential of invaded forests to act as refuges for native biota, including threatened species. Experiments that remove invasive species such as *Cedrela* can elucidate the processes that result in differences in plant species distribution in invaded habitats, and inform how particular species transform communities. Finally, experiments that evaluate effects of *Cedrela* removal on environmental conditions and the recruitment and persistence of native plant species are essential for determining if invader-dominated sites in Galápagos are beyond the threshold for practical restoration (Hobbs et al. 2009) or if managerial actions can help to reestablish historical conditions of these unique an endangered forests.

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