

THE ROLE OF EVOLUTIONARY HISTORY AND NICHE DIFFERENTIATION  
IN STRUCTURING SPECIES CO-OCCURRENCE IN  
NEW ZEALAND *PITTOSPORUM* (PITTOSPORACEAE)

By

Kristen Marie Nolting

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## ABSTRACT

### THE ROLE OF EVOLUTIONARY HISTORY AND NICHE DIFFERENTIATION IN STRUCTURING SPECIES CO-OCCURRENCE IN NEW ZEALAND *PITTOSPORUM* (PITTOSPORACEAE)

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Understanding the processes that shape the spatial distribution of species, and their co-existence in communities, remains one of the biggest challenges that ecologists face today. Investigations of co-existence typically treat species as independent entities, thereby ignoring their shared evolutionary history, niche preferences and functional similarity. This limits the ability of ecologists to make strong inferences regarding co-existence mechanisms. It is more useful to employ a pluralistic approach that integrates phylogenetic information and species-specific environmental and trait associations. In this study I evaluated the role of evolutionary history and environmental and functional trait differentiation in predicting species co-occurrence in the New Zealand plant genus *Pittosporum*. I hypothesized that co-occurring species would be more distantly related than non co-occurring species, given that closely related species are likely to be more ecologically similar as a result of their shared ancestry, and thus competitive interactions would preclude them from co-occurring. Similarly, I predicted that co-occurring species would be more divergent in their functional traits to enable co-existence. I found that co-occurring species were no different than non co-occurring species with respect to their phylogenetic dissimilarity, that co-occurring species had higher environmental niche overlap than non co-occurring species, and that for most traits measured there was no difference in trait dissimilarity among co-occurring and non co-occurring species. Approximate maximum vessel length and leaf nitrogen content, however, showed convergence among co-occurring species.

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## INTRODUCTION

Describing patterns of biodiversity and identifying the processes that shape the geographic distribution of species has been a major source of scientific intrigue for centuries (eg. Darwin 1859, Wallace 1869). Despite this interest, understanding the mechanisms underlying these patterns remains one of the biggest challenges that biologists face today (Ricklefs 1987, Emerson and Gillespie 2008, Sutherland et al. 2013). Addressing this problem requires us to understand both the origins of biodiversity, as well as the factors that act to govern the distributions of species across spatial and temporal scales. The spatial distribution of species itself is determined by species' interactions with the abiotic and biotic environment. In other words, ecologists are challenged to explain why species occur where they do, as well as how they manage to co-exist given that they may compete for the same limited resources.

A central goal in community ecology is to identify the processes that act to structure community assemblages (Weiher and Keddy 1995), and similarly, those that are responsible for maintaining species co-existence (reviewed in Mittelbach 2012). Traditionally, there have been two main paradigms that have been suggested as processes acting to structure the distribution of species into communities. First, competitive interactions preclude ecologically similar species from occupying the same space, such that species must differ substantially along one or more important niche axes in order to maintain stable co-existence, *sensu* limiting similarity (MacArthur and Levins 1967). However, recent work suggests that competitive interactions can lead to ecologically similar species co-existing when performance differences are small (Chesson 2000, Mayfield and Levine 2010), but this is thought to only occur at very local scales and when the environment is highly homogenous (HilleRisLambers et al. 2012). Alternatively, species

occupying the same habitat may also be ecologically similar as a result of an abiotic filter acting to limit the types of phenotypes, and thus species, that are able to survive in the focal environment (Keddy 1992). In any scenario, species assemblages at the local scale should be a non-random subset of the species pool, or a larger set of species that can potentially colonize this study site (Diamond 1975).

Early studies aimed at understanding community assembly used species lists, distribution records, and a null model approach to identify instances of non-random species associations (eg. Diamond 1975, Gilpin and Diamond 1982, Connor and Simberloff 1983, Gotelli 2000). More recently, researchers have incorporated additional information related to species' phylogenetic relationships (eg. Webb 2000), environmental associations (John et al. 2007), and species-specific traits (eg. Weiher et al. 1998) to further elucidate the mechanisms acting to structure species distributions. Evaluation of the phylogenetic structure of communities provides a way to potentially test whether abiotic filters or biotic interactions are more important in the assembly process. Under the assumption that closely related species are more ecologically similar than more distantly related species given their shared ancestry (Darwin 1859), it is inferred that communities that are more phylogenetically overdispersed than a null model are indicative of competitive interactions. Alternatively, those communities that are more phylogenetically clustered are inferred to be indicative of abiotic filtering (Webb 2000). In a similar way, we can evaluate the phylogenetic dissimilarity of individual species pairs that are either co-occurring (showing positive associations) or non co-occurring (showing negative associations). If co-occurring species pairs are less phylogenetically similar than non co-occurring pairs, competitive interactions are inferred to be acting, whereas abiotic filtering is attributed if co-occurring species are more phylogenetically related than non co-occurring pairs (eg. Winston 1995, Peres-



Neto 2004, Tobias et al. 2013). However, it is important to also evaluate species' traits themselves as they may not be conserved, and thus patterns of trait distributions may indicate different mechanisms of assembly and coexistence (Cavender-Bares et al. 2004).

Although a phylogenetic approach provides a quick and potentially informative way to evaluate community assembly mechanisms, it is also valuable to assess the distributions of species-specific traits themselves in assemblages (Swenson 2013). In particular, community phylogenetics investigations assume that the traits associated with abiotic filtering and biotic interactions are phylogenetically conserved (Webb 2000). While there has been evidence presented for broad patterns of niche conservatism across taxa and spatial scales (Peterson et al. 1999, Wiens et al. 2010), there is also a great deal of evidence for trait divergence among closely related species (Losos 2008). Thus it is preferable to test for phylogenetic signal in traits as opposed to assuming trait conservatism is the norm (Losos 2008). Additionally, by evaluating the distribution of traits themselves, we can identify which ecological aspect of a species is acting to structure its distribution (Swenson 2013). It is even possible for some traits to be structured by abiotic filtering and others to be structured by biotic interactions, as demonstrated in multiple studies of assembly in plant (Weiher et al. 1998, Cavender-Bares et al. 2004, Swenson and Enquist 2009) and animal (Tobias et al. 2013) communities. Lastly, it is important to consider the phylogenetic and trait distributions in the context of species' environmental associations, as this provides information about the abiotically-defined aspects of a species niche (Grinnell 1917). This allows one to determine whether or not traits are associated with environmental variables, and thus strengthens our understanding of how abiotic filters are operating to limit species distributions.

In this study I integrate knowledge regarding the phylogenetic relatedness among species, species-specific functional traits, and environmental niche occupancy to explore the mechanisms of co-existence in the Pacific Basin plant genus, *Pittosporum* (Pittosporaceae), in New Zealand. Instead of looking at whole plant communities, I evaluate the mechanisms contributing to co-occurrence and non co-occurrence of species pairs in a single group of closely related species. This is advantageous as it is likely that closely related species are more strongly interacting given their shared ancestry and thus putative ecological similarity. Further, most community phylogenetics studies to date have evaluated distributions of species that did not evolve together in the study region, that are highly divergent and thus have been unable to robustly link the evolution of traits to co-existence due to poor taxonomic sampling. By investigating mechanisms of co-existence in a single, densely sampled, and endemic group of species, we can make stronger inferences about how evolutionary processes have contributed to current patterns of species distributions and co-existence (Swenson 2013).

Specifically, I aim to evaluate (1) whether or not phylogenetic similarity predicts species co-occurrence, and (2) how niche dissimilarity, as measured through trait differences and environmental niche overlap, contributes to species co-occurrence. I predict that closely related species will not co-occur, and that species that do co-occur will differ substantially along one or more important niche axes.

## METHODS

### *Study System*

This study examined the role that phylogenetic relatedness and niche differentiation – as quantified through functional trait dissimilarity and environmental niche overlap – play in structuring species distributions and co-occurrence in the genus *Pittosporum* (Pittosporaceae) throughout New Zealand. The genus *Pittosporum* consists of approximately 200 species that are widely distributed throughout the Pacific Basin, in tropical to temperate climates. Species are found in disparate geographic regions such as Africa, Asia and Malesia, and Hawai'i, but the largest centers of diversity are located in New Caledonia (50 species), and New Zealand (26 species) (Gemmill et al. 2002). The genus shows a tremendous amount of variation in morphology and habitat preference within New Caledonia and New Zealand (Cooper 1956; Gemmill et al. 2002), ranging from prostrate shrubs to subcanopy trees, and occupying coastal to subalpine regions (Cooper 1956; Gemmill et al. 2002; Chandler et al. 2007).

The New Zealand *Pittosporum* represent an ideal group for investigating how phylogenetic dissimilarity and niche differentiation contribute to species co-existence. The New Zealand species are all endemic, and recent work has shown that the diversity of the genus throughout the country is the result of only two colonization events (Gemmill et al. in prep). This high level of endemism and presence of just two monophyletic groups mean that the observed species diversity, and diversity in traits and habitat associations, is the result of divergence within New Zealand in which all species arose in the study region and have interacted with a similar suite of species and environments. This allows for the investigation not only of present-day co-existence among species pairs, but also the role that evolution has played

in generating the diversity in this genus. Lastly, the morphological diversity and the wide range of habitats and climates occupied by species suggest that niche differentiation could be acting to maintain co-existence.

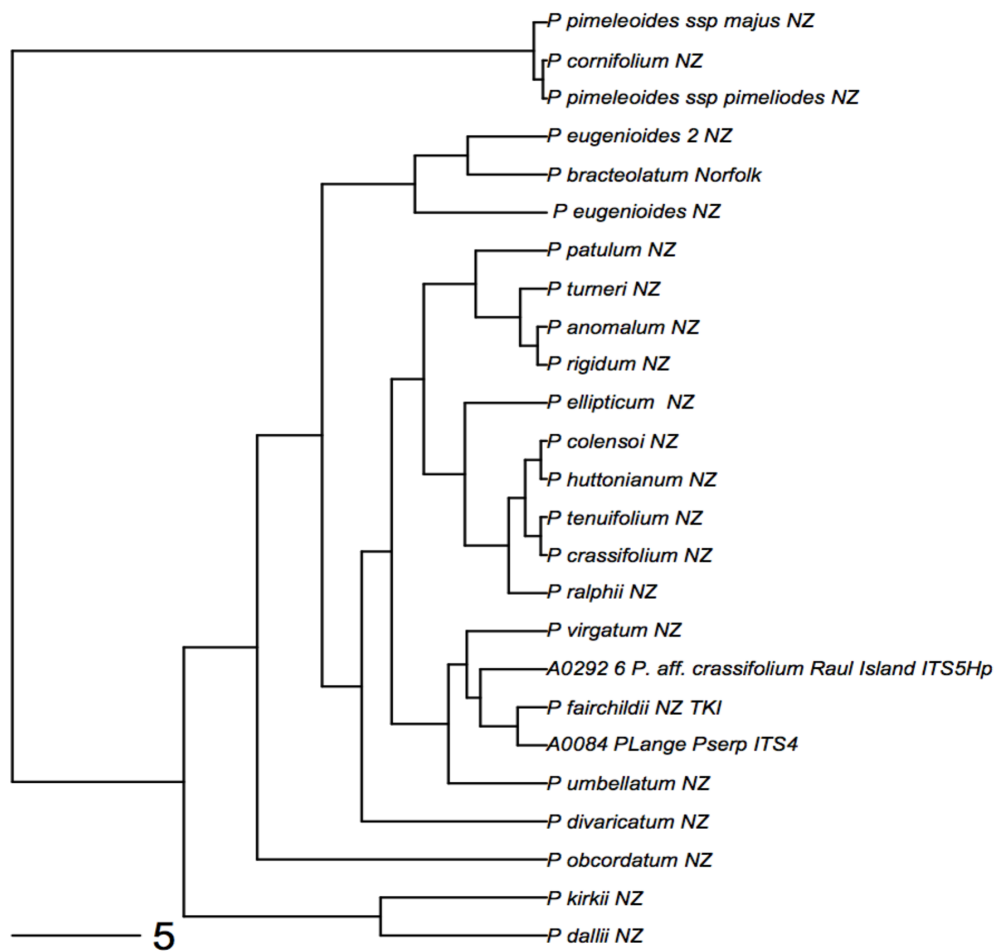
### *Phylogenetic Inference*

A recent phylogenetic treatment of the group indicates that the *Pittosporum* as a whole are monophyletic (Gemmill et al. in prep). The New Zealand *Pittosporum* have arisen as a result of two colonization events and subsequent radiations. The main radiation, consisting of 20 species, arose approximately 20 million years (my) ago, with the putative ancestor colonizing from Australia (Gemmill et al. in prep). The second radiation, consisting of just two species and one subspecies, is approximately 10 my old and is hypothesized to have arisen as a result of a back colonization event from New Caledonia (Gemmill et al. in prep). The present work will utilize the chronogram produced by Gemmill et al. (in prep). The phylogeny was generated using the ITS gene region and a Bayesian reconstruction. The phylogeny contains 22 of the 24 known species of New Zealand *Pittosporum* (Figure 1).

For this study I evaluated the degree of differentiation between all pairwise species combinations in the New Zealand *Pittosporum*. As the New Zealand *Pittosporum* are not monophyletic, I conducted the analyses with and without the clade representing the second colonization event. The results showed indistinguishable patterns so I only present data from the analysis combining both clades.

## Species Functional Traits

A total of 12 functional traits known to be associated with various aspects of plant ecological strategies were selected to evaluate the functional differentiation among species. Previous work



**Figure 1.** *Phylogenetic relationships of the 24 New Zealand species of Pittosporum.* The tree is based off of ITS sequence data and was constructed using a Bayesian inference. The scale bar at the bottom represents age since the origination of the genus.

has demonstrated that many of these traits are often correlated with climatic gradients and are therefore expected to relate to the climatic niches of species (eg. Reich et al. 1997, Wright et al. 2004, Moles and Westoby 2006, Swenson and Enquist 2007, Moles et al. 2009). In this way, functional traits provide a link from the environment to the organism itself. Plant ecologists use functional traits to evaluate how species are partitioning resources differently, through the comparison of these ecologically important traits. In this study, four traits associated with wood characteristics and hydraulics were measured (wood density, stem hydraulic conductance, approximate maximum vessel length, and bark thickness), in addition to eight leaf traits (chlorophyll content, leaf thickness, leaf density, leaf dry matter content, leaf mass per area (LMA), leaf area, leaf nitrogen content and leaf carbon content).

The LMA and leaf nitrogen content are commonly referred to in the context of the ‘leaf economics spectrum’ (Wright et al. 2004), a suite of traits that represent a continuum along which all plant species lie (Reich et al. 1997; Wright et al. 2004). Leaves with high LMA tend to have a longer lifespan than those with low LMA (eg. Reich et al. 1997, Wright et al. 2004). Leaf nitrogen content relates to photosynthetic capacity, as nitrogen is the major component of many compounds, such as RuBisCO, that are essential for, and constrain the rate of, photosynthesis (Lambers et al. 1998). Leaf thickness and leaf density together can be used to calculate LMA, and in turn are related to photosynthetic capacity (Niinemets 2001). Both traits, however, represent independent axes of function along which species can differentiate. Increases in leaf thickness are primarily driven by increases in numbers and lengths of photosynthetically active mesophyll cells, thus increasing photosynthetic capacity (Pieters 1974, De Lillis and Valletta 1985, Korner et al. 1989, Niinemets 1999, Niinemets 2001). In contrast, increases in leaf density are often correlated with decreases in photosynthetic capacity. Higher leaf density

relates to mesophyll cells with thicker cell walls, leading to fewer photosynthetically active cells that may also decrease gas exchange into the cells (Syvertsen et al. 1995). Higher density leaves are thought to represent those species that are shade tolerant (Alvarez-Clare and Kitajima 2007) and/or more resistant to herbivores (Kitajima and Poorter 2010). Leaf dry matter content (LDMC) has also been shown to be an important trait representing variation along a resource-use gradient (Wilson et al. 1999), where species with high LDMC are fast-growing in less resource limited environments (Grime et al. 1997, Wilson et al. 1999, Garnier et al. 2001). Although chlorophyll content of leaves is not included in the ‘leaf economics spectrum,’ it also positively relates the photosynthetic capacity of leaves. Leaf carbon content represents the ability of leaves to assimilate and store carbon (Elser et al. 2010), and is negatively correlated with vegetative growth rate (Lambers et al. 1998). Lastly, leaf area relates to resource capture, with larger area leaves being able to capture more sunlight. Larger leaves are also associated with lower boundary layer conductance, meaning that there is less transfer of heat from the leaf to the surrounding environment, resulting in an increase in leaf temperature (Lambers et al. 1998). Increases in sunlight capture and leaf temperature lead to higher photosynthetic rates, but high irradiance and high leaf temperatures may slow photosynthetic processes due to photoinhibition and decreased stomatal conductance, respectively.

In response to the development of the ‘leaf economics spectrum,’ there has been a push to evaluate wood traits in a similar trade-off framework. In this ‘wood economics spectrum,’ Chave et al. (2009) suggest that woody plants have developed and optimized anatomical traits and physiological functions that lead to increased performance and survival in different habitats. As with the ‘leaf economics spectrum’ it is suggested that there is a trade-off in wood traits that either contribute to fast growth or to slower growth but increased survival. Species that have the

ability to maximize resource transport and grow quickly typically have lower density wood and high hydraulic conductance (Baralato et al. 2010), whereas species that are resistant to disturbance and have greater mechanical support have higher density wood, but lower hydraulic conductance and thus grow more slowly (Hacke et al. 2001). It is valuable to evaluate wood traits in addition to leaf traits, as they have been shown to directly relate to plant growth and survival (Poorter et al. 2009).

In this study I quantified wood density and hydraulic conductance, in addition to approximate maximum vessel length (AMVL) and bark thickness of stems. As described above, wood density and hydraulic conductance relate to competitive ability and resistance to mechanical failure. In a study of 42 rainforest trees Poorter et al. (2009) found that growth rate was positively correlated with hydraulic conductance and negatively related to wood density, but wood density was positively related to survival. Although less emphasized in studies of functional ecology, AMVL and bark thickness are also indicators of different plant strategies. Indeed, Comstock and Sperry (2000) argue that xylem conduit length, here referred to as AMVL, represents a ‘neglected dimension’ for understanding the hydraulic architecture of plants and thus a major performance axis. Their review of the literature suggests that variation in vessel length is indicative of a trade-off between hydraulic conductance and safety. While long vessels minimize resistance and thus maximize flow, trees with long vessels are more susceptible to mechanical failure that results from cavitation or damage due to herbivores and pathogens (Comstock and Sperry 2000). Bark thickness may also be important for plant performance in different environments, and thus be an indicator of species niche differentiation. There is evidence to suggest that thicker bark may be beneficial for species that are in habitats frequented by fires (Hare 1965, Harmon 1984), but it may also be related to structural support and herbivore



and pathogen resistance. In their study of wood and leaf functional traits of tree species in French Guiana, Baralato et al. (2010) found a negative relationship between bark thickness and wood density. They suggest that species with less dense wood may benefit from the structural support of thicker bark, but more likely fast growing trees with less dense wood may be more susceptible to herbivore and pathogen attacks, and thus have thicker bark to mitigate the effects of this damage (Baralato et al. 2010, Paine et al. 2010).

### *Functional Trait Measurements*

Leaf functional trait data were collected from 72 individuals and wood trait data were collected from 67 individuals representing 22 of the 24 species of *Pittosporum* in New Zealand. Samples were taken from saplings grown in the shadehouse at the University of Waikato in Hamilton, New Zealand, from the Oratia Native Plant Nursery, or from native plant gardens in the surrounding region. When possible, I collected wood and leaf samples from three or more individuals per species, but for several uncommon species I was only able to collect from one to two individuals.

Leaf traits were measured for three leaves per individual and these values were averaged to obtain an individual mean trait value. All measurements were conducted on fresh, fully mature sun leaves as suggested in Cornelissen et al. (2003). I measured traits on leaves both with and without petioles, but as there was no significant difference in trait means between the samples, I present data only from leaves with petioles. Leaf chlorophyll content was measured using a SPAD-502 chlorophyll meter. Three measurements were taken on each leaf, avoiding the mid-vein when possible. These values were averaged to obtain a single mean leaf value.

Leaves from *P. divaricatum* and *P. turneri* were too small to obtain accurate measurements. Leaf thickness was measured using a digital micrometer, and as with chlorophyll content, three measurements were taken to obtain an average value for each leaf. Leaf area, defined as the surface area of the upper lamina of the leaf, was measured using LI-3100 leaf area meter (Lincoln, Nebraska USA). In order to calculate LMA, I weighed leaves that had been dried in a 70 degree Celsius oven for three or more days. For very small leaves, I determined the total area and dry mass of 20 – 30 leaves and took an average to determine LMA. Leaf density was calculated as LMA divided by leaf thickness (Kitajima and Poorter 2010), and leaf dry matter content was calculated as the oven dry mass of a leaf divided by its fresh mass (Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013). Mass-based leaf percent nitrogen and carbon were analyzed at the Cornell Isotope Laboratory using a Thermo Delta V isotope ratio mass spectrometer (IRMS) interfaced to a NC2500 elemental analyzer.

Wood traits were measured on a single stem per individual, and all traits were measured on the same sample. When possible, measurements were taken on samples from lateral branching stems, but for a few individuals with small diameter stems I sampled from the main stem. Wood density was measured as dry mass per unit fresh volume of stems with the outer cortex removed (Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013). I quantified stem volume using the dimensional method (Perez-Harguindeguy et al. 2013), with volume calculated as  $\pi \times L \times (0.5D)^2$ , where  $L$  is the length of the stem and  $D$  is its diameter. Stem sections sampled were of regular shape making this an appropriate way to measure stem wood density. To further ensure the accuracy of our values, diameter was measured using vernier calipers at five points along the stem and averaged. Stems were dried at 100 degrees Celsius for five days before being weighed on an analytical balance. Bark thickness was measured on both ends of

the stem section and the values averaged. Bark was defined as in Perez-Haguindeguy et al. (2013) as the tissue external to the wood or xylem, and includes the phloem. Approximate maximum vessel length was measured using the ‘air method’ as described in Ewers and Fisher (1989). Air was forced through a stem section that was placed underwater and was cut back incrementally until bubbles emerged. While an interesting trait in itself, AMVL was also used to determine the stem length of the samples measured for hydraulic conductance. In all but a few instances samples used were longer than the AMVL, thus preventing the problem of overestimation of hydraulic conductance. Samples measured that were not longer than the AMVL had similar  $K_s$  values as other individuals of the same species, and thus were not excluded from the analyses. Sapwood-specific conductivity was calculated as

$$K_s = J \times L \times A^{-1} \times \Delta\Psi^{-1},$$

where  $J$  is the rate of water flow through the stem ( $\text{kg s}^{-1}$ ),  $L$  is the length of the stem (m),  $A$  is the mean cross-sectional area of the stem ( $\text{m}^2$ ) and  $\Delta\Psi$  is the difference in hydrostatic pressure (MPa). All measurements were taken following the protocol outlined in Perez-Haguindeguy et al. (2013). In this gravitational method, a known pressure head is used to force a 10 mM KCl solution through a sample with a known stem diameter and length for a known period of time. The volume of the liquid forced through the stem was measured using a micro-pipette. All stem samples were purged with filtered and degassed water for twenty minutes at a pressure of 60 - 100 kPa before  $K_s$  was measured to clear the stem section of potential embolisms.

### *Species-Specific Climatic Niche Envelopes*

The primary goal of this work was to determine the phylogenetic, trait, and environmental niche dissimilarity among co-occurring and non co-occurring species in the genus *Pittosporum*. To evaluate the degree of environmental niche differentiation I first estimated climatic niches for each species using an ecological niche modeling approach. Specifically, I used the species distribution modeling software, Maxent (ver. 3.3.3k; Phillips et al. 2006, Phillips and Dudik 2008), to estimate the optimal environmental envelope occupied by each species. Using habitat and/or climatic data and species occurrence data as input variables, Maxent employs a maximum entropy approach to predict species geographic ranges as determined by habitat suitability (Phillips et al. 2006). Maxent is an ideal program to use in this study as it operates under the assumption of presence-only data, performs well with relatively small sample sizes (Hernandez et al. 2006, Pearson et al. 2007), and has proven a robust method in a recent comparison of multiple habitat modeling methods (see Elith et al. 2006).

The Maxent algorithm requires geo-referenced occurrence data for each species. Geo-referenced species occurrence records were obtained via the Global Biodiversity Information Facility (GBIF) database (<http://data.gbif.org>) with additional data coming from individual herbaria throughout New Zealand. Through the use of the GBIF database and herbaria records I was able to utilize over 5000 geo-referenced occurrence records for 16 *Pittosporum* species of the 24 species found in New Zealand. Although the number of occurrences varied for each species, I only included those species that have greater than 10 occurrence records in our analyses. The original geo-referenced data come from multiple institutions that have provided their data to GBIF for re-distribution to the public. The majority of the occurrence data came

from the National Vegetation Survey (<https://nvs.landcareresearch.co.nz>). This databank comprises survey data from over 19000 permanent plots sampled over 50 years. I used the 19 BIOCLIM variables developed by Hijmans et al. (2005, <http://www.worldclim.org>), in addition to altitude, as the environmental covariates defining the background data for the Maxent models. Combining and summarizing temperature and precipitation data, these 19 bioclimatic variables inform us about the climatic tolerances associated with different species. All environmental layers in the model were defined using a raster grid size of 30 arc-seconds.

### *Quantifying Predicted Niche Occupancies*

I used the results from the Maxent models to quantify the multi-dimensional climatic niche space occupied by each species and to compare niche overlap between species. Incorporating the locality data and environmental background data, the Maxent algorithm generates a predicted geographic range map. The probability of occurrence of the focal species within any given grid cell within the specified range is indicated using a heat map color scheme with warmer colors indicating a higher probability of occurrence in a grid cell. It is possible to extract the “raw probabilities” from the predicted Maxent range map/model. Following the methods developed by Evans et al. (2009) I binned the raw probabilities assigned to each grid cell on the range map to obtain a “predicted niche occupancy” (PNO; Evans et al. 2009) associated with each of the environmental variables studied for each species. The resulting unit area histograms allow for the visualization of the expected distribution of individuals of a given species along a specified environmental axis. The PNOs were subsequently used to determine niche overlap of all pairwise species comparisons for all environmental variables included in the Maxent model.

### *Determining Pairwise Species Differentiation*

The phylogenetic distance between each pair of species was calculated as the branch lengths separating the species and calculated using the cophenetic function in the R package “ape” (v3.1 – 1; Paradis et al. 2004).

I quantified climatic niche overlap for species pairs using the *I* niche overlap metric described in Warren et al. (2008). This similarity statistic, which is an adaptation of the Hellinger distance metric (van der Vaart 1998, page 211), ranges from 0 (no niche overlap) to 1 (complete niche overlap) and is calculated as

$$I(p_x, p_y) = 1 - \frac{1}{2} \sqrt{\sum_i (\sqrt{p_{x,i}} - \sqrt{p_{y,i}})^2}$$

where  $p_x$  and  $p_y$  denote the probability that a species will occur in location  $i$ . This metric is often preferred as it carries no biological assumptions about the population densities of species in a given habitat unlike other metrics that are commonly used, such as Schoener’s *D* statistic (Warren et al. 2008). Additionally, this metric proves especially useful in this study as I can use the output from the PNO plots to determine the probability of occurrence in each habitat for each species. I also determined overall niche overlap among species pairwise comparisons by evaluating niche overlap of entire environmental niche models. All calculations were carried out using the “phyloclim” package in R (v0.9-4; R Development Core Team 2013).

Functional trait differentiation for all pairwise species comparisons was determined for each trait individually by calculating the Euclidean distance between two species’ traits using the

“stats” package in R (v3.0.2; R Development Core Team 2013). I also conducted a principal components analysis (PCA) to summarize the multivariate associations among all functional traits and used the first four components in our evaluation of trait differentiation among co-occurring, non co-occurring, and randomly distributed species pairs. Lastly I calculated a Gower’s dissimilarity to estimate the overall dissimilarity in traits among species pairs. I used the Gower’s dissimilarity index on the PCA output instead of on all individual traits combined as the PCA removes the redundancy in traits. The Gower calculation was implemented in the “FD” package in R (v1.0-11; R Development Core Team 2013).

#### *Determining Co-occurrence vs. Non Co-occurrence*

To determine whether species pairs are co-occurring more than expected, non co-occurring more than expected, or randomly distributed I first binned all geo-referenced occurrence data into 0.25 x 0.25 degree (latitude and longitude) grid cells and calculated Schoener's Co-occurrence index ( $C_{ij}$ ) from the present-absence data matrix (Schoener 1968). The observed  $C_{ij}$  values were then compared to a distribution of 999 random  $C_{ij}$  values generated by implementing an independent swap null model. Briefly, the independent swap randomizes the presence-absence matrix of species while maintaining the species richness observed in a map grid cell and the occupancy rates of individual species across map grid cells in the study system. I then calculated whether each pair of species co-occurs more or less than expected given the null expectation using the ranks of the observed  $C_{ij}$  values in the null distribution of 999 random  $C_{ij}$  values. Co-occurrence calculations were implemented in the R package “picante” (v1.6-2; R Development Core Team 2013).

## Statistical Analyses

To test for significant phylogenetic, functional trait, and environmental niche dissimilarity between co-occurring, random, and non co-occurring species pairs, I implemented separate linear mixed effects models (LMMs) using all pairwise comparisons as data points ( $n = 124$ ). LMMs are useful for examining relationships among data points that exhibit non-independence and represent multiple comparisons (Faraway 2005). Using this approach, I assigned occurrence designation as a fixed factor but was able to account for non-independence of data points by including species 1 and species 2 as random effects. I used Honest Significant Difference Tukey tests to determine post-hoc differences among occurrence categories. Calculations were carried out using the “lme4” (v1.0-6; R Development Core Team 2013) and “multcomp” (v1.3-2; R Development Core Team 2013) packages in R.

**Table 1.** Results from the LMM analysis of trait dissimilarity differences among co-occurring, non co-occurring and randomly distributed species pairs.

Trait	Co-occurring and Non Co-occurring		Co-occurring and Random		Non Co-occurring and Random	
	z - score	p -value	z - score	p -value	z - score	p -value
Chlorophyll Content	0.551	0.845	-0.530	0.856	-1.184	0.46
Leaf Thickness	0.716	0.754	-0.635	0.801	-1.445	0.317
Leaf Density	0.525	0.859	-0.171	0.984	-0.757	0.729
Leaf Dry Matter Content	0.417	0.908	-1.057	0.540	-1.534	0.274
Leaf Mass per Area (LMA)	0.615	0.811	0.777	0.717	0.105	0.994
Leaf Area	1.796	0.170	1.081	0.525	-0.934	0.618
Leaf Carbon Content	1.048	0.546	0.484	0.879	-0.667	0.782
Leaf Nitrogen Content	4.080	< 0.001	3.541	0.001	-0.899	0.640
Approx. Max Vessel Length	8.780	< 0.001	4.275	< 0.001	-5.674	0.001
Hydraulic Conductance	0.272	0.960	1.396	0.342	1.151	0.482
Wood Density	-0.494	0.874	-0.062	0.998	0.487	0.887
Bark Thickness	1.886	0.142	0.806	0.699	-1.275	0.409



## RESULTS

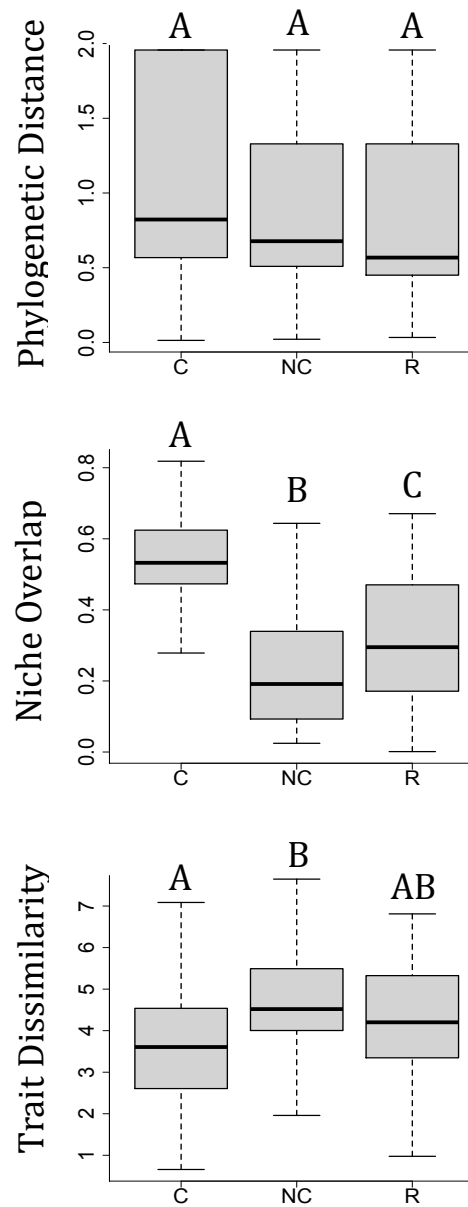
I evaluated a total of 120 species pairwise comparisons to determine if species co-occurred more than expected based on a null distribution, did not co-occur more than expected, or were distributed randomly with respect to each other. Species were considered co-occurring if they had a Cij value that fell in the upper tail of the null distribution (0.975 and above) and non co-occurring when they fell in the lower tail of the distribution (0.025 and below). Thirty-three species pairs were described as co-occurring, 32 were described as non co-occurring, and 55 were described as randomly distributed.

### *Phylogenetic Relatedness and Co-occurrence*

I found no significant difference in mean pairwise phylogenetic distance between co-occurring, non co-occurring, and randomly distributed species (Figure 2), indicating that phylogenetic relatedness does not predict whether or not species co-occur in this genus. The same result was obtained when the clade consisting of *P. pimelioides ssp. pimelioides* and *P. cornifolium* (ie: the

**Table 2.** Results from the LMM analysis of trait dissimilarity of the first four principal components among co-occurring, non co-occurring and randomly distributed species pairs.

Trait	Co-occurring and Non Co-occurring		Co-occurring and Random		Non Co-occurring and Random	
	z - score	p -value	z - score	p -value	z - score	p -value
Principal Component 1	1.659	0.221	0.617	0.810	-1.230	0.434
Principal Component 2	-0.149	0.988	-0.901	0.639	-0.747	0.735
Principal Component 3	-0.267	0.961	1.640	0.228	1.956	0.123
Principal Component 4	3.185	0.004	1.834	0.158	-1.752	0.185
Multivariate PCA	2.956	0.009	1.240	0.429	-2.032	0.104

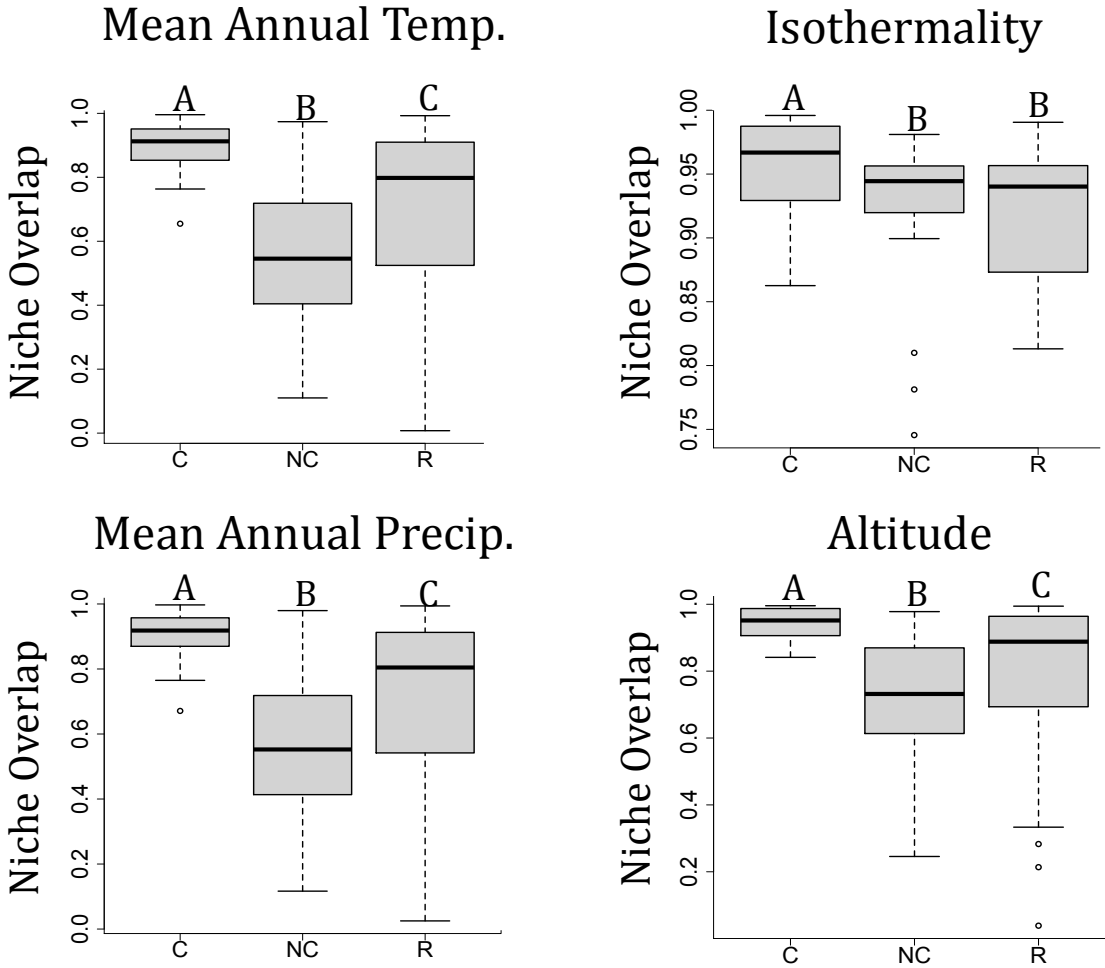


**Figure 2.** The mean phylogenetic distance, environmental niche overlap and trait dissimilarity among co-occurring (C), non co-occurring (NC) and randomly distributed (R) species pairs. The environmental niche overlap and trait dissimilarity are represented by a multivariate summary of all variables and traits, respectively.

second colonization event) was included and excluded. Thus I only show the results with the clade included.

### *Niche Overlap and Co-occurrence*

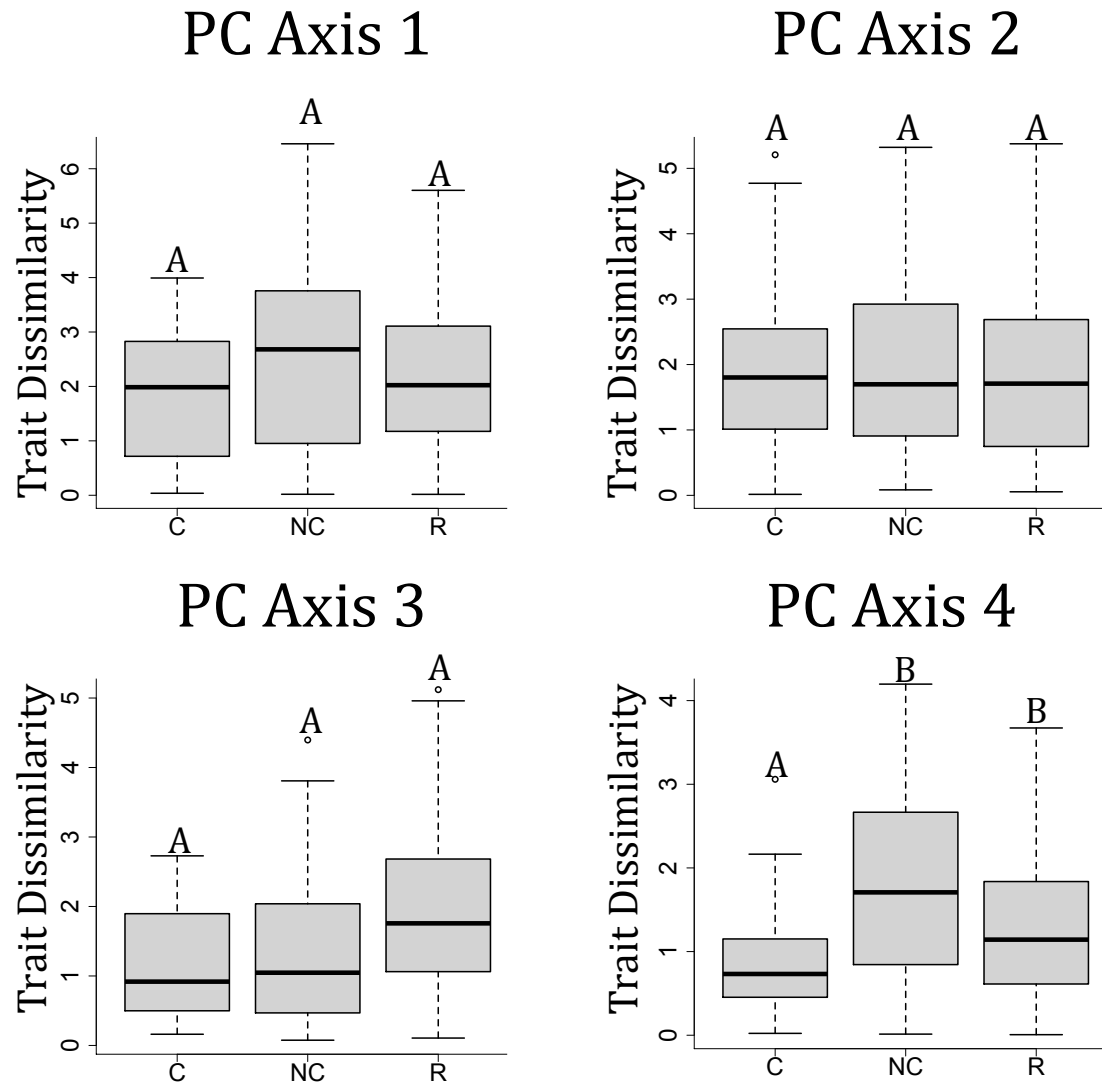
There was a significant difference in degree of overall niche overlap between occurrence classifications, with those that co-occur having very high niche overlap (Figure 2). When evaluating overlap of individual environmental variables, co-occurring species always had higher niche overlap than non co-occurring species, but there were some instances in which differences were not significantly different than those species pairs that were randomly distributed (Figure 3).



**Figure 3.** Mean environmental niche overlap among co-occurring (C), non co-occurring (NC) and randomly distributed (R) species pairs for four independent environmental variables: mean annual temperature (Bio1), isothermality (Bio3), mean annual precipitation (Bio12), and altitude.

#### *Trait Dissimilarity and Co-occurrence*

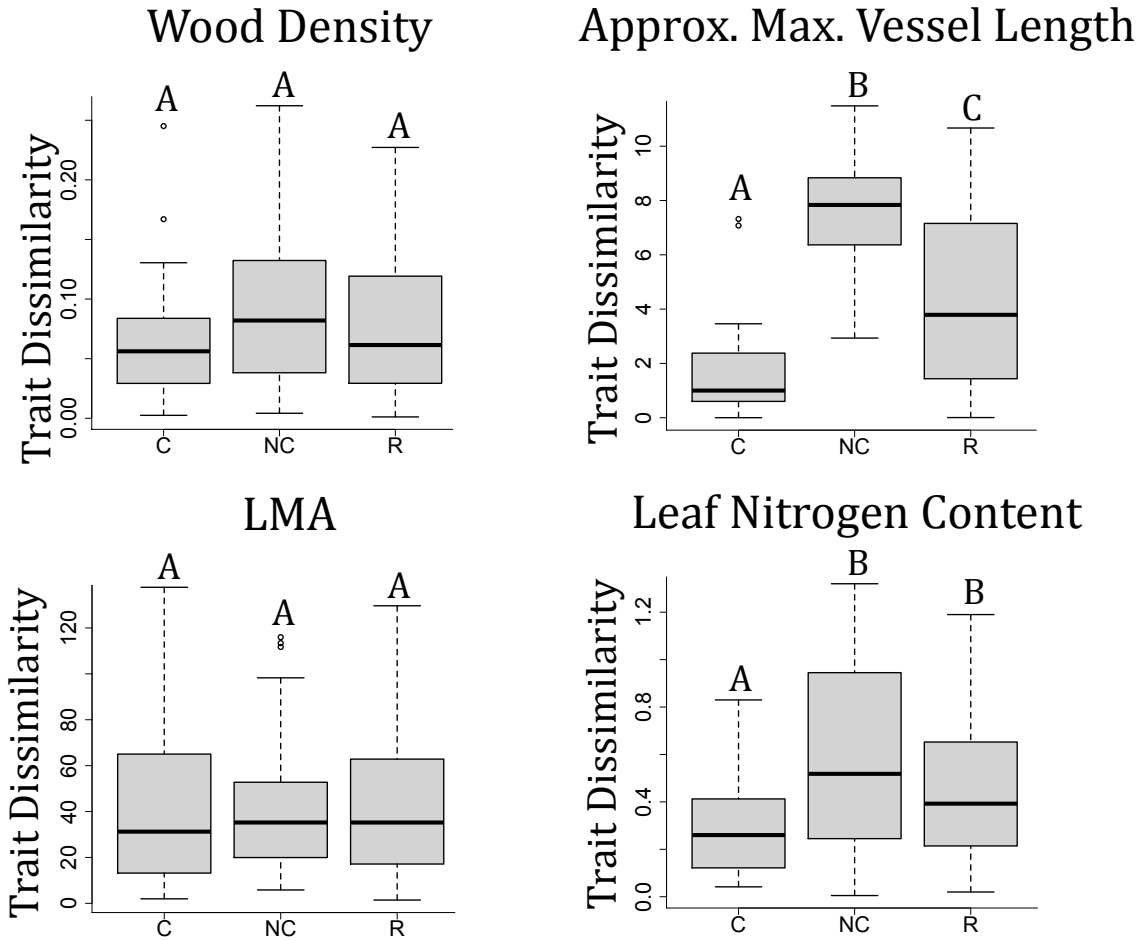
I evaluated trait dissimilarity for all 12 functional traits independently, in addition to evaluating dissimilarity along individual principal component axes and Euclidean distance in multivariate PCA space. For the principal components analysis, I used the first four components. These four components explained 92 percent of the variation, with each component explaining between 12



**Figure 4.** Mean trait dissimilarity among co-occurring (C), non co-occurring (NC) and randomly distributed (R) species pairs for the first four principal components. Components one through three represent “leaf axes” whereas component four represents a “wood axis.”

and 35 percent of the variation (see Appendix 1, Tables A1 and A2 for summary of PCA).

Principal components one through three can be described as “leaf axes” whereas principal component four had wood density and approximate maximum vessel length loading most heavily, and thus I describe this component as a “wood axis.” There was no significant



**Figure 5.** Mean trait dissimilarity among co-occurring (C), non co-occurring (NC) and randomly distributed (R) species pairs for four independent functional traits: wood density, approximate maximum vessel length, LMA, and leaf nitrogen content.

difference in mean trait dissimilarity between co-occurring, non co-occurring, and randomly distributed species pairs for components one through three, the leaf axes (Figure 4, Table 2), but there was a significant difference between co-occurring and non co-occurring species pairs for component four, the wood axis (Figure 4, Table 2). Co-occurring species pairs were more similar than non co-occurring species pairs for this axis. The same result was observed when evaluating dissimilarity in the multivariate principal component axis (Figure 1, Table 2). When

evaluating the traits independently, approximate maximum vessel length and leaf nitrogen content were the only traits that were significantly different between co-occurring and non co-occurring species pairs, again, with these traits being more similar in co-occurring versus non co-occurring species pairs (Figure 5, Table 1).

## DISCUSSION

In this study I assessed mechanisms of co-existence in the New Zealand *Pittosporum*. Specifically, I evaluated whether phylogenetic relatedness, environmental niche overlap, and functional trait dissimilarity could explain patterns of species co-occurrence and non co-occurrence. I found that there was no difference in mean phylogenetic distance between co-occurring and non co-occurring species (Figure 1). Co-occurring species had a higher degree of niche overlap than non co-occurring species (Fig. 1), but the relative difference in mean niche overlap between the groups differed based on the environmental axis examined (Figure 2). Lastly, when evaluating all traits simultaneously, co-occurring species had a lower degree of trait dissimilarity than non co-occurring species (Figure 1). However, when the traits were evaluated independently we see that approximate maximum vessel length and leaf nitrogen content are the only traits that exhibit patterns of low trait dissimilarity in co-occurring species. There was no difference in trait dissimilarity between co-occurring and non co-occurring species with the other traits considered (Table 1). As leaf nitrogen content was not included in the principal components analysis, this suggests that approximate maximum vessel length is a major driver contributing to the pattern of trait similarity in co-occurring species when evaluating the traits together. Below I discuss possible explanations behind the observed results in the context of species co-occurrence mechanisms in the New Zealand *Pittosporum*.



### *Phylogenetic Relatedness and Species Associations*

I expected that due to shared ancestry closely related species would be more ecologically similar to each other than to distantly related species (Darwin 1959), and thus not be able to co-occur. Instead, the results show no difference in phylogenetic relatedness among co-occurring and non co-occurring species. One explanation for this result is that the assumption of niche conservatism is not upheld in this group. That is, the traits that are important for co-existence may not have phylogenetic signal and thus closely related species are actually less similar than expected based on phylogenetic relatedness. This lack of trait phylogenetic signal and its implications for species co-existence and community assembly have been observed and explored in other study systems including Floridian oak (Cavender-Bares et al. 2004) and Caribbean *Anolis* communities (Losos et al. 2003) where the phylogenetic patterns of co-existence can only be understood in the context of convergent trait and environmental niche evolution. I therefore will now discuss patterns of environmental niche and functional trait similarity observed in the genus *Pittosporum*.

### *Environmental Niche Similarity and Co-Occurring Species*

It is not surprising that I observed high climatic niche overlap among co-occurring species, and lower climatic niche overlap among non co-occurring and randomly distributed species, given that the co-occurring species occupy the same environments. It is interesting to note, however, that for several variables there was still a relatively high degree of niche overlap for non co-occurring species. This suggests that either these variables represent a strong environmental

filter for the entire genus, in that there is only a certain range of environmental space that these species can occupy, or that all species occupy the whole range of environmental space and thus there is no differentiation along these niche axes. In either scenario, this lack of niche differentiation might be limiting the number of species in the genus through lack of diversification into different habitats, and also the ability of these species to co-exist across New Zealand.

### *Trait Convergence in Co-Occurring Species*

I expected that regardless of phylogenetic dissimilarity, co-occurring species would be less similar to each other with respect to their traits than non co-occurring species as a result of biotic interactions. Instead, I found that co-occurring species are either more similar in traits, or that there is no difference in trait dissimilarity between co-occurring and non co-occurring species pairs. The high degree of trait similarity for approximate maximum vessel length and leaf nitrogen content is likely due to abiotic filtering where only a small range of trait values are suitable for the given abiotic environment. High trait similarity among co-occurring plant species has been previously shown suggesting an important role for abiotic filtering in community assembly (e.g. Weiher et al. 1998, Grime 2006, Kraft et al. 2008, Swenson and Enquist 2009).

In studies of plant functional traits, it is recognized that species tend to have trait values that fall along a ‘leaf economics spectrum’ (Wright et al. 2004) as well as a ‘wood economics spectrum’ (Chave et al. 2009). The extremes of this spectrum can be described with respect to different growth and survival strategies. On one end, species are highly conservative in their

traits, meaning that they have lower growth rates but higher survival. On the other end of the spectrum, species are more acquisitive, and tend to have higher growth rates but lower survival. These plant strategies, and the traits associated with each, have been explored in theoretical models (Sterck et al. 2011) as well as in many empirical studies (eg. Reich et al. 1999, Wright et al. 2004, Ordoñez et al. 2009, Markesteijn et al. 2011). In the case of leaf nitrogen content and approximate maximum vessel length in the present study, I believe that species are exhibiting different growth and survival strategies in differing environments, leading to the observed pattern of ecological trait convergence among co-occurring species.

Leaf nitrogen content is positively related to photosynthetic capacity (Reich et al. 1999). In this study, species with high leaf nitrogen content are often found in cooler, relatively wet habitats, whereas species with low leaf nitrogen content are more often found in warmer, drier habitats (data not shown). This suggests that species in the cooler, wetter environments are investing more energy in photosynthetic machinery in order to maximize growth rates. In contrast, species in the drier, warmer habitats may be restricted in their photosynthetic capacity. Drought limited species are prone to hydraulic failure if there is too much stomatal conductance, as this increases the negative pressure in the xylem and can thus lead to cavitation (Tyree and Sperry 1989, Sperry and Sullivan 1992). It is noted, however, that other studies have shown no relationship between leaf nitrogen content and climatic variables (Ordoñez et al. 2009), and even a negative correlation between leaf nitrogen content and precipitation (Cunningham et al. 1999), suggesting that this is a trait-environment relationship that needs further investigation.

Approximate maximum vessel length represents a tradeoff between water conductance and safety, and thus an acquisitive and conservative strategy, respectively. Species with long vessels maximize hydraulic conductance by minimizing resistance, but they are also more

susceptible to cavitation and mechanical failure (reviewed in Comstock and Sperry 2000, Markesteijn et al. 2011). Cavitation is caused by both drought and freezing, as drought may induce air seeding in the conduit, and freeze-thaw events can result in embolisms (Tyree and Sperry 1989, Sperry and Sullivan 1992). In this study system those species with the shortest vessels occur in wetter habitats, suggesting that drought is not a factor limiting distributions. However, they are also found in the cooler habitats, which are subjected to freezing temperatures during the coldest months, suggesting that temperature could be an abiotic filter causing the observed convergence in traits in co-occurring species. However, more information about vessel diameter will be needed to make any conclusive inferences about the hydraulic strategies of each species.

It has also been suggested that competitive interactions can lead to ecological trait convergence among co-existing species when performance differences are small (Chesson 2000, Mayfield and Levine 2010). However, this is likely to occur on very local scales and in a homogenous environment (HilleRisLambers 2012). The designation of co-occurrence versus non co-occurrence in this study was defined at a scale of 0.25 X 0.25 longitude and latitude grid cells. While this scale is useful in describing patterns of co-occurrence, it does not define local co-existence. Additionally, New Zealand is climatically heterogeneous therefore it is unlikely that co-occurring species were restricted to identical environments. Lastly, these two traits show strong correlations with both precipitation and temperature variables (data not shown) and thus I conclude that it is most likely that abiotic filtering effects are acting to structure species and trait distributions in these environments.

### *Trait Dissimilarity and Species Associations*

Interestingly, all individual traits, with the exceptions of approximate maximum vessel length and leaf nitrogen content, showed no difference in the degree of dissimilarity between co-occurring and non co-occurring species. There are several possible explanations for this result. First, the level of trait dissimilarity observed among co-occurring species may be enough to allow for niche differentiation. One of the limitations of this, and many other functional trait studies, is that it is difficult to identify a minimum threshold of dissimilarity needed for co-existence. Thus, the trait dissimilarity observed here could be great enough to explain co-occurrence. This does not, however, explain why co-occurring and non co-occurring species have the same mean trait dissimilarity. I suggest that two mechanisms are acting to cause the observed results. As discussed above, the degree of dissimilarity in co-occurring species could be driven by biotic interactions and niche differentiation, as has been observed in other plant (Cavender-Bares et al. 2004) and animal (Tobias et al. 2013) systems. In contrast, the dissimilarity in traits among non co-occurring species could be driven by environmental differences in the habitats in which the species occur. Both scenarios could lead to similar trait dissimilarities between co-occurring and non co-occurring species pairs.

Another possible explanation for the observed results is that many of the traits I measured can be plastic (reviewed in Berg and Ellers 2010), and thus may differ within a species among varying environments. Natural populations likely grow in environments different from the environments in which the study individuals were grown. If I was to take trait measurements from species in these varying environments, we may see a very different pattern of trait dissimilarity among co-occurring species. Traits may be more overdispersed if competitive

interactions are at play (see Burns and Strauss 2012), but traits could also be more convergent owing to the prevalent occurrence of trait-environment relationships (Ordoñez et al. 2009).

Lastly, it is possible that I am missing some important axis or axes of trait differentiation that are mediating co-occurrence. This could be especially important in this system, as I am looking at species in a single genus as opposed to species across a broader taxonomic scale. The species are recently diverged, and so have had less time to accumulate trait and environmental niche differentiation. It may be possible that these closely related species are maintaining continued co-existence by differing along a reproductive trait axis, such as flower type, flower timing, and/or seed size.

#### *Community Assembly in the New Zealand Pittosporum*

Historically researchers have used lists of species, knowledge of their distributions, and a null model approach to try and understand the processes responsible for structuring species assemblages in general, and species co-occurrence, specifically (eg. Diamond 1975). In recent years the inclusion of trait and phylogenetic data has greatly enhanced our power to elucidate the actual mechanisms acting that lead to observed community assemblages (eg. Weiher et al. 1998, Gotelli and Ellison 2002, Cavender-Bares et al. 2004, Peres-Neto 2004, Tobias et al. 2013). The results from this study suggest that neither phylogenetic dissimilarity nor dissimilarity in the measured traits alone predict patterns of species co-occurrence in the New Zealand *Pittosporum*. Although we do see trait clustering in co-occurring species for leaf nitrogen content and approximate maximum vessel length, we do not observe any pattern of high trait dissimilarity among co-occurring species. It will be interesting to reevaluate this study system with the

inclusion of additional traits that may exhibit patterns of trait divergence as has been observed in other systems (Losos et al. 2003, Cavender-Bares 2004, Tobias et al. 2013).

Additionally, the inclusion of evolutionary history into this and other studies of mechanisms of co-occurrence will inform us about how species and trait diversification have led to patterns of diversity and distributions we observe today. Preliminary analysis of the data in this study suggests that many of the functional traits evaluated are not conserved (data not shown) suggesting that phenotypic convergence over time is potentially confounding the signal of phylogenetic dissimilarity among co-occurring species. Information about the evolutionary history of a radiation can also inform us about how (ie: the magnitude and timing of diversification) species have diverged along functional trait and environmental niche axes as they radiated across New Zealand. Lastly, I suggest that additional studies of trait evolution and species co-existence be conducted across different lineages to evaluate whether the same patterns are observed, and thus the same mechanisms are acting to structure the spatial distributions of species.

## APPENDIX



**Table A1.** *The percent of variation explained by each of the four first components from the principal components analysis conducted on the 12 functional traits investigated in this study.*

Comp 1	Comp 2	Comp 3	Comp 4	<b>TOTAL</b>
0.3522	0.2645	0.1781	0.1222	0.9170

**Table A2.** *The loadings from the principal components analysis conducted on the 12 functional traits investigated in this study.*

Trait	Comp 1	Comp 2	Comp 3	Comp 4
Approx. Max Vessel Length	-0.288	-0.172	-0.26	0.599
Bark Thickness	-0.458	-	0.261	-
Chlorophyll Content	-	0.517	0.289	-0.183
Hydraulic Conductance	-0.267	-0.373	-0.266	-0.336
Leaf Density	0.131	-0.336	0.58	-
Leaf Dry Matter Content	0.135	-0.464	0.417	-
Leaf Mass per Area	-0.405	0.103	0.407	0.167
Leaf Thickness	-0.431	0.333	-	0.125
Wood Density	0.332	-	-	0.662
Leaf Area	-0.37	-0.321	-0.167	-

**Table A3.** Results from the LMM analysis of environmental niche overlap differences among co-occurring, non co-occurring and randomly distributed species pairs.

Environmental Variable	Co-occurring and Non Co-occurring		Co-occurring and Random		Non Co-occurring and Random	
	z - score	p -value	z - score	p -value	z - score	p -value
Bio1 - Annual Mean Temp.	-7.687	<0.001	-3.835	<0.001	4.668	<0.001
Bio2 - Mean Diurnal Range	-4.728	<0.001	-1.606	0.242	3.624	<0.001
Bio3 - Isothermality	-2.904	0.010	-3.216	0.004	-0.028	1.000
Bio4 - Temp. Seasonality	-6.494	<0.001	-3.623	0.001	3.528	0.001
Bio5 - Max. Temp. of Warmest Month	-6.218	<0.001	-2.712	0.018	4.160	<0.001
Bio6 - Min. Temp. of Coldest Month	-7.588	<0.001	-4.259	<0.001	4.114	0.001
Bio7 - Temp. Annual Range	-7.366	<0.001	-3.476	0.002	4.682	<0.001
Bio8 - Mean Temp. of Wettest Quarter	-7.865	<0.001	-4.024	0.002	4.669	<0.001
Bio9 - Mean Temp. of Driest Quarter	-7.332	<0.001	-3.971	<0.001	4.109	<0.001
Bio10 - Mean Temp. of Warmest Quarter	-5.994	<0.001	-3.653	<0.001	2.943	0.009
Bio11 - Mean Temp. of Coldest Quarter	-8.022	<0.001	-4.048	<0.001	4.852	<0.001
Bio12 - Annual Precipitation	-7.577	<0.001	-3.733	<0.001	4.652	<0.001
Bio13 - Precip. of Wettest Month	-7.797	<0.001	-3.949	<0.001	4.671	<0.001
Bio14 - Precip. of Driest Month	-4.687	<0.001	-1.984	0.116	3.193	0.004
Bio15 - Precip. Seasonality	-4.249	<0.001	-2.685	0.020	1.996	0.113
Bio16 - Precip. of Wettest Quarter	-4.339	<0.001	-2.185	0.074	2.604	0.025
Bio17 - Precip. of Driest Quarter	-6.104	<0.001	-3.421	0.002	3.319	0.003
Bio18 - Precip. of Warmest Quarter	-4.280	<0.001	-2.833	0.013	1.881	0.144
Bio19 - Precip. of Coldest Quarter	-5.015	<0.001	-1.818	0.163	3.727	0.001
Altitude	-6.300	<0.001	-3.133	0.005	3.835	<0.001
Multivariate Niche Overlap	-8.945	<0.001	-5.922	<0.001	3.957	<0.001

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