



Predicting Extinction Risk of Brazilian Atlantic Forest Angiosperms

TARCISO C. C. LEÃO,*† CARLOS R. FONSECA,‡ CARLOS A. PERES,§
AND MARCELO TABARELLI* **

*Departamento de Botânica, Universidade Federal de Pernambuco, Recife, PE, 50670-901, Brazil

†Department of Forest Resources, University of Minnesota, St. Paul, MN, 55108, U.S.A.

‡Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, RN, 59072-970, Brazil

§School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, United Kingdom

Abstract: *Understanding how plant life history affects species vulnerability to anthropogenic disturbances and environmental change is a major ecological challenge. We examined how vegetation type, growth form, and geographic range size relate to extinction risk throughout the Brazilian Atlantic Forest domain. We used a database containing species-level information of 6,929 angiosperms within 112 families and a molecular-based working phylogeny. We used decision trees, standard regression, and phylogenetic regression to explore the relationships between species attributes and extinction risk. We found a significant phylogenetic signal in extinction risk. Vegetation type, growth form, and geographic range size were related to species extinction risk, but the effect of growth form was not evident after phylogeny was controlled for. Species restricted to either rocky outcrops or scrub vegetation on sandy coastal plains exhibited the highest extinction risk among vegetation types, a finding that supports the hypothesis that species adapted to resource-limited environments are more vulnerable to extinction. Among growth forms, epiphytes were associated with the highest extinction risk in non-phylogenetic regression models, followed by trees, whereas shrubs and climbers were associated with lower extinction risk. However, the higher extinction risk of epiphytes was not significant after correcting for phylogenetic relatedness. Our findings provide new indicators of extinction risk and insights into the mechanisms governing plant vulnerability to extinction in a highly diverse flora where human disturbances are both frequent and widespread.*

Keywords: comparative method, geographic range size, growth form, plant traits, tropical flora, vegetation types, vulnerability

Predicción del Riesgo de Extinción de Angiospermas del Bosque Atlántico Brasileño Leão *et al.*

Resumen: *El entendimiento del efecto de la historia de vida de las plantas sobre la vulnerabilidad de las especies a las perturbaciones antropogénicas y el cambio ambiental es un reto ecológico mayor. Examinamos cómo el tipo de vegetación, la forma de crecimiento y el tamaño de rango geográfico se relacionan con el riesgo de extinción a lo largo del dominio del Bosque Atlántico Brasileño. Usamos una base de datos que contenía información a nivel de especie de 6,929 angiospermas dentro de 112 familias y filogenia funcional con bases moleculares. Usamos árboles de decisión, regresión estándar y regresión filogenética para explorar las relaciones entre los atributos de especie y el riesgo de extinción. El tipo de vegetación, la forma de crecimiento y el tamaño de rango geográfico estuvieron relacionados con el riesgo de extinción de la especie, pero el efecto de la forma de crecimiento no fue evidente de que se controlara la filogenia. Las especies restringidas a afloramientos rocosos o vegetación de matorral sobre planicies costeras arenosas exhibieron el riesgo de extinción más alto entre los tipos de vegetación, un hallazgo que apoya la hipótesis de que todas las especies adaptadas a ambientes de recursos limitados son más vulnerables a la extinción. Entre las formas de crecimiento, las epífitas estuvieron asociadas con el riesgo más alto de extinción en los modelos de regresión no-filogenética, seguidas de los árboles, mientras que los arbustos y las trepadoras estuvieron asociadas con el riesgo de extinción más bajo. Sin embargo, el riesgo más alto de extinción de las epífitas no fue significativo después de corregir la conectividad filogenética. Nuestros resultados proporcionan nuevos indicadores de*

**Address correspondence to Marcelo Tabarelli, email mtrelli@ufpe.br

Paper submitted December 18, 2012; revised manuscript accepted December 24, 2013.

riesgo de extinción y aclaraciones sobre los mecanismos que dominan la vulnerabilidad de las plantas a la extinción en flora altamente diversa donde las perturbaciones humanas son frecuentes y extensas.

Palabras Clave: Flora tropical, forma de crecimiento, método comparativo, rasgos vegetales, tamaño de rango geográfico, tipos de vegetación, vulnerabilidad

Introduction

Terrestrial ecosystems worldwide are experiencing high species extinction rates caused by the growing extent and intensity of anthropogenic activities (Pereira et al. 2010). Habitat conversion and overexploitation are the leading drivers of species extinctions in tropical forests (Brook et al. 2008). Although human disturbances often push species toward population decline, species vulnerability to extinction is often associated with both species attributes and evolutionary history (McKinney 1997). Although some species are undergoing rapid population decline, others are expanding their population and distribution (McKinney & Lockwood 1999). A key question arising from these opposite species responses is how life history of different species can predict their vulnerability to current disturbances and environmental change (Henle et al. 2004; Brook et al. 2008).

Geographic range size is the most evident predictor of global-scale species extinction risk. The smaller the species range size, the higher the probability that disturbances and environmental changes will affect the entire species range (Gaston & Blackburn 2000). Extent of occurrence and area of occupancy are among the most useful and widely adopted measures of geographic range size and the most common criteria used by the International Union for Conservation of Nature (IUCN) to assign threat status (Gaston & Fuller 2009). Understanding differences in extinction risk among species therefore critically depends on a robust measure of geographic range size, particularly the extent of occurrence and area of occupancy.

Although several studies have identified some species attributes as strong predictors of extinction risk, most of them have focused on animals (Henle et al. 2004), and little is known about how plant attributes are associated with extinction risk (Stork et al. 2009). For example, large vertebrates are widely considered to be most vulnerable in faunal assemblages because they tend to have low population densities and large spatial requirements, exhibit low fecundity, and be more prone to overexploitation, characteristics that predispose them to high extinction risk (Turner 1996; Stork et al. 2009). Although finding consistent relationships between plant attributes and extinction risk has been difficult (Murray et al. 2002), evidence from both plant and animal studies suggests that attributes related to population size and rates of growth and mortality should be correlated with species vulnerabilities (Pimm 1991; Henle et al. 2004). For trop-

ical forest trees, which comprise the best-known group of tropical plants, shade tolerance, per capita mortality rate, population growth rate, and dispersal capacity are consistently among the most important determinants of population persistence in disturbed environments (Henle et al. 2004). In general, species characterized by small population sizes, high demographic fluctuations, low competitive ability, low dispersal ability, and specialization to restricted habitats are expected to be more vulnerable to extinction in fragmented and disturbed habitats (Henle et al. 2004).

Differences in habitat type and growth form can be associated with differences in relative growth rate (Grime & Hunt 1975; Galmés et al. 2005), another key predictor of extinction risk. Habitats associated with elevated environmental stress, such as excessive droughts or nutrient scarcity, tend to host species with inherently limited growth rates imposed by evolutionary adaptations to stress tolerance (Grime 1977; Arendt 1997; Fonseca et al. 2000). Thus, growth forms adapted to stressful microhabitats, such as some epiphytes and herbs restricted to rocky outcrops, exhibit inherently low growth rates (Grime & Hunt 1975; Benzing 1990). For instance, growth rates of some epiphytes can be lower than those of forest trees that are renowned for their slow growth (Schmidt & Zotz 2002; Laube & Zotz 2003). Because slow-growing stress-tolerant plants often recover slowly from disturbance events (Grime 1977), slow growth rates are expected to render species more vulnerable to extinction in frequently disturbed habitats (Pimm 1991).

The Atlantic Forest of Brazil is one of the world's biodiversity hotspots. In this area many global extinctions are imminent (Mittermeier et al. 2004). Within the boundaries of the Brazilian Atlantic Forest, there are at least 5 major vegetation types (Fig. 1), including several forest and nonforest natural habitats that cover a wide range of elevation, precipitation, and temperature gradients and soil types (IBGE 2008; see Methods for details). The Atlantic Forest formerly occupied approximately 1,500,000 km², 12% of which remains as secondary and old-growth forest distributed across more than 245,000 forest fragments. These forest remnants are typically small (80% are <50 ha), are influenced by edge effects, and consist of secondary forests at intermediate stages of regeneration (Ribeiro et al. 2009). However, the Atlantic Forest still hosts over 15,000 plant species, 45% of which are endemic (Stehmann et al. 2009) and 10% of which are threatened with extinction (Fundação Biodiversitas 2005),

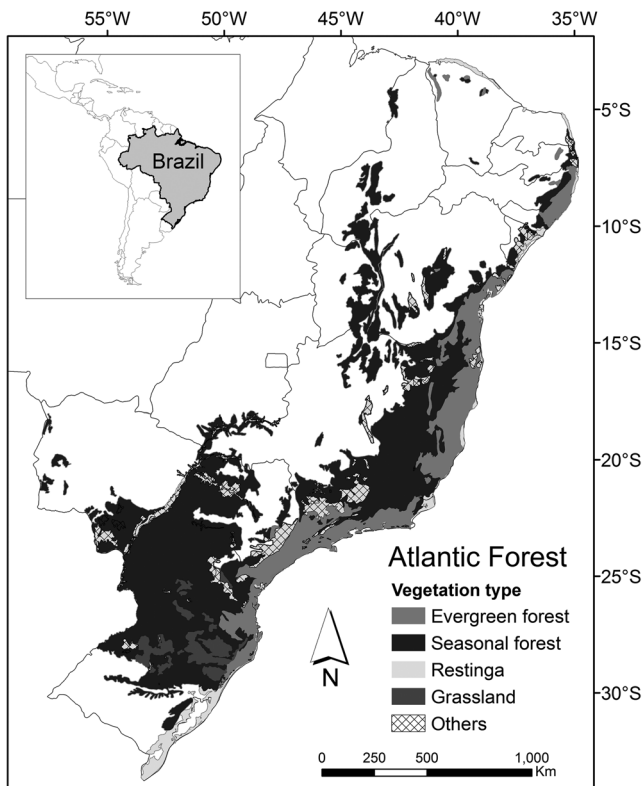


Figure 1. *Phytogeographic boundaries and main vegetation types of the Brazilian Atlantic Forest domain (IBGE 2008).*

although the Brazilian government officially recognizes fewer threatened species.

We examined how vegetation type and growth form relate to expert-defined species extinction risk throughout the Brazilian Atlantic Forest domain. We also investigated the additional relevance of these attributes in explaining extinction risk after controlling for geographic range size and explicitly considering the phylogenetic nonindependence among species. Finally, we sought to provide evidence to support an appropriate use of life-history attributes as indicators of species extinction risk and evidence-based insights into the mechanisms behind plant vulnerability to extinction.

Methods

Database and Extinction Risk

The database we used included 6929 species within 112 angiosperm families of the Brazilian Atlantic Forest flora. This represents roughly 50% of the total number of species and more than 50% of the families of native angiosperms known to the Brazilian Atlantic Forest domain (Stehmann et al. 2009). We classified extinction risk following the Brazilian Checklist of Threatened and Endan-

gered Flora, which was reviewed by 180 expert botanists and published by Fundação Biodiversitas (2005). We detected that the number of consulted specialists per family was significantly related to the number of threatened species within each family, even after controlling for family size as a covariate ($t = 2.38$, $df = 193$, $p = 0.02$). Therefore, we excluded from the database 92 families because either their level of extinction risk failed to be evaluated by any specialist or the number of consulted specialists was significantly different from the overall mean (chi-square, $p < 0.10$).

We treated the threat status as a continuous response: 0, nonthreatened species; 1, vulnerable; 2, endangered; 3, critically endangered; 4, extinct in the wild or globally extinct. Species classified as data deficient in the risk assessment were not included. We estimated the species extent of occurrence and area of occupancy to examine possible effects of geographic range size on the relationships between plant attributes and conservation status. To estimate species-specific extent of occurrences and area of occupancy, we used herbarium data collected from over 60 herbaria through the SpeciesLink network (available in Supporting Information), which contains 260,690 occurrences of 6,270 species that have been geo-referenced at the municipal county scale across all 26 Brazilian states (≈ 8.5 million km^2). The extent of occurrence for each species was calculated according to the minimum convex polygon (or convex hull) method. Area of occupancy was calculated according to a sliding scale grid cell width with the CAT (Conservation Assessment Tools) extension within ArcView 3.1 (Moat 2007).

Species Attributes

We placed each species into categories of growth form, vegetation type, and level of geographic endemism (Table 1). We distinguished 5 growth form categories: climber (including scandents), epiphyte, herb, shrub, and tree. Aquatic and parasitic growth forms were excluded from the analyses because of large errors in model effect estimates due to small numbers of species in these categories. Growth form is one of the most easily distinguishable plant traits and is related to several functional responses in plants (Diaz & Cabido 1997). We distinguished 6 categories of vegetation type according to Stehmann et al. (2009): ombrophilous (evergreen) forest, semideciduous (seasonally dry forest), rocky outcrop, restinga (i.e., scrub vegetation on sandy coastal plains), grassland, and habitat generalist (i.e., species occurring in more than one vegetation type). These categories cover all major plant habitat types across the Brazilian Atlantic Forest (IBGE 2008), and each vegetation type is associated with a distinct set of environmental conditions (Veloso et al. 1991). The main aggregate sources of information were the Atlantic Forest Vascular Plant Endemism Project (<http://sagui.icb.ufmg.br/bot/mataatlantica/>),

Table 1. Breakdown of angiosperm species into categories of plant traits, extinction risk, and extent of occurrence.

Plant traits	Red List category		Extent of occurrence	
	<i>threatened</i> ^a (%)	<i>not threatened</i> (%)	<i>rare</i> ^b (%)	<i>not rare</i> (%)
Growth form				
climber	46 (4.3)	1026 (95.7)	234 (24.6)	716 (75.4)
epiphyte	85 (15.3)	471 (84.7)	301 (58.7)	212 (41.3)
herb	144 (6.3)	2126 (93.7)	730 (38.8)	1153 (61.2)
shrub	66 (4.9)	1288 (95.1)	396 (33.3)	792 (66.7)
tree	97 (6)	1520 (94)	354 (23.5)	1150 (76.5)
aquatic	1 (1.9)	53 (98.1)	6 (12.2)	43 (87.8)
parasite	0 (0)	103 (100)	30 (34.9)	56 (65.1)
Vegetation type				
rocky outcrops	43 (19.1)	182 (80.9)	125 (69.4)	55 (30.6)
grasslands	46 (5.1)	862 (94.9)	291 (40.6)	426 (59.4)
semideciduous forests	30 (6.2)	456 (93.8)	121 (29.1)	295 (70.9)
ombrophilous forests	191 (7.1)	2517 (92.9)	1040 (45.3)	1256 (54.7)
coastal restingas	33 (12.9)	222 (87.1)	73 (32.4)	152 (67.6)
habitat generalist	101 (4)	2424 (96)	451 (18.9)	1940 (81.1)
Endemism				
endemic ^c	383 (10.7)	3211 (89.3)	1556 (51.3)	1475 (48.7)
nonendemic	61 (1.7)	3509 (98.3)	550 (17)	2689 (83)
Total	444 (6.2)	6720 (93.8)	2106 (33.6)	4164 (66.4)

^aAccording to Fundação Biodiversitas (2005).

^bSpecies with extent of occurrence of <20,000 km² were defined as rare, according to the criteria for species categorization adopted by the IUCN.

^cSpecies were classified as endemic if they were restricted to the Atlantic Forest domain (Stebmann et al. 2009).

SpeciesLink (<http://www.splink.org.br/>), the World Checklist of Selected Plant Families (<http://apps.kew.org/wcsp/home.do>), the Brazilian List of Rare Plants (Giulietti et al. 2009), and the Species List of the Brazilian Flora (Forzza et al. 2012).

Phylogenetic Tree

We constructed a dated phylogenetic tree with all species, whereby the branch length was equivalent to the estimated age of each lineage according to Wikström et al. (2001). The topology of the tree containing all species was pruned from the megatree R20100701.new (available at <http://svn.phylodiversity.net/tot/megatrees/>) with the phylomatic tool (Webb & Donoghue 2005) as implemented in Phylocom version 4.2 (Webb et al. 2008). Clades with unresolved nodes were treated as polytomies, which reduced the power of the phylogenetic statistics tests and possibly overestimated phylogenetic conservatism (Davies et al. 2011b). The species and family trees (available in Supporting Information & Fig. 2) showing the phylogenetic distribution of plant attributes and extinction risk were constructed with iTOL (Letunic & Bork 2007).

Data Analyses

We measured the strength of the phylogenetic signal in extinction risk, area of occupancy, and extent of occurrence according to the Pagel's λ method and tested for significance with the *phylosig* function in *phytools* pack-

age (Pagel 1999; Revell 2012). This method estimates the phylogenetic signal and the likelihood value for each trait in both the original tree and the transformed tree with no phylogenetic signal (i.e., $\lambda = 0$). The likelihood ratio test was then used to compare these trees and test the null hypothesis that there is no phylogenetic signal.

We first explored the relationships between plant attributes and extinction risk with decision-tree analysis, as recommended by Sullivan et al. (2006). We used the QUEST method implemented in SPSS AnswerTree 3.0. The cross-validation procedure was applied 10 times, and the cost of misclassification in decision trees was the same for all trait groups. Further discussions on the use of decision trees to predict extinction risk from species traits can be found in Bielby et al. (2010). We also performed standard and phylogenetic regressions to test the relationship between traits and risk because both of these approaches can be usefully interpreted (Westoby et al. 1995). The use of phylogenetic regression allowed us to test how the independent evolution of certain life history and ecological traits affects present-day variation among species in levels of extinction risk. Phylogenetic regressions were performed using the *compar.gee* function available in the package *ape* version 3.0–8 for R (Paradis et al. 2011). This function uses the generalized estimating equation to apply a phylogenetic correction according to a variance-covariance matrix, which specifies the nonindependence among pairs of species based on their phylogenetic distance (Paradis & Claude 2002). The variance-covariance matrix was constructed using the *corPagel* function, and the λ value was set equal to

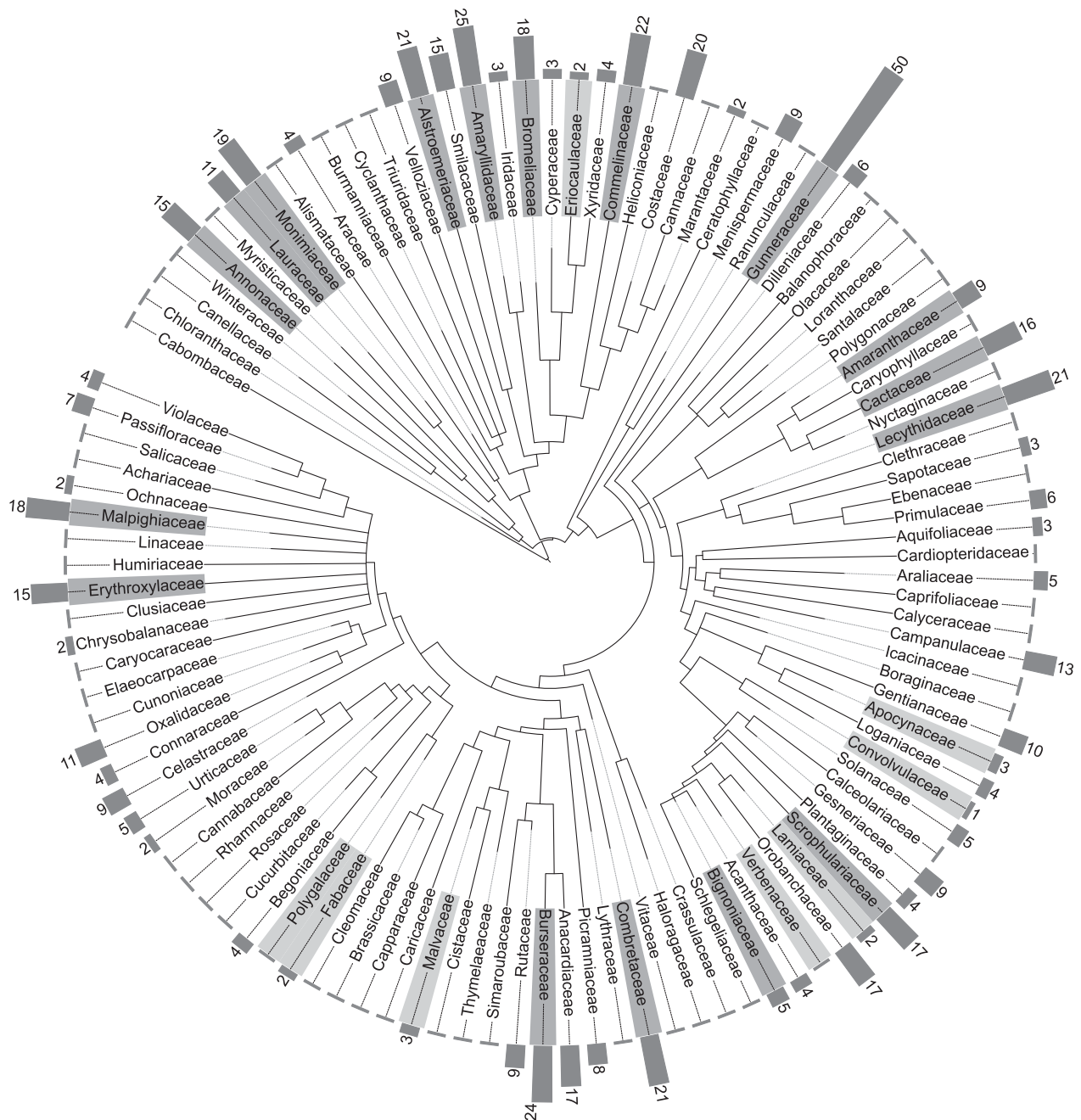


Figure 2. Phylogeny and family level extinction risk of 112 plant families from the Brazilian Atlantic Forest ($N = 6929$ study species). Family level extinction risk is represented by percentages of threatened species (the percentage value is shown at the end of bars). Shaded families showed either significantly higher (dark grey) or significantly lower (light grey) percentages of threatened species compared with the overall mean (Pearson's chi-square tests, $p < 0.05$).

the phylogenetic signal in extinction risk ($\lambda = 0.14$; see Freckleton et al. 2002).

Results

Phylogenetic Signal of Extinction Risk

Of 6929 species of Atlantic Forest plants in our data set, 6.4% were deemed threatened. The estimated extinction

risk was higher among close relatives than expected by chance, as evidenced by the phylogenetic signal test ($\lambda = 0.14$, $p < 0.001$, see phylogenetic tree in Supporting Information). Significant phylogenetic signal was also detected in the extent of occurrence ($\lambda = 0.54$, $p < 0.001$) and area of occupancy ($\lambda = 0.47$, $p < 0.001$), meaning that closely related species tended to share similar range sizes. The family phylogenetic tree illustrates how extinction risk was skewed toward some lineages (Fig. 2). From

all 112 plant families examined, 17 were associated with a higher species extinction risk than the overall mean (Pearson's chi-square tests, $p < 0.05$), whereas 8 families were associated with a significantly lower extinction risk. For example, Bromeliaceae, Cactaceae, Malpighiaceae, Amaryllidaceae, Annonaceae, and Lauraceae had more extinction-prone species than other clades selected by chance. In contrast, Fabaceae, Lamiaceae, Malvaceae, and Verbenaceae had fewer high-risk species than other clades.

Decision Tree Analysis

The decision tree analysis indicated that area of occupancy was the most powerful overall predictor of extinction risk, although a significant portion of the variation in extinction risk was additionally explained by other plant attributes. Vegetation type and growth form improved the predictive power of models and explained extinction risk under different classes of area of occupancy (Fig. 3). Species occurring in rocky outcrops were always more extinction prone than those in other vegetation. Epiphytes also had higher extinction risk than other growth forms. Differences among other vegetation types and extent of occurrence also explained some variation of extinction risk among species.

Overall, 16% of the epiphytes, and 20% and 13% of the species restricted to rocky outcrops and coastal restingas, respectively, were threatened with extinction. These fractions were 2- to 3-fold higher than the overall average. Some species groups were under relatively little threat, including climbers (4%) and habitat generalists (4%). This pattern of risk can be partially explained by the geographic distributions of these plant groups because 56% of the rocky outcrop endemics, 44% of all epiphytes, and 24% of the coastal restinga endemics were restricted to an area of occupancy smaller than the critical IUCN value ($<2000 \text{ km}^2$). Conversely, habitat generalists and trees were associated with relatively few narrowly distributed species (12% and 17%, respectively).

Standard Regression Models

As expected, extent of occurrence and area of occupancy were important predictors of extinction risk (Table 2). Vegetation type and growth form were also related to extinction risk in simple uncontrolled models, where plants restricted to either rocky outcrops or restingas and epiphytes were associated with significantly higher extinction risk than other plants.

According to the nonphylogenetic multiple regression model that included the 4 predictors, area of occupancy remained an important predictor of risk, whereas extent of occurrence explained no additional variation in extinction risk. Vegetation type and growth form also significantly explained extinction risk even after controlling

for both estimates of geographic range size. In particular, species restricted to rocky outcrops and coastal restingas were still associated with the highest extinction risk, whereas other habitat categories showed no differences among each other. Moreover, in the nonphylogenetic full model, epiphytes were still the single most extinction-prone growth form. Conversely, climbers and shrubs showed significantly lower extinction risk than both trees and epiphytes. Specifically, vegetation type and growth form accounted for 22% of the total variation explained by the full model after the effects of area of occupancy and extent of occurrence had been taken into account. When area of occupancy and extent of occurrence were removed from the full model, most predictors became more positively related to extinction risk, which clearly showed that part of the variation explained by plant attributes in uncontrolled models reflected differences in range size.

Phylogenetic Regression Models

Phylogenetic regression analyses reinforced the results that geographic range size and vegetation type were important predictors of extinction risk. Similarly to the nonphylogenetic full model, area of occupancy was negatively related to extinction risk, whereas extent of occurrence was not significant. Furthermore, species from coastal restingas and rocky outcrops still remained highly threatened after taking into account the phylogenetic nonindependence of the species. In contrast, the phylogenetic regressions produced very different results for growth form. In fact, none of the phylogenetic models detected differences in extinction risk among growth forms. In particular, the higher extinction risk of epiphytes detected in nonphylogenetic models was not significant when the non-independence of the species was taken into account. Again, by removing extent of occurrence and area of occupancy from the full model, it was possible to confirm that part of the predictive power attributed to plant traits was due to their correlation with geographic range size.

Discussion

Vegetation type and growth form were related to extinction risk in angiosperms across the Brazilian Atlantic Forest, even after controlling for variation in geographic range size; thus, these attributes could be used as indicators of extinction risk. For a given range size, plants endemic to either rocky outcrops or restingas were more likely to be at risk of extinction than plants in any other vegetation type. Likewise, epiphytes comprised the most extinction-prone growth form. However, threat status had a significant phylogenetic signal, indicating that some families and lineages concentrated a disproportionately

Table 2. Summary of standard and phylogenetic regression models predicting the threat status of plant species in the Brazilian Atlantic Forest.

Model Predictor	Standard regression						Phylogenetic regression					
	SLR models		full model		no-GRS model		SLR models		full model		no-GRS ^a model	
	B	SE	B	SE	B	SE	B	SE	B	SE	B	SE
Extent of occurrence ^b	-0.013***	0.001	-0.001	0.002	-	-	-0.011***	0.001	-0.001	0.002	-	-
Area of occupancy ^b	-0.016***	0.001	-0.015***	0.002	-	-	-0.014***	0.001	-0.013***	0.002	-	-
Vegetation type												
coastal restingas ^c	0.168***	0.030	0.124***	0.030	0.178***	0.030	0.168***	0.029	0.118***	0.029	0.157***	0.030
grasslands	0.021	0.018	-0.023	0.020	0.019	0.018	0.061*	0.021	0.014	0.022	0.062	0.023
habitat generalist ^d	-	-	-	-	-	-	-	-	-	-	-	-
ombrophilous forests	0.053***	0.013	-0.019	0.013	0.050***	0.013	0.044***	0.013	-0.021	0.013	0.041*	0.013
rocky outcrops	0.342***	0.032	0.212***	0.035	0.312***	0.033	0.254***	0.033	0.165***	0.036	0.258***	0.036
semideciduous forests	0.064*	0.023	0.039	0.023	0.070**	0.023	0.071*	0.022	0.044	0.023	0.078**	0.023
Growth form												
climber	-0.035	0.018	-0.051***	0.018	-0.035	0.018	-0.033	0.024	-0.051	0.024	-0.047	0.024
epiphyte	0.200***	0.023	0.083**	0.023	0.189***	0.023	0.008	0.034	-0.079	0.035	-0.072	0.036
herb	0.028	0.015	-0.018	0.016	0.013	0.016	-0.011	0.022	-0.039	0.023	-0.030	0.023
shrub	-0.009	0.017	-0.050*	0.017	-0.016	0.017	0.013	0.020	-0.033	0.020	-0.017	0.020
tree	-	-	-	-	-	-	-	-	-	-	-	-
Intercept	-	-	0.335***	0.021	0.055***	0.013	-	-	0.355	0.054	0.101	0.053
Observations ^e	-	-	5943		6742		-	-	5943		5943	
R ²	-	-	0.079		0.035		-	-	-		-	

Note: Only species with complete attribute data were considered in each model. The table includes simple linear regressions (SLR models), multiple regressions including all variables (full models), and multiple regressions including only area type and growth form, which did not include geographic range size (no-GRS models).
 Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (p values adjusted for multiple comparisons with Benjamini-Hochberg method).

^aGeographic range size.
^bLog2 extent of occurrence, log2 area of occupancy.
^cRestingas refers to the scrub vegetation on sandy coastal plains.
^dReference category.
^eMissing cases omitted.

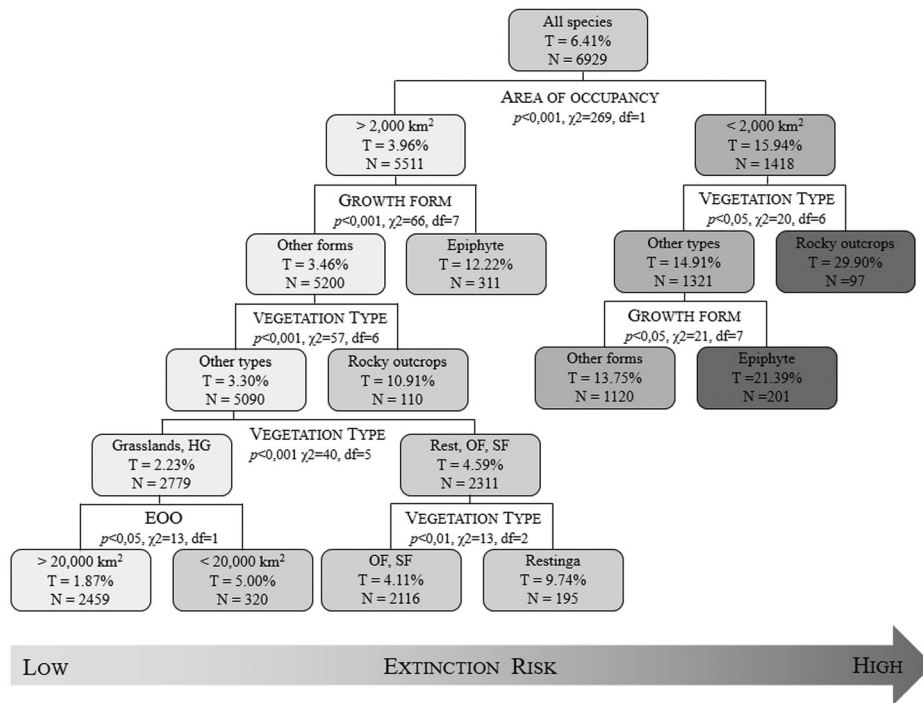


Figure 3. Hierarchical tree resulting from a decision-tree analysis. The tree shows how geographic range size and life history enhance partitioning of the species pools into groups with different levels of extinction risk. The tree clearly shows how life history can improve the prediction of extinction risk over and above the area of occupancy and extent of occurrence (EOO). Each tree node contains the predictor variable category, percentage of threatened species (T), and total number of species (N). Abbreviations: Rest, coastal restinga; OF, ombrophilous (evergreen) forest; SF, semideciduous forest; HG, habitat generalist.

high fraction of the threatened species. Taking into account this phylogenetic structure did not affect the relationship between habitat type and risk of extinction; rather, it rendered differences among growth forms non-significant. This stresses the consistency of rocky outcrops and restingas as areas associated with high vulnerability to extinction but indicates that the observed trend for higher extinction risks in epiphytes might not be causal.

Vegetation Type and Extinction Risk

Species extinction proneness varied substantially across vegetation types, even when area of occupancy and extent of occurrence were held constant and the phylogenetic structure of all species was considered. Specifically, species restricted to rocky outcrops were most threatened, which is only partially explained by the higher proportion of range-restricted species in this habitat type. This suggests that intrinsic properties of rocky outcrops may be important to understand the mechanisms underlying plant vulnerability to extinction. Rocky outcrops are montane islands facing extremely xeric conditions within a surrounding matrix of humid vegetation and safeguard some of the highest levels of plant endemism anywhere in the tropics (Burke 2003). High levels of beta diversity and endemism in rocky outcrops, along with an increasing frequency of disturbances such as fire, grazing, biological invasions, mining, and overexploitation of plants for trade, are the main determinants of high extinction risk in this habitat type (Meirelles et al. 1999; Jacobi et al. 2007). Like other montane areas, rocky outcrops

may also be more vulnerable to species loss due to climate change compared with low-elevation areas (Thuiller et al. 2005).

In coastal restinga plant communities, rarity was relatively unimportant in explaining extinction risk compared with other vegetation types because the risk associated with plants endemic to restingas was still significant after area of occupancy and extent of occurrence were controlled for. Land-use change is one of the main drivers of extinction risk across restinga plant communities because restinga is the most densely settled vegetation type and is likely experiencing the highest level of anthropogenic pressure in eastern Brazil (Rocha et al. 2007). The risk associated with species endemic to coastal restingas was also largely independent of phylogeny, emphasizing the role of habitat characteristics in explaining extinction risk. In contrast, extinction risk associated with species endemic to seasonally dry or evergreen forests were closely related to geographic range size, emphasizing the importance of range size as a predictor of vulnerability to extinction in these 2 forest types.

Species extinction risk varies greatly across habitat types worldwide, particularly due to differences in habitat size and rates of habitat loss (Duncan & Young 2000; Sodhi et al. 2008). Although habitat loss is a key determinant of extinction, observed differences in extinction risk can be partially explained by habitat-specific environmental conditions. Habitats exposed to marked environmental stress—such as severe droughts in rocky outcrops (Porembski & Barthlott 2000), restingas (Zamith & Scarano 2006) and forest canopy microhabitats associated with epiphytes (Benzing 1990; Zotz & Ziegler,

1997)—tend to be primarily occupied by slow-growing species (Grime & Hunt 1975; Arendt 1997), which likely exhibit low rates of population recovery following pulses of disturbance. Because repeated disturbance events are often relentless in areas facing high anthropogenic pressure, such as the Brazilian Atlantic Forest, more species will likely be extirpated in less resilient communities (Pimm 1991).

Growth form and Extinction Risk

Extinction risk varied among growth forms only when phylogenetic relationships were unaccounted for. We believe, however, that the results from both nonphylogenetic and phylogenetic models are useful if properly interpreted. For conservation purposes, in particular, nonphylogenetic models can be used to produce surrogates of extinction risk. For example, the nonphylogenetic regression models indicated that, in general, epiphytes are likely at higher risk of extinction than other growth forms even after controlling for geographic range size. This corroborates results of previous studies in Southeast Asia that show epiphytes concentrate most extinction-prone species (Turner et al. 1994; Sodhi et al. 2008).

From an evolutionary perspective, however, our phylogenetic models showed there was no evidence of functional relationships between growth forms and extinction risk. The apparently high extinction risk of epiphytes was due to the fact that a few speciose phylogenetic lineages of epiphytes concentrated more high-risk species. Our findings therefore failed to support the notion that epiphytism per se results in higher vulnerability to extinction. For example, among the epiphyte families, Bromeliaceae and Cactaceae concentrated high levels of extinction risk (18% and 16% of all species were threatened, respectively), whereas Gesneriaceae and Araceae were far less extinction prone (9% and 4%, respectively). Moreover, phylogenetically related traits not considered here may be important in explaining differences in extinction risk among epiphytes. For example, Bromeliaceae and Cactaceae include a large number of species with crassulacean acid metabolism (CAM), whereas this photosynthetic pathway is less prevalent in Araceae and Gesneriaceae species (Zotz & Ziegler 1997). Species with crassulacean acid metabolism typically grow slower than those with other photosynthetic pathways (i.e., C3 and C4; Lüttge 2004), and CAM epiphytes are also expected to have smaller population sizes relative to other epiphytes (Zotz 2004). In addition, we did not consider patterns of speciation that could be related to extinction risk, such as the age and rate of evolution of different phylogenetic lineages (Davies et al. 2011a).

Trees were the second most threatened growth form across the Brazilian Atlantic Forest according to non-

phylogenetic models. Although not significant, trees appeared as the most threatened growth form in the full phylogenetic model. This contrasts with previous findings that herbs other than grasses (Wiegmann & Waller 2006) and shrubs (Duncan & Young 2000; Kolb & Diekmann 2005) are often more extinction prone. Key mechanisms driving trees toward extinction are forest loss and fragmentation, decline of pollinators and seed dispersers, and timber extraction (Tabarelli et al. 2004).

The amount of variation explained by our models was limited, but this could be improved by incorporating other life history traits such as dispersal ability (Duncan & Young 2000) and dependence on specific modes of animal seed dispersal and pollination vectors (Bond 1994; Sodhi et al. 2008). However, we expect that a large amount of variation in extinction risk cannot be explained by any combination of biological traits because of the complex and idiosyncratic nature of human-imposed threats and uncertainties associated with estimates of species extinction risk. Despite such limitations, we found evidence for a unifying mechanism explaining plant extinction risk across the Atlantic Forest domain. High extinction risk and slow growth life histories appear to be disproportionately concentrated in plants restricted to rocky outcrops and restingas and in the most drought-adapted epiphyte lineages (e.g., Bromeliaceae and Cactaceae). In ecosystems where disturbances are both frequent and diffuse, such as the Atlantic Forest, low-resilience species associated with low rates of net population recovery are likely to be most vulnerable to extinction. An increasingly severe regime of human-induced disturbances and community hyperdynamism across the Atlantic Forest may therefore disproportionately aggravate threats to species expressing an intrinsically low capacity for population recovery. We hope our findings can aid future attempts to identify extinction-prone species in highly diverse tropical floras, thereby refining regional-scale conservation planning across one of the world's most important biodiversity hotspots.

Acknowledgments

We are especially grateful to J. Stehmann (Atlantic Forest Vascular Plant Endemism Project) and R. Govaerts (Kew Garden) for facilitating the plant attribute data acquisition process. We thank A. Ives and B. Santos for their advice with phylogenetic analyses and 2 anonymous reviewers. T.L. received scholarships from CNPq and Conservation International do Brasil and is currently supported by a scholarship from CAPES (BEX 1145/12-6). C.R.F. received support from CNPq (Productivity Fellowship 303714/2010-7), and C.A.P. was funded by a Brazilian Ministry of Education grant (PVE 004/2012).

Supporting Information

The list of herbaria providing data (Appendix S1), and the phylogenetic tree containing all species and plant attributes (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than omitted material) should be directed to the corresponding author.

Literature Cited

- Arendt, J. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology* **72**:149–177.
- Benzing, D. 1990. *Vascular epiphytes*. Cambridge University Press, New York.
- Bielby, J., M. Cardillo, N. Cooper, and A. Purvis. 2010. Modelling extinction risk in multispecies data sets: phylogenetically independent contrasts versus decision trees. *Biodiversity and Conservation* **19**:113–127.
- Bond, W. J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions: Biological Sciences* **344**:83–90.
- Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**:453–460.
- Burke, A. 2003. Inselbergs in a changing world—global trends. *Diversity and Distributions* **9**:375–383.
- Davies, T. J., et al. 2011a. Extinction risk and diversification are linked in a plant biodiversity hotspot. *PLoS Biol* **9**:e1000620.
- Davies, T. J., N. J. B. Kraft, N. Salamin, and E. M. Wolkovich. 2011b. Incompletely resolved phylogenetic trees inflate estimates of phylogenetic conservatism. *Ecology* **93**:242–247.
- Diaz, S., and M. Cabido. 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* **8**:463–474.
- Duncan, R. P., and J. R. Young. 2000. Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology* **81**:3048–3061.
- Fonseca, C. R., J. M. Overton, B. Collins, and M. Westoby. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* **88**: 964–977.
- Forzza, R. C., et al. 2012. New Brazilian floristic list highlights conservation challenges. *Bioscience* **62**:39–45.
- Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* **160**:712–726.
- Fundação Biodiversitas. 2005. *Lista da flora brasileira ameaçada de extinção*. Fundação Biodiversitas.
- Galmés, J., J. Cifre, H. Medrano, and J. Flexas. 2005. Modulation of relative growth rate and its components by water stress in Mediterranean species with different growth forms. *Oecologia* **145**:21–31.
- Gaston, K. J., and T. M. Blackburn. 2000. *Pattern and process in macroecology*. Blackwell Science, Cambridge.
- Gaston, K. J., and R. A. Fuller. 2009. The sizes of species' geographic ranges. *Journal of Applied Ecology* **46**:1–9.
- Giulietti, A. M., A. Rapini, M. J. G. D. Andrade, L. P. D. Queiroz, and J. M. C. D. Silva. 2009. *Plantas raras do Brasil*. Conservação Internacional, Belo Horizonte.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* **111**:1169–1194.
- Grime, J. P., and R. Hunt. 1975. Relative growth-rate: its range and adaptive significance in a local flora. *Journal of Ecology* **63**:393–422.
- Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* **13**:207–251.
- IBGE. 2008. *Mapa da área de aplicação da Lei nº 11.428 de 2006*. Instituto Brasileiro de Geografia e Estatística.
- Jacobi, C., F. do Carmo, R. Vincent, and J. Stehmann. 2007. Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. *Biodiversity and Conservation* **16**:2185–2200.
- Kolb, A., and M. Diekmann. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. *Conservation Biology* **19**:929–938.
- Laube, S., and G. Zotz. 2003. Which abiotic factors limit vegetative growth in a vascular epiphyte? *Functional Ecology* **17**:598–604.
- Letunic, I., and P. Bork. 2007. Interactive Tree Of Life (iTOL): an online tool for phylogenetic tree display and annotation. *Bioinformatics* **23**:127–128.
- Lüttge, U. 2004. Ecophysiology of Crassulacean acid metabolism (CAM). *Annals of Botany* **93**:629–652.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* **28**:495–516.
- McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**:450–453.
- Meirelles, S. T., V. R. Pivello, and C. A. Joly. 1999. The vegetation of granite rock outcrops in Rio de Janeiro, Brazil, and the need for its protection. *Environmental Conservation* **26**:10–20.
- Mittermeier, R. A., P. R. Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreaux, and G. A. B. Fonseca. 2004. *Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions*. Cemex and University of Chicago Press, Chicago, Illinois.
- Moat, J. 2007. Conservation assessment tools extension for ArcView 3.x, version 1.2 in G. Unit, editor. Royal Botanic Gardens, Kew. Available from: <http://www.rbgb.org.uk/gis/cats>
- Murray, B. R., P. H. Thrall, and A. B. Nicotra. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecology* **27**:291–310.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401**:877–884.
- Paradis, E., and J. Claude. 2002. Analysis of comparative data using generalized estimating equations. *Journal of Theoretical Biology* **218**:175–185.
- Paradis, E., et al. 2011. Package 'ape'—analyses of phylogenetics and evolution.
- Pereira, H. M., et al. 2010. Scenarios for global biodiversity in the 21st century. *Science* **330**:1496–1501.
- Pimm, S. L. 1991. *The balance of nature?: Ecological issues in the conservation of species and communities*. The University of Chicago Press, Londres.
- Porembski, S., and W. Barthlott. 2000. Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. *Plant Ecology* **151**:19–28.
- Revell, L. J. 2012. *phytools: an R package for phylogenetic comparative biology (and other things)*. *Methods in Ecology and Evolution* **3**:217–223.
- Ribeiro, M. C., J. P. Metzger, A. C. Martensen, F. J. Ponzoni, and M. M. Hirota. 2009. The Brazilian Atlantic forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* **142**:1141–1153.
- Rocha, C., H. Bergallo, M. Van Sluys, M. Alves, and C. Jamel. 2007. The remnants of restinga habitats in the Brazilian Atlantic Forest of Rio de Janeiro state, Brazil: habitat loss and risk of disappearance. *Brazilian Journal of Biology* **67**:263–273.
- Schmidt, G., and G. Zotz. 2002. Inherently slow growth in two Caribbean epiphytic species: a demographic approach. *Journal of Vegetation Science* **13**:527–534.

- Sodhi, N., et al. 2008. Correlates of extinction proneness in tropical angiosperms. *Diversity and Distributions* **14**:1–10.
- Stehmann, J. R., R. C. Forzza, M. S. Alexandre Salino, D. P. D. Costa, and L. H. Y. Kamino. 2009. Plantas da Floresta Atlântica. Jardim Botânico do Rio de Janeiro, Rio de Janeiro.
- Stork, N. E., J. A. Coddington, R. K. Colwell, R. L. Chazdon, C. W. Dick, C. A. Peres, S. Sloan, and K. Willis. 2009. Vulnerability and resilience of tropical forest species to land-use change. *Conservation Biology* **23**:1438–1447.
- Sullivan, M., M. Jones, D. Lee, S. Marsden, A. Fielding, and E. Young. 2006. A comparison of predictive methods in extinction risk studies: contrasts and decision trees. *Biodiversity and Conservation* **15**:1977–1991.
- Tabarelli, M., J. M. C. Silva, and C. Gascon. 2004. Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodiversity and Conservation* **13**: 1419–1425.
- Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* **102**:8245–8250.
- Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence *The Journal of Applied Ecology* **33**:200–209.
- Turner, I. M., H. T. Tan, Y. C. Wee, A. B. Ibrahim, P. T. Chew, and R. T. Corlett. 1994. A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. *Conservation Biology* **8**:705–712.
- Veloso, H. P., A. R. Filho, and J. A. Lima. 1991. Classificação da vegetação brasileira, adaptada a um sistema universal. IBGE, Rio de Janeiro.
- Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* **24**:2098–2100.
- Webb, C. O., and M. J. Donoghue. 2005. Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* **5**:181–183.
- Westoby, M., M. R. Leishman, and J. M. Lord. 1995. On misinterpreting the ‘phylogenetic correction’. *Journal of Ecology* **83**:531–534.
- Wiegmann, S. M., and D. M. Waller. 2006. Fifty years of change in northern upland forest understories: Identity and traits of winner” and “loser” plant species. *Biological Conservation* **129**:109–123.
- Wikström, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**:2211–2220.
- Zamith, L. R., and F. R. Scarano. 2006. Restoration of a Restinga Sandy Coastal Plain in Brazil: survival and growth of planted woody species. *Restoration Ecology* **14**:87–94.
- Zotz, G. 2004. How prevalent is crassulacean acid metabolism among vascular epiphytes? *Oecologia* **138**:184–192.
- Zotz, G., and H. Ziegler. 1997. The occurrence of crassulacean acid metabolism among vascular epiphytes from Central Panama. *New Phytologist* **137**:223–229.