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The Relationship between Local Abundance and Distribution of Rain Forest Trees across Environmental Gradients in India

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ABSTRACT

We tested whether local abundance of rain forest trees in the medium elevation wet forests of the southern Western Ghats (WG) was related to environmental tolerance, life form, and geographical range. We selected trees in medium elevation wet forests (750–1700 m asl) of the southern WG, using two data bases: a small plot (30 × 30 m) data base of 288 species of trees ($\geq$ 3 cm dbh) in 33 plots totaling 2.97 ha, and a data base of 135 species of tree ($\geq$ 10 cm dbh) in larger plots of 1 ha each, totaling 4.84 ha. The species density per hectare and number of records in the plot network was used in a factor analysis to give a measure of the local abundance of each species. The altitude and seasonality ranges of these species in the WG was assessed from independent data bases and used to generate an environmental tolerance score. Results indicated that as a species became locally more abundant, it occurred across a wider range of environmental gradients, but regional distribution was not related to geographical distribution. Understory species tended to be rarer with smaller range sizes and lower environmental tolerances than overstory species. Climate change is predicted to have drastic effects on restricted range species with limited environmental tolerances.

Key words: climatic gradients; commonness and rarity; environmental tolerance; restricted range species; tropical rain forest; Western Ghats.

THE RELATIONSHIP BETWEEN LOCAL ABUNDANCE AND SPATIAL DISTRIBUTION at the macro-scale can provide insights into the ecological processes that determine the abundance and distribution of species (Brown 1984). A species that is abundant at the local scale also tends to occur in more sites (Gaston *et al.* 1997). This pattern is consistent across scales and taxa suggesting that similar processes might regulate local and regional abundances of species (Hanski 1982, Bock & Ricklefs 1983, Brown 1984, Lacy & Bock 1986, Bock 1987, Gaston 1996, Gaston *et al.* 1997, Jankowskil & Rabenold 1997).

The mechanisms underlying this pattern are not clear (Gaston *et al.* 1997). Brown (1984) had proposed that species with broader niches and environmental tolerances would be able to use a wider range of resources, attain higher local densities, and survive in more places. However, since environmental conditions change over regions, this relationship would weaken at larger scales. A species that is well adapted locally might not necessarily be abundant in sites where different environmental conditions prevail (see Gaston *et al.* 1997). Johnson (1998) suggested that species that are locally rare and with small range sizes are more prone to extinction, thereby resulting in a positive relationship between range size and abundance.

Trees in hyperdiverse tropical rain forests tend to be locally rare (Hubbell & Foster 1986). Local rarity has been linked to pest pressure because species-specific pests reduce recruitment near conspecific adults due to density-dependent predation (Janzen 1970, Connell 1971). However, rarity at larger scales increases with increasing dry season lengths and altitude (up to 1500 m), indicating that seasonality and altitude are the two axes regulating the distribution of species in the Western Ghats (WG) rain forests (Gimaret-Carpentier *et al.* 2003, Davidar *et al.* 2005). Dry season length decreases in mid elevations of the southern WG making this region relatively aseasonal and a center for plant diversity and endemism (Gimaret-Carpentier *et al.* 2003, Davidar *et al.* 2005).

Severe drought in the dry season has drastic consequences on rain forest trees (Condit *et al.* 1995), particularly for shallow rooted understory treelets and shrubs (Wright 1992, Engelbrecht & Kursar 2003). Sensitivity to drought varies among species and is considered an important regulator of tree distributions in rain forests (Engelbrecht *et al.* 2007). Widespread species have been shown to be less prone to drought stress (Baltzer *et al.* 2008).

Widespread species in the Neotropical rain forests tended to be tall trees with higher sapling survivorship rates in the shade (Pitman *et al.* 2001, Svenning *et al.* 2004, Macia & Svenning 2005). Taller canopy trees in the rain forests of the WG of India tended to have

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higher levels of similarity across sites than trees of the understory (Davidar *et al.* 2007), suggesting a wider range size. There were relatively fewer understory species in the seasonal wet forests of the central WG of India compared with the aseasonal forests in the southern region.

Tall trees could be better competitors for light and less resource limited than shorter understory trees and shrubs (Kelly 1996). Thomas and Bazzaz (1999) have shown that tall canopy trees in a Malaysian rain forest have higher photosynthetic capacity relative to understory species. Dominant trees in temperate forests also tend to have similar traits (Kobe 1996, Koike 2001), indicating that similar processes might regulate tree distributions in tropical and temperate forests.

In tropical Asian forests, large-scale patterns of tree species distributions and diversity were correlated with seasonality (Davidar *et al.* 2005, Baltzer *et al.* 2008). However, the relationship between the distribution of species across climatic gradients is difficult to assess in hyper diverse forests due to uncertainty in species identifications and lack of information on their range sizes (Ruokolainen *et al.* 2002). The rain forest tree flora of the WG of India is well known, and species identifications can be done with a certain amount of confidence due to many floras and herbaria. Plot-based tree inventories conducted in different parts of the WG can provide fairly unambiguous information on the distribution of species across geographical and environmental gradients.

We selected tree species ($\geq$ 3 cm dbh) in a 33-plot network in medium altitude rain forests of the *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum* type, which is restricted to the less seasonal sites in the southern WG of India (Pascal 1988). We assessed plant rarity at the local scale and environmental tolerance at the scale of the WG, and tested the null hypothesis that local rarity was not associated with environmental tolerance, life form, and geographical range size (Hanski 1982; Brown 1984; Gaston & Kunin 1997; Pitman *et al.* 1999, 2001).

METHODS

STUDY AREA.—The WG, a biodiversity hotspot (Myers, 1990), is a narrow chain of mountains running parallel to the western coast of the Indian peninsula 8–21°N, about 1600 km in length (Fig. 1). The rain forests, known locally as wet evergreen forests, occur as a ribbon running north to south along the slopes and valleys of the WG from *ca* 8°23–16°N. Much of the forests have been destroyed but pristine forests remain in the inaccessible slopes and valleys. The southern Western Ghats (SWG) lie south of the Palghat Gap (10°30′ N), a 30-km-wide break in the mountain chain. Further south at around 9°N is the Shencottah gap, a small break that segregates the species rich forests of Tirunelveli and Travancore from the northern section. Due to their relative inaccessibility, a comparatively larger proportion of these forests are fairly pristine.

Annual rainfall is highest in the Central regions decreasing both northwards and southwards. The length of the dry season increases from the South to the North (Davidar *et al.* 2005).

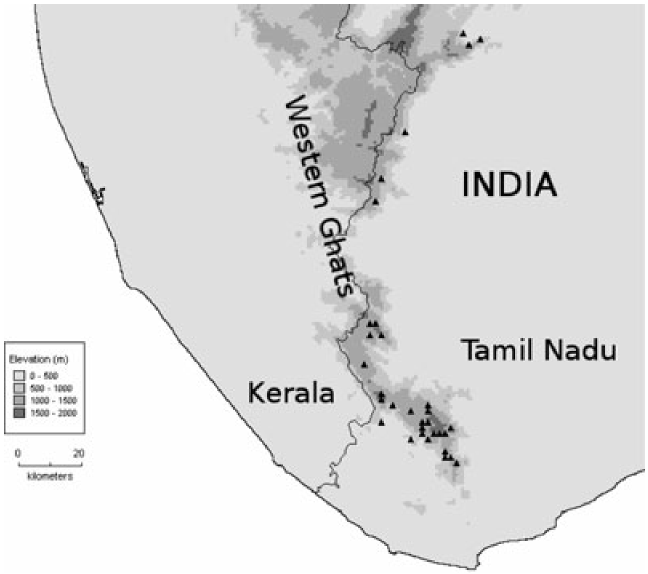

FIGURE 1. Map of the Indian subcontinent showing the location of the plots in the southern Western Ghats.

We studied commonness and rarity among trees in the *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum* type of forest common in medium elevations in regions (700–1700 m asl) with short dry seasons (1–3.5 mo dry season) in the southern part of the WG.

The data base for the study was from 33 unpublished small plot inventories. We also used data from two published inventories located in the same region to counter-check our results on the relationship between environmental tolerance and species rarity. The small plot inventories were conducted between 1999 and 2002, and consisted of 33 randomly laid plots of total area 2.97 ha in medium elevation forest sites (8°23′–9°50′ N) where all trees ($\geq$ 3 cm dbh) had been inventoried. This region lies south of the Palghat Gap in the districts of Tirunelveli, Ramnathapuram, and Kanyakumari of Tamil Nadu state (Fig. 1). Only five of the small plots were in Kalakad-Mundanthurai Tiger Reserve (KMTR) and the rest were in Reserved Forests, which have a lower level of protection, but which had minimal human disturbance.

The published inventories (four consolidated plots of total area 3.84 ha and a 1 ha plot) were located at about 8°33′ N, 1200 m asl and were conducted in the early to mid 1990s. These plots were located within undisturbed stretches of medium elevation wet forests in the KMTR, which was relatively under sampled in the small plot inventories. These published inventories (trees $\geq$ 10 cm dbh) were a 1 ha plot laid in undisturbed medium elevation forests in Sengaltheri (Parthasarathy 1999) and a composite of plots totaling 3.84 ha in Kakachi about 10 km away (Ganesh *et al.* 1996).

Sites where the inventories were conducted have annual rainfall averaging 3000–6000 mm and dry seasons of 1–3 mo. These sites had not been logged as per the records of the Working Plans of the Tamil Nadu Forest Department. Otherwise the sites showed little or no current human impact.

THE TREE INVENTORIES.—Species in the small plot inventories were identified through a voucher specimen collected from each tree and deposited at the herbarium of the Department of Ecology and Environmental Sciences, Pondicherry University (for details see Davidar *et al.* 2005). Published information on species and their abundances were obtained directly from source publications.

We assembled a species distribution matrix for each data set. The number of individuals per species was summed over all the plots and then divided by 2.97 ha (33 plots × 0.09 ha) for the small plots and by 4.84 for the published plots, to convert the values into density per hectare. As the density data were not normally distributed, we log transformed (natural logarithm) the values. Occurrence was measured as the number of plots in which each species was recorded. The log density and occurrence data for each species were reduced to a factor score and these scores were used as a measure of commonness and rarity. Species at the low end of the scale were those with low densities and records in the plot network, whereas abundant and widespread species were at the high end of the scale. We classified life-forms as upper story: emergent, canopy and subcanopy trees with maximum height ≥ 15 m and understory trees as those with maximum height < 15 m.

ENVIRONMENTAL RANGES.—We assessed the environmental tolerance of each species from an independent data base consisting of published and unpublished tree distributions in the WG.

The independent plot based data base on tree distributions extended from 8°23′ to 15°00′ N and covered a total area of 53 ha. These plot-based data included 116 published (Pascal 1988; Pascal & Pelissier 1996; Parthasarathy & Karthikeyan, 1997; Ayyappan & Parthasarathy 1999; Garrigues 1999; Parthasarathy 1999, 2001; Srinivas & Parthasarathy 2000) and unpublished inventories (P. Davidar, unpubl. data). The second data base was generated by the Atlas of Endemic trees of the WG where the geographical and altitudinal ranges of the endemic trees of lower dbh limit ≥ 10 cm were noted using records from 12 different herbaria in India and abroad, published data, and field surveys (Ramesh *et al.* 1997, Puyravaud *et al.* 2003). In addition, regional floras were consulted for corroborating the information on the distributional limits of species (Gamble & Fischer 1915–1936; Matthew 1981, 1982, 1999).

The geographical coordinates of the plots where the tree inventories were made were used as reference points for location. Information on the geographical coordinates and altitude of each site was directly obtained or was noted from the source publications. Meteorological data on each site were obtained through Governmental sources, private companies, or through source publications. Rainfall data were obtained from rain gauges located fairly close (< 5 km) to the study plots. Using the available data, mean monthly and annual rainfall were computed for each site. Dry season length was defined as the number of consecutive months with monthly rainfall averaging < 100 mm (see Davidar *et al.* 2005, 2007 for further information).

ENVIRONMENTAL TOLERANCES OF SPECIES.—The minimum and maximum distributional limits of each species across latitudinal, altitude, and seasonality gradients was computed from the data base using Microsoft Access. A species distribution across seasonality and altitudinal ranges were used as an indicator of their environmental tolerance. To assess the environmental tolerance of a species, the difference between its minimum and maximum altitude and seasonality limit was estimated and reduced in a factor analyses to obtain a factor score. These factor scores were used as a measure of the environmental tolerances of species. Scores at the low end of the scale had narrower distributions across environmental gradients than those with higher scores. Only evergreen trees were used for the analyses. Species that had poor distributional records across the WG, were also not included. We used both the small plot and the published data base for the analyses.

GEOGRAPHICAL DISTRIBUTIONS.—We assessed whether rare species tended to have a higher proportion of WG endemics compared with common species. The geographical ranges of species was categorized as: (1) endemic to the WG; and (2) nonendemics, distributed over the Indian peninsula, Sri Lanka, Indo-Malesia, and other tropical regions. We used published literature to determine the global ranges of species (Whitmore 1972, 1973; Ng 1978; Saldanha 1984; Ahmedullah & Nayar 1986; Ramesh *et al.* 1997).

COMMON AND RARE SPECIES.—We identified common and rare species using the small plot network (≥ 3 cm dbh). We classified species with single records as rare, and those with factor scores $>$ 1.9 as common. We excluded deciduous species and those predominantly from the lower elevations, since these species tend to be transients in this forest. We assessed whether common species tended to belong to certain life-forms as compared with rare species.

DATA ANALYSES.—We used regression analyses to assess the relationship between local abundance and distribution in the plot network, and rarity and environmental tolerances at larger scales. Using *t*-tests we tested whether: (1) WG endemics/nonendemics; (2) understory/overstory; and (3) rare/common species differed in latitudinal range sizes and environmental tolerances (Sokal & Rohlf 1981). Systat version 10 (2000) was used for the statistical analyses.

RESULTS

GENERAL PATTERNS.—The small plot data base (≤ 3 cm dbh) used in this study consisted of 3903 trees from 288 species, 158 genera, and 59 families. Of these, 266 were evergreen and 22 deciduous trees. The deciduous trees were not included in the analyses since they were very rare and probably transients (mean rarity scores of –0.65, compared with 0.05 for the evergreen trees). Introduced species were not represented in this data base. Therefore the analysis was restricted to the remaining 266 species. The two large plots (≤ 10 cm dbh) consisted of 2956 trees representing 135 species. There were a total of 325 species in both data bases with 101 (31%) species in common.

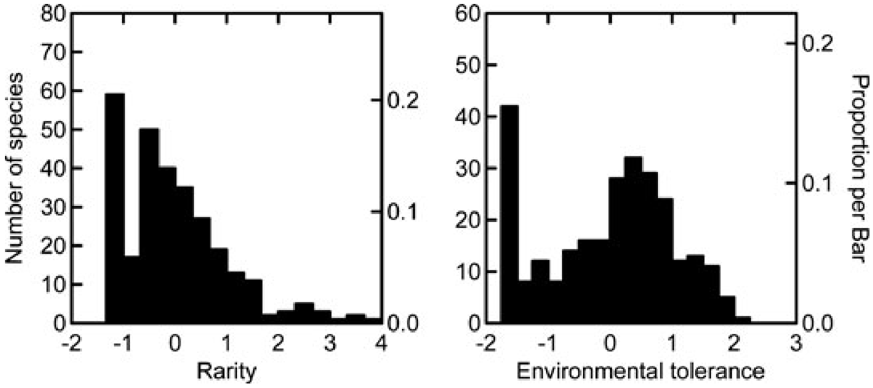

FIGURE 2. Distribution of (A) rarity factor scores and (B) environmental tolerance scores for tree species in the southern Western Ghats.

Species with broader environmental tolerances tended to occur across a wider latitudinal range ($y = -0.61 + 0.21x$, $N = 264$, $R^2 = 0.30$, $P < 0.0001$), indicating that species that ranged widely in the WG tolerated a wide range of environmental conditions. Range size and environmental tolerance appear to be continuous variables, but both were strongly skewed toward the left with 40–60 species having narrow environmental tolerances and being very rare (Fig. 2A, B). Some rare species had broader environmental tolerances. When species with very narrow environmental tolerances were excluded, the data did not significantly differ from normality (Wilks Shapiro test = 0.986, $P > 0.05$; Fig. 2B), indicating that tolerance to a range of environmental conditions varied continuously (Fig. 2). Some species were very rare and others were very common, whereas most species had intermediate values of rarity. This suggests that very rare species and very common species were exceptional (Fig. 2B).

Log density and frequency of distribution in the plot network was significantly related (Table 1), but more strongly for the small plots (≤ 3 cm dbh) than the published data base (≤ 10 cm dbh). There was a significantly positive relationship between local rarity factor scores and environmental tolerance at higher scales (Table 1; Fig. 3). However, some of the locally rare species had broader environmental tolerances (Fig. 3).

RARE AND COMMON SPECIES.—We identified 45 rare and 17 common species from the small plot data base. Common species had over twice the latitudinal range as rare species (hereafter mean ± SD; rare: 2.06 ± 2.48; common: 4.37 ± 2.25, $t = 3.5$, df = 31.6, $P < 0.001$; Fig. 4). Common species had wider environmental tolerance scores than rare species (rare: –0.56 ± 0.84; common: 1.10 ± 0.44, $t = 10.1$, df = 53.7, $P < 0.0001$; Fig. 4).

GEOGRAPHICAL RANGES.—WG endemics did not significantly differ from nonendemics in the local rarity factor (endemic rarity: 0.01 ± 0.93; nonendemic rarity: 0.11 ± 1.10, $t = 0.77$, df = 240, ns) or in environmental tolerance (endemic tolerance: –0.01 ± 0.92; nonendemic tolerance: 0.08 ± 1.04, $t = 0.74$, df = 233, ns; Table 1; Fig. S1). The geographical ranges of the rare and common species did not significantly differ ($\chi^2 = 1.12$, df = 1, ns). However the relationship between the local rarity factor and

TABLE 1. *The relationship between rarity and environmental tolerance at the local scale and the large scale.*

Data base	Dependent variable	Independent variable	Intercept	Slope	N	R^2	P
Tree species (≤ 3 cm dbh)	occurrence	log density	2.17	+1.94	288	0.58	< 0.0001
Tree species (≤ 10 cm dbh)	occurrence	log density	1.1.5	+0.11	132	0.16	< 0.0001
Tree species (≤ 3 cm dbh)	rarity	environmental tolerance	0.06	+0.52	256	0.26	< 0.0001
Tree species (≤ 10 cm dbh)	rarity	environmental tolerance	0.02	+0.33	131	0.11	< 0.0001
Western Ghats endemics (≤ 3 cm dbh)	rarity	environmental tolerance	0.01	+0.36	103	0.12	< 0.0001
Nonendemics (≤ 3 cm dbh)	rarity	environmental tolerance	0.06	+0.62	153	0.34	< 0.0001

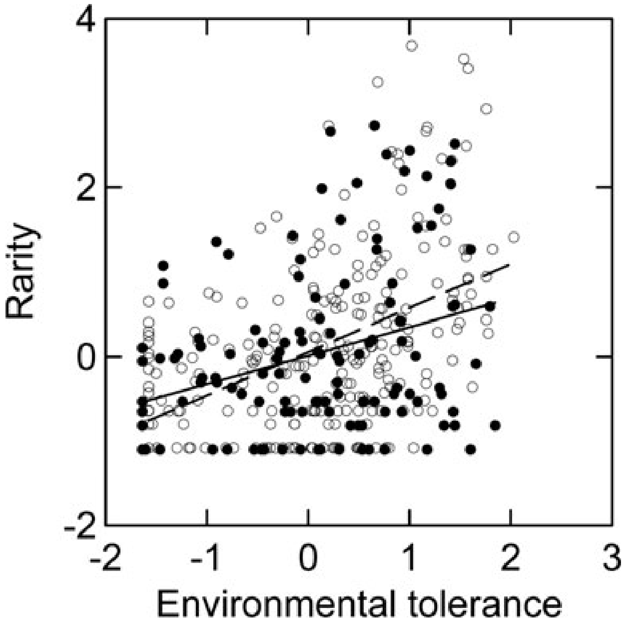

FIGURE 3. The relationship between rarity and environmental tolerance (black circles, dashed line = species from 33 small plots [≤ 3 cm dbh], open circles, continuous line = species from published plots [≤ 10 cm dbh]).

environmental tolerance was stronger for nonendemics than endemics (Table 1; Fig. S1).

SPECIES ATTRIBUTES.—Species were equally divided between the overstory (152 species) and the understory (136 species). Understory species tended to have significantly lower local rarity factor scores than overstory species (understory: –0.016 ± 0.81; overstory: 0.15 ± 1.12, $t = 2.7$, df = 273, $P = 0.01$), and lower levels of environmental tolerances (understory: –0.015 ± 1.01; overstory: 0.14 ± 0.98, $t = 2.41$, df = 268, $P = 0.02$). Understory species had significantly smaller latitudinal range sizes (understory: 2.6 ± 2.57; overstory: 3.49 ± 2.57, $t = 2.81$, df = 262, $P = 0.01$) and occurred over smaller ranges in seasonality (understory: 2.16 ± 1.32; overstory: 2.5 ± 1.38; $t = 2.10$, df = 262, $P = 0.04$) than overstory species.

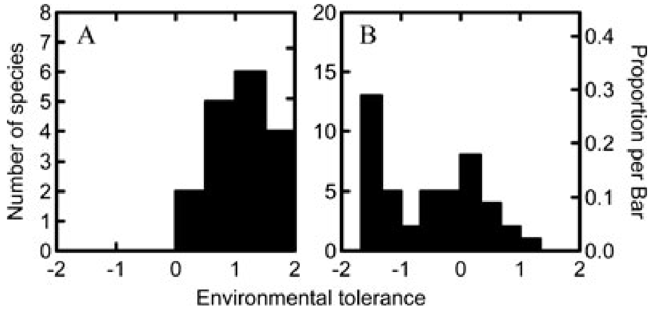

FIGURE 4. The environmental tolerances of common and rare tree species (≤ 3 cm dbh).

DISCUSSION

GENERAL PATTERNS.—Our study shows that while there is a continuum of environmental tolerances among species, rare species have more restricted environmental ranges and tend to be from the forest understory whereas common species tended to have wider distributions and tend to be larger overstory trees. This trend is consistent across scales: species that were locally common and widespread also tended to be common and widespread at regional scales. Studies have shown that widespread species that are adapted to climatic variations at the larger scale might not do well locally on particular edaphic features (Baltzer *et al.* 2007). However, our study indicates that widespread species are also locally abundant, and this might be because local populations tend to be adapted to local conditions (Fox & Morrow 1981, Ayres & Scriber 1994).

Gaston and Kunin (1997) have proposed mechanisms that could explain the interspecific relationship between abundance and range size. Niche-based mechanisms would not operate at all scales because environmental conditions that promote local adaptation could change. However, adaptation to moisture and thermal gradients could be better predictors of range sizes and local abundances of species since these factors are relatively independent of scale.

Tolerance to seasonal drought could be an important factor regulating tree distributions in tropical rain forests (Engelbrecht *et al.* 2007). A study in the SE Asian rain forests has shown that drought-resistant trees tended to be more widely distributed than those that were drought intolerant (Baltzer *et al.* 2008). Generally, taller species tend to be more drought-resistant than small shallowly rooted species of the understory (Wright 1992, Condit *et al.* 1995, Engelbrecht & Kursar 2003). Our study shows that smaller understory species were rarer, had smaller latitudinal and seasonality ranges, and had lower levels of environmental tolerance than taller overstory species. In the WG rain forests, understory tree species richness was higher in aseasonal forests compared with more seasonal forests (Davidar *et al.* 2007), suggesting that the moist conditions through the year promote the survival of understory trees and saplings. Shrubs on BCI 50-ha plot in Panama tended to suffer higher mortality than trees (Condit *et al.* 1995). The distribution of the Melastomataceae and the pteridophytes, which are smaller taxa, in Western Amazonian forests were largely environmentally determined (Tuomisto & Ruokolainen 1994). Therefore severe drought in tropical rain forests could differentially affect smaller trees (Condit *et al.* 1995, Engelbrecht & Kursar 2003), resulting in local rarity. Johnson (1998) suggested that local extinction of rare species could result in the observed abundance-range size relationship.

Tall trees could also be better competitors for light and less resource limited than shorter understory trees and shrubs (Kelly 1996). Studies in Neotropical lowland rain forests have indicated that a set of tall trees dominate local scales and large scales (Pitman *et al.* 2001, Svenning *et al.* 2004, Macia & Svenning 2005). These species had higher sapling survivor rates in the shade (Svenning *et al.* 2004). Thomas and Bazzaz (1999) have shown that tall canopy trees in a Malaysian rain forest have higher photosynthetic capacity relative to understory species. Dominants in temperate forests tend to have similar traits (Kobe 1996, Koike 2001), indicating that taller trees might be less prone to stress caused by thermal variation or rainfall seasonality. Gimaret-Carpentier *et al.* (2003) in their study of the distribution of endemic tree species across altitudinal and seasonality gradients in the WG, found that endemic species richness was highest in the mid elevation forests (800–1800m asl) with short dry season characteristic of the southern WG. However, there were endemics restricted to regions with long dry seasons. Therefore species could be adapted to short, long, and all seasonality regimes.

Climate change that result in unpredictable local weather conditions could adversely affect rare species particularly narrow ranging endemics restricted to particular temperature and rainfall seasonality regimes. Therefore conservation action should focus on identifying species that could be more vulnerable to change in climatic conditions.

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SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

FIGURE S1. The relationship between rarity and environmental tolerance for trees in the Western Ghats.

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