Choosing favorites: the host preference of a vascular epiphyte (*Didymoglassum tahitense*)

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Background. The specific relationships between hosts and epiphytes are fairly unknown. Biotic factors contributing to epiphytic distribution have generally been considered secondary predictors to epiphyte growth and range. Invasive species pose risk to the biodiversity of epiphytes by altering the very specific environments epiphytes require to grow, which could ultimately harm the ecosystem as a whole. This study investigates the relationship between a tropical island vascular epiphyte, *Didymoglassum tahitense*, to wood density, bark phosphorus and host species in order to understand the specific interactions between host and epiphyte. **Methods.** Epiphytic surveys were conducted on the two native trees *N. forsteri* and *I. fagifer* and two invasive trees *S. campanulata* and *P. falcataria* to test for *D. tahitense* abundance and presence. Wood density for all tree species was calculated with the equation density=mass/volume, where volume was found using the displacement method and the mass by calculating dry mass. Phosphorus concentrations in the bark and epiphyte were found using an elemental analyzer. **Results.** The study found that *D. tahitense* preferred to live on the two native species *N. forsteri* and *I. fagifer* and that no *D. tahitense* grew on the invasive trees *S. campanulata* and *P. falcataria*. Of these four tree species, the two native trees had lower bark density and higher phosphorus concentrations where the invasive trees had higher bark density and lower phosphorus amounts. **Discussion.** With these findings, I assume that *D. tahitense* is host specific to species with high phosphorus in their wood.

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PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2679v1 | CC BY 4.0 Open Access | rec: 2 Jan 2017, publ: 2 Jan 2017

Abstract

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Methods. Epiphytic surveys were conducted on the two native trees *N. forsteri* and *I. fagifer* and two invasive trees *S. campanulata* and *P. falcataria* to test for *D. tahitense* abundance and presence. Wood density for all tree species was calculated with the equation density=mass/volume, where volume was found using the displacement method and the mass by calculating dry mass. Phosphorus concentrations in the bark and epiphyte were found using an elemental analyzer.
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Introduction

Tropical forests are powerhouses of biodiversity. Unfortunately, these systems are under constant threat as humans continually utilize and change the environment. Introduced species are one of the many threats to tropical forest structure and one of the largest problems facing tropical island forest ecosystems. In a lowland forest on a Hawaiian island, invasive species are heavily influencing native biodiversity; creating concern for the native forests' future survival (Michaud et al. 2015). The same is true for mid-elevation forests in the Opunohu valley on the island of Mo'orea, French Polynesia (Khan et al. 2015). The entire forest today is a second growth forest, rich in invasive trees so that the community is now drastically different from the native forest that once existed. This change in forest composition causes potential problems for the diversity of epiphytes which in turn affects nutrient cycling and water balance for the forest (Benitez et al. 2015). Epiphytes contribute to the high biodiversity that exists in tropical ecosystems and due to their sensitivity to microclimate (Shashidhar and Kumar 2009) and success in mature forests (Benavides, Wolf and Duivenvoorden 2006) are under constant threat as their habitats risk change. Understanding how trees interact with the epiphyte community is critical to understanding the importance that this relationship has to ecosystem diversity and function.

Epiphytes are plants spatially removed from terrestrial soil and the resources associated with it. Vascular epiphytes especially, being attached to their hosts, have adapted many strategies to acquire the necessary nutrient and water amounts (Cardelus and Mack 2010). Most of the epiphyte diversity and variance found is explained by climate (Ding et al. 2015). Although it is understood that abiotic factors have the largest role in epiphytic species composition, biotic factors such as host species have been observed to influence community composition as well

(Ding et al. 2015; Dislich and Mantovani 2016). In Mo'orea, a study demonstrated that epiphytic communities are more abundant on native trees than on invasive trees (Cushing 2002). Cushing identified host characteristics that may contribute to a higher epiphyte abundance and found that host species was the most indicative factor in predicting epiphyte abundance. Corroborating Cushing's finding, epiphyte abundance and composition was also found to be significantly influenced by host species in a study measuring the effects of host features in a forest in São Paulo, Brazil (Dislich and Mantovani 2016).

Throughout the study the terms native, non-native and invasive will be continually utilized, for clarification these terms will be defined. A Native species is a species of indigenous origin or growth to (a) location(s). Non-native species are species that have been introduced into new areas that have not historically been part of their native range. An invasive species is an organism that causes ecological or economic harm in a new environment where it is not native. This study will be including *Inocarpus fagifer* into the group called native throughout the paper, however it should be noted that this species is a non-native species introduced by Polynesians around 950 BC (Khan et al. 2015) but has been completely naturalized on the island.

A study on quaking aspen (Gustafsson and Eriksson 1995) revealed that there are strong correlations between terrestrial soil chemistry and bark chemistry. This suggests that soil chemistry might still indirectly influence the epiphytic community. More recently, researchers found strong evidence that terrestrial soil influenced the epiphytic community on a tree in a montane Hawaiian rainforest (Benner and Vitousek 2007). In this study, growth of epiphytes was measured after fertilizing terrestrial soil with nitrogen and phosphorus. Similarly, a study that investigated the wood nutrients along a tropical soil nutrient gradient also indicated a correlation between the two (Heineman et al. 2016). Moreover, increasing wood density is correlated with declining phosphorus concentrations, suggesting that low phosphorus amounts and dense wood are traits associated with tree species living on nutrient-poor soils. The study also suggested that the concentrations of macronutrients in the outer layer of bark is high in respect to inner-wood nutrients. These studies indicate that soil nutrient concentrations determine wood nutrient concentrations; and thus epiphytes may receive necessary nutrients directly from the wood itself.

Phosphorus has been found to be the most limiting factor in epiphytic growth, and has been found to significantly predict epiphyte richness (Boelter et. Al 2014). Increases in this nutrient is the most likely factor to causes epiphyte blooms (Benner and Vitousek 2007). With this said, it is possible that epiphytes prefer hosts with higher phosphorus in their wood (Benner 2011) and that phosphorus concentrations in ferns are correlated with the phosphorus concentrations in their host trees (Cardelus and Mack 2010). The information found in these studies suggests that it may be possible that vascular epiphytes prefer trees with higher phosphorus and that nutrients found in the wood will mirror the nutrients in the vascular epiphyte. P While nitrogen, on the other hand, plays a lesser role for epiphytes. Epiphytic ferns were found to have lower nitrogen content than their terrestrial counterparts (Wegner et al. 2003); however, epiphytes are rarely nutrient stressed and epiphytic ferns are rarely nitrogen limited.

From the past literature, it is clear that the movement from soil to tree to epiphyte is occurring in forest ecosystems. However, the answer to whether or not epiphytes demonstrate host specificity due to these bark transfers is unclear. In my initial gathering of data, I was able to conclude that only one vascular epiphyte, *Didymoglassum tahitense* (see Appendix for all species), was a worthy predictor of whether or not its host was invasive or native/non-native.

This finding proves useful because I am able to ask the question of what mechanisms are behind this vascular epiphyte selecting certain hosts. As *D. tahitense* only appeared only on native/non-native trees in multiple microclimates, I hypothesize that *D. tahitense* will have a preference for the native/non-native trees *Neonauclea forsteri,* and *Inocarpus fagifer* over the invasive trees *Spathodea campanulata* and *Paraserianthes falcataria.* I also hypothesize that *N. forsteri* and *I. fagifer* have less dense wood and therefore higher concentrations of phosphorus than *S. campanulata* and *P. falcataria* in their wood.

Methods

Field site and sampling

Sampling took place in the tropical rain forest around the Belvedere look out (17°32'25.93"S 149°49'36.09"W) between 190m and 260m in Mo'orea, French Polynesia (Fig. 1). Utilized trails included: Three Coconuts trail and Three Pines trail. Both trails are accessible from the Belvedere look out. The forest was divided into three different areas estimated to represent differing microclimates, as found with GPS and Google Maps. Area one occurs on a north facing slop and has a dryer microclimate (Fig. 1). Area two has a wetter microclimate and occurs in a watershed along the Three Coconuts trail. Area three also has a wetter microclimate but is in an adjacent watershed along Three Pines trail. Once the three areas encompassing different microclimates were established, surveys of epiphytic communities on native trees *Incocarpus Fagifer*, *Neonauclea forsteri,* and invasive trees *Spathodea campanulata,* and *Paraserianthes falcataria* were recorded as outlined below.

Epiphyte survey

Forty trees from each of the four focal tree species in the three designated microclimate areas were surveyed for a total of 160 trees. Pilot studies revealed that the vascular epiphyte *Didymoglassum tahitense* was selective of host trees *I. fagifer* and *N. fosteri*. Thus, observations were focused in part to determine the accuracy of preliminary work by surveying the populations of *D. tahitense* on *I. fagifer* and *N.forsteri* as well as the invasive *S. campanulata* and *P. falcataria*. The method of sampling was standardized on a per- individual tree basis. Specifically, a 36 x 36 cm quadrat was placed on each individual tree in an area of the tree that was most representational of the percent cover and *D. tahitense* abundance. One of the most important influences on epiphytic communities is vertical height (Dilsch and Mantovani 2016), thus, each sampled tree was divided into two heights of 1.3m and 0.65m to assess differences in percent cover and abundance between heights. When the epiphyte *D. tahitense* became too numerous to count in the quadrat grid, sub-sampling was used by dividing the grid into halves or quarters and then multiplying the number of ferns counted by 2 or 4 to estimate across the entire grid. Again, while sub-sampling, the quadrat would be divided so that abundance was representational of the true abundance at tree heights of 1.3 and 0.65 m.

Wood collection and density calculation

To collect wood samples, focal tree species above 4 in. in diameter at breast height were randomly chosen to have sections cut from the bark with a hand saw. A total of 35 wood samples were collected. *Didymoglassum tahitense* was also collected if a sampled tree had the plant growing on it. To calculate wood density, the equation density=mass/volume was used following the methods of (Chave et al. 2016). In order to estimate mass, each sample air dried for at least 24 hours, then samples were placed in an oven at 103° C for 5 hours. Mass was immediately calculated after removal from the oven on a scale to obtain the most accurate reading. Volume of the bark was taken with the displacement method. Water level readings were taken using a 300 ml graduated cylinder with 5 ml increments. The bark piece was submerged to avoid hitting the sides of the cylinder. Final water level was subtracted from initial water level to calculate the volume of the bark piece. Averages and standard deviation of wood density was calculated for each species.

Wood and epiphyte nutrient analysis

Once density was estimated, relative densities were used to predict the level of phosphorus in the wood. Specifically, because phosphorus levels decline as wood becomes denser (Heineman, Turner and Dalling 2016). The average density of wood for each species was used to predict abundance of phosphorus in the wood based upon the work done by Heineman, Dalling and Turner.

Statistical analysis

For analysis of *D. tahitense* host preference, an ANOVA and a regression analysis tested the predictor variable of tree species with *D. tahitense* abundance. For wood density analysis a t-test was used to test differences between invasive and native wood; and an ANOVA was also used to test differences of means between all four species. To analyze dependency of the presence or absence of *D. tahitense* on wood density and therefore phosphorus concentration a T-test was conducted. All tests were performed using R studio (R Core Team 2013).

Results

Epiphyte Survey

Native trees *N. forsteri* and *I. fagifer* had 100% higher abundance of *D. tahitense* than invasive trees *S. campanulata* and *P. falcataria*. (Fig. 2, ANOVA, $F_{3/142} = 4.2$, $p<.001$). The abundance of *D. tahitense* between *N. forsteri* and *I. fagifer* were found to be similar (T-test, t=0.017, df=137, p>0.05). With regard to percentage of total epiphyte cover native trees had a higher number of trees that had greater coverage of epiphytes than invasive trees (Fig.3, T-test, t=-7,df=239.5, p<0.001).

In respect to microclimate, abundance of *D. tahitense* on *N. forsteri* and *I. fagifer* was similar in the three different areas with the exception that Area Three had higher *D. tahitense* abundance than Area One (Fig. 4, ANOVA, Post-Hoc test, $df_{5/140}=1.9$, $p<.01$). Abundance at the two separate heights of 0.65m and 1.3m were also similar (ANOVA, $df_{2/143}=0.185$, $p>0.1$).

Bark Density and Nutrient Concentrations

The mean bark density of *N. forsteri* was 0.26 g/ml^3 smaller than the mean bark density of *S. campanulata* while *I. fagifer* was 0.50 g/ml^3 smaller. *Neonauclea forsteri* was 0.35 g/ml^3 and *I. fagifer* was 0.60g/ml^3 smaller than *P. falcataria* (Fig. 5, Post-Hoc test, p<.05). The bark densities between the two native trees were within 0.25g/cm^3 of each other and the densities between the two invasive trees were 0.08 g/ml^3 of each other (Fig. 5). *Parserianthes falcataria* and *S. campanulata* had the highest density and therefore the lowest phosphorus where *Neonauclea forsteri* and *I. fagifer* had lower bark density and therefore higher phosphorus amounts under the assumption of Heineman, Turner, and Dalling's confirmed relationship between wood density and phosphorus amounts.

Didymoglassum tahitense was found to be present only at low wood densities and therefore at higher phosphorus concentrations. Where *D. tahitense* was primarily absent at high wood densities and therefore lower phosphorus concentrations (Fig. 6, T-test, t= 4.13, df=28, p<.001).

Discussion

Didymoglassum tahitense was found to prefer trees *I. fagifer* and *N. forsteri* and was found to have no preference for *S. campanulata* and *P. falcataria* (Fig. 2). The abundance of *D. tahitense*, therefore appears to be affected by host species. An explanation to *D. tahitense's* preference of *N. forsteri* and *I. fagifer* is that the vascular epiphyte has adapted to live in trees naturalized on the island. The data suggests that *D. tahitense* requires hosts with low density wood and high phosphorus. This can be supported by previous studies in the literature. For example, it is believed that epiphytes prefer hosts with high phosphorus amounts and that epiphytes bloom with increases in phosphorus compared to nitrogen (Benner and Vitousek 2007, Benner 2011). This epiphyte may have adapted to live on certain high phosphorus hosts due to fluxing and unstable P concentrations in the tropical forest ecosystem. Furthermore, it is possible that some tropical epiphytes may have evolved luxury P storage to deal with the limited concentrations (Wanek and Zotz 2011). It is possible that *D. tahitense* has evolved to prefer *N. forsteri* and *I. fagifer* trees in order to utlilize P but also to store P, regardless if the plant is nutrient stressed.

In line with the hypothesis, invasive trees *P. falcataria* and *S. campanulata* had higher density wood and lower phosphorus concentrations than *I. fagifer* and *N. forste*ri. Phosphorus concentrations based upon wood density are assumed based upon the work done by Heineman, Dalling, and Turner in 2016. Of which a correlation between the density of tropical wood and phosphorus concentrations was found (Table 1). This data suggests that *D. tahitense* has adapted to grow on high phosphorus substrates and that the two invasive trees are inept to support the epiphyte's growth and nutrient desires. In an unprecedented study on wood density, it was found that average wood density of an entire forest changed with geographical location. For example, wet forests have significantly lower wood densities than dry forests and high elevation forests have lower wood density than low elevation forests. The study also found that variation in wood density of different species could be traced back to genus level. Meaning, that individuals in different genus levels will have differening wood density (Chave et. al 2006). This provides an insight into why the invasive trees *S. campanulata* and *P. falcataria* have higher wood densities than the native/nonnative trees. The invasive trees are adapted to living in different forests and are in different genuses. It is apparent that *D. tahitense* lives on the native/nonnative trees because they provide the exact environment needed for the plant to survive.

Futhermore, although *I. fagifer* is not native to Mo'orea *D. tahitense* still grows and prefers this tree. This suggests that *D. tahitense* responds to a specific range of phosphorus in wood and that the fern is indeed highly host specific based upon P abundance. Suggesting that tree species is less of a predictor of whether or not the epiphyte grows on the tree than P concentrations are. It appears that *I. fagifer* has adapted mechanisms for P storage and bark interactions as the native *N. forsteri* has, providing insight into why *I. fagifer* has been so successful on Mo'orea.

A similarity existed in *D. tahitense* abundance between *N. forsteri* and *I. fagifer* (Table 1). The bark densities of these species were similar and differences in epiphyte abundance on the two trees was not found. The data also illustrates that P in the wood affects both abundance and presence of *D. tahitense* on its host. Where invasive *P. falcataria* and *S. campanulata* were found to have absolutely no *D. tahitense* present, *I. fagifer* and *N. forsteri* were found to have both zero abundance and high abundance of *D. tahitense*. This proposes that P may not be the only predictor variable for abundance. However, high host P is a worthy predictor of presence or absence of the vascular epiphyte on a host species. Furthermore, percent cover of total epiphytes was found to be higher on native/non-native trees than on invasive trees (Fig. 3). This data further suggests that native/non-native trees provide a more suitable environment for high epiphytic abundance than the invasive trees.

Microclimate may be another predictor in determining *D. tahitense* abundance. This study, by discovering D. tahitense in every microclimate on the native/non-native trees, was able to control for abiotic factors affecting the presence or absence of the epiphyte. Therefore, allowing the study to look at biotic factors in isolation. However, the abundance of *D. tahitense* appears to be influenced by both abiotic and biotic conditions. Dry Area one and wet area three were found to have significantly different abundances of *D. tahitense* on hosts (Fig 4), where area one had much lower abundances of the vascular epiphyte than area three. This data demonstrates the influences that abiotic factors have on the distribution of *D. tahitense*. The small difference (p=.1) in *D. tahitense* abundance between between dry area one and wet area two illustrates that dualistic nature of microclimate on *D. tahitense* abundance. Meaning that microclimate acts as both a determining factor and a supplementary factor in the epiphyte's abundance and that the biotic factor of host species influences abundance as equally. Therefore, it can be concluded that the abundance of *D. tahitense* on *N. forsteri* and *I. fagifer* is predicted by an interaction of biotic and abiotic conditions.

Although bark phosphorus concentrations are predictive of *D. tahitense* presence and absence, other bark characteristics could aid an explanation for the epiphyte's presence. The plant itself lies completely against the bark surface, and it may be a morphological adaptation to bark texture or water exchange that explains why the plant chooses to live on the bark of *N. forsteri* and *I. fagifer*. It is also very likely that one biotic factor would never completely explain the distribution of an epiphyte, and that instead many biotic and abiotic factors are at play. This explanation is supported by the data. The presence or absence of *D. tahitense* appears to be affected by bark phosphorus (Fig. 7) where the abundance appears to be influenced by a combination of biotic and abiotic conditions (Fig. 2 and Fig. 4). Further investigation into how biotic and abiotic factors affect vascular epiphyte distribution is worthy of study.

The fact that *D. tahitense* selected for trees with less dense wood and assumed higher phosphorus in the wood is suggestive of mechanisms behind the mutualism between host tree and epiphyte. With this information we can continue to study the intricacies of this relationship and the importance it plays for ecosystem functions such as nutrient cycling. For example, other studies have also found correlations of P concentrations between ferns and host trees indicating how bound the nutrient cycling of phosphorus may be (Cardelus and Mack 2010, Benner 2007). This nutrient is very limited in tropical ecosystems, and has repeatedly been found to be a greater limiting factor for epiphytes than nitrogen (Benner 2007). Since *D. tahitense* is selective of trees with high phosphorus, future research could be done on possible ways that the plant utilizes this phosphorus and the extent of benefits the fern contributes to its environment through possible cycling pathways of P from soil to epiphyte.

Conclusion

This study aimed to illustrate that an invaded forest could change the species composition of not only the trees, but of the vascular epiphytes that grow on them. Invasive species pose risk to the biodiversity of epiphytes by altering the very specific environments epiphytes require to grow, which could ultimately harm the ecosystem as a whole. The fact that *D. tahitense* only occurs on *N. forsteri* and *I. fagifer* is important to understanding the specificity that organisms have in tropical forests and the implications that this specificity has for the ecosystem at large. This specificity creates multitudes of questions about the cascading effect of diversity. Meaning, how does this plant effect the health and therefore biodiversity of the forest? Invasive trees threaten the unknown answer to this question, simply because they pose a danger to biodiversity. Vascular epiphytes are the silent powerhouse of tropical diversity and the unique relationships between host and epiphyte are only beginning to be understood. This important plants can only continue to thrive and function if we protect tropical forests from invasive trees.

Acknowledgements

I would like to thank Cindy Looy, Justin Brasheres, Jonathan Stillman, Patrick O'Grady, Eric Armstrong, Natalie Stauffer-Olsen, and Ignacio Escalante for their guidance while my classmates and I learned the ropes of researching. This experience on Mo'orea was eye-opening and it would have been impossible without the professors and graduate students. I would also like to thank all of my 22 other classmates, I definitely could not have written this paper without ever single one of you. You have all brought me so much joy and wisdom.

Appendix

Photographs illustrating organisms found in this study:

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Figure 1(on next page)

Map of Mo'orea and study sites

An outline of the island of Mo’orea, the location of the belvedere lookout and study sites one, two and three.

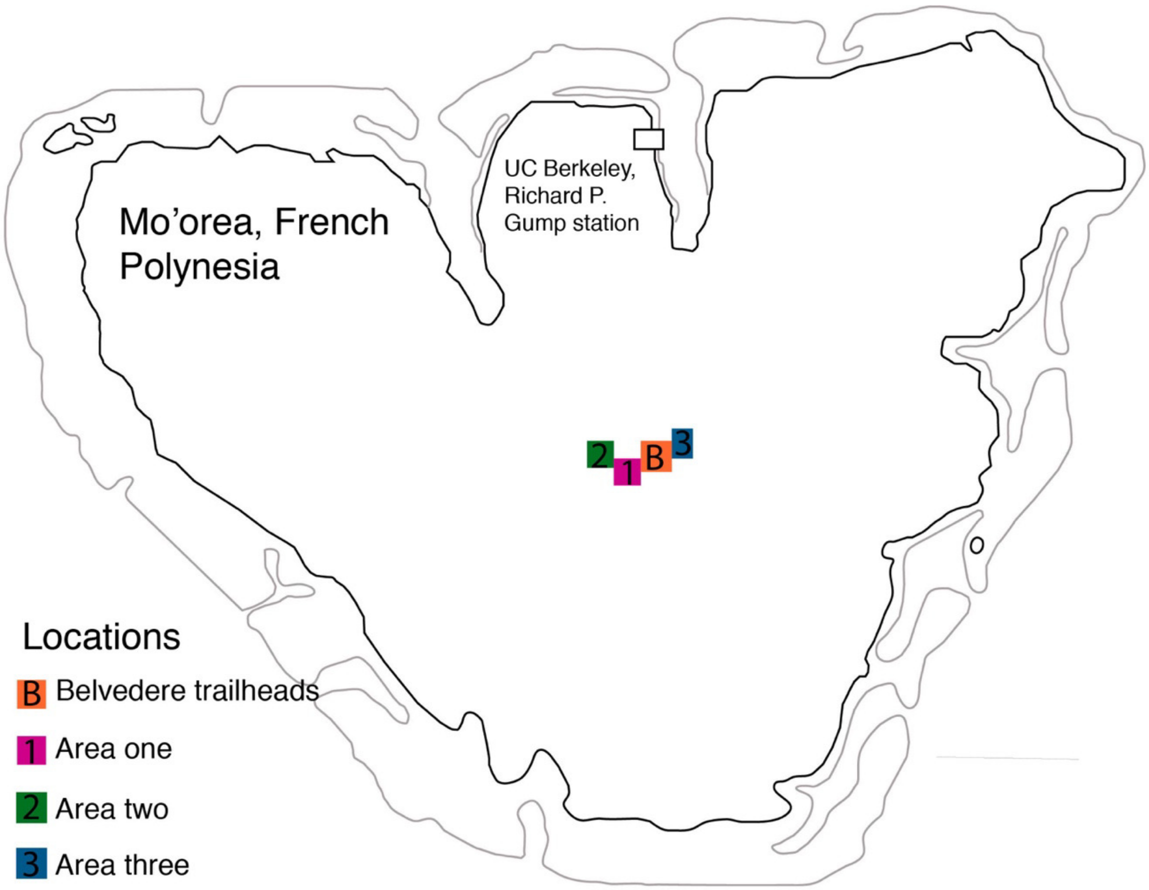

UC Berkeley, Richard P. Gump station
Mo’orea, French Polynesia
2
1
B
3
Locations
B Belvedere trailheads
1 Area one
2 Area two
3 Area three

Figure 2 (on next page)

D. tahitense abundance on different native and invasive tree species

Illustrates epiphyte abundance on each species with the points representing mean host abundance of *D. tahitense* and the standard error bars with 95% confidence.

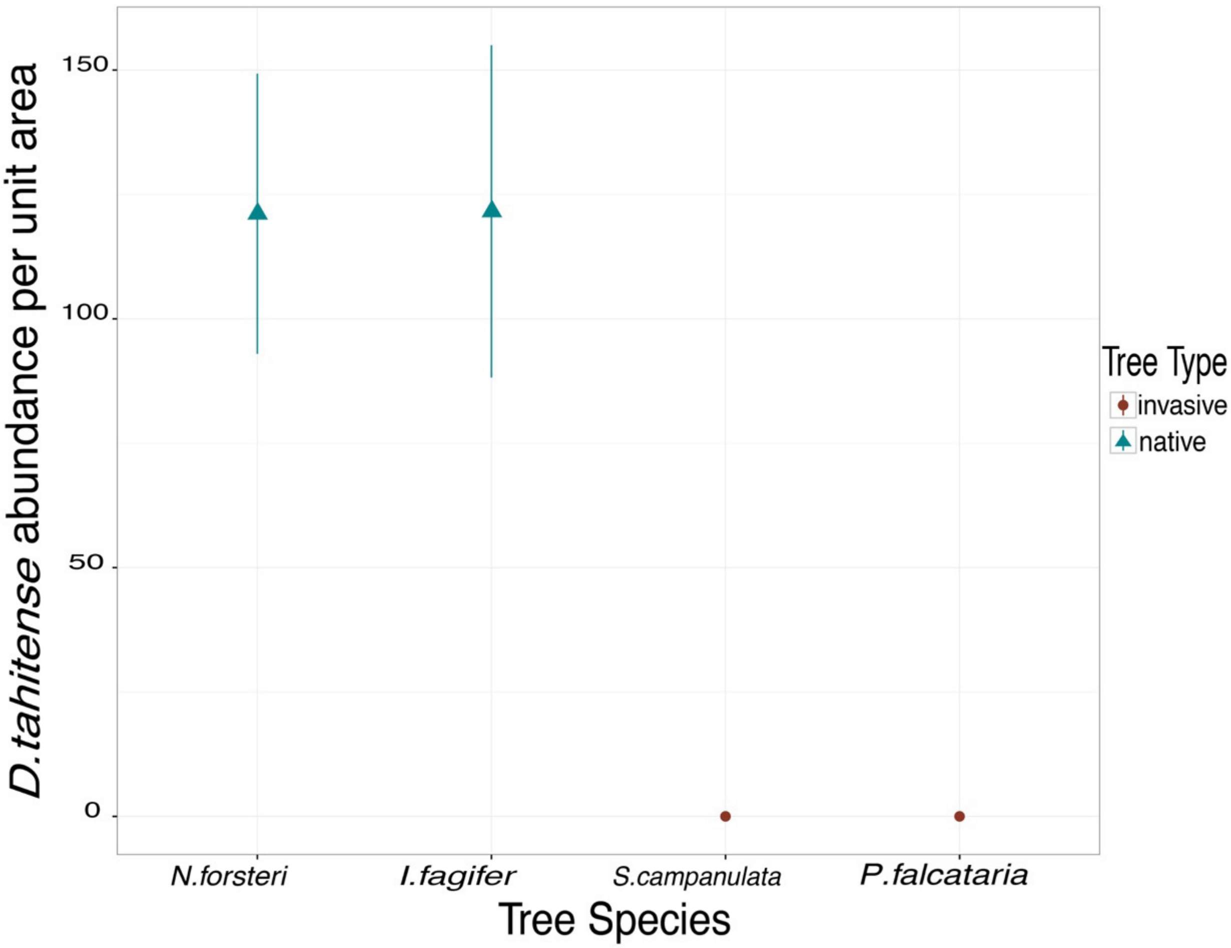
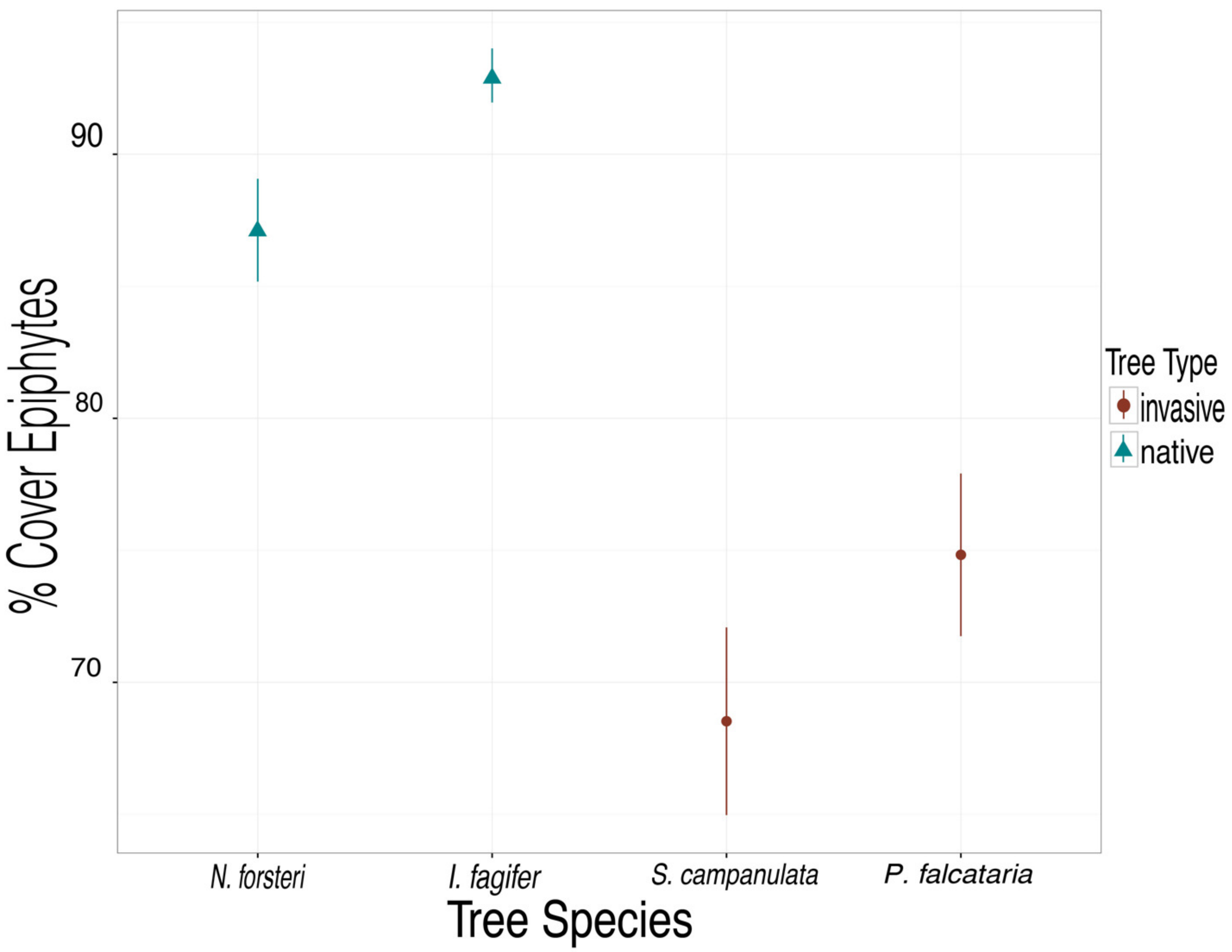

D.tahitense abundance per unit area
150
100
50
0
N.forsteri
I.fagifer
S.campanulata
P.falcataria
Tree Species
Tree Type
invasive
native

Figure 3 (on next page)

Percent cover of epiphytes on native and invasive tree species

Mean percent cover of total epiphytes on each native and invasive tree species. Lines represent standard error.



90
80
70
% Cover Epiphytes
N. forsteri
I. fagifer
S. campanulata
P. falcataria
Tree Species
Tree Type
invasive
native

Figure 4(on next page)

Affect of microclimate on *D. tahitense* abundance

Illustrates abundance of *D. tahitense* with respect to microclimate. Area one is the driest existing on a ridge line, where Areas two and three are in adjacent watersheds. Lines represent 95% confidence intervals of standard error, points represent mean abundance of *D. tahitense*.

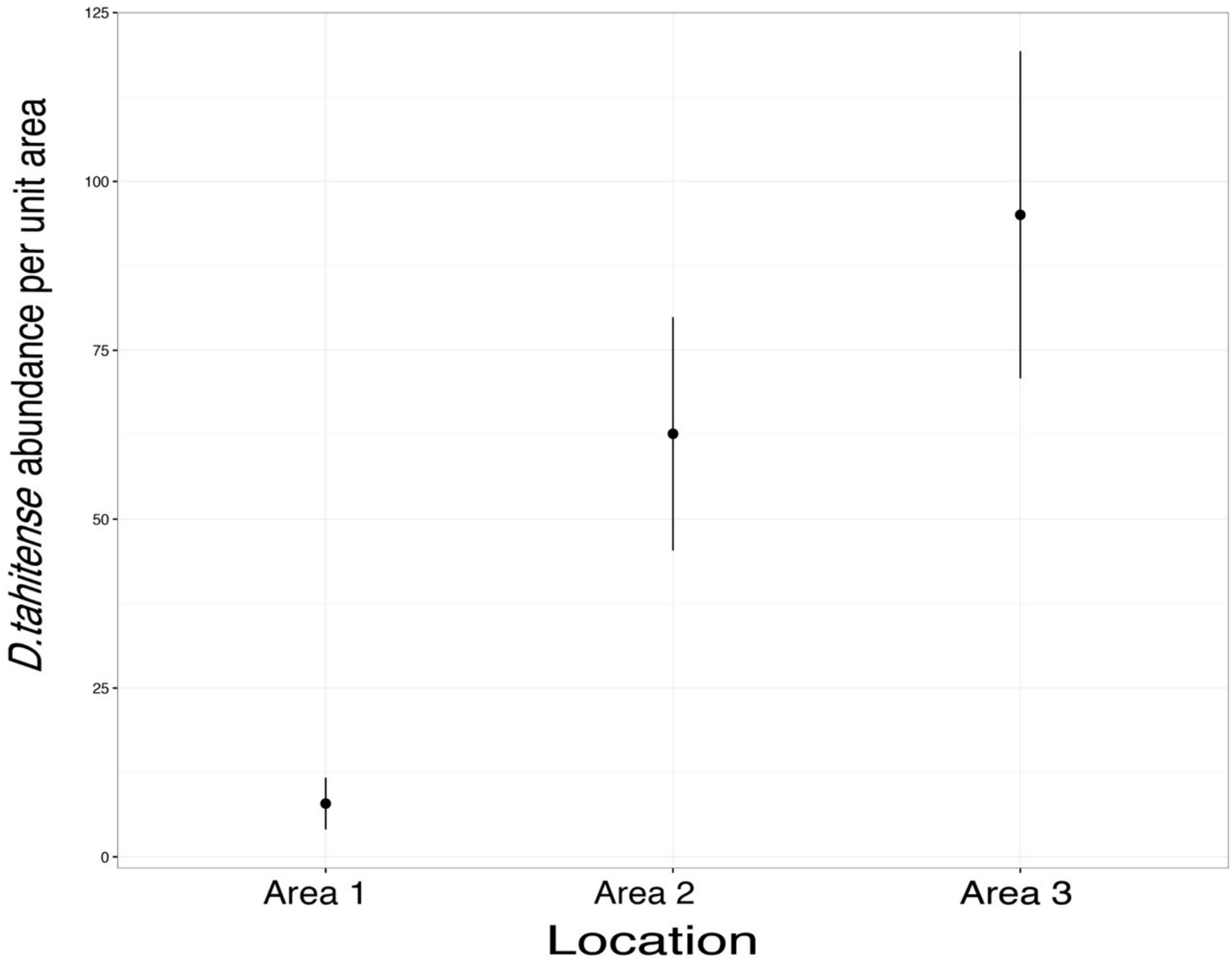


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Figure 5(on next page)

Bark density of each native and invasive tree species.

Differing bark densities of the four tree species, the whiskers represent the range of bark densities calculated. Vertical lines represent 95% confidence interval; boxes represent interquartile range.

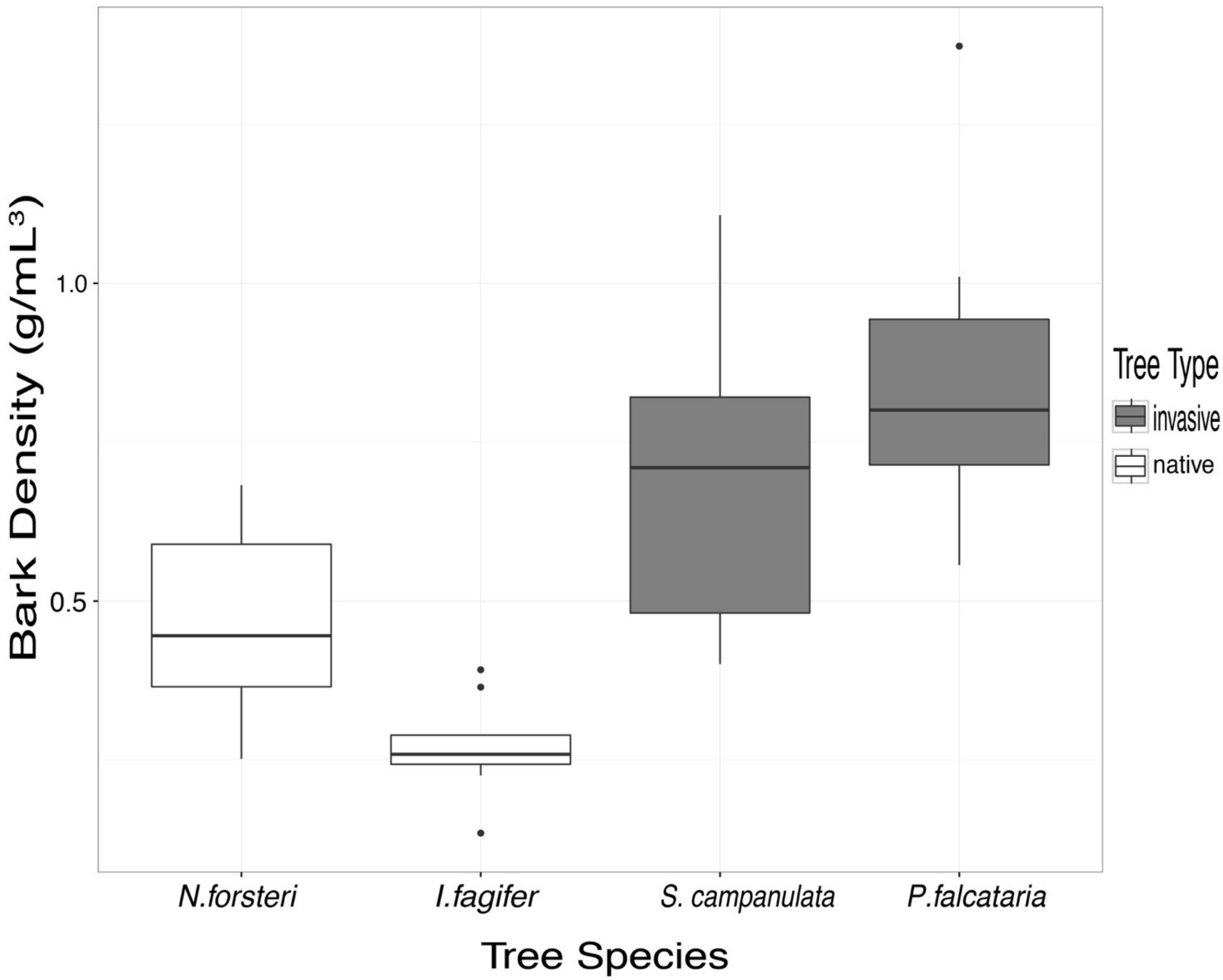

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Figure 6(on next page)

Affect of wood density on absence or presence of D. tahitense

The points illustrate the mean wood density at which you would find an absence or presence of *D. tahitense.* The lines represent 95% confidence of standard error.

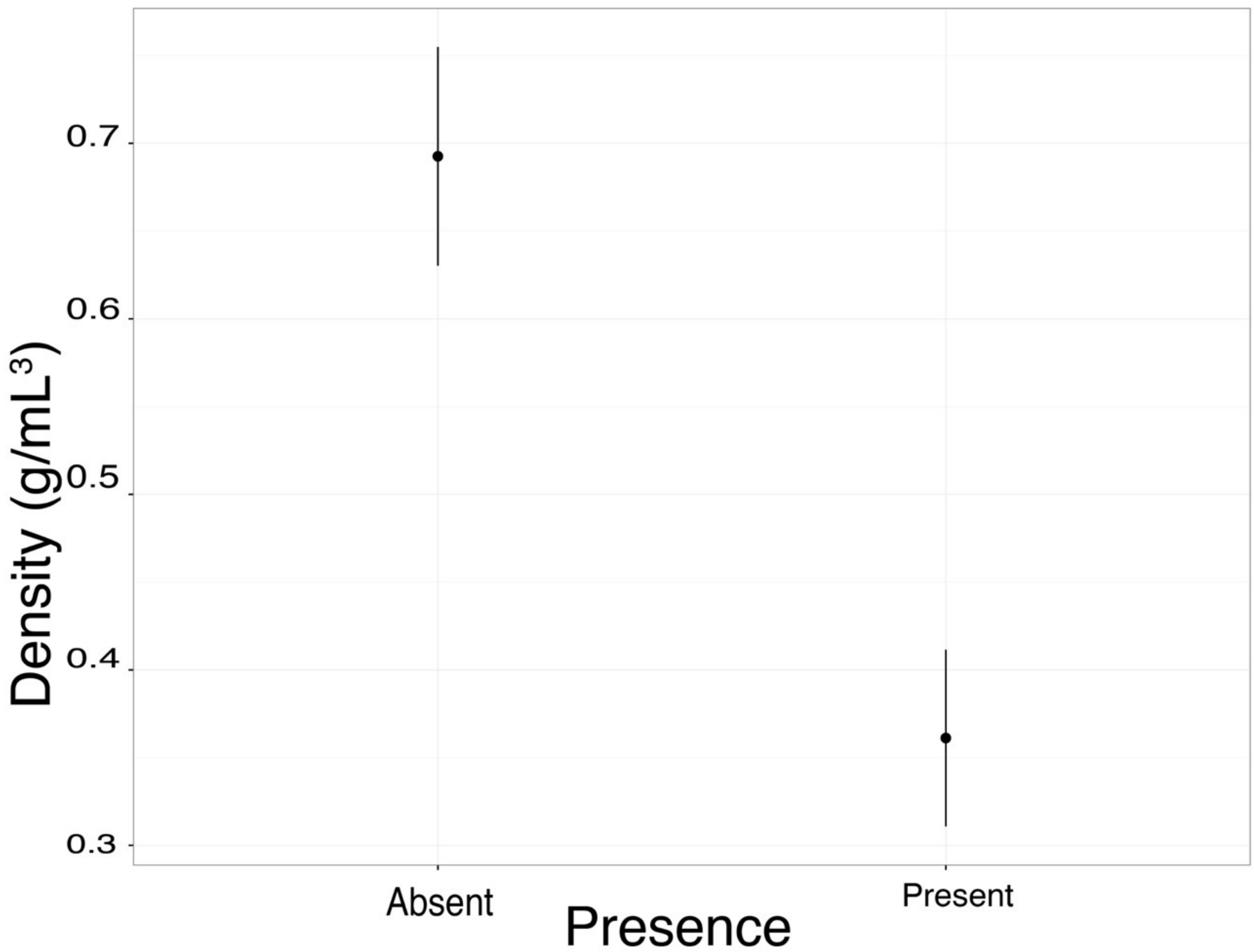
0.7
0.6
0.5
0.4
0.3
Density (g/mL^3)
Absent
Present
Presence

Table 1(on next page)

Table summarizing the graphs previously shown.

summarizes the wood density, relative phosphorus concentrations (Heineman et. Al 2016) and abundance of *D. tahitense* data shown in previous graphs.

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Tree Species	Mean Density with standard error	Mean *D. tahitense* abundance with standard error	Relative Phosphorus concentrations
Inocarpus fagifer	0.27 g/mL^3+/- 0.02	121.6+/-33.4	X X X X Highest
Neonauclea forsteri	0.46 g/mL^3+/- 0.04	121.11+/-28.15	X X X High
Spanthodeas campanulata	0.70 g/mL^3+/- 0.06	0	X X Low
Paraserthanes falcataria	0.86 g/mL^3+/- 0.1	0	X Lowest

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Figure 7 (on next page)

Images of all organisms found in this study

a. *Didymoglassum tahitense*

b. Inocarpus fagifer

c. Neonauclea forsteri

d. Spathodea campanulata

e. Parserianthes falcataria


1
INCHES 2

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