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Traits and Resource Use of Co-Occurring Introduced and Native Trees in a Tropical Novel Forest

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Abstract: Novel forests are naturally regenerating forests that have established on degraded lands and have a species composition strongly influenced by introduced species. We studied ecophysiological traits of an introduced species (*Castilla elastica* Sessé) and several native species growing side by side in novel forests dominated by *C. elastica* in Puerto Rico. We hypothesized that *C. elastica* has higher photosynthetic capacity and makes more efficient use of resources than co-occurring native species. Using light response curves, we found that the photosynthetic capacity of *C. elastica* is similar to that of native species, and that different parameters of the curves reflected mostly sun light variation across the forest strata. However, photosynthetic nitrogen use-efficiency as well as leaf area/mass ratios were higher for *C. elastica*, and both the amount of C and N per unit area were lower, highlighting the different ecological strategies of the introduced and native plants. Presumably, those traits support *C. elastica*'s dominance over native plants in the study area. We provide empirical data on the ecophysiology of co-occurring plants in a novel forest, and show evidence that different resource-investment strategies co-occur in this type of ecosystem.

Keywords: introduced species; leaf C and N densities; novel forests; photosynthetic nitrogen use-efficiency; leaf mass per area

1. Introduction

The Anthropocene Epoch is associated with rapidly changing environmental conditions and high rates of species introductions, leading to the formation of novel forests [1]. These emerging forests contain species assemblages that include co-occurring introduced and native tree species [2,3]. Novel forests comprise about 35% of global terrestrial ecosystems [4] and are expected to become more common in the future. There has been much debate in recent years about the implications of novel forests for biodiversity. However, little empirical data are yet available to understand how the tree biota might respond to changing environmental conditions and how this might affect the functioning of present and future forests [5,6].

It is well known that introduced species—commonly the dominant tree species in novel forests—are generally considered a risk for biodiversity due to their ability to outperform native species in terms of productivity, reproductive capacity, and recruitment (e.g., [7,8]). In general, studies report faster growth, higher maximum assimilation rate at saturating light intensities, higher dark respiration and transpiration, more efficient use of resources, and faster nutrient cycling for introduced species compared to native species [9–17]. Usually, introduced species act as pioneers [18] during succession, giving them an advantage in the colonization of disturbed and degraded sites. The ecophysiology of

native species can be influenced by the effects that introduced species have on novel ecosystems [19], which may be large when introduced species are abundant and dominate the plant community [19,20].

Less is known about species traits and mechanisms that allow native plants to survive and thrive when a novel forest is formed. In a community containing co-occurring native and introduced species, those able to compete efficiently for the same resources, and/or use them in different ways are more likely to persist [10,15]. Presumably, native and introduced species occupy different positions in the leaf economic spectrum [10,21–24], which describes the nutrient and organic matter investment of plants on leaf structure and functioning. However, we are unaware of empirical studies demonstrating this pattern in tropical mature novel forests.

We chose a novel forest in Puerto Rico dominated by the introduced tree *Castilla elastica* Sessé, to study the ecophysiology of co-occurring native and introduced trees. Based on previous studies in the area [20,25] and on the literature, we anticipate that *C. elastica* has a strong influence on the abiotic conditions in this community, which might have effects on the ecophysiology of native species. We hypothesize that *C. elastica* has higher photosynthetic capacity than native species, probably related to its highly efficient use of resources; and that *C. elastica* and native species occupy different regions of the leaf economic spectrum, particularly regarding to leaf area/mass ratios and concentrations of C and N per unit leaf area. To test our hypotheses, we use photosynthesis light-response curves, and resource use and resource investment indexes to compare species in the community. We also measure the light availability across the forest.

2. Materials and Methods

2.1. Castilla elastica—A Dominant Introduced Tree

Castilla elastica is one example of a dominant introduced naturalized tree in Puerto Rico, originally from Central and South America [26,27]. The introduction of *C. elastica* to Puerto Rico happened at the beginning of 20th century according to the local Agricultural Experiment Station in Mayagüez, Puerto Rico. Originally, the government attempted unsuccessfully to produce latex from *C. elastica*, but also used it as shade tree in coffee plantations. Today, novel forests of *C. elastica* are present throughout Puerto Rico, concentrating in the humid northwest region. These forests covered about 100 hectares in the 1990s, corresponding to less than one percent of the country's land area [26].

2.2. Study Area

We studied plants at the biological reserve El Tallonal located in the municipality of Arecibo (18°24′27″ N 66°43′53″ W), which is classified as a subtropical moist forest [28]. The predominant soil type at the sinkholes of El Tallonal, where *C. elastica* is dominant, is the Oxisol of the series *Almirante* [29]. The annual mean temperature and precipitation are 25.5 °C and 1295 mm, respectively. The dry season is from January to April, and the wettest months are July to September.

Agriculture and cattle grazing were common activities at El Tallonal until the 1950s, and it is likely that *C. elastica* was introduced in the area around 1940s and then abandoned few years later. Forest regeneration occurred naturally after land abandonment, and aerial photographs show that areas covered by novel forests of *C. elastica* had been growing for about 50 years by 2005. Currently, *C. elastica* has a mean species Importance Value Index of 37% (a composite index of relative density, cover, and frequency) in these forests, indicating that the species occupies a dominant position [25]. The forest is referred to hereafter as *Castilla* novel forest. Modifications on species composition and functioning in the study area have been associated with the dominance of this species [20,25].

2.3. Sampling

We measured in situ photosynthetic light responses of leaves of *C. elastica* and of co-occurring native species (Table 1). To that end, we took advantage of two 26 m-tall meteorological towers standing in the study site that allowed data collection at different heights or forest strata, i.e., canopy = 25 m in

height, subcanopy = 15 m in height and understory = ground level to two meters in height. Large trees ($\geq$10 cm of diameter at breast height (DBH)), assumed as adult trees, were measured in the canopy and in the subcanopy. Saplings (1.5 $\leq$ DBH < 2.5 cm , between one and two m in height), and juvenile plants (seedlings and young individuals of 10 to 40 cm in height) were measured in the understory. The number of trees and species that could be measured and sampled from the towers was limited, imposing restrictions on the statistical analyses. However, the same trees could be repeatedly measured throughout an entire year, compensating partially for the small number of individuals measured.

Sampling campaigns were performed during periods of contrasting rainfall and temperature. For practical purposes, below we refer to each measuring period as follows: December to January as December 2008; March to April as March 2009; June to July as June 2009; and October to November as November 2009.

In the canopy, we selected two trees of *C. elastica* and two of native species. In the subcanopy, we measured a *C. elastica* tree and one tree of native species (the only one present at this forest stratum). In the understory, we measured four saplings: two of *C. elastica* and two of native species. For juvenile plants, we selected six individuals on each sampling event (three of *C. elastica* and three of native species), and measured one leaf per individual, instead of two. Each pair of leaves and trees (native and introduced) was measured at the same level to ensure they were exposed to a similar light environment. In total, we obtained at least two light response curves, per species, per measuring period (except in the case of a few juvenile plants that were represented by a single curve), for a total of 92 light response curves. Plants in the subcanopy and understory were only measured during December 2008, March 2009, and June 2009.

Table 1. List of species analyzed, their botanical families, and the forest stratum at novel *Castilla* forests. Taxonomic classification follows [26,30].

Species	Family	Forest Stratum
Casearia guianensis (Aubl.) Urban [N]	Flacourtiaceae	Us
Casearia sylvestris Sw. [N]	Flacourtiaceae	SC
Castilla elastica Sessé [In]	Moraceae	C, SC, Us
Chrysophyllum argenteum Jacques [N]	Sapotaceae	Us
Cordia alliodora (Ruiz & Pav.) [N]	Boraginaceae	C
Faramea occidentalis (L.) A. Rich [N]	Rubiaceae	Us
Guarea guidonia (L.) Sleumer [N]	Meliaceae	Us
Ocotea floribunda (Sw.) Mez [N]	Lauraceae	C
Ocotea leucoxylon (Sw.) Mez [N]	Lauraceae	C
Thouinia striata Radlk [Ne]	Sapindaceae	Us
Trichilia pallida Sw [N]	Meliaceae	Us

In = introduced naturalized, N = native, and Ne = native endemic species; C = Canopy, SC = Subcanopy and Us = Understory.

Environmental data were recorded using a HOBO micro-station data logger (H21-002, Onset Computer Corporation, Bourne, MA, USA). Three micro stations were installed in each tower and forest strata: canopy (26 m in height), subcanopy (15 m) and understory (1.5 m). Air temperature ($^\circ$C), photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) and air relative humidity (percent) were recorded from December 2008 to November 2009. Care was taken to ensure that environmental data recorded by loggers were representative of leaf conditions.

2.4. Light Response Curves and Leaf Harvesting Protocol

Light response curves were measured in the field, using a portable infrared gas analyser (LC*pro+*, ADC BioScientific Ltd., Hertfordshire, UK). The LC*pro+* analyses the difference between ambient CO_2 concentration and the concentration of CO_2 in a leaf chamber (Δc), and calculates CO_2 assimilation rate (A, in μmol m^{-2} s^{-1}) and stomatal conductance to water vapour (gs, in mol m^{-2} s^{-1}).

Gas exchange measurements were performed in the morning, after leaves had received natural illumination for at least two hours. In the canopy and subcanopy, we measured CO_2 assimilation in response to increasing light intensity from dark conditions (zero) to 2000 µmol m^{-2} s^{-1} of photosynthetic photon flux density (PPFD), using the following sequence: 0, 100, 250, 500, 1000, 1500 and 2000 µmol m^{-2} s^{-1}. In the understory, we used PPFD from zero to 600 µmol m^{-2} s^{-1}, using the following sequence: 0, 50, 100, 200, 400 and 600 µmol m^{-2} s^{-1}. We allowed enough time between changes in light intensity to ensure leaf equilibration. Temperature was kept constant at 25 °C and CO_2 concentration was maintained at about 380 volume per million (vpm) to avoid short term variations that would render measurements meaningless. After conducting each light response curve, leaves were harvested to measure the leaf area, leaf mass and leaf carbon and nitrogen concentrations.

Light response curve data were then analysed using a non-linear mixed model as follows: $A = A_{max} * (1 - e^{-\alpha\,(PPFD-LCP)})$ [31]. Sigma Plot (v.11.0, Systat Software Inc., San Jose, CA, USA) was used to fit the curves and calculate the following parameters: maximum photosynthetic rate at saturating light intensities (A_{max}), light compensation point (LCP), light saturation point (LSP), dark respiration and quatum yield. We also calculated the stomatal conductance of water vapour at maximum A rates (gs_{max}, in mol m^{-2} s^{-1}), the intrinsic water use efficiency at maximum rates (WUE_i) as the molar ratio of A_{max} and gs_{max} (in µmol mol^{-1}), and the photosynthetic nitrogen use efficiency (PNUE) per unit of leaf nitrogen at maximum assimilation rates (PNUE = A_{max}/nitrogen content, in µmol mol^{-1} s^{-1}).

2.5. Samples Processing

Leaf area of fresh leaves was measured using a leaf area meter (LI-3100, LI-COR Biosciences, Lincoln, NE, USA). After that, leaves were dried in the oven at 65 °C for at least three days, and then weighed to obtain their dry mass. Leaf surface area (m^2), leaf dry mass (kg), and leaf mass per area (LMA in kg m^{-2}), were determined to compare leaf structure among species and groups [32]. Leaf carbon and nitrogen concentrations were measured by macro dry combustion using a LECO CNS-2000 analyser (LECO Corporation, St. Joseph, MI, USA). Molar N concentrations are given on both area (m^2) and mass basis (kg).

2.6. Statistical Analyses

All analyses were performed using JMP 13.0 (SAS Institute Inc., Cary, NC, USA). Differences in environmental conditions between forest strata were tested using an Analysis of Variance (ANOVA) and posterior Tukey test for differences among measuring periods. Normality tests showed that biological parameters were not normally distributed, therefore we used nonparametric tests analogous to one-way analysis of variance (Wilcoxon/Kruskal-Wallis test, at maximum $p = 0.05$), or multiple pair-wise contrasts (Wilcoxon z), for comparing the photosynthetic capacity parameters, LMA, and C and N concentrations.

The set of native species available for measurement around the tower area was treated as a single group as there were no significant statistical differences in their photosynthetic parameters. This group was compared to the set of *C. elastica* measurements at every sampling season and stratum (canopy, subcanopy and understory). Linear regression analysis was used to test the relationship between leaf area and leaf mass, and the concentrations of C and N.

3. Results

3.1. Environmental Conditions

Mean precipitation and temperature range for each period were the following: December (149 mm, and 18 to 27 °C), March (33 mm, and 20 to 28 °C), June (144 mm, and 23 to 31 °C) and November (189 mm, and 22 to 30 °C). Throughout the year, mean temperature varied from 20 to 24 °C with a peak in June. The relative humidity was over 80% for almost the entire study period.

Light intensity (PPFD$_{mean}$) varied from the understory to the canopy by two orders of magnitude: from about 6 to more than 700 μmol m^{-2} s^{-1} (Figure 1). The average PPFD$_{mean}$ per day in the canopy was 686 μmol m^{-2} s^{-1}, and the average daily PPFD$_{sum}$ was 30 mol m^{-2} day^{-1}. The PPFD$_{mean}$ received in the subcanopy and in the understory were only 10% and 1% of that received in the canopy, respectively. The photoperiod (the total hours in a day during which the PAR sensors record incident and diffuse sunlight in each stratum), varied throughout the year between 12 and 13 h in the canopy and subcanopy, and between 8 and 11 in the understory. Both the PPFD$_{mean}$ and PPFD$_{sum}$ did not differ between dates in the canopy, but they were significantly higher during March and June season in both the subcanopy and the understory, coinciding with the pronounced leaf shedding of *C. elastica* trees [20,25].


(A)

(B)
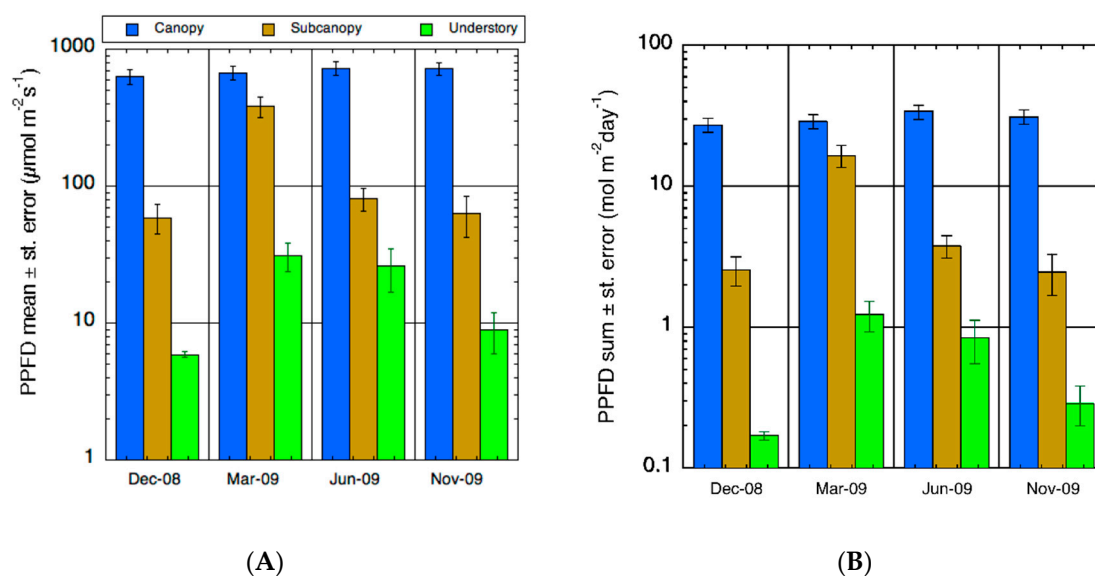
Figure 1. Environmental variables at *Castilla* novel forest. (**A**) Mean photosynthetic photon flux density (PPFD$_{mean}$) and (**B**) total photosynthetic photon flux density (PPFD$_{sum}$) per day for the different forest strata during four measuring periods (*n* = 60–62).

3.2. Leaf Dimensions

Castilla elastica produced larger and heavier leaves compared to the group of native species (Figure 2). In addition, their LMA was lower and decreased 3.3 times from the canopy to the understory. For the group of native species, the same pattern was observed but the decrease in LMA was less pronounced (2.2 times), indicating lower plasticity of this parameter.

### 3.3. Concentration of C and N, and C:N Ratios

Median C concentration of the native species was 43 mol kg^{-1}, ranging from 35 to 47 mol kg^{-1}, whereas *C. elastica* had a narrower range (34 to 40 mol kg^{-1}) and a lower median (38 mol kg^{-1}) (Groups differed significantly: Wilcoxon/Kruskal-Wallis $\chi^2 = 35$, $0.001 < \chi^2 < p$). In the case of leaf N concentration, grouped native species had a median of 1.7 (range: 1.2 to 2.2 mol kg^{-1}), whereas *C. elastica* had a significantly larger median leaf N concentration (2.05 mol kg^{-1}) and a range between 1.3 and 2.4 mol kg^{-1} (Wilcoxon/Kruskal-Wallis $\chi^2 = 16$, $0.001 < \chi^2 < p$).
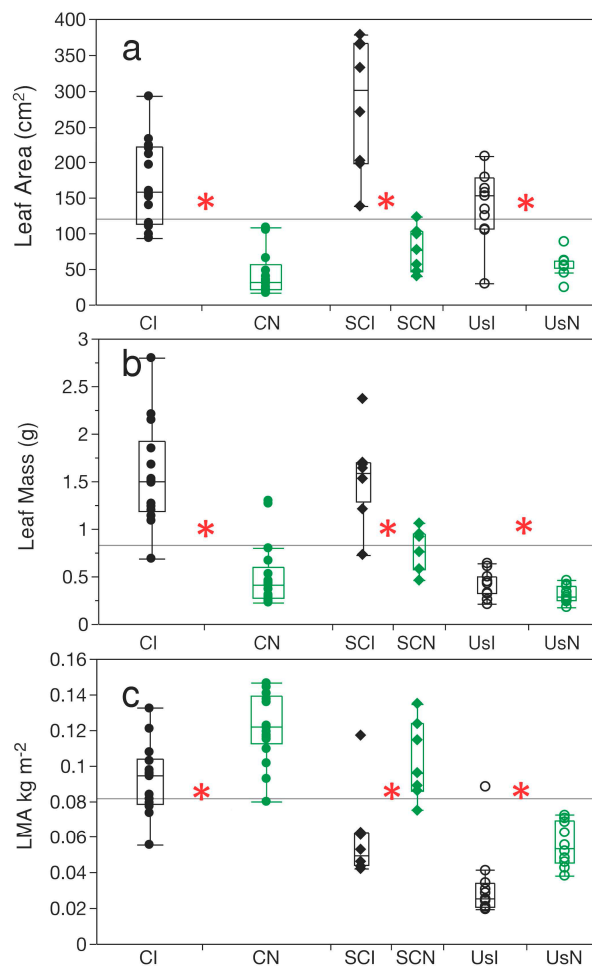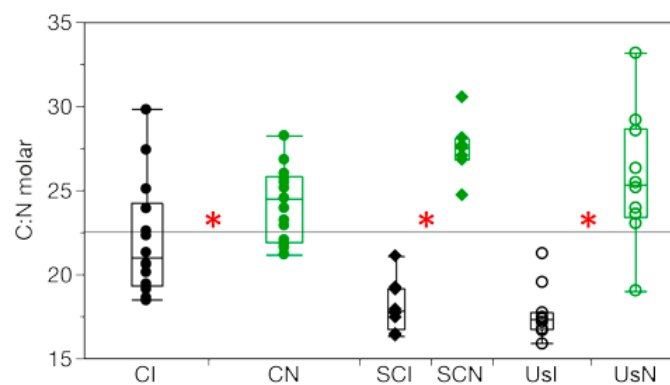
Figure 2. (**a**) Leaf area; (**b**) leaf mass and (**c**) leaf mass per area (LMA) of *C. elastica* (I) (black symbols) and group of native species (N) (green symbols) measured in the canopy (C), subcanopy (SC), and understory (Us) of a *Castilla* novel forest. Number of samples: CI = 14, CN = 16, SCI = 8, SCN = 7, UsI = 11, UsN = 10. The red asterisks indicate significant differences between groups within each stratum (Wilcoxon z, *p* < 0.01).

The LMA values of both groups increased from the understory to the canopy, and as expected, C concentration per unit area was linearly correlated with the LMA in both groups, with a slightly higher slope for grouped native species (Figure 3). The same pattern was observed in the case of N concentration per area (N_{area}), although the models explained lower percentages of data variance in comparison to those for C concentrations. The continuous and rapid increase of C and N per unit area from the understory to the canopy in both groups is expected as a response to the higher light energy available for photosynthesis in the upper forest strata.

Within each stratum, median C:N ratios were significantly lower for *C. elastica* (Figure 4). For this species, the ratio decreased markedly from the canopy to the understory, whereas no uniform pattern was observed for the grouped native species.
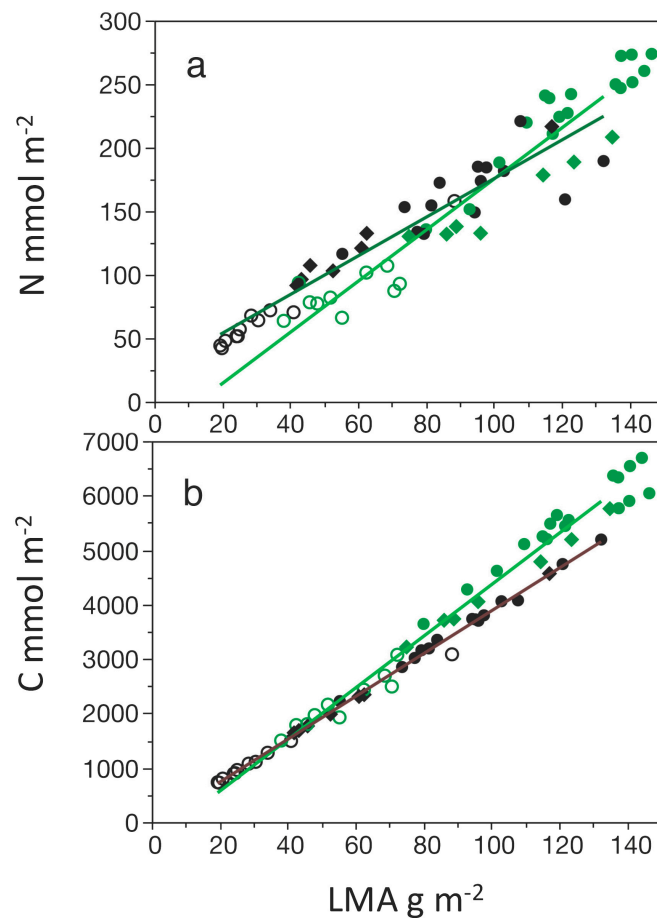
Figure 3. Variations of the relationship between leaf mass per area (LMA) and (**a**) N and (**b**) C concentrations per unit area in the vertical profile of the *Castilla* novel forest. Green symbols: native species; black symbols: *C. elastica*. Open circles (Us), squares (SC), closed circles (C). For, native species: C = −380 + 47,000 LMA, R^2 = 0.97; and N = −26 + 2000 LMA, R^2 = 0.92 (*n* = 34). For *C. elastica*: C = −53 + 39,000 LMA, R^2 = 0.99; and N = 23.4 + 1500 LMA, R^2 = 0.91 (*n* = 33).

Figure 4. Vertical variation in leaf C:N ratios for *C. elastica* (I) (black symbols) and grouped native species (N) (green symbols) measured in the canopy (C), sub-canopy (SC), and understory (Us) of a *Castilla* novel forest. The stars indicate significant differences between groups within each stratum (Wilcoxon test, *p* < 0.05). Overall comparison between *C. elastica* and the group of native species: Wilcoxon/Kruskal-Wallis test χ^2 = 44, 0.001 < χ^2 < *p*.

3.4. Comparisons Among Photosynthetic Capacity and Other Physiological Traits

We found no differences among species and across measuring periods when comparing photosynthetic parameters from the controlled light response curves. However, these parameters varied between forest strata and were always higher in the canopy than in the subcanopy and understory, respectively (Table 2). The lack of differences among groups within each forest stratum indicates similar adaptability of the photosynthetic apparatus in both introduced and native species. In addition, both gs_{max} (0.24 to 0.40 mol m^{-2} s^{-1} for all species) and WUE_i (89 to 51 and 11 to 63 μmol mol^{-1}, for *C. elastica* and grouped native species respectively) overlapped in both the introduced and native species groups, across all strata and measuring periods.

Photosynthetic rate per area was linearly and positively related to the N concentration per unit area in both groups (Figure 5a), with a slightly greater gradient for *C. elastica*. Unexpectedly, the regression between A_{max} and N concentration per unit mass was significant only for *C. elastica* (Figure 5b).

Table 2. Median ± Median Absolute Deviation (number of observations) for the main photosynthetic parameters in the Castilla forest at El Tallonal. Medians differed between group of species per stratum, except for A_{max} per unit mass.

Stratum	Amax μmol kg^{-1} s^{-1}	Amax μmol m^{-2} s^{-1}	LCP μmol m^{-2} s^{-1}	LSP μmol m^{-2} s^{-1}
Canopy	104.4 ± 18.8 (31)	11.3 ± 1.6 (34)	22.6 ± 3.2	927 ± 57
Subcanopy	113.8 ± 25.4 (15)	7.6 ± 1.7 (19)	15.2 ± 3.5	775 ± 122
Understory	127.1 ± 42.6 (21)	4.9 ± 1.0 (26)	9.6 ± 1.9	275 ± 57
χ^2 Wilcoxon/Kruskal-Wallis	$p = 0.462$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
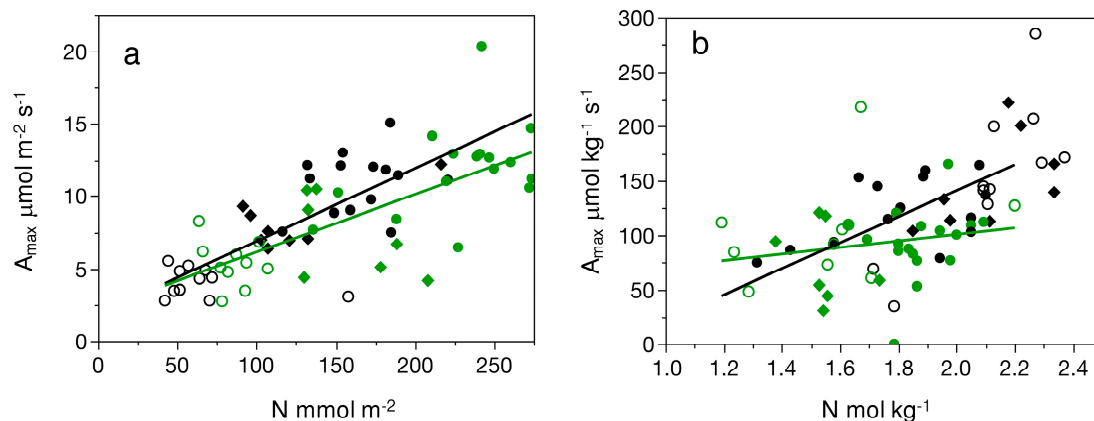
Figure 5. Relationship between A_{max} and N concentration per unit area ($A_{max\ area}$, (**a**)), and unit mass ($A_{max\ mass}$, (**b**)). Symbols as in Figure 3. For *C. elastica*, $A_{max\ area} = 1.87 + 0.05\ N_{area}$, $R^2_{adj} = 0.59$, F = 47, $p > F < 0.0001$, $n = 33$; $A_{max\ mass} = -97.9 + 119.4\ N_{mass}$, $R^2_{adj} = 0.38$, F = 21, $p > F < 0.0001$. For the group of native species, $A_{max\ area} = 2.18 + 0.04\ N_{area}$, $R^2_{adj} = 0.50$, F = 31, $p > F < 0.0001$, $n = 33$; $R^2_{adj} = 0.005$, not significant.

3.5. Photosynthetic Nitrogen Use-Efficiency

Within each stratum, *C. elastica* had median values above the overall mean, but significant differences between *C. elastica* and the native species group were found only at the canopy level (Figure 6a). *Castilla elastica* showed a higher PNUE compared to all native species when data was pooled together (median of 67.5 and 53.7 μmol CO_2 mol^{-1} N s^{-1}, for *C. elastica* and grouped native species, respectively) (Figure 6b).
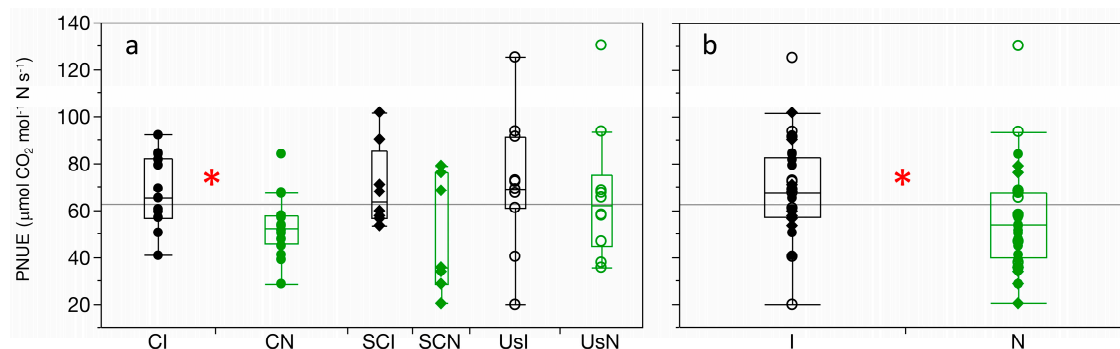
Figure 6. Comparison of photosynthetic nitrogen use-efficiencies for *Castilla elastica* = (I) (black symbols) and group of native species (N) (green symbols). The red asterisk indicates significant differences between groups of species (Wilcoxon and Wilcoxon/Kruskal-Wallis tests). (**a**) Photosynthetic nitrogen use efficiency per stratum and groups of species (CI > CN, Wilcoxon z value = 2.66, $p = 0.0078$) and (**b**) comparison between I and N (Wilcoxon/Kruskal-Wallis $\chi^2 = 8.8$, $p > \chi^2 = 0.0031$).

4. Discussion

4.1. Castilla elastica Influences the Irradiance Below the Canopy

The novel forest under study has been regenerating for at least 60 years and already presents a complex canopy structure [25]. This complex canopy drives the vertical differences in PPFD across strata. The understory only receives a tiny proportion of the total irradiance that reaches the canopy (~1%). Clark et al. [33], in a study of mature tropical forests, also reported that only 1% to 2% of the photosynthetically active radiation reaches the understory.

Below the canopy, the PPFD varied across seasons, probably because of changes in leaf area index. The fact that *C. elastica* is a deciduous tree, and loses its leaves during the dry season [20,26,34], promotes high variation in the irradiance received in the subcanopy (8–50%) and in the understory throughout the year (<1% to 4%). These changes probably influence the ecophysiology of the whole plant community in the area.

4.2. Similar Photosynthetic Capacity and Water Use Among Species

Species groups varied little in their photosynthetic capacities and water use (A_{max}, gs_{max}, and WUE_i) when comparing plants within the same forest stratum. This resulted in similar carbon gain among species. This similarity in photosynthetic capacities was unexpected, because introduced species often have higher photosynthetic capacity and resource gain than native species [9,15,35]. Instead, the differences that were found across forest strata demonstrated leaf adjustment to the large differences in irradiance and reflected the different stages of plant development.

Photosynthetic characteristics of upper canopy leaves of *C. elastica* in moist forests in Panama were studied in detail by Kitajima et al. [36]. Leaves developed in the early wet season were compared to those developed in the pre-dry season. The study showed that *C. elastica* did not exhibit seasonal phenotypes. There were no significant differences from early wet season to pre-dry season for the following indicators: light saturated oxygen evolution, nitrogen content per unit mass, photosynthetic N use efficiency, and LMA. Maximum CO_2 assimilation rates and nitrogen concentrations of *C. elastica* canopy leaves in Panama overlap the values reported here. However, LMA values are much lower in Panama (0.065–0.077 kg m^{-2}) than in our study (0.093 kg m^{-2}), which can probably be explained by the different methods used for measuring the leaves.

4.3. Nitrogen Use-Efficiency and Leaf Area Are Advantages for Castilla elastica

Castilla elastica adult trees showed the most efficient use of nitrogen in photosynthesis, particularly at the canopy and subcanopy strata, where light energy was not limiting photosynthesis. Thus,

similarly to introduced species in general, *C. elastica* outperformed native species in this aspect. This feature could contribute to explain *C. elastica*'s dominance in this novel forest. It is remarkable that we found significant linear relationships between N and photosynthesis per unit area but not per unit mass, as is usually reported in other sites [37]. Values of PNUE for the native species group reported here are comparable to those of late successional species elsewhere (29–84 vs. 56 μmol CO_2 mol^{-1} N s^{-1}) [37], while those of *C. elastica* are much lower than those of early successional species (41–92 vs. 216 μmol CO_2 mol^{-1} N s^{-1}).

Leaf mass per area of *C. elastica* was significantly lower than that of native species. This shows that *C. elastica*'s leaves are less expensive because they attain similar photosynthetic rates as that of native species while investing a lot less C and N. Moreover, *C. elastica* showed higher plasticity than native species, by adjusting to the different irradiance across forest strata, as suggested by the different leaf mass/area relationships across strata. Phenotypic plasticity is usually high in introduced species for a number of traits, including LMA [38]. Although high plasticity does not always indicate better performance, this is usually the case and can give an advantage to introduced species in their new habitat [14,39]. In the case of *C. elastica*, plasticity in LMA seems to have contributed to its dominance in the new range.

Leaf mass per area of *C. elastica* adult plants was in the range of variation for those reported by Reich et al. [39] for deciduous and pioneer woody plants in tropical forests (0.03–0.4 kg m^{-2}). We found even lower LMA for saplings and juvenile plants of *C. elastica* (0.015–0.02 kg m^{-2}). Low LMA is often associated with a high relative growth rate and invasiveness [40–47]. Investing resources in less expensive leaves (i.e., low LMA) might result in more efficient light interception for *C. elastica* in comparison to native species.

5. Conclusions

Overall, photosynthetic capacity was unexpectedly similar among species in the *Castilla* novel forest. High PNUE and low LMA support *C. elastica*'s higher competitive capacity over native species and could explain its dominance in this novel ecosystem. These results contradict our hypothesis of higher photosynthetic capacity for *C. elastica*, but support the hypothesis of more efficient use of resources (C and N) by the introduced species. The results also indicate that introduced and native species do not occupy overlapping positions in the leaf economic spectrum.

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Conflicts of Interest: The authors declare no conflict of interest.

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