

ECOLOGY OF LEAF TEETH: A MULTI-SITE ANALYSIS FROM AN AUSTRALIAN SUBTROPICAL RAINFOREST¹

DANA L. ROYER,^{2,6} ROBERT M. KOOYMAN,^{3,4} STEFAN A. LITTLE,⁵ AND PETER WILF⁵

²Department of Earth and Environmental Sciences, Wesleyan University, Middletown, Connecticut 06459 USA; ³Department of Biological Sciences, Macquarie University, Sydney, NSW 2109 Australia; ⁴National Herbarium of NSW, Sydney, NSW 2000 Australia; and ⁵Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania 16802 USA

Teeth are conspicuous features of many leaves. The percentage of species in a flora with toothed leaves varies inversely with temperature, but other ecological controls are less known. This gap is critical because leaf teeth may be influenced by water availability and growth potential and because fossil tooth characters are widely used to reconstruct paleoclimate. Here, we test whether ecological attributes related to disturbance, water availability, and growth strategy influence the distribution of toothed species at 227 sites from Australian subtropical rainforest. Both the percentage and abundance of toothed species decline continuously from riparian to ridge-top habitats in our most spatially resolved sample, a result not related to phylogenetic correlation of traits. Riparian lianas are generally untoothed and thus do not contribute to the trend, and there is little association between toothed riparian species and ecological attributes indicating early successional lifestyle and disturbance response. Instead, the pattern is best explained by differences in water availability. Toothed species' proportional richness declines with proximity to the coast, also a likely effect of water availability because salt stress causes physiological drought. Our study highlights water availability as an important factor impacting the distribution of toothed species across landscapes, with significance for paleoclimate reconstructions.

Key words: Australia; disturbance; fire; leaf physiognomy; leaf teeth; lianas; life history traits; paleoclimate; rainforest; riparian habitats.

The sensitivity of leaf teeth to climate is well known and widely reported. Notably, a significant, negative correlation between the percentage of nonmonocot (“dicot”) woody angiosperms in mesic floras with toothed leaves and mean annual temperature (MAT) has been observed in East Asia, the Americas, Europe, and Australia (Bailey and Sinnott, 1915, 1916; Webb, 1959; Wolfe, 1979, 1993; Wilf, 1997; Gregory-Wodzicki, 2000; Kowalski, 2002; Greenwood et al., 2004; Greenwood, 2005a; Traiser et al., 2005; Hinojosa et al., 2006; Adams et al., 2008; Aizen and Ezcurra, 2008). Recent work in present-day eastern North American forests demonstrates that the size and number of teeth also correlate negatively with MAT (Huff et al., 2003; Royer et al., 2005, 2008). However, despite leaf teeth being strongly linked to temperature, less is known about their sensitivity to most other ecological variables (e.g., Halloy and Mark, 1996; Kappelle and Leal, 1996; Royer et al., 2008).

¹ Manuscript received 18 August 2008; revision accepted 11 December 2008.

This research arose from a working group of the ARC-NZ Research Network for Vegetation Function, supported by the Australian Research Council; the authors thank M. Westoby (Macquarie University) for organizing the Network. They also thank C. Allen (Royal Botanic Gardens, Sydney) for constructing Fig. 1, R. Gallagher (Macquarie University) for extracting interpolated climate data, and R. Burnham and D. Greenwood for helpful reviews. Work was supported in part by funding from Rainforest Rescue (to R.M.K.) and by grants from the National Science Foundation (grants DEB-0345750 to P.W. and EAR-0742363 to D.L.R.), the David and Lucile Packard Foundation (to P.W.), and the Petroleum Research Fund of the American Chemical Society (grant 40546-AC8, to P.W. and D.L.R.). This paper is dedicated to the memory of Professor Len J. Webb (1920–2008) and his contributions to rainforest botany and ecology. His work valued the role of leaves in understanding the lives of trees and linked paleobotany, neobotany, and ecology in the exploration of evolutionary patterns.

⁶ Author for correspondence (e-mail: droyer@wesleyan.edu)

The primary goal of this study is to examine how ecological attributes related to disturbance, water availability, and growth strategy influence the distribution of toothed species at 227 sites in the humid Australian subtropics (Fig. 1). Specifically, we determine how topographic position (ridge crest to creek/gully) and distance to coastline impact the relative richness and abundance of toothed species, including possible underlying causes. Because attributes of fossil leaf teeth, particularly the percentage of toothed species at a single locality, are important components of several paleoclimate methods (e.g., Bailey and Sinnott, 1915; Wolfe, 1979, 1993; Wilf, 1997; Royer et al., 2005; Greenwood, 2007), we discuss how our results may affect these approaches. For example, habitat-related differences in the distribution of toothed species may generate errors in paleoclimate reconstruction if habitats differ greatly between calibration and fossil sites. Our work also contributes to knowledge on leaf-teeth ecology in Gondwanan floras, a topic little studied by comparison to the northern hemisphere (e.g., Webb, 1968; Greenwood et al., 2004; Aizen and Ezcurra, 2008).

Our study area encompasses two forest community types (sensu Webb, 1968, 1978): simple notophyll vine forest (SNVF) and complex notophyll vine forest (CNVF). Because MAT varies minimally across sites (<3°C), we can closely examine the influences of more subtle factors on leaf teeth using dense sampling. Measured attributes include six environmental variables (topographic position, soil depth, slope, elevation, fire return frequency, disturbance; see Table 1), growth form (liana, tree, shrub), and eight life-history traits (seed and fruit size, fruit type, dispersal mode, ability to resprout after disturbance, and leaf size, lobing, and compounding; see Table 2). Our specific hypotheses are outlined next.

Freshwater-margin hypothesis—Burnham et al. (2001) observed that the percentage of toothed species at one lake margin and three riparian sites in the Ecuadorian lowlands was ~15% higher than at two nearby distal floodplain and terra firme sites.

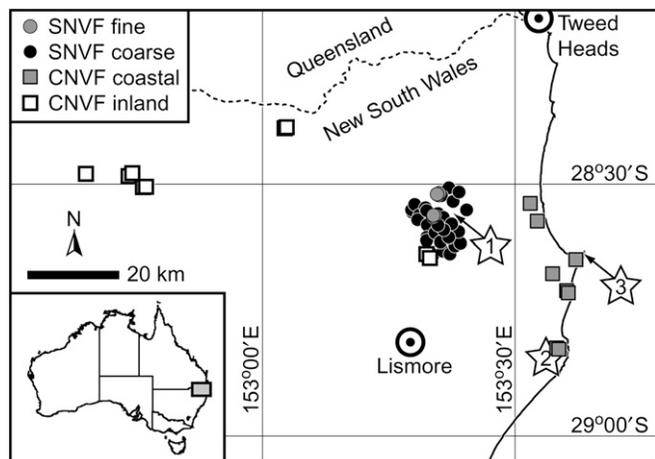


Fig. 1. Map of study area. Sites are coded by sample: SNVF fine ($N = 100$ sites), SNVF coarse (92), CNVF coastal (11), CNVF inland (24). Numbers within stars represent climate stations used in study: 1 = Whian Whian/Rummary Park; 2 = Ballina Airport; 3 = Byron Bay. Tweed Heads and Lismore are cities.

Greenwood (2005b) reported a similar pattern for leaf litter samples from seven riparian and 30 nonriparian sites in eastern Australia (northern Queensland to Victoria). Kowalski and Dilcher (2003) also observed relatively higher proportions of toothed species at three eastern North American sites adjacent to lakes or swamps. The presence of this “freshwater effect” is important because, if pervasive, it implies that many paleoreconstructions of MAT based on the percentage of toothed species may be too cold, because habitats adjacent to rivers, lakes, and swamps are infrequently included in extant calibrations but are the dominant depositional setting of fossil leaf assemblages (Wolfe, 1977; Burnham et al., 2001; Kowalski and Dilcher, 2003; Greenwood, 2005b). A difference of 15% in toothed species translates to a $\sim 4.5^\circ\text{C}$ difference in estimated MAT using most calibrations.

Kowalski and Dilcher (2003) postulated that differences in water availability (e.g., soil moisture) across a landscape can explain the freshwater effect. It has long been noted that water availability impacts the presence of leaf teeth (but usually to a lesser degree than MAT; Wolfe, 1993): humid to mesic sites often contain a greater fraction of toothed species than drier sites with the same MAT (Bailey and Sinnott, 1915; Wolfe, 1993). This effect may therefore explain the preponderance of toothed species at freshwater-margin sites with high water tables relative to nearby, better-drained sites.

Most studies that address why leaves have teeth are consistent with colder and/or wetter environments containing proportionately more toothed species, and with teeth being major sites

TABLE 1. Environmental variables and rankings (modified after Rossetto and Kooyman, 2005). Two environmental variables, slope ($^\circ$) and elevation (m a.s.l.), were measured directly and not ranked.

Topographic position	Soil depth (cm)	Fire return frequency (yr)	Disturbance
1 Creek/gully	1 <30	1 <100	1 None
2 Lower slope	2 30–50	2 100–250	2 Light
3 Midslope	3 50–80	3 250–500	3 Moderate
4 Upper slope	4 >80	4 >500	4 Heavy
5 Crest		5 No fire	

of water loss. The possible role of heightened transpiration in leaf teeth was noted over a century ago (Billings, 1905; Bailey and Sinnott, 1916; Canny, 1990; Wolfe, 1993). More recently, Feild et al. (2005) observed that leaf teeth in the herbaceous basal angiosperm *Chloranthus japonicus* prevent the flooding of intercellular airspaces via guttation of excess fluid. In this case, teeth are probably adaptive in wet and seasonally freezing environments where positive root pressure and freeze–thaw embolisms, respectively, are common (Feild et al., 2005). In a separate study, Royer and Wilf (2006) measured rates of photosynthesis and transpiration in 60 woody dicot species from two differing climates in eastern North American deciduous forest, finding high rates in teeth early in the growing season; moreover, these early season rates were typically higher in the plants native to the colder climate. In this case, teeth are probably adaptive for rapidly acquiring carbon in cold, mesic environments, where growing-season length is limiting but access to water is not (Royer and Wilf, 2006; see also Baker-Brosch and Peet, 1997).

Burnham et al. (2001) suggested that the diversity of lianas in riparian and lake-margin habitats may also help to explain the freshwater effect because, at their Ecuadorian sites, a high proportion of liana species are toothed. Liana diversity in these environments is likely controlled, in part, by water availability because lianas typically have long, wide vessels that make them prone to water stress (Wheeler and LaPasha, 1994; Carlquist, 2001). The interaction between lianas, habitat position, and toothed leaves has not been investigated outside of Ecuador, and so the geographic extent of this liana effect is unknown.

However, lianas do not fully account for the freshwater effect in the Ecuadorian lowlands (Burnham et al., 2001). Therefore, Burnham et al. (2001) additionally argued that the disturbed, open character of many habitats adjacent to freshwater (especially lakes and rivers) may select against untoothed species (see also Kappelle and Leal, 1996). This putative selection occurs because rapid growth is often advantageous in disturbed, open environments (e.g., Grime, 1977, 2001; Garnier et al., 2004), and leaf teeth may facilitate periods of fast growth (Royer et al., 2005; Royer and Wilf, 2006; see previous discussion about tooth function).

TABLE 2. Life history traits and rankings (modified after Rossetto and Kooyman, 2005).

Teeth	Seed size (mm)	Fruit size (mm)	Fruit type	Dispersal mode*	Resprout**	Leaf size***	Lobed leaves	Compound leaves
0 No	1 <1	1 <1	0 Nonfleshy	0 Wind	0 No	1 Nanophyll	0 No	0 No
0.5 Sometimes†	2 1–6	2 1–6	1 Fleshy††	1 Frugivore	1 Yes	2 Microphyll	0.5 Juvenile only	1 Yes
1 Yes	3 6–15	3 6–15				3 Notophyll	0.75 Sometimes	
	4 15–30	4 15–30				4 Mesophyll	1 Yes	
	5 >30	5 >30				5 Macrophyll		

Notes: * All other dispersal modes excluded (e.g., scatter-horde, ants); ** Restricted to resprouting in response to disturbance; *** After Webb (1978), juvenile plants excluded; † Includes species whose leaves are toothed in juvenile plants but untoothed in adults; †† Includes arils.

Here, we investigated the association between leaf teeth and riparian habitats, including possible underlying mechanisms. We focused primarily on a subset of sites where other environmental gradients that may impact the presence of leaf teeth are minimal ("SNVF fine" sample; see Materials and Methods for descriptions of this and three supplemental samples). This work builds on previous research in four significant ways. First, we analyzed a large number of sites ($N = 227$ total [100 sites in SNVF fine] vs. 6 for Burnham et al. [2001] and 37 for Greenwood [2005b]). Second, we coded our sites for five topographic positions from ridge crest to creek/gully (Table 1), which contrasts with the binary coding of previous studies; thus, our methodology allows for testing the influence of a more continuous habitat gradient on leaf teeth. Third, we coded all species for relative abundance as well as presence vs. absence; this allows for a more thorough analysis of community dynamics, including, for example, whether toothed species compose a greater fraction of the canopy in riparian vs. nonriparian habitats. Fourth, we tested whether phylogenetically inherited syndromes may be a factor influencing the relative abundance of toothed taxa with other traits across sites. It is generally assumed that phylogenetic history has minimal impact, relative to climate, on the prevalence of teeth in a flora (Bailey and Sinnott, 1916; Wolfe, 1993), but this assumption has only recently begun to be tested (Little et al., 2008).

Salt stress hypothesis—Salt stress is a form of physiological water stress (Larcher, 1995); thus, as a general extension of the water-availability hypothesis, toothed species should be less common in salt-stressed environments. This relationship has been reported anecdotally (e.g., Bailey and Sinnott, 1915), but here we quantify the strength of correlation with 11 coastal sites that are directly impacted by salt spray ("CNVF coastal" sample; Fig. 1).

Leaf teeth and variables related to growth strategy—We also test whether environmental and life history variables that are commonly associated with rapid growth and an early successional status are correlated with the presence of leaf teeth. This test helps to assess the disturbance explanation for the freshwater effect because rapidly growing, early successional species often dominate in disturbed habitats (discussed earlier). Examples of appropriate variables measured here include fire return frequency, ability to resprout after disturbance, presence of lobed and compound leaves, seed and fruit size, fruit type (fleshy vs. nonfleshy), and seed dispersal mode (wind vs. animal) (Tables 1, 2). Early successional species are common in fire-dominated landscapes, even when the fire return frequency exceeds a century (Engelmark et al., 1998; Falster and Westoby, 2005; Spencer and Baxter, 2006). Compound leaves are considered to be common in habitats with light gaps where there is a premium on rapid growth because they can be easily shed when overtopped, leaving fewer understory branches behind, thereby conserving water and structural resources (Givnish, 1978b, 1984), and lobed leaves are considered abundant in rapidly growing, early successional forests (Givnish, 1978a). Small, nonfleshy, wind-dispersed seeds are more common in disturbed, open habitats than in closed forests (Baker, 1972; Salisbury, 1974; Foster and Janson, 1985; Westoby et al., 1992; Givnish et al., 2005), and fruit size typically tracks seed size very closely (Wright et al., 2007). In combination with direct measurements of site disturbance (Table 1) and with published observations of growth rate and successional status, these associations allow a

multifaceted analysis of the possible link between leaf teeth and growth strategy.

Toothless Australia hypothesis—The correlation between the percentage of toothed species and MAT is as strong in eastern Australian rainforests as elsewhere, but Greenwood et al. (2004) reported a generally lower percentage (~15%) of toothed species for a given MAT relative to the global norm (different y -intercept). Greenwood et al. (2004) used 113 rainforest sites from Webb et al. (1984) that span from north Queensland to Tasmania. Here we compare the patterns observed by Greenwood et al. (2004) to a data set with a higher spatial resolution and more limited climatic and geographic range. We predict similar patterns but with greater scatter because of our increased emphasis on capturing secondary factors that affect the presence of toothed species (e.g., topographic position, elevation).

MATERIALS AND METHODS

Study area—Our study area is in northern New South Wales, eastern Australia (Fig. 1). It is located on the eroded Mt. Warning (Wollumbin) volcanic caldera, which is comprised of rhyolitic cliffs and basaltic plateaus deeply dissected by eroded stream bases; these streams form an almost circular radiating network of valleys around the central caldera. The geological history is described in Stevens (1977), and detailed soil mapping is provided in Morand (1994, 1996). The climate is subtropical with seasonally (summer-autumn) high rainfall (mean annual precipitation [MAP] ≈ 2000 mm) and generally mild temperatures (MAT $\approx 18^\circ\text{C}$; annual range in mean monthly temperatures $\approx 10^\circ\text{C}$); Nix (1991) places the area in the Mesotherm bioclimatic region.

Both the simple notophyll vine forest (SNVF) and complex notophyll vine forest (CNVF) community types were intensively sampled by R. M. Kooyman across a range of environmental and life history gradients (Tables 1, 2). The SNVF has relatively low complexity in regard to structure and floristics and is often dominated by just a few species. Cunoniaceae are the dominant canopy trees; other families present in the canopy include Elaeocarpaceae, Lauraceae, Monimiaceae, Myrtaceae, Rutaceae, and Atherospermataceae. The CNVF community type is the most species-rich and diverse rainforest in the region with strong floristic affinities to the more tropical northeastern Australian rainforests; dominant families include (as examples) Malvaceae, Myrtaceae, Ebenaceae, Moraceae, Lauraceae, Rutaceae, Rubiaceae, Sapindaceae, and Euphorbiaceae. Due to the minor presence of *Araucaria cunninghamii* at our sites, the formal community types are "SNVF $\pm A. cunninghamii$ " and "CNVF $\pm A. cunninghamii$ " (sensu Webb, 1968), but for convenience we adopt SNVF and CNVF throughout. Because species composition varies within the SNVF and CNVF community types along the Australian east coast (Webb, 1959, 1968), all patterns attributed here to the SNVF and CNVF refer specifically to our study area. All analyses are restricted to woody dicots because they are the basis of most previous work on tooth variation and paleobotanical leaf-climate methods.

SNVF samples—The SNVF was sampled at two spatial scales. The fine-scale sample, here termed "SNVF fine", includes 100 sites from two 4-ha areas within the Nightcap National Park and Mt. Jerusalem National Park (Fig. 1; Kooyman, 2005). Each 4-ha area was divided into a grid of 200×200 m squares using the Central Mapping Authority 1:25000 topographical map (Hunbrook Map Sheet 9540-1-N). Ten grid squares were chosen at random for both areas; in each square, five 20×20 m quadrats were located in differing topographical positions representing crest, upper slope, midslope, lower slope, and creek/gully. A total of 50 quadrats were established at each of the two locations, making a total of 100 quadrats (sites) in the combined sample. Species richness among woody dicots ranges from 20 to 47 (median = 34) and among lianas from 0 to 8 (median = 4). Important environmental gradients in this sample include topographic position, slope (range: $3\text{--}35^\circ$), and soil depth (range: <30 to >80 cm); variation in site elevation is minimal (565–800 m a.s.l.).

We largely restrict our interpretations of how topographic position impacts the presence of toothed species to the SNVF fine sample because, in contrast to the other three samples, site selection was based on topographic position and all topographic categories are evenly represented. Also, because the SNVF fine

sample is the most geographically restricted (Fig. 1), other environmental gradients that may potentially impact the presence of leaf teeth are generally weaker and less likely to be influential than in the other samples.

The coarse-scale SNVF sample (SNVF coarse) covers 9.2 ha and is comprised of 92 (50 × 20 m) quadrat plots, with nested 20 × 20 m subplots (Fig. 1; see also Rossetto and Kooyman, 2005). Compared to the fine-scale SNVF, this sample includes a broader mix of environmental gradients and species composition. Species richness among woody dicots ranges from 18 to 61 (median = 38.5) and among lianas from 0 to 10 (median = 4). Important environmental gradients in this sample include disturbance, fire return frequency (range: <100 yr to no fire), and elevation (160–790 m a.s.l.). The MAT for sites in both SNVF samples is approximately 17.5°C (Whian Whian/Rummery Park climate station), but MAT is more variable among sites in the coarse-scale SNVF sample because of its larger elevation gradient (range in interpolated MAT across sites = 1.9 and 0.3°C for SNVF coarse and SNVF fine samples, respectively; Hijmans et al., 2005; see Appendix S1 in Supplemental Data with the online version of this article). All SNVF sites occur on rhyolite-derived (acid volcanic) soils.

CNVF samples—The CNVF sites represent 20 × 20 m nested subplots within 50 × 20 m plots (Fig. 1; see Kariuki and Kooyman, 2005; Kariuki et al., 2006; Kooyman and Rossetto, 2006). All CNVF sites are on basalt-derived soils. We partitioned sites into two samples based on distance to coastline. The CNVF coastal sample contains 11 sites that are within 1.5 km of the coast; these plant communities are directly impacted by salt spray. The MAT at these sites is 19.7°C, and the MAP is 1735 mm (Byron Bay and Ballina Airport climate stations). Species richness among woody dicots ranges from 22 to 89 (median = 36) and among lianas from 5 to 11 (median = 6).

The CNVF inland sample contains 24 sites. The climate is somewhat cooler (MAT = 17.5°C) and wetter (MAP = 2319 mm; Whian Whian/Rummery Park climate station; stations closer to the western sites are unsuitable because they are not in forested terrain and thus are substantially drier) than the coastal sample owing to its higher elevation (190–875 m a.s.l.). Species richness among woody dicots ranges from 58 to 92 (median = 79) and among lianas from 9 to 20 (median = 13.5). Disturbance and elevation are the strongest environmental gradients in this sample; variation in topographic position is minimal, particularly in comparison to the fine-scale SNVF sample.

Across all samples, soils are wetter at creek/gully sites than at ridge-crest sites (R. M. Kooyman, personal observation), due in part to creek/gully sites having higher water tables and deeper soils (one-way ANOVA: $F_{4,198} = 8.9$, P

< 0.001 for all samples combined except CNVF inland, where soil depth was not measured). Thus, there is a water availability gradient for plants at our sites, controlled by topographic position.

We interpolated from climate station data that MAT varies ~3°C across all 227 sites (Hijmans et al., 2005; online Appendix S1). A 3°C change in MAT can account for an ~11% shift in the percentage of toothed species (using the Australia-specific calibration of Greenwood et al., 2004), which is small compared to the measured 45% range across our sites (Fig. 2). This disparity suggests that factors other than MAT (such as those measured for this study; see Tables 1, 2) are important for explaining the variability in the percentage of toothed species at our sites.

Data collection—All vascular plant species were identified to species level by R. M. Kooyman. Species cover codes (modified from Braun-Blanquet, 1932) were entered using a cover abundance scale (1–6), where 1 = cover <5% of site and rare, 2 = cover <5% of site and common, 3 = cover 6–20% of site, 4 = cover 21–50% of site, 5 = cover 51–75% of site, and 6 = cover 76–100% of site. In total, our study includes 344 woody dicot species and 7944 species-site pairs. Species lists and cover abundance data for each site are available in online Appendix S1.

Plant life-history traits were extracted by R. M. Kooyman from published sources provided in species taxonomic descriptions (e.g., Floyd, 1989; Harden, 1990–2002 with revisions) and, wherever possible, were based on measured data from published floras. The traits chosen reflect the dispersal dimension (seed and fruit size, fruit type, dispersal mode), persistence (resprouting), leaf size, and leaf growth form (lobed, simple/compound, presence of teeth) (Table 2; see online Appendix S1 for trait values of species). Because the gradients in life history traits are broadly similar across samples (in contrast with the environmental gradients, which vary in strength across samples, as described earlier), we place equal weight on all samples when interpreting the relationships between these traits and the presence of leaf teeth.

Environmental variables were quantified by R. M. Kooyman from field observations. The categorization of discrete environmental variables is described in Table 1, and site means of all environmental variables are available in online Appendix S1.

Phylogenetic analyses—A composite tree (Sanderson et al., 1998) was assembled by S. A. Little for the species in the fine-scale SNVF sample; we focused on this sample because of our interest in topographic position (discussed earlier). A backbone family phylogeny was obtained from the large-scale anal-

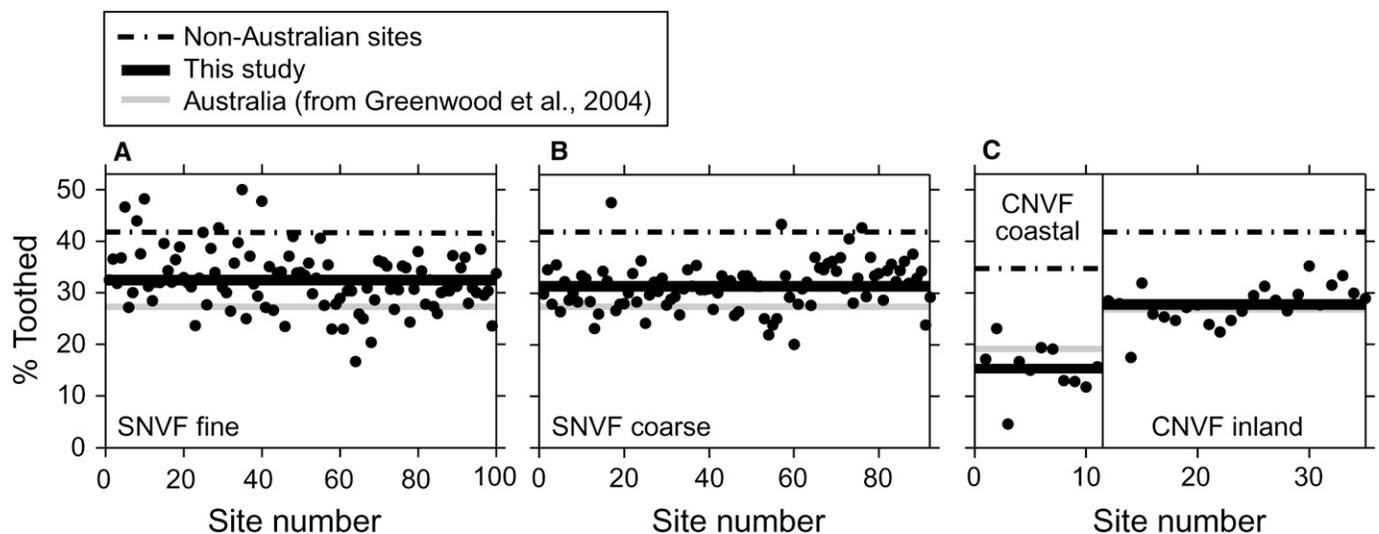


Fig. 2. Percentage of toothed species at sites. Dots represent individual sites grouped by sample: (A) SNVF fine, (B) SNVF coarse, (C) CNVF coastal and inland. For each sample, the solid black line represents the mean of all sites; solid gray line represents the sample mean prediction of percentage of toothed species based on the regression relating MAT to percentage of toothed species from eastern Australian rainforests (Greenwood et al., 2004); dashed line represents the sample mean prediction of percentage of toothed species using a worldwide compilation of the relationship between MAT and percentage of toothed species, but excluding Australian data. Worldwide compilation is from Green (2006) supplemented by Wolfe (1979), Wilf (1997), and Royer et al. (2005) ($N = 303$ data points); data from Wolfe (1979) were extracted from his fig. 8 using Engauge Digitizer open-source software (<http://digitizer.sourceforge.net>) (see online Appendix S1 for extracted data).

ysis of Soltis et al. (2007). The tree was further augmented by the insertion of clades resolved at lower taxonomic levels (glucosinolate-producing clade: Ronse De Craene and Haston, 2006; Malvales: Alverson et al., 1999; Sapindales, Biebersteiniaceae: Muellner et al., 2007; Rutaceae: Chase et al., 1999; Scott et al., 2000; Apocynaceae: Potgieter and Albert, 2001; Cunoniaceae: Bradford and Barnes, 2001; Lauraceae: Chandrabali et al., 2001; Li et al., 2004; Nie et al., 2007; Myrtaceae: Ladiges et al., 1999; Wilson et al., 2001, 2005; Lucas et al., 2007; Leguminosae: Wojciechowski et al., 2004; Proteaceae: Hoot and Douglas, 1998; Barker et al., 2007; Rosaceae (supertree): Vamossi and Dickinson, 2006; Rubiaceae: Bremer and Manen, 2000; Mouly et al., 2007). The program Mesquite (Maddison and Maddison, 2008) was used to assemble the tree by hand using only relationships between taxa that were present in the consensus trees from each study (Fig. 5); no apparent conflicts between tree topologies were noted. Where the relationships between species were poorly resolved or unknown, clades were entered as polytomies. All genera were assumed to be monophyletic and entered as a polytomy, except Lauraceae, where species of *Endiandra* and *Beilschmiedia* were entered as a polytomy (Chandrabali et al., 2001).

The mirror tree module in Mesquite (Maddison and Maddison, 2008) was used to visualize traits for apparent evolutionary correlation of the tooth character with the other variables (e.g., Fig. 5; for all trees see Appendix S2 in Supplemental Data with the online version of this article). No traits appeared to consistently co-occur with the tooth trait on the phylogeny of SNVF fine. Nonetheless, we binarized traits for use in Pagel's (1994) test of correlated evolution of traits to acquire significance values. Species that occasionally have toothed or lobed leaves were simply scored as toothed and lobed, respectively (see Table 2 for definitions of traits). For seed and fruit size, a threshold of 15 mm was used: species with a fruit or seed size <15 mm were placed in one category (categories 1–3 from Table 2) and >15 mm were placed in the other category (categories 4 and 5 from Table 2). For leaf size, species with nanophyll and microphyll leaves composed one category (categories 1 and 2 from Table 2) and notophyll, mesophyll, and macrophyll leaves the other (categories 3–5 from Table 2). Tests based on different categorical thresholds for seed, fruit, and leaf size returned similar results (online Appendix S2). For environmental variables, analyses were based on the mean state for each species across all sites (see Table 1 for definitions of variables); tests based on the mode state returned similar results (Appendix S2). For topographic position, we used a categorical threshold of 3 (creek/gully to midslope vs. midslope to crest); for soil depth and disturbance, we adopted 30 cm and 2 (none to light vs. light to heavy) as thresholds, respectively. Tests based on different categorical thresholds returned similar results (Appendix S2).

We ran Pagel's (1994) test for correlated evolution in discrete characters, as implemented in Mesquite's *correl* module (Midford and Maddison, 2006). Each of the binarized life history traits and environmental averages were analyzed with the leaf-margin trait (toothed vs. untoothed leaves). The test compares the ratio of likelihoods of two models: one model where the rates of change in each character are independent of the state of the other, and a sec-

ond model where rates of change depend on the state of the other character. The significance of the ratio is tested by comparison with simulated data. Simulations are run to obtain a null distribution of likelihood values, where the rates of character change are independent. The null distribution is then used to assess if the more complex model, where character changes are not independent, is significantly different (Midford and Maddison, 2006). We present *P*-values for 100 simulations with 10 likelihood search iterations per simulation and with all branch lengths equal to one (Table 3). Simulations performed with 1000 simulations, or longer branch lengths, did not improve significance.

RESULTS

Patterns in the percentage of toothed species across samples—Across all 227 sites, the percentage of toothed species ranges from 5% to 50% (Fig. 2). Ninety-five percent of sites in the SNVF fine, SNVF coarse, and CNVF inland samples contain between 22% and 43% toothed species; using the relationship between the percentage of toothed species and MAT from Australian rainforests (Greenwood et al., 2004), this translates to a 5.5°C local variability in estimated MAT. The percentage of toothed species at CNVF coastal is distinctly lower than the other three samples (Fig. 2; $t_{225} = -9.8$, $P < 0.0001$). Within the CNVF coastal sample, sites closest to the coast contain the lowest percentage of toothed species (Fig. 3).

Correlation between leaf teeth and topographic position—In the fine-scale SNVF sample, where topographic position is the strongest environmental gradient, the percentage of species with teeth declines continuously from riparian to ridge-crest habitats (Fig. 4; Table 4). This topographic gradient is only weakly resolved in the SNVF coarse and CNVF inland samples and is not resolved at all in the CNVF coastal sample (Table 4); however, topographic position is not the principal environmental gradient in these three samples (see Materials and Methods). Importantly, in the SNVF fine sample, the possession of leaf teeth and average topographic position for a species do not appear to be a phylogenetically coinherited

TABLE 3. Tests of correlated evolution of environmental and life history traits vs. leaf-margin character (toothed vs. untoothed) at fine-scale simple notophyll vine forest (SNVF) sites. Pagel's 94 test, as implemented in Mesquite's *correl* module, was used to assess significance for the two traits having correlated evolution (see Materials and Methods for details). No trait pairs consistently co-occur on the composite tree ($P > 0.05$ for all trait pairs; see online Appendix S2 for all tree comparisons). See Tables 1 and 2 and Materials and Methods for descriptions of variables.

Variable	<i>P</i>
Topographic position	0.57
Soil depth	0.79
Disturbance	0.76
Seed size	0.30
Fruit size	0.62
Fruit type	0.36
Dispersal mode	0.60
Resprout	0.61
Leaf size	0.29
Lobed leaves	0.69
Compound leaves	0.63

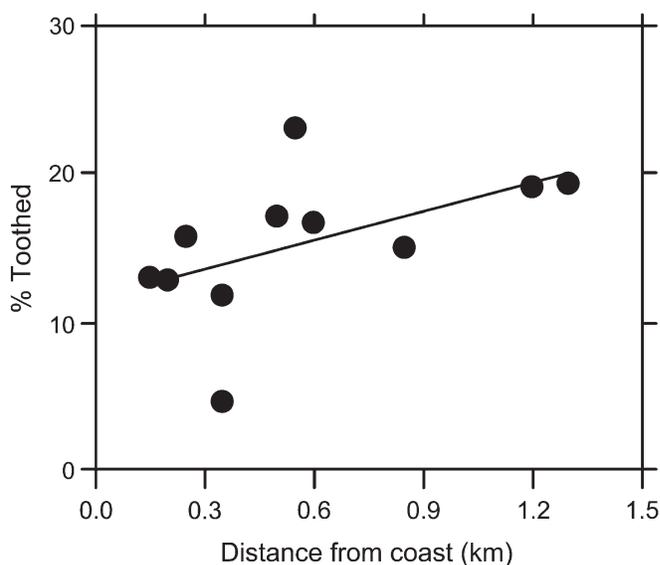


Fig. 3. Relationship between the percentage of toothed species and distance from coast for the CNVF coastal sample. Dots represent individual sites. Least-squares linear regression statistics: $r^2 = 0.27$, $P = 0.10$.

TABLE 4. Correlations between environmental variables and the percentage of toothed species. Correlations are based on site means for each sample. Correlations for topographic position, soil depth, fire return frequency, and disturbance were calculated using one-way ANOVA; correlations for slope and elevation were computed using least-squared linear regression. *N* = number of sites; *m* = slope of correlation; NA = not applicable, fire return frequency does not vary strongly in these samples; NM = not measured. Boldfaced correlations are statistically significant ($P \leq 0.05$). See Table 1 for descriptions of variables.

Sample	<i>N</i>	Topographic position		Soil depth		Slope			Elevation			Fire return frequency		Disturbance	
		<i>m</i>	<i>P</i>	<i>m</i>	<i>P</i>	<i>m</i>	<i>r</i> ²	<i>P</i>	<i>m</i>	<i>r</i> ²	<i>P</i>	<i>m</i>	<i>P</i>	<i>m</i>	<i>P</i>
SNVF fine	100	+	<0.001	+	<0.001	+	0.04	0.05	+	0.00	0.57	NA		+	0.24
SNVF coarse	92	+	0.11	+	0.14	+	0.01	0.33	–	0.07	0.01	+	0.006	–	0.54
CNVF inland	24	+	0.10	NM		+	0.12	0.10	+	0.16	0.05	NA		+	0.10
CNVF coastal	11	–	0.78	–	0.10	+	0.00	0.90	+	0.01	0.78	NA		–	0.90

syndrome, and thus are not likely to be causing the correlation across sites (Fig. 5; Table 3; online Appendix S2).

The strong association between leaf teeth and topographic position in the SNVF fine sample is retained even when quantified in terms of relative abundance: toothed species are more abundant in riparian settings than in ridge-crest settings (Fig. 6A). A species that highlights this pattern is *Sloanea australis* (Elaeocarpaceae), which grows almost exclusively in riparian habitats, where it is locally dominant (Fig. 6B). However, some species occur in all topographic positions and thus do not contribute substantially to the patterns observed in Figs. 4 and 6A; for example, *Ceratopetalum apetalum* (Cunoniaceae) is locally dominant at all 100 sites (Fig. 6C). The abundance of toothed species and topographic position are not strongly linked in the other three samples (see Fig. 7 for CNVF inland; analyses for other two samples are not shown). In the CNVF inland sample, elevation has a stronger impact on the abundance of toothed species than does topographic position (Fig. 7).

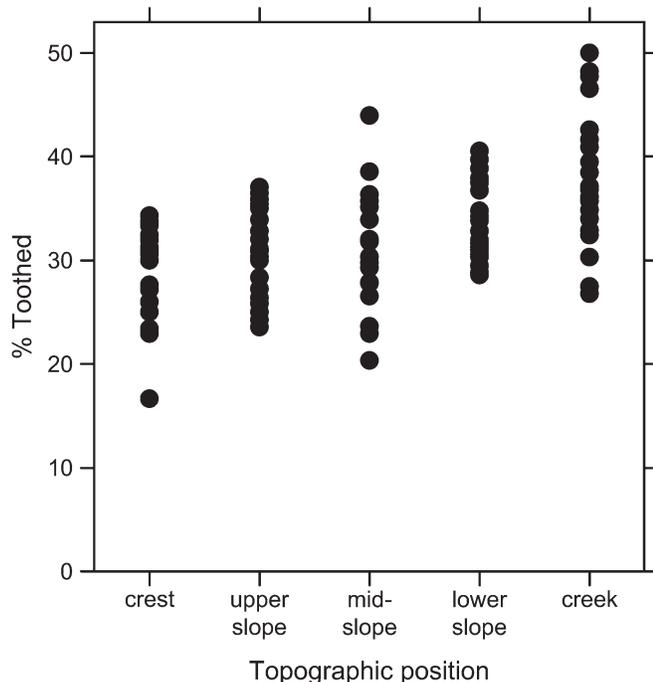


Fig. 4. Relationship between the percentage of toothed species and topographic position for the fine-scale SNVF sample. Dots represent individual sites. One-way ANOVA: $F_{4,95} = 9.8$, $P < 0.001$ (Table 4).

Correlation of leaf teeth to other ecological variables—There are few strong correlations between leaf teeth and other ecological attributes (Tables 4, 5). In the SNVF fine sample, sites with a higher percentage of toothed species correlate significantly with deeper soils and steeper slopes, and toothed species tend to have larger leaves than untoothed species. In the SNVF coarse sample, toothed species are more common in fire-influenced environments at the rainforest edge and at low elevation, and toothed species are linked with smaller seeds. In both CNVF samples, toothed species correlate with smaller fruit size, and in the CNVF inland sample toothed species are more likely to resprout after disturbance. None of these correlations appear to be driven by coevolved combinations of traits (Table 3; online Appendix S2).

Correlation between leaf teeth and growth form—Lianas are disproportionately untoothed at sites in the SNVF fine sample (Fig. 8; $t_{31} = -7.4$, $P < 0.0001$ for comparing lianas to all species at sites; sites with <5 liana species excluded). Untoothed lianas that are common in SNVF fine include Apocynaceae, Aristolochiaceae, Bignoniaceae, Fabaceae, and Menispermaceae, families all known to contain very few or no toothed species globally (e.g., Heywood et al., 2007). A significant topographic gradient is also present in the fine-scale SNVF sample: lianas are proportionally more abundant near creeks than on ridge crests (Fig. 9). At sites in the SNVF coarse and CNVF inland samples, the percentage of liana species that are toothed is not statistically distinguishable from the site means of all species (Fig. 8; SNVF coarse: $t_{40} = 0.70$, $P = 0.49$; sites with <5 liana species excluded; CNVF inland: $t_{23} = 1.2$, $P = 0.23$). In contrast, at sites in the CNVF coastal sample, lianas are disproportionately toothed relative to site means of all species (Fig. 8; $t_{10} = 2.6$, $P = 0.03$), primarily due to the presence of Vitaceae.

DISCUSSION

General patterns across samples—The percentage of toothed species observed across all four samples is comparable with previously published data for eastern Australian rainforests (Greenwood, 1992; Greenwood et al., 2004; compare gray and black lines in Fig. 2). This further corroborates the reported observation that Australian rainforest vegetation typically has a lower proportion of toothed species at a given MAT than vegetation elsewhere (Greenwood et al., 2004; compare solid and dashed black lines in Fig. 2).

Sites in the CNVF coastal sample contain proportionally fewer toothed species than sites in the other samples (Fig. 2), but the MAT for these sites is somewhat higher (~19.7°C vs.

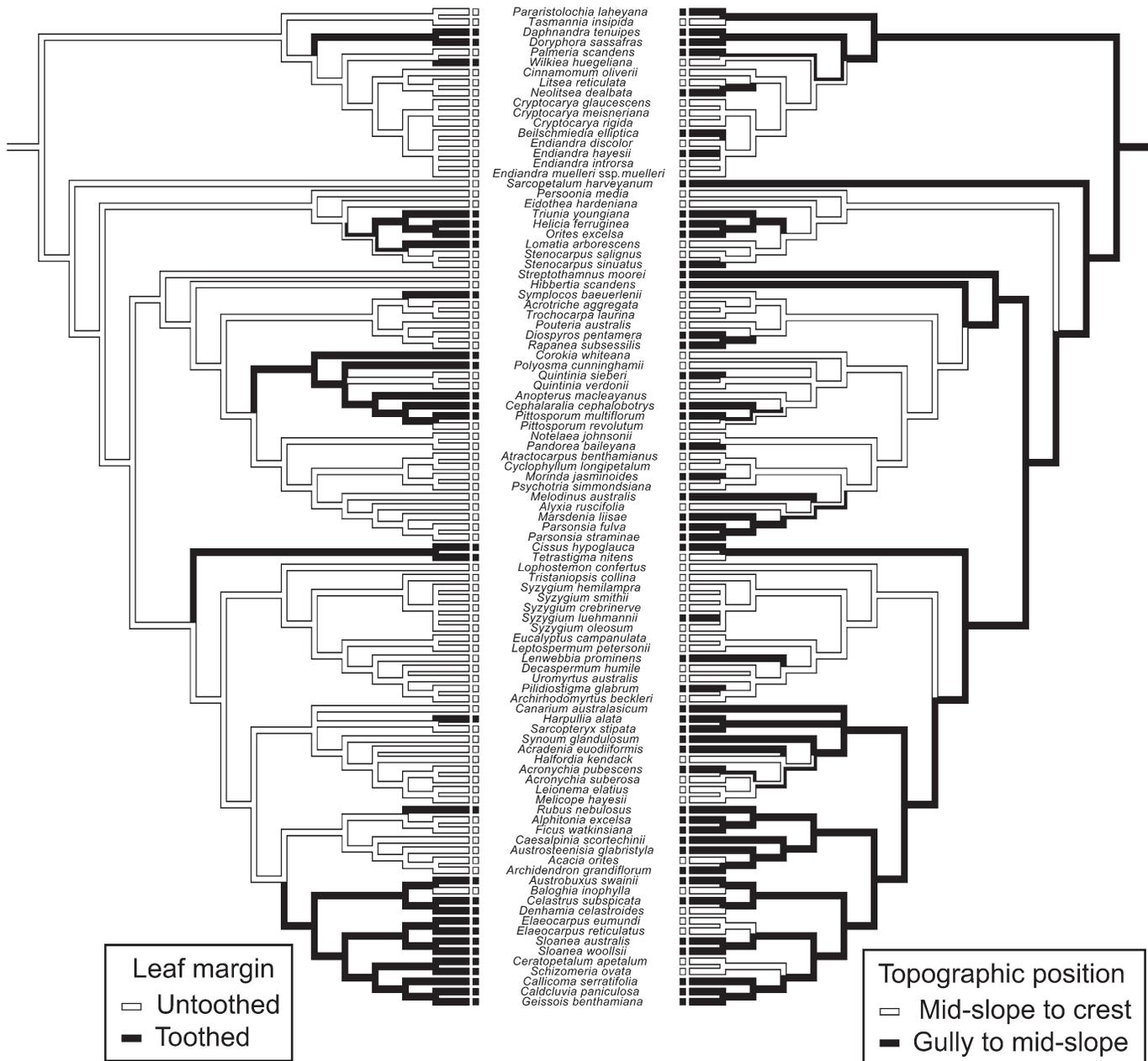


Fig. 5. Composite phylogeny of woody dicots analyzed from the fine-scale SNVF sample, showing leaf-margin trait (untoothed vs. toothed) contrasted with average topographic position on a mirror tree. Average topographic position and leaf teeth do not have a consistent relationship to each other ($P = 0.57$; see Table 3). See online Appendix S2 for trees of all trait comparisons.

~17.5°C for sites in the other three samples); MAT may therefore partially explain these differences. However, if the percentage of toothed species is predicted from MAT using the Australian rainforest calibration of Greenwood et al. (2004), it is overpredicted by 4% for sites in the CNVF coastal sample and underpredicted by ~3% for the other samples (compare black and gray lines in Fig. 2); the CNVF coastal sample is therefore disproportionately untoothed relative to most Australian rainforest vegetation, even after correcting for MAT. Furthermore, within the CNVF coastal sample, sites closest to the coast tend to have the fewest toothed species, although the trend is significant only at the 90% level (Fig. 3). Together, these data

suggest that salt stress selects against toothed species; this selection probably occurs because salt stress is linked to physiological drought, and leaf teeth are expensive with respect to water use (Royer and Wilf, 2006). We note that coastal sites are generally windier than other sites, and their canopy is shorter and more open and exposed to the sun; these factors may also increase transpirational loss and physiological water stress.

Leaf teeth and growth form—Liana species are less likely to be toothed than trees and shrubs in the fine-scale SNVF sample; in the CNVF coastal sample, lianas are more likely to be toothed, but there is no statistically significant pattern in the

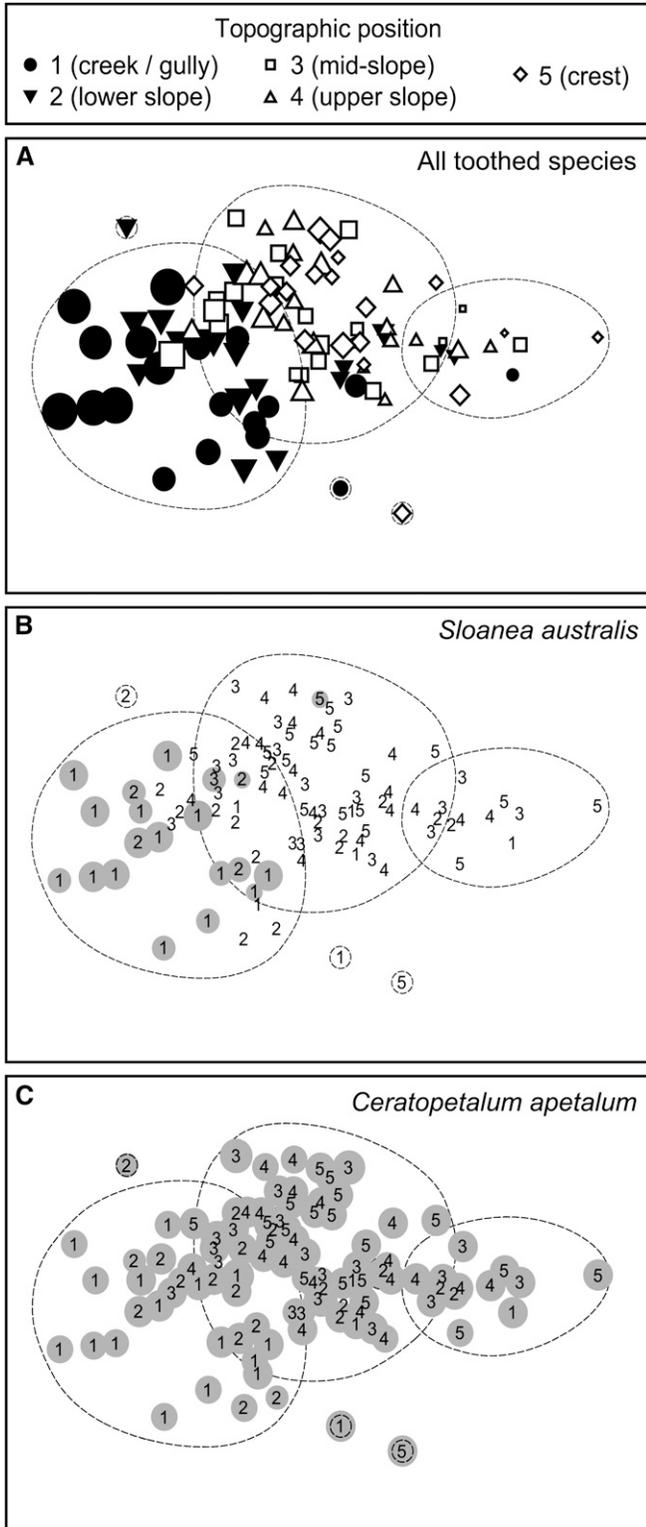


Fig. 6. Nonmetric multidimensional scaling (nMDS) ordination showing the relationship between topographic position and the abundance of toothed species in the fine-scale SNVF sample. All three panels show the same ordination. Each symbol or number represents a single site; symbol sizes scale proportionately with an estimate of cover abundance (CA) by toothed species (calculated as the fraction of summed CA of toothed spe-

SNVF coarse and CNVF inland samples (Fig. 8). With the exception of the observed richness ($N = 5$ species) and abundance of Vitaceae in the CNVF coastal sample, lianas in our samples tend to be shared across community types, and they characteristically lack or only rarely have teeth. In comparison, Burnham et al. (2001) observed that lianas are disproportionately toothed in an Ecuadorian rainforest; the most common families at their riparian and lake-margin sites belong to Sapindaceae, which are mostly toothed, and Fabaceae, which are exclusively untoothed in their data set. We conclude that in our study area differences among growth forms in the relative proportions of toothed species are not strongly controlled by ecological factors; instead, phylogenetic differences offer a better explanation.

Leaf teeth and growth strategy—Toothed species at our sites are rarely rapidly growing, early-phase species. In the SNVF, some of the most common and/or abundant toothed species include the canopy trees *Ceratopetalum apetalum*, *Schizomeria ovata* (both Cunoniaceae), and *Orites excelsa* (Proteaceae), the understory shrubs *Wilkiea huegeliana* (Monimiaceae) and *Triunia youngiana* (Proteaceae), and the small trees *Helicia ferruginea* (Proteaceae) and *Daphnandra tenuipes* (Atherospermataceae). All these species are present (and often dominant) in riparian habitats, yet all are slow-growing (mostly), mature-phase species (Kooyman, 2005; R. M. Kooyman, unpublished data). The CNVF has more untoothed canopy trees and early phase species with toothed leaves, for example, *Dendrocnide excelsa* (Urticaceae) and *Polyscias murrayi* (Araliaceae). However, the number and abundance of early-phase, toothed species is generally low, and there is no trend toward more early-phase species in riparian areas. In fact, as with the SNVF, the majority of toothed species belong to the slower-growing, mature-phase canopy and subcanopy groups (Kooyman, 2005; R. M. Kooyman, unpublished data).

The analysis of environmental and life history variables commonly associated with rapid growth and early successional status also indicates a weak link between growth strategy and leaf teeth (Tables 4, 5). Seed size, fruit type (fleshy vs. nonfleshy), dispersal mode (wind vs. frugivore), ability to resprout after disturbance, and leaf lobing and compounding generally correlate poorly with the leaf-margin character (untoothed vs. toothed). The two exceptions to this pattern are fire return frequency, where toothed species are more common in fire-prone areas in the one sample where fire return frequency composes an important gradient (SNVF coarse; Table 4), and fruit size, where toothed species are more likely to have smaller fruits in the two CNVF samples (but not in the two SNVF samples; Table 5). Phylogenetic patterns of inheritance of these life his-

←
cies relative to all species; CA for individual species is modified from Braun-Blanquet, 1932; see Materials and Methods for details; scaling of symbol sizes differs between panels). Dashed lines represent the 60% similarity slice through the classification (clustering) dendrogram based on the underlying resemblance matrix. (A) General patterns for site-level means of all species. The ordination shows a clear association between sites with abundant coverage by toothed species and low topographic position. (B, C) Relationship between topographic position and CA for the individual species (B) *Sloanea australis* (Elaeocarpaceae), a toothed species with clear riparian tendencies, and (C) *Ceratopetalum apetalum* (Cunoniaceae), a toothed species with broad topographic occurrence. Sites with no bubbles do not contain the species (CA = 0).

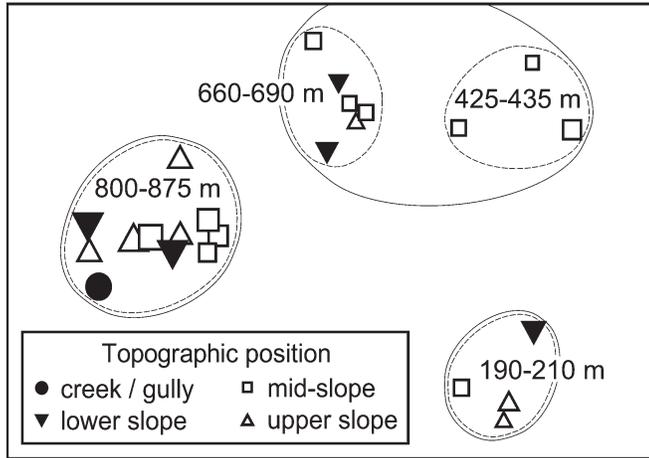


Fig. 7. Nonmetric multidimensional scaling (nMDS) ordination showing the relationship between topographic position and the abundance of toothed species in the CNVF inland sample. Symbols represent individual sites; symbol sizes scale proportionately with an estimate of cover abundance (CA) by all toothed species (calculated as the fraction of summed CA of toothed species relative to all species; CA for individual species is modified from Braun-Blanquet, 1932; see Materials and Methods for details). Solid and dashed lines represent the 50% and 60% similarity slices, respectively, through the classification (clustering) dendrogram based on the underlying resemblance matrix. The elevation range for each site cluster is marked. The ordination shows no clear association between the canopy coverage of toothed species and topographic position; instead, the relative abundance of toothed species tracks elevation.

tory traits do not appear to have significantly coevolved with the presence of leaf teeth (Table 3; Appendix S2), and therefore also do not support a strong link between growth strategy and leaf teeth. Importantly, a general measure of site disturbance (Table 1) shows no clear association with the percentage of toothed species (Table 4), even though disturbance is an important gradient in the SNVF coarse and CNVF inland samples.

Taken together (observations of growth rate and successional status, measurement of traits linked to growth rate and successional status, and observations of disturbance), there is no strong association between toothed species and growth strat-

egy. In comparison with eastern North American forests, where the association may be more important (Royer et al., 2005; Royer and Wilf, 2006), this poor correlation may be driven in the SNVF by the lack of a well-developed successional flora. Here, existing species of the mature (undisturbed) forest generally regenerate immediately following disturbance. However, in cases where soil disturbance is significant, *Acacia orites* (Fabaceae, untoothed phyllodes) and/or *Callicoma serratifolia* (Cunoniaceae, toothed) can dominate the regeneration because both have long-lived seed reserves (Kooyman, 2005). Thus, *Callicoma serratifolia* provides the only example of a toothed species that is both fast growing and reliant on larger-scale disturbance for regeneration in SNVF assemblages.

Leaf teeth and topographic position—At the SNVF fine sites, riparian habitats contain a higher percentage and greater abundance of toothed species than nonriparian habitats; our data also establish, for the first time, a continuous gradient controlled by topography between wetter and drier sites (Figs. 4, 6A; Table 4). The correlation between topographic position and leaf teeth does not appear to be an inherited syndrome, and thus the influence of evolutionary history probably cannot explain the general pattern (Fig. 5, Table 3; Appendix S2). These associations emphasize the need to account for topographic position when calibrating the relationship between the percentage of toothed species and MAT in present-day forests for application to fossil plant sites, because fossil leaves overwhelmingly are derived from the lowest topographic positions on the landscape (Burnham et al., 2001; Kowalski and Dilcher, 2003; Greenwood, 2005b). Probably the most appropriate calibration sites are those from the lowest topographic positions.

The SNVF coarse and CNVF inland samples have similar, but not statistically significant correlations between toothed species and topographic position; no correlation is seen in the CNVF coastal sample (Table 4). These weaker signals are expected because site selection for these samples was not determined by topographic position (see Materials and Methods, *SNVF samples* and *CNVF samples*). Also, other environmental gradients are larger in the other samples than in the fine-scale SNVF sample, and these large gradients can confound the relationship between leaf teeth and topographic position. For example, in the CNVF coastal sample, salt effects (as proxied by proximity to coast) probably overwhelm any effect of topo-

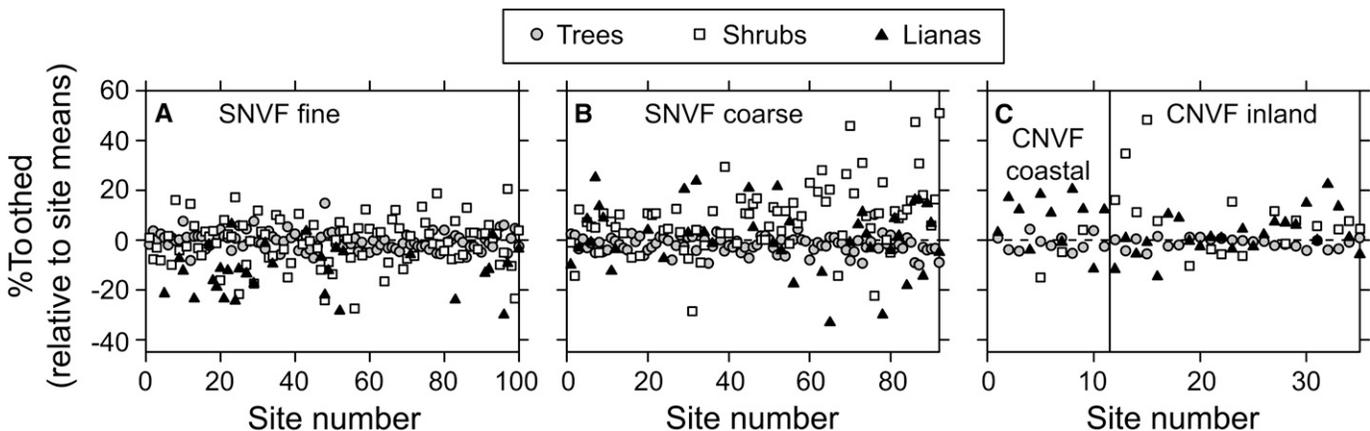


Fig. 8. Percentage of toothed species by growth form. Each symbol represents the departure for each growth form relative to the site mean. Sites are grouped by sample: (A) SNVF fine, (B) SNVF coarse, (C) CNVF coastal and inland. Sites with <5 species of a growth form are excluded.

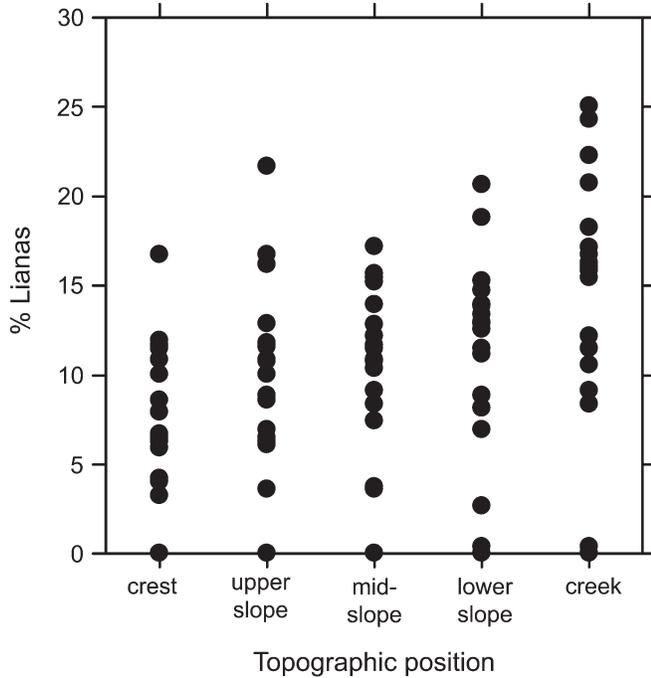


Fig. 9. Relationship between the percentage of liana species and topographic position for the fine-scale SNVF sample. Dots represent individual sites. One-way ANOVA: $F_{4,95} = 4.5$, $P = 0.002$.

graphic position (see earlier discussion). In the CNVF inland sample, elevation is more important than topographic position for explaining patterns in the proportional abundance of toothed species (Fig. 7). Elevation is also critical in the coarse-scale SNVF sample, as is fire return frequency (Table 4). In summary, topographic position has a moderate-to-significant impact on the percentage and abundance of toothed species at our sites, and these signals are most clearly resolved when other environmental gradients are minimized. We hypothesize that if the CNVF community type were sampled in a manner similar to the fine-scale SNVF sample, a stronger relationship between leaf teeth and topographic position would emerge.

Webb (1968) and Greenwood et al. (2004) observed that Australian rainforest sites with nutrient-rich bedrock (e.g., basalt, limestone) contain a slightly higher percentage of toothed species (~5%) than sites with nutrient-poor bedrock (e.g., rhyolite, sandstone). In our study area, each community type is associated with a single bedrock type (SNVF: rhyolite; CNVF: basalt; see Materials and Methods), and thus bedrock cannot explain the correlations between topographic position and toothed species. Moreover, there are no strong differences in

the percentage of toothed species between the SNVF and CNVF inland sites (Fig. 2), despite differing bedrock. However, we did not measure directly the soil nutrient status at our sites. Soil depth is sometimes, but not always, linked with soil fertility (e.g., Jenny, 1994); in the SNVF fine sample, sites with deep soils are positively correlated with a high percentage of toothed species (Table 4), even when topographic position is factored out ($F_{1,96} = 10.5$, $P = 0.002$; one-way ANCOVA, topographic position covariate). Thus, it is possible that soil fertility influences the proportion of toothed species in our study area. However, the correlation between the percentage of toothed species and topographic position remains highly significant even after removing the influence of soil depth ($F_{4,94} = 6.0$, $P = 0.0002$; one-way ANCOVA, soil depth covariate), and deep soils are also linked to greater water availability (via increased water holding capacity and root volume; e.g., Pimentel et al., 1995; Schulze et al., 1996). Given that the percentage of toothed species does not vary strongly across bedrock type in our study area, it is likely that the influence of soil depth on leaf teeth is more related to water availability than to soil fertility.

To summarize, there are at least three explanations for the abundance of toothed species at riparian sites (the freshwater effect; see introduction): increased availability of water (soil moisture), higher diversity of toothed lianas, and selection against untoothed species in disturbed environments. Our data most strongly support the first explanation, which is consistent with the hypothesis that leaf teeth are expensive with respect to water use (Royer and Wilf, 2006; see introduction). We can reject the disturbance hypothesis as an explanation for the freshwater effect in our study area based on direct observations of disturbance, growth rate, and successional status, and on environmental and life history traits commonly associated with growth rate and successional status. With regards to the second (liana) explanation, liana species are indeed more common in riparian environments (Fig. 9), but they are disproportionately toothed relative to other growth forms in only one sample, due to the local richness of a single family (Vitaceae in CNVF coastal; Fig. 8). Therefore, the likely explanation for the freshwater effect in our study area is water availability. Kowalski and Dilcher (2003) suggest a similar cause at their eastern North American sites, whereas Burnham et al. (2001) consider the liana and disturbance effects to be more important at their Ecuadorian sites. Together, this suggests multiple causes for the freshwater effect in different settings.

Summary—Mean annual temperature exerts the principal control over the percentage of toothed species across most mesic sites worldwide (Wolfe, 1993; Greenwood, 2005a). In our study area, where MAT varies ~3°C across sites, the percentage of toothed species ranges from 5 to 50%; thus, factors in addition to MAT are critical. Our data implicate topographic

TABLE 5. Correlations among species between life history traits and the leaf-margin character (untoothed vs. toothed). Correlations are based on all species in a sample and were calculated using one-way ANOVA. N = species richness (woody dicots); m = slope of correlation. Boldfaced correlations are statistically significant ($P \leq 0.05$). See Table 2 for descriptions of traits.

Sample	N	Seed size		Fruit size		Fruit type		Dispersal mode		Resprout		Leaf size		Lobed leaves		Compound leaves	
		m	P	m	P	m	P	m	P	m	P	m	P	m	P	m	P
SNVF fine	99	-	0.24	-	0.28	-	0.30	-	0.65	+	0.84	+	0.04	+	0.95	+	0.34
SNVF coarse	172	-	0.03	-	0.12	-	0.33	-	0.43	+	0.52	+	0.06	+	0.71	+	0.35
CNVF inland	213	-	0.52	-	<0.001	+	0.41	-	0.45	+	0.02	+		+	0.31	+	0.58
CNVF coastal	179	-	0.39	-	0.002	+	0.12	-	0.30	+	0.11	-	0.63	-	0.41	+	0.44

position, soil depth, and distance to coast as important factors for influencing the distribution of toothed species. The high percentage of toothed species in riparian habitats (the freshwater effect) is likely controlled by water availability, not phylogeny, growth form (lianas, shrubs, trees), or growth strategy (fast vs. slow growth rates); likewise, the low percentage of toothed species in coastal areas is probably also related to water availability via salt stress. This sensitivity to water availability is consistent with experiments that show that leaf teeth in many eastern North American species are conduits for significant water loss, particularly early in the growing season (Royer and Wilf, 2006).

Our observed freshwater effect has been previously observed on three continents: Australia (Greenwood, 2005b), South America (Burnham et al., 2001), and North America (Kowalski and Dilcher, 2003). Broadly, this suggests that the effect is not phylogenetically inherited, a conclusion also supported by quantitative tests for species within our study area. Also, our results support previous observations (Greenwood et al., 2004) that Australian rainforest vegetation has proportionately fewer toothed species at a given MAT than vegetation elsewhere; the cause of this difference is unknown, but several historical hypotheses have been suggested (Greenwood et al., 2004). We also find no strong evidence for an association between the presence of leaf teeth and fast-growing, early-phase species. This syndrome is most often reported from North American vegetation (e.g., Royer et al., 2005; Royer and Wilf, 2006), and thus our data present regional differences needing further study.

Our study highlights water availability as a factor that should be taken into account when reconstructing climate from the analysis of teeth in fossil leaves. The original growth settings for most fossil leaf assemblages are edaphically wet (Spicer, 1981) and topographically low on the landscape. Thus, the influence of topographic position on the distribution of toothed species is probably more uniform in most fossil leaf deposits than what we observed here. Nevertheless, because leaf-climate methods are mostly calibrated in distal floodplain and upland habitats, a consistent bias toward falsely cool inferred paleotemperatures is probably present (Burnham et al., 2001; Kowalski and Dilcher, 2003; Greenwood, 2005b); further, we show here that the magnitude of the bias will vary, in part, due to the topographic positions of the calibration floras. Thus, recalibration initiatives should emphasize the lowest topographic positions. Also, coastal fossil deposits should be treated with care because even in edaphically wet settings, the impact of salt spray will probably reduce the presence of toothed species.

LITERATURE CITED

- ADAMS, J. M., W. A. GREEN, AND Y. ZHANG. 2008. Leaf margins and temperature in the North American flora: Recalibrating the paleoclimatic thermometer. *Global and Planetary Change* 60: 523–534.
- AIZEN, M. A., AND C. EZCURRA. 2008. Do leaf margins of the temperate forest flora of southern South America reflect a warmer past? *Global Ecology and Biogeography* 17: 164–174.
- ALVERSON, W. S., B. A. WHITLOCK, R. NYFFELER, C. BAYER, AND D. A. BAUM. 1999. Phylogeny of the core Malvales: Evidence from *ndhF* sequence data. *American Journal of Botany* 86: 1474–1486.
- BAILEY, I. W., AND E. W. SINNOTT. 1915. A botanical index of Cretaceous and Tertiary climates. *Science* 41: 831–834.
- BAILEY, I. W., AND E. W. SINNOTT. 1916. The climatic distribution of certain types of angiosperm leaves. *American Journal of Botany* 3: 24–29.
- BAKER, H. G. 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53: 997–1010.
- BAKER-BROSH, K. F., AND R. K. PEET. 1997. The ecological significance of lobed and toothed leaves in temperate forest trees. *Ecology* 78: 1250–1255.
- BARKER, N. P., P. H. WESTON, F. RUTSCHMANN, AND H. SAUQUET. 2007. Molecular dating of the 'Gondwanan' plant family Proteaceae is only partially congruent with the timing of the break-up of Gondwana. *Journal of Biogeography* 34: 2012–2027.
- BILLINGS, F. H. 1905. Precursory leaf serrations of *Ulmus*. *Botanical Gazette (Chicago, Ill.)* 40: 224–225.
- BRADFORD, J. C., AND R. W. BARNES. 2001. Phylogenetics and classification of Cunoniaceae (Oxalidales) using chloroplast DNA sequences and morphology. *Systematic Botany* 26: 354–385.
- BRAUN-BLANQUET, J. 1932. Plant phytosociology. McGraw-Hill, New York, New York, USA.
- BREMER, B., AND J. F. MANEN. 2000. Phylogeny and classification of the subfamily Rubioideae (Rubiaceae). *Plant Systematics and Evolution* 266: 233–252.
- BURNHAM, R. J., N. C. A. PITMAN, K. R. JOHNSON, AND P. WILF. 2001. Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest. *American Journal of Botany* 88: 1096–1102.
- CARLQUIST, S. 2001. Comparative wood anatomy: Systematic, ecological, and evolutionary aspects of dicotyledon wood, 2nd ed. Springer-Verlag, Berlin, Germany.
- CANNY, M. 1990. What becomes of the transpiration stream? *New Phytologist* 114: 341–368.
- CHANDERBALI, A. S., H. VAN DER WERFF, AND S. S. RENNER. 2001. Phylogeny and historical biogeography of Lauraceae: Evidence from the chloroplast and nuclear genomes. *Annals of the Missouri Botanical Garden* 88: 104–134.
- CHASE, M. W., C. M. MORTON, AND J. A. KALLUNKI. 1999. Phylogenetic relationships of Rutaceae: A cladistic analysis of the subfamilies using evidence from *rbcL* and *atpB* sequence variation. *American Journal of Botany* 86: 1191–1199.
- ENGELMARK, O., A. HOFGAARD, AND T. ARNBORG. 1998. Successional trends 219 years after fire in an old *Pinus sylvestris* stand in northern Sweden. *Journal of Vegetation Science* 9: 583–592.
- FALSTER, D. S., AND M. WESTOBY. 2005. Tradeoffs between height growth rate, stem persistence and maximum height among plant species in a post-fire succession. *Oikos* 111: 57–66.
- FEILD, T. S., T. L. SAGE, C. CZERNIAK, AND W. J. D. ILES. 2005. Hydathodal leaf teeth of *Chloranthus japonicus* (Chloranthaceae) prevent guttation-induced flooding of the mesophyll. *Plant, Cell & Environment* 28: 1179–1190.
- FLOYD, A. G. 1989. Rainforest trees of mainland south-eastern Australia, 268–270. Inkata Press, Sydney, Australia.
- FOSTER, S. A., AND C. H. JANSON. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 66: 773–780.
- GARNIER, E., J. CORTEZ, G. BILLÈS, M.-L. NAVAS, C. ROUMET, M. DEBUSSCHE, G. LAURENT, ET AL. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630–2637.
- GIVNISH, T. J. 1978a. Ecological aspects of plant morphology: Leaf form in relation to environment. *Acta Biotheoretica (Supplement: Folia Biotheoretica No. 7)* 27: 83–142.
- GIVNISH, T. J. 1978b. On the adaptive significance of compound leaves, with particular reference to tropical trees. In P. B. Tomlinson and M. H. Zimmermann [eds.], *Tropical trees as living systems*, 351–380. Cambridge University Press, New York, New York, USA.
- GIVNISH, T. J. 1984. Leaf and canopy adaptations in tropical forests. In E. Medina, H. A. Mooney, and C. Vázquez-Yanes [eds.], *Physiological ecology of plants of the wet tropics*, 51–84. Dr. W. Junk, The Hague, Netherlands.
- GIVNISH, T. J., J. C. PIRES, S. W. GRAHAM, M. A. MCPHERSON, L. M. PRINCE, T. B. PATTERSON, H. S. RAI, ET AL. 2005. Repeated evolution of net venation and fleshy fruits among monocots in shaded

- habitats confirms *a priori* predictions: Evidence from an *ndhF* phylogeny *Proceedings of the Royal Society of London, B, Biological Sciences* 272: 1481–1490.
- GREEN, W. A. 2006. Loosening the CLAMP: An exploratory graphical approach to the Climate Leaf Analysis Multivariate Program. *Palaeontologia Electronica* 9.2.9A: 1–17.
- GREENWOOD, D. R. 1992. Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates. *Review of Palaeobotany and Palynology* 71: 149–190.
- GREENWOOD, D. R. 2005a. Leaf form and the reconstruction of past climates. *New Phytologist* 166: 355–357.
- GREENWOOD, D. R. 2005b. Leaf margin analysis: taphonomic constraints. *Palaios* 20: 498–505.
- GREENWOOD, D. R. 2007. Fossil angiosperm leaves and climate: From Wolfe and Dilcher to Burnham and Wilf. *Courier Forschungsinstitut Senckenberg* 258: 95–108.
- GREENWOOD, D. R., P. WILF, S. L. WING, AND D. C. CHRISTOPHEL. 2004. Paleotemperature estimation using leaf-margin analysis: Is Australia different? *Palaios* 19: 129–142.
- GREGORY-WODZICKI, K. M. 2000. Relationships between leaf morphology and climate, Bolivia: Implications for estimating paleoclimate from fossil floras. *Paleobiology* 26: 668–688.
- GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.
- GRIME, J. P. 2001. Plant strategies, vegetation processes, and ecosystem properties, 2nd ed. John Wiley & Sons, Chichester, UK.
- HALLOY, S. R. P., AND A. F. MARK. 1996. Comparative leaf morphology spectra of plant communities in New Zealand, the Andes and the European Alps. *Journal of the Royal Society of New Zealand* 26: 41–78.
- HARDEN, G. J. 1990–2002 with revisions. Flora of New South Wales, vols. 1–4. University of New South Wales Press, Sydney, Australia.
- HEYWOOD, V. H., R. K. BRUMMITT, A. CULHAM, AND O. SEVERG. 2007. Flowering plant families of the world. Firefly Books, Richmond Hill, Ontario, Canada.
- HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.
- HINOJOSA, L. F., J. J. ARMESTO, AND C. VILLAGRÁN. 2006. Are Chilean coastal forests pre-Pleistocene relicts? Evidence from foliar physiognomy, palaeoclimate, and phytogeography. *Journal of Biogeography* 33: 331–341.
- HOOT, S. B., AND A. W. DOUGLAS. 1998. Phylogeny of the Proteaceae based on *atpB* and *atpB-rbcL* intergenic spacer region sequences. *Australian Systematic Botany* 11: 301–320.
- HUFF, P. M., P. WILF, AND E. J. AZUMAH. 2003. Digital future for paleoclimate estimation from fossil leaves? Preliminary results. *Palaios* 18: 266–274.
- JENNY, H. 1994. Factors of soil formation: A system of quantitative pedology. Dover, New York, New York, USA.
- KAPPELLE, M., AND M. E. LEAL. 1996. Changes in leaf morphology and foliar nutrient status along a successional gradient in a Costa Rican upper montane *Quercus* forest. *Biotropica* 28: 331–344.
- KARIUKI, M., AND R. M. KOOYMAN. 2005. Floristic changes and regeneration patterns for a 12-year period during the 3rd and 4th decades following selection logging in a subtropical rainforest. *Austral Ecology* 30: 844–855.
- KARIUKI, M., M. ROLFE, R. G. B. SMITH, J. K. VANCLAY, AND R. M. KOOYMAN. 2006. Diameter growth performance varies with species functional-group and habitat characteristics in subtropical rainforests. *Forest Ecology and Management* 225: 1–14.
- KOOYMAN, R. M. 2005. The ecology and population biology of *Uromyrtus australis* A.J. Scott. M.Sc. thesis, University of New England, Armidale, Australia.
- KOOYMAN, R. M., AND M. ROSSETTO. 2006. Factors influencing species selection for littoral rainforest restoration: Do environmental gradients matter? *Ecological Restoration and Management* 7: 113–122.
- KOWALSKI, E. A. 2002. Mean annual temperature estimation based on leaf morphology: A test from tropical South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 188: 141–165.
- KOWALSKI, E. A., AND D. L. DILCHER. 2003. Warmer paleotemperatures for terrestrial ecosystems. *Proceedings of the National Academy of Sciences, USA* 100: 167–170.
- LADIGES, P. Y., G. I. MCFADDEN, N. MIDDLETON, D. A. ORLOVICH, N. TRELOAR, AND F. UDOVICIC. 1999. Phylogeny of *Melaleuca*, *Callistemon*, and related genera of the *Beaufortia* suballiance (Myrtaceae) based on 5S and ITS-1 spacer regions of nrDNA. *Cladistics* 15: 151–172.
- LARCHER, W. 1995. Physiological plant ecology. Springer-Verlag, Berlin, Germany.
- LI, J., D. C. CHRISTOPHEL, J. G. CONRAN, AND H.-W. LI. 2004. Phylogenetic relationships within the ‘core’ Laureae (*Litsea* complex, Lauraceae) inferred from sequences of the chloroplast gene *matK* and nuclear ribosomal DNA ITS regions. *Plant Systematics and Evolution* 246: 19–34.
- LITTLE, S. A., S. KEMBEL, P. WILF, AND D. L. ROYER. 2008. Phylogenetic signal in leaf traits and its influence on leaf–climate correlations. Botany 2008: Annual Meeting of the Botanical Society of America, Vancouver, Canada [online abstract]. Website <http://2008.botanyconference.org/engine/search/index.php?func=detail&aid=626>.
- LUCAS, E. J., S. A. HARRIS, F. F. MAZINE, S. R. BELLISHAM, E. M. N. LUGHADHA, A. TELFORD, P. E. GASSON, AND M. W. CHASE. 2007. Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* 56: 1105–1128.
- MADDISON, W. P., AND D. R. MADDISON. 2008. Mesquite: A modular system for evolutionary analysis, version 2.5. Website <http://mesquiteproject.org> [accessed April 2008].
- MIDFORD, P., AND W. P. MADDISON. 2006. Correl package for Mesquite, version 1.1; module used within Mesquite, [website <http://mesquiteproject.org>, accessed April 2008].
- MORAND, D. T. 1994. Soil landscapes of the Lismore–Ballina 1:100,000 sheet. Department of Conservation and Land Management, Sydney, Australia.
- MORAND, D. T. 1996. Soil landscapes of the Murwillumbah–Tweed Heads 1:100,000 sheet. Department of Conservation and Land Management, Sydney, Australia.
- MOULY, A., S. G. RAZAFIMANDIMBISON, F. ACHILLE, T. HAEVERMANS, AND B. BREMER. 2007. Phylogenetic placement of *Rhopalobrachium fragrans* (Rubiaceae): Evidence from molecular (*rps16* and *trnT-F*) and morphological data. *Systematic Botany* 32: 872–882.
- MUELLNER, A. N., D. D. VASSILIADES, AND S. S. RENNER. 2007. Placing Biebersteiniaceae, a herbaceous clade of Sapindales, in a temporal and geographic context. *Plant Systematics and Evolution* 266: 233–252.
- NIE, Z. L., J. WEN, AND H. SUN. 2007. Phylogeny and biogeography of *Sassafras* (Lauraceae) disjunct between eastern Asia and eastern North America. *Plant Systematics and Evolution* 267: 191–203.
- NIX, H. A. 1991. An environmental analysis of Australian rainforests. In G. Werren and P. Kershaw [eds.], The rainforest legacy: Australian national rainforests study, vol. 2, 1–26. Australian Government Publishing Service, Canberra, Australia.
- PAGEL, M. 1994. Detecting correlated evolution on phylogenies: A general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London, B, Biological Sciences* 255: 37–45.
- PIMENTEL, D., C. HARVEY, P. RESOSUDARMO, K. SINCLAIR, D. KURZ, M. MCNAIR, S. CRIST, ET AL. 1995. Environmental and economic costs of soil erosion and conservation benefits. *Science* 267: 1117–1123.
- POTGIETER, K., AND V. A. ALBERT. 2001. Phylogenetic relationships within Apocynaceae s.l. based on *trnL* intron and *trnL-F* spacer sequences and propagule characters. *Annals of the Missouri Botanical Garden* 88: 523–549.
- RONSE DE CRAENE, L. P., AND E. HASTON. 2006. The systematic relationships of glucosinolate-producing plants and related families: A cladistic investigation based on morphological and molecular characters. *Botanical Journal of the Linnean Society* 151: 453–494.
- ROSSETTO, M., AND R. M. KOOYMAN. 2005. The tension between dispersal and persistence regulates the current distribution of rare pa-

- laeo-endemic rain forest flora: a case study. *Journal of Ecology* 93: 906–917.
- ROYER, D. L., J. C. MCELWAIN, J. M. ADAMS, AND P. WILF. 2008. Sensitivity of leaf size and shape to climate within *Acer rubrum* and *Quercus kelloggii*. *New Phytologist* 179: 808–817.
- ROYER, D. L., AND P. WILF. 2006. Why do toothed leaves correlate with cold climates? Gas exchange at leaf margins provides new insights into a classic paleotemperature proxy. *International Journal of Plant Sciences* 167: 11–18.
- ROYER, D. L., P. WILF, D. A. JANESKO, E. A. KOWALSKI, AND D. L. DILCHER. 2005. Correlations of climate and plant ecology to leaf size and shape: Potential proxies for the fossil record. *American Journal of Botany* 92: 1141–1151.
- SALISBURY, E. J. 1974. Seed size and mass in relation to environment. *Proceedings of the Royal Society of London, B, Biological Sciences* 186: 83–88.
- SANDERSON, M. J., A. PURVIS, AND C. HENZE. 1998. Phylogenetic supertrees: Assembling the trees of life. *Trends in Ecology & Evolution* 13: 105–109.
- SCHULZE, E.-D., H. A. MOONEY, O. E. SALA, E. JOBBAGY, N. BUCHMANN, G. BAUER, J. CANADELL, ET AL. 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* 108: 503–511.
- SCOTT, K. D., C. L. MCINTYRE, AND J. PLAYFORD. 2000. Molecular analyses suggest a need for a significant rearrangement of Rutaceae subfamilies and a minor reassessment of species relationships within *Flindersia*. *Plant Systematics and Evolution* 223: 15–27.
- SOLTIS, D. E., M. A. GITZENDANNER, AND P. S. SOLTIS. 2007. A 567-taxon data set for angiosperms: The challenges posed by Bayesian analyses of large data sets. *International Journal of Plant Sciences* 168: 137–157.
- SPENCER, R.-J., AND G. S. BAXTER. 2006. Effects of fire on the structure and composition of open eucalypt forests. *Austral Ecology* 31: 638–646.
- SPICER, R. A. 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England. *U.S. Geological Survey Professional Paper* 1143: 1–77.
- STEVENS, N. C. 1977. Geology and landforms. In R. Monroe and N. C. Stevens [eds.], *The Border Ranges: A land use conflict in regional perspective*, 1–6. Royal Society of Queensland, Brisbane, Australia.
- TRAISSER, C., S. KLOTZ, D. UHL, AND V. MOSBRUGGER. 2005. Environmental signals from leaves—A physiognomic analysis of European vegetation. *New Phytologist* 166: 465–484.
- VAMOSI, J. C., AND T. A. DICKINSON. 2006. Polyploidy and diversification: A phylogenetic investigation in Rosaceae. *International Journal of Plant Sciences* 167: 349–358.
- WEBB, L. J. 1959. A physiognomic classification of Australian rain forests. *Journal of Ecology* 47: 551–570.
- WEBB, L. J. 1968. Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology* 49: 296–311.
- WEBB, L. J. 1978. A general classification of Australian rainforests. *Australian Plants* 9: 349–363.
- WEBB, L. J., J. G. TRACEY, AND W. T. WILLIAMS. 1984. A floristic framework of Australian rainforests. *Australian Journal of Ecology* 9: 169–198.
- WESTOBY, M., E. JURADO, AND M. LEISHMAN. 1992. Comparative evolutionary ecology of seed size. *Trends in Ecology & Evolution* 7: 368–372.
- WHEELER, E. A., AND C. A. LAPASHA. 1994. Woods of the Vitaceae: Fossil and modern. *Review of Palaeobotany and Palynology* 80: 175–207.
- WILF, P. 1997. When are leaves good thermometers? A new case for leaf margin analysis. *Paleobiology* 23: 373–390.
- WILSON, P. G., M. M. O'BRIEN, P. A. GADEK, AND C. J. QUINN. 2001. Myrtaceae revisited: A reassessment of infrafamilial groups. *American Journal of Botany* 88: 2013–2025.
- WILSON, P. G., M. M. O'BRIEN, M. M. HESLEWOOD, AND C. J. QUINN. 2005. Relationships within Myrtaceae sensu lato based on a *matK* phylogeny. *Plant Systematics and Evolution* 251: 3–19.
- WOJCIECHOWSKI, M. F., M. LAVIN, AND M. J. SANDERSON. 2004. A phylogeny of legumes (Leguminosae) based on analyses of the plastid *matK* gene resolves many well-supported subclades within the family. *American Journal of Botany* 91: 1846–1862.
- WOLFE, J. A. 1977. Paleogene floras from the Gulf of Alaska region. *U.S. Geological Survey Professional Paper* 997: 1–108.
- WOLFE, J. A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. *U.S. Geological Survey Professional Paper* 1106: 1–37.
- WOLFE, J. A. 1993. A method of obtaining climatic parameters from leaf assemblages. *U.S. Geological Survey Bulletin* 2040: 1–71.
- WRIGHT, I. J., D. D. ACKERLY, F. BONGERS, K. E. HARMS, G. IBARRA-MANRÍQUEZ, M. MARTÍNEZ-RAMOS, S. J. MAZER, ET AL. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99: 1003–1015.