

Vertical gradients in leaf trait diversity in a New Zealand forest

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Abstract Leaves come in a remarkable diversity of sizes and shapes. However, spatial patterns in leaf trait diversity are rarely investigated and poorly resolved. We used a hierarchical approach to evaluate vertical variability in leaf morphology (i.e., leaf trait diversity) in 16 common tree and shrub species inhabiting a New Zealand forest. Height-related heterogeneity in leaf area, specific leaf area, circularity and length to width ratio was analyzed at three scales: (1) among leaves within plants, (2) among plants within species and (3) among species within functional groups (i.e., trees vs. shrubs). Results were scale dependent. Among-leaf morphological diversity was unrelated to plant height. Among-individual morphological diversity increased with the average height of each species, indicating that taller plant species express a greater range of leaf traits than shorter species. Among-species morphological diversity was higher in shrubs than in trees. We hypothesize that scale-dependent patterns in leaf trait diversity result from scale-dependent adaptations to forest environmental conditions. As trees grow from the forest floor into the canopy, they are exposed to a range of environmental conditions, which may select for a range of leaf traits through ontogeny. Conversely, shrubs never reach the forest canopy and may instead be differentially adapted to suites of environmental conditions associated with different stages of forest recovery from tree-fall disturbances. Overall results indicate that vertical patterns in leaf trait diversity exist. However, their strength and

directionality are strongly scale-dependent, suggesting that different processes govern leaf shape diversity at different levels of ecological organization.

Keywords Diversity · Functional group · Leaf trait · Morphology · New Zealand · Scale · Specific leaf area

Introduction

A central goal in ecology is to explain spatial patterns in biological diversity. Biological diversity is typically defined taxonomically. However, there are many other types of biodiversity. For example, plant leaves exhibit an extraordinary diversity of size and shape, yet spatial patterns in leaf morphological diversity are rarely investigated.

A variety of morphological traits covary in most plants (see Niklas 1993; Westoby et al. 2002; Enquist et al. 2007). In particular, specific leaf area (the ratio of leaf area to leaf mass) increases concomitantly with leaf nutrient concentrations, turnover rates and mass-dependent carbon assimilation rates, which collectively comprise a world-wide leaf economic spectrum (Grubb 2002; Wright et al. 2004, 2005). Leaf trait correlations associated with specific leaf area represent an important component of plant life history strategies, and interspecific differences in this suite of plant traits may promote coexistence within plant communities (Wilson et al. 1999; Ackerly 2004; Burns 2004; Ackerly and Cornwell 2007; Shipley et al. 2006; Guohong 2007). On larger scales, spatial variation in these traits may represent community-wide adaptations to environmental conditions (Fonseca et al. 2000; Wright et al. 2002; Luo et al. 2005; Franco et al. 2005; Bertiller et al. 2006; Warren et al. 2006; Santiago and Wright 2007).

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Despite these important insights into leaf form and function, spatial patterns in leaf trait diversity (i.e., variability in the size and shape of co-occurring leaves) remain poorly resolved. However, naturalists have long been interested in spatial variation in leaf trait diversity gradients. MacArthur (1972) argued that tropical leaves are less diverse morphologically than temperate leaves. Janzen (1975) suggested that leaf morphological diversity is lower in undisturbed areas of Costa Rican rainforest than in canopy gaps or clearings. Cody (1986) noted that leaf shape diversity is broadly similar in Mediterranean-climate scrub in different parts of the globe, yet leaf shapes can differ markedly among localities, species and genders within regions.

Here, we quantified spatial variation in leaf trait diversity in a New Zealand forest. However, unlike previous observations we tested for vertical patterns in leaf trait diversity, or gradients in dissimilarity of leaf size and shape stretching from the forest floor into the canopy (i.e., the uppermost, continuous layer of leaves). Leaf area, specific leaf area, circularity and length to width ratio were measured on 2,612 leaves collected from 263 plants belonging to 16 common tree and shrub species. Vertical gradients in leaf trait diversity were then assessed at three scales of resolution: (1) among leaves within plants, (2) among plants within species, and (3) among species with plant functional groups (shrubs vs. trees). Results were used to establish whether vertical gradients in leaf trait diversity exist and whether they differ among each scale of analysis.

Materials and methods

Study site

All data were collected in Otari-Wilton's Bush on the southern tip of the North Island of New Zealand (41°14'S, 174°45'E). Otari-Wilton's Bush is a forest reserve comprised of 75 ha of mature and regenerating conifer-broadleaf forest (see Burns and Dawson 2005). The parent material is greywacke; steeper slopes are comprised of a stony colluvium and valley bottoms are covered in silty loam. Mean annual temperatures average approximately 12.8°C, and range from an average daily minimum of 6.3°C in July, to an average daily maximum of 20.6°C in February. Annual rainfall averages approximately 1,250 mm. Rainfall occurs year-round; however, most (~75%) falls in winter (May–September). Frosts and snow are uncommon and last between 1–3 days (<5 events per year).

The vertical structure of New Zealand conifer-broadleaf forest is highly heterogeneous and similar to that of tropical forests (see Dawson 1988). While it is comprised mostly of species that grow to 7–10 m in height, several 'canopy

emergent' species grow to substantially greater heights (15–30 m) and extend well above the canopy. A variety of small tree and shrub species inhabit the forest floor and are sometimes found in tree-fall gaps that are formed by strong winds in winter. Therefore, the vertical distribution of leaf area is fairly uniform, with little open space within the forest's vertical profile (see Wardle 2002). Although vertical changes in environmental conditions have yet to be quantified at this site, McDonald and Norton (1992) describe forest environmental conditions at several other sites supporting similar forest. All species included in the study are evergreen.

Data collection

Morphological measurements were made on 9–10 leaves collected from 7–24 individuals of the 16 most common tree and shrub species (Table 1) following the protocol outlined by Cornelissen et al. (2003). Leaf selection methods deviated slightly from the random transect method due to accessibility problems arising from steep terrain coupled with our desire for large sample sizes. We traversed a series of footpaths spanning the reserve between November 2006 and February 2007, and stopped in areas devoid of steep slopes (>40°, $n = 20$). In each of these sampling areas, a maximum of three individuals per species was selected for measurement. To promote a full representation of different-sized individuals from each species in the dataset, a stratified sampling design was adopted, whereby by small individuals (<the average height of each species at reproductive maturity) and large individuals (>the average height) were sampled alternately. While this sampling design gives an accurate representation of leaf morphology through ontogeny, it also yields estimates of plant height that are lower than their average height at reproductive maturity.

First, the height of each individual was measured to the nearest 0.1 m with an extendible ruler. Next, 3–4 small stems were cut from the top of each plant. Selected stems contained 2–20 leaves depending on the species, from which 10 leaves were randomly selected, sealed in plastic bags and transported to laboratory conditions for measurement. Leaves were refrigerated within 2 h of collection and completely analyzed within 36 h of being refrigerated. Analyses were restricted to undamaged leaves that were produced in the current growing season.

Leaves were individually placed on an hp scanjet 5400c computer scanner and a high resolution, black and white image was generated. Images were imported into ImageJ (Abramoff et al. 2004) and their length, width, area and perimeter were measured. Leaves were then dried to a constant mass in a drying oven (30°C), and leaf mass was measured to the nearest 0.01 mg with an electronic

Table 1 Functional group membership, sample sizes and average morphology (\pm SD) of study species

Species	Functional group	No. of plants sampled	No. of leaves sampled	Plant height	Leaf area (cm ²)	Specific leaf area (cm ² /gm)	Leaf circularity	Length to width ratio
<i>Beilschmiedia tawa</i> , Lauraceae	Tree	20	197	6.2 \pm 4.15	10.0 \pm 2.56	10.1 \pm 2.49	0.36 \pm 0.07	5.2 \pm 1.89
<i>Corynocarpus laevigatus</i> , Corynocarpaceae	Tree	19	190	4.6 \pm 2.80	62.3 \pm 2.70	11.5 \pm 2.89	0.66 \pm 0.05	2.2 \pm 0.21
<i>Dysoxylum spectabile</i> , Meliaceae	Tree	18	179	4.9 \pm 3.19	70.3 \pm 22.23	15.8 \pm 4.02	0.72 \pm 0.02	1.9 \pm 0.12
<i>Elaeocarpus dentatus</i> , Elaeocarpaceae	Tree	18	178	6.3 \pm 2.84	16.2 \pm 7.09	7.8 \pm 3.62	0.44 \pm 0.09	4.1 \pm 1.35
<i>Knightia excelsa</i> , Proteaceae	Tree	23	228	5.5 \pm 3.58	32.3 \pm 5.46	7.3 \pm 3.35	0.22 \pm 0.09	8.3 \pm 3.40
<i>Melicytus ramiflorus</i> , Violaceae	Tree	24	236	4.2 \pm 2.53	37.6 \pm 14.62	17.7 \pm 5.41	0.52 \pm 0.04	2.6 \pm 0.19
<i>Oleria rani</i> , Asteraceae	Tree	18	179	3.4 \pm 2.20	31.4 \pm 11.49	14.6 \pm 4.42	0.53 \pm 0.07	2.3 \pm 0.17
<i>Pittosporum eugenioides</i> , Pittosporaceae	Tree	21	210	4.7 \pm 3.49	21.5 \pm 3.82	11.8 \pm 4.26	0.53 \pm 0.04	2.8 \pm 0.22
<i>Brachyglottis repanda</i> , Asteraceae	Shrub	12	120	2.5 \pm 1.04	102.8 \pm 30.36	14.0 \pm 1.74	0.67 \pm 0.02	1.4 \pm 0.09
<i>Coprosma areolata</i> , Rubiaceae	Shrub	11	110	2.4 \pm 1.69	1.2 \pm 0.39	33.3 \pm 3.99	0.83 \pm 0.02	1.3 \pm 0.09
<i>Coprosma grandifolia</i> , Rubiaceae	Shrub	12	119	3.1 \pm 1.31	74.4 \pm 16.73	16.9 \pm 2.90	0.66 \pm 0.04	2.1 \pm 0.23
<i>Coprosma rhamnoides</i> , Rubiaceae	Shrub	7	70	0.8 \pm 0.24	0.4 \pm 0.07	23.0 \pm 4.13	0.74 \pm 0.05	1.8 \pm 0.32
<i>Coprosma robusta</i> , Rubiaceae	Shrub	11	110	2.4 \pm 1.22	34.1 \pm 16.45	11.3 \pm 3.10	0.63 \pm 0.04	2.3 \pm 0.24
<i>Geniostoma ligustrifolium</i> , Loganiaceae	Shrub	15	149	2.5 \pm 1.35	19.3 \pm 5.26	33.1 \pm 4.45	0.60 \pm 0.04	2.3 \pm 0.17
<i>Macropiper excelsum</i> , Piperaceae	Shrub	12	118	2.9 \pm 1.56	56.9 \pm 8.27	29.9 \pm 4.74	0.76 \pm 0.02	1.1 \pm 0.03
<i>Myrsine australis</i> , Myrsinaceae	Shrub	22	219	4.0 \pm 2.50	6.4 \pm 1.34	13.8 \pm 3.78	0.59 \pm 0.04	2.2 \pm 0.19

Nomenclature follows (Allan 1961 and Moore and Edgar 1970)

balance. From these measures, four dependent variables were calculated: total leaf area (cm²), specific leaf area (cm² g⁻¹), leaf circularity [$4\pi(\text{area} \cdot \text{perimeter}^{-2})$] and length to width ratio (length \cdot width⁻¹). One species (*Dysoxylum spectabile*) produces very large compound leaves that are too big to be scanned; we therefore restricted analyses to leaflets in this species, which were just small enough to fit on a standard computer scanner and are likely to be functionally equivalent to leaves (see Bongers and Popma 1990; Niinemets et al. 2007).

Analyses

Leaf trait diversity among leaves within individuals was investigated by obtaining the coefficient of variation (CV) of leaf area, specific leaf area, circularity and length to width ratio among all leaves collected from each individual. Two analyses were then conducted to test for vertical

gradients in leaf trait diversity at this scale. First, separate general linear models were conducted on the CV of each dependent variable, using height above the ground as a covariate and species as a fixed factor. Second, the four dependent variables were reduced into a single axis using principal component analysis. If the first principal component captured substantial amount of information contained in the four dependent variables, it was subjected to the same general linear model procedure applied to each dependent variable. Dependent variables were log₁₀ transformed when necessary to conform to homoscedasticity assumptions.

Leaf trait diversity among individuals within species was investigated by first obtaining the average value of each dependent variable for each individual. The coefficient of variation (CV) among individual averages for each dependent variable was calculated for each species and treated as the dependent variable in two statistical analyses.

First, the among-individual CV for each species was regressed against the average height of each species using least-squares regression. Separate analyses were conducted on each dependent variable. Second, the four dependent variables were reduced into a single axis using principal component analysis. If the first principal component captured a substantial amount of information contained in the four dependent variables, it was subjected to the same regression procedure used previously with each dependent variable. Data were again \log_{10} transformed to conform to assumptions, where necessary.

Leaf trait diversity among species within plant functional groups was assessed after amalgamating species into two growth form categories. ‘Trees’ were specifically defined as species that are typically >5-m tall at maturity. ‘Shrubs’ were defined as species that rarely, if ever, grow above 5 m. Trees were typically singled-stemmed and less than 1 m in diameter. Shrubs were typically rooted by multiple stems that had smaller diameters. To characterize interspecific morphological diversity within each guild, species averages for leaf area, specific leaf area, circularity and length to width ratio were subject to PROXAL multi-dimensional scaling (MDS) analyses in SPSS (2002). MDS is a multivariate procedure that is conceptually similar to principal components analysis, in that it reduces the information contained in the four dependent variables into a smaller number of variables, in this case two variables, which are referred to as dimensions. This inevitably results in the loss of some information, which is quantified by an inverse goodness-of-fit measure called ‘stress’. Stress values under 0.1 indicate that the two dimensions accurately reflect morphological differences among species (Sturrock and Rocha 2000). The relative positions of species in two (low stress) dimensions reflect overall differences in their morphology. Points situated close together represent morphologically similar species, while widely separated points represent morphologically divergent species.

To test for interspecific differences in leaf trait diversity among functional groups, the Euclidean distances between each species and its group centroid were calculated according to the following formula:

$$\sqrt{(p_x - q_x)^2 + (p_y - q_y)^2},$$

where ‘ p ’ is the mean value for the functional group, ‘ q ’ is the value for a given species and ‘ x ’ and ‘ y ’ are MDS dimensions one and two, respectively. Euclidean distances between each species and its group centroid were then subjected to single factorial ANOVA. A functional group containing species with greater average Euclidean distances would indicate higher morphological diversity than a group with lower Euclidean distances.

Results

Scale-dependent vertical gradients in leaf trait diversity were observed. At the smallest scale of resolution, morphological diversity was unrelated to plant height. The coefficient of variation among leaves within individuals differed among species, but was unrelated to plant height in all four leaf traits (Table 2). The first principal component (PC1) captured 46% of the variation contained in all four leaf traits (Eigen value = 1.836), and was positively associated with leaf area ($R = 0.475$), circularity ($R = 0.865$), length to width ratio ($R = 0.928$), but not specific leaf area ($R = -0.012$). PC1 was also unrelated to plant height (Fig. 1; Table 2).

Leaf trait diversity increased vertically at the intermediate scale. The coefficient of variation increased with the average height of each species for specific leaf area ($R^2 = 0.493$, $F_{1,14} = 15.567$, $P = 0.001$), leaf circularity ($R^2 = 0.305$, $F_{1,14} = 7.583$, $P = 0.016$) and length to width ratio ($R^2 = 0.202$, $F_{1,14} = 4.804$, $P = 0.046$). However, the coefficient of variation in leaf area ($R^2 < 0.001$, $F_{1,14} = 0.156$, $P = 0.699$) did not increase with plant height. The first principal component captured 62% of the variation contained in leaf traits (Eigen value = 2.481), and was positively associated with specific leaf area ($R = 0.847$), length to width ratio ($R = 0.915$) and circularity ($R = 0.962$), but not leaf area ($R = -0.011$). PC1 also increased with plant height (Fig. 1; $R^2 = 0.356$, $F_{1,14} = 9.309$, $P = 0.009$).

At the largest scale, leaf trait diversity was higher in shrubs than in trees. A relatively low level of stress was generated in multi-dimensional scaling analysis (stress = 0.051). Therefore, when plotted in the two corresponding dimensions, distances separating species accurately reflect differences in their morphology (Fig. 2). Euclidean distances between each species and the centroid for each functional group were higher in shrubs than in

Table 2 Results of general linear model analyses of among-individual variation in leaf morphology (i.e. the coefficient of variation among leaves within plants) using plant height as a covariate and species as a fixed factor

Effect	df	Area	SLA	Circularity	Length to width ratio	PC1
Height	1, 231	<0.1	0.2	0.8	<0.1	0.1
Species	15, 231	3.3*	1.6 ^{ns}	9.3*	4.1*	7.2*

Separate analyses were conducted on leaf area (cm^2), specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$), leaf circularity [$4\pi(\text{area} \cdot \text{perimeter}^{-2})$], leaf length to width ratio ($\text{length} \cdot \text{width}^{-1}$) and the first axis generated by principal component analysis of the four leaf traits (PC1), which captured 46% of the variation among the four dependent variables

^{ns} = $P > 0.20$, * $P < 0.001$

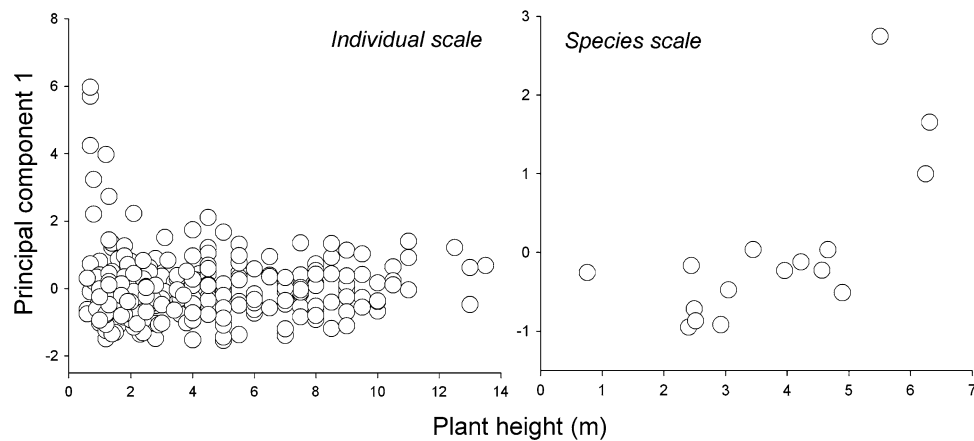
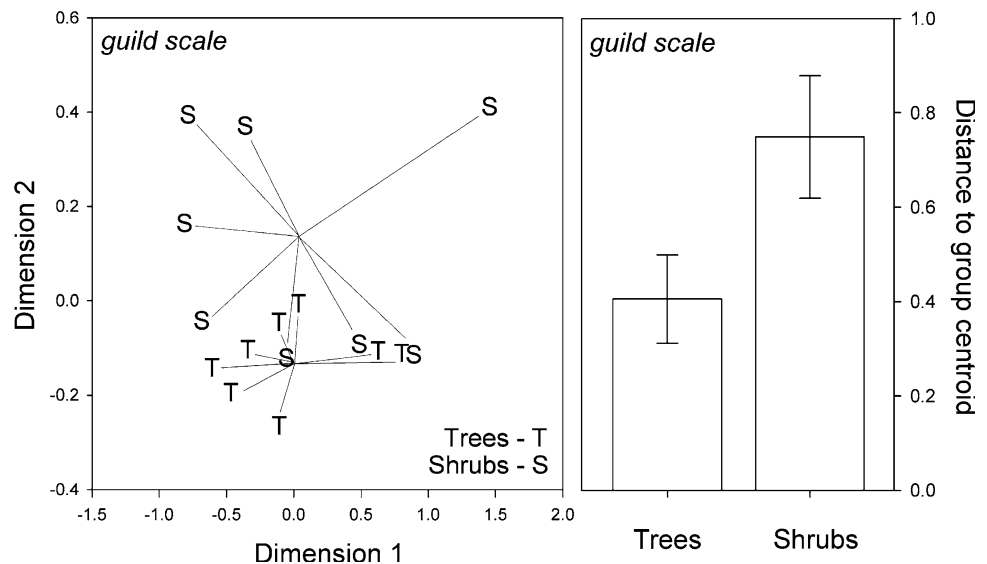


Fig. 1 Vertical patterns in leaf trait diversity at the small (*left*) and intermediate (*right*) scales of analysis. The y-axis is the first axis generated by principal component analysis of the coefficient of variation (CV) of leaf area, circularity, length to width ratio and specific leaf area. At the small scale, it accounts 46% of the variation

in among-leaf CV's of the four leaf traits and is positively correlated with leaf area, circularity and length to width ratio. At the intermediate scale it accounts 62% of the variation in among-individual CV's of the four leaf traits and is positively correlated with specific leaf area, circularity and length to width ratio

Fig. 2 a Species averages of leaf area, circularity, length to width ratio and specific leaf area reduced onto two dimensions using multi-dimensional scaling. Different symbols are used for different functional groups (*T* trees, *S* shrubs). Lines connect each species to their functional group centroid. **b** Average Euclidean distances between each species and the centroid for each functional group (\pm SE)



trees ($F_{1,14} = 4.609$, $P = 0.049$), indicating that the smaller functional group had higher leaf trait diversity than the taller group.

Discussion

Vertical gradients in leaf trait diversity were observed; however, they were strongly scale-dependent. Height-related trends were not observed at the smallest scale. Leaf trait diversity increased vertically at the intermediate scale, with taller species showing greater among-individual diversity than shorter plant species. Conversely, leaf trait diversity decreased vertically at the largest scale, with

shrubs showing greater morphological diversity than trees. Therefore, vertical patterns in leaf trait diversity were reversed on the two scales where they occurred.

The absence of a diversity gradient at the smallest scale indicates that morphological differences among immediately adjacent leaves were unrelated to their vertical location within the forest canopy. At this relatively small spatial scale, environmental conditions such as light, temperature and humidity are relatively homogeneous (see Chazdon and Fetcher 1984; Kira and Yoda 1989; Oshima et al. 1997). Therefore, if leaf shape diversity increased with environmental heterogeneity, consistent changes in leaf trait diversity with plant height might not be expected at this scale. This interpretation is consistent with previous

work on intracanopy variation in leaf morphology, which illustrates that leaf traits are more closely associated with light availability than to canopy height per se (Niinemets 1998; Sack et al. 2006).

Although among-leaf morphological diversity did not vary with plant height, average trait values did vary vertically (Burns and Beaumont 2008). Average leaf area and specific leaf area (SLA) declined with plant height. These patterns are consistent with previous research on the adaptive significance of both traits. Large, high SLA leaves harvest low levels of diffuse radiation more efficiently than small, low SLA leaves, which perform more efficiently in high light environments (see Burns 2004 and references within). Additionally, at this scale, leaf circularity increased with plant height, while length–width ratios declined. Leaf shape also varies vertically within species at other locales and could be associated with vertical changes in light, temperature or mechanical costs (Vogel 1970; Givnish 1987; Kincaid et al. 1998; Ali and Kikuzawa 2005; Sack and Frole 2006; Niinemets et al. 2007). Alternatively, it could be associated with herbivory (Rauscher 1978). Heteroblasty (i.e., sudden, significant changes in morphology during ontogeny) is a common feature in the New Zealand flora (see Cockayne 1912; Day 1998; Burns and Dawson 2006). Heteroblasty is often attributed to extinct browsing birds (see Givnish et al. 1994; Bond et al. 2004; Bond and Silander 2007). Extant ratites swallow leaves by positioning them in their bill and then snapping their head forwards to orient leaves down their oesophagus, in a manner similar to herons when swallowing fish (Bond et al. 2004). Long, narrow leaves could therefore be more difficult for toothless birds to swallow, and are produced by juvenile plants of many heteroblastic species (Burns and Dawson 2006), including two of the three largest tree species studied here (*Eleaocarpus dentatus* and *Knightia exsisa*).

Results from the intermediate scale showed that taller plant species express a greater range of SLA, leaf circularity and length to width ratios than shorter plant species. Leaf trait diversity gradients at this scale result from greater differentiation between individuals, which often differed in size. Although a range of different-sized individuals was sampled in all species, samples from shorter species necessarily came from a smaller range of heights above the forest floor, because shorter species inhabit a smaller range of the forest's vertical profile. Conversely, individuals from taller species occupy a greater range of the forest's vertical profile. Many environmental characteristics, including light, temperature and humidity, change vertically in forested environments (Chazdon and Fetcher 1984; Kira and Yoda 1989; Oshima et al. 1997). Therefore, greater leaf trait diversity in taller species likely results from increased morphological plasticity associated with greater variation in environmental conditions across the

forest's vertical profile. Similar results have been found elsewhere (Osada et al. 2001; Yáñez-Espinosa et al. 2003), including Popma et al. (1992) and Valladares et al. (2000) who found that gap-dependent shrubs have greater morphological plasticity than understory shrubs, which may be attributed to greater environmental heterogeneity in tree-fall gaps.

In addition to vertical gradients in leaf trait diversity, average trait values also varied among species (Burns and Beaumont 2008). While average leaf area was unrelated to the average height of each species, taller species had lower SLA, which likely increases photosynthetic efficiency in high light environments. Leaves from taller species were also less circular and had greater length to width ratios. Greater leaf elongation in canopy species may enhance leaf structural support in high winds (see Jaffe and Forbes 1993; Niinemets et al. 2007) or reduce heat stress by promoting conductance (Sack and Frole 2006).

Results from the largest scale indicate that shrubs have greater leaf trait diversity than trees. Tree-fall gaps are a common feature of New Zealand forests and promote spatio-temporal variation in environmental conditions (Martin and Ogden 2006). Immediately after tree-fall, light and temperature increase while soil moisture levels decline (see Canham et al. 1990). However, these changes are not permanent and conditions gradually revert back as the fallen tree is replaced. Shrub species could be differentially adapted to exploit suites of environmental conditions that occur at particular stages of recovery from tree-fall gaps (Denslow 1980). Some species may have leaf traits that enable them to maximize growth and reproduction immediately following tree-fall, while others may be better able to exploit undisturbed forest patches (Bragg and Westoby 2002; Houter and Pons 2005). Although affinities to light have yet to be quantified for the study species, interspecific differences in environmental preferences seem pronounced, with some species being found mostly in disturbed, high light environments (e.g., *Mrysiene australis*), while others occur mostly in the forest understory (e.g., *Geniostoma ligustrifolium*). Conversely, trees are likely to experience both gap and undisturbed conditions as they recruit into the canopy. Taller plants generally grow more slowly than shorter plants (Brown et al. 2004), so trees are unlikely to reach the forest canopy during a single tree-fall gap recovery sequence. Long-lived trees are likely to be exposed to a wide range of environmental conditions during growth, which may promote intraspecific variation within leaf traits in this functional group. Conversely, short-lived shrubs may complete their life cycle within particular stages of tree-fall gap recovery.

Future work on leaf trait diversity gradients may benefit from investigating several other leaf traits that were not considered here. For example, leaf inclination and

growth rate responses to increases in irradiance are important structural traits and may contribute substantially to leaf trait diversity patterns (Niinemets 1998; Poorter and Bongers 2006). Within-crown variation in leaf morphology was also not considered here, but could be an interesting source of variation in leaf trait diversity (Gratani et al. 2006). Similarly, differences in plasticity between life history stages (i.e., seedlings vs. adults) could also be investigated.

Similar to studies on species diversity, the patterns observed in this study are not easily amenable to manipulations. Therefore, the processes responsible for the leaf trait diversity gradients observed here are difficult to pinpoint. Although results from all three scales can be interpreted as scale-dependent adaptations to environmental conditions, other explanations are possible. For example, biotic interactions such as competition and herbivory could also be important (see Cody 1986; Hanley et al. 2007). A second feature of this study that is similar to studies of species diversity is that patterns in leaf trait diversity differed strongly among scales. Scale-dependent results are a common feature of biodiversity research and gradients in species diversity often differ in space and time (Blackburn and Gaston 2002). Spatial variation in leaf trait diversity gradients is currently unresolved and additional work is needed to determine whether similar gradients occur in other forests.

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