

Geographical distributions in tropical trees: can geographical range predict performance and habitat association in co-occurring tree species?

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ABSTRACT

Aim A major floristic and climatic transition from aseasonal to seasonal evergreen tropical forest (the Kangar–Pattani Line; KPL) exists in the Indo-Sundaic region of Southeast Asia. Mechanisms constraining species distribution here are at present poorly understood, but it is hypothesized that species differ in their tolerances of abiotic factors, in particular water availability. Under this hypothesis, we anticipate differences in performance or habitat preferences, or both, of species differing in distribution with respect to the KPL. The aim of this study is to test whether geographical distributions can be used to explain variation in growth, mortality and habitat preferences in co-occurring tree species differing in their distribution in relation to the KPL.

Location Pasoh Forest Reserve, Negeri Sembilan, Malaysia; south of the KPL.

Methods All tree species within a 50-ha forest dynamics plot were classified as widespread or southern based upon their distributions in relation to the KPL and as habitat specialists or generalists based on spatial association with soil-based habitat categories. Growth and mortality rates, variation in growth and mortality with respect to soil type, and levels of habitat association were quantified for species with different geographical distributions.

Results Differences existed in species performance based upon geographical distributions. Specifically, widespread species had lower growth rates than did species restricted to the aseasonal forests. Mortality rates did not differ as a function of geographical distribution. The growth responses of species to soil habitats also diverged, such that differences in performance of widespread species among soil types were more conservative than those of species restricted in their distribution to the aseasonal forests. However, the proportion of species showing positive habitat associations did not differ significantly between widespread and southern species.

Main conclusions Distribution-based differences in species performance and response to soil type support the hypothesis that species tolerant of wider climatic variation perform less well in any given environment due to limitations on plasticity. These performance differences provide quantitative evidence of the role of climatic transitions in determining tree species distributions in relation to the Kangar–Pattani Line in the Indo-Malay region. Such differences in performance have important implications for our understanding of biodiversity gradients and responses of Indo-Sundaic forests to climate change.

Keywords

Abiotic resource requirements, geographical range, habitat association, plasticity, rainfall seasonality, Southeast Asia, stress tolerance, performance trade-offs, tropical trees.

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INTRODUCTION

The Indo-Sundaic region contains exceptional floristic diversity and comprises two distinct 'biological hotspots' of Asia (Myers *et al.*, 2000). A recognized climatic and floristic transition, initially documented by Van Steenis (1950) and subsequently named the Kangar–Pattani Line (KPL) by Whitmore (1984), exists between Indo-Burma and Sundaland and bisects the Malay–Thai Peninsula close to the Malaysian border (Fig. 1). At the KPL there is a transition from a perhumid climate in the south to a seasonally dry climate (albeit having only a 2–3 month dry season) to the north with little or no change in total annual rainfall (Whitmore, 1984; Ashton, 1997). Forests to the north and south of the line are classified as seasonal and aseasonal evergreen tropical forests, respectively (Ashton, 1995). A dramatic floristic transition occurs across this line that is exemplified by the Dipterocarpaceae. South of the KPL, 157 species of Dipterocarpaceae are found, only 27 of which cross the line into the Indochinese floristic zone (Ashton, 1997). An additional 19 Dipterocarpaceae not present in the aseasonal forests of Malaya are found north of the line (Ashton, 1997). Similar phytogeographical patterns are found in numerous other taxa in this region. Specifically, 375 genera occurring south of the line reach their northern limits and 200 from north of the line reach their southern limits at the KPL (Van Steenis, 1950). Despite these striking distributional patterns, the underlying mechanisms have been insufficiently investigated, and the primary causes of these changes in species richness and composition remain unknown.

Previous examinations of biogeographical patterns in this region have focused upon historical factors as primary drivers

of floral and faunal species distributions (Hughes *et al.*, 2003; Woodruff, 2003). Specifically these studies have proposed past dispersal boundaries caused by ancient seaways during periods of high sea levels. A second mechanism that is hypothesized to contribute to the existence and maintenance of the KPL is that species distributions correspond to the change from a climate that is effectively aseasonal to one that contains a short, seasonal period of water stress (Whitmore, 1984; Ashton, 1995; Richards, 1996). These hypotheses are by no means mutually exclusive and could both contribute to present-day distributions. However, if dispersal limitation alone were maintaining the current floristic transition then we would expect no systematic differences in the ecology of species having differing distributions in relation to the transition. The present study will provide the first test, to our knowledge, of the potential role of this seasonality gradient in determining species distributions.

Climate has been repeatedly implicated in latitudinal gradients of species richness and composition in a variety of environments worldwide (reviewed in Gaston, 2003; Hawkins *et al.*, 2003; Willig *et al.*, 2003). However, within any particular climatic region, range size as well as tolerance to environmental factors (i.e. niche breadth, *sensu* Hutchinson, 1957) is highly variable among co-occurring species (Brown *et al.*, 1996; Gaston, 1996). Species niche breadth, primarily determined by physiological tolerances to abiotic stresses, has been identified as a strong correlate of geographical range size in trees, although focus has been primarily on temperate species (Aizen & Woodcock, 1996; Pither, 2003; Mathews & Bonser, 2005). In the example of the KPL described above, species co-occurring in the aseasonal forests of Malaysia differ greatly in their northern distributional limits and thus will experience substantial variation in the degree of seasonality of rainfall that they must endure. Differences in the climatic tolerances of co-occurring species based on geographical range size may be predicted to affect two aspects of stand dynamics: tree species performance (i.e. growth and mortality) and habitat preferences or associations.

Increased tolerance to abiotic stress has been shown to trade off against growth and competitive abilities in plants (Bazzaz, 1979; Grime, 1979). The basis of this trade-off is thought to be inherent variation in allocation strategies corresponding to the resource limitations faced by plants occupying different environments (Kobe, 1997; Veneklaas & Poorter, 1998; Walters & Reich, 2000). Increased stress tolerance has repeatedly been shown to correspond to more conservative patterns of growth and physiology (Grime, 1977; Reich *et al.*, 1999; Wright *et al.*, 2004; Baltzer *et al.*, 2005; Russo *et al.*, 2005). Does this pattern hold for species occupying different portions of the seasonality gradient of the Malay–Thai peninsula? Species having sufficient plasticity to persist in both seasonal and aseasonal climates might be expected to incur some cost in terms of fitness or reduced performance (i.e. reduced growth or increased mortality) as a consequence of limitations to plasticity (reviewed in Dewitt *et al.*, 1998).

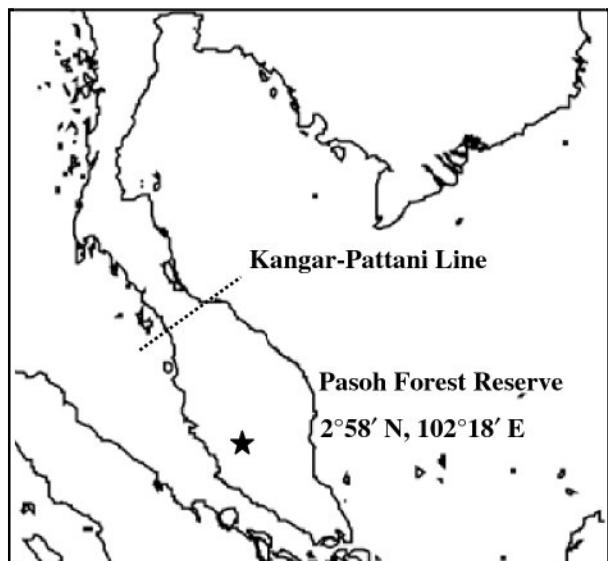


Figure 1 Map of the location of the Kangar–Pattani Line (KPL) on the Thai–Malay Peninsula. The region to the north of the KPL has largely seasonal rainfall while the region to the south is primarily aseasonal.

Tolerance of a broad range of abiotic factors may reduce habitat specificity. A species with broad climatic tolerances might be expected to be less sensitive to local variation in resource availability or edaphic characteristics than a species restricted in its distribution to a narrower range of environmental conditions. In other words, a negative relationship should exist between the degree of local habitat specialization and geographical range size (Brown, 1984). This pattern has been demonstrated for numerous faunal taxa (Eeley & Foley, 1999; Pyron, 1999; Gaston & Spicer, 2001; Krasnov *et al.*, 2005) but its extension to plant communities and specifically tropical forests is not well documented and the results are not as clear (Thompson *et al.*, 1999; Thompson & Ceriani, 2003; Kolb *et al.*, 2006). This pattern should only hold true, however, if the same factors (in this case water availability) are dictating species distributions at both local and geographical scales. If, for example, availability of soil nutrients (e.g. Palmiotto *et al.*, 2004) or biotic agents (e.g. Fine *et al.*, 2004) are driving local patterns of habitat use then there should be no relationship between local and regional distributions.

Explaining how some taxa can traverse climatic gradients while others cannot is central to understanding latitudinal gradients in species richness and composition. Conversely, determining the role that species responses to resource variation associated with geography plays in shaping performance and local habitat preferences is equally important to understanding local forest dynamics and potential responses of species to changing climatic conditions (Noss, 2001; Terwilliger, 2003; Thuiller *et al.*, 2005). In the present study we make use of long-term forest dynamics data from a forest south of the KPL to examine potential relationships between species geographical distributions, performance and local distributions (i.e. habitat associations). We test two specific hypotheses: (1) that performance (growth and mortality) differences exist between species restricted to the aseasonal forests south of the KPL and those capable of traversing this apparent barrier, and (2) that species occurring in both seasonal and aseasonal forests will be less specialized with respect to edaphic habitats than species restricted to aseasonal forests south of the KPL.

METHODS

Study site and data sets

The study area is located within the Pasoh Forest Reserve (hereafter Pasoh, 2°58' N, 102°18' E) in Negeri Sembilan, Malaysia. Pasoh is located approximately 400 km south of the KPL. The core of the reserve consists of 650 ha of primary lowland dipterocarp forest surrounded by approximately 1400 ha of forest that was selectively logged between 1956 and 1959 (Kochummen *et al.*, 1990; Okuda *et al.*, 2003; Manokaran *et al.*, 2004). The eastern edge of the reserve is bordered by primary hill forest. Maximum and minimum daily temperatures for Pasoh are 33.2°C and 22.7°C while maximum and minimum temperatures at a permanent forest dynamics

plot (Khao Chong Forest Reserve) just north of the KPL are 32.6°C and 22.7°C.

In 1985, a 50-ha (1000 m by 500 m) forest inventory plot was established following protocols of the Center for Tropical Forest Science (Condit, 1998; Ashton *et al.*, 1999; Manokaran *et al.*, 2004). Every stem ≥10 mm in diameter was tagged, mapped, measured and identified to species (Condit, 1998). Repeat censuses have since been conducted at 5-year intervals. Floristic descriptions can be found in Kochummen *et al.* (1990) and Davies *et al.* (2003). The topography of the plot and surrounding forest consists of gently rolling hills. Soils are derived from sedimentary rocks (Triassic shales) and riverine granitic alluvium in the lower areas (Allbrook, 1973; Ashton, 1976; Manokaran & Swaine, 1994). Soil sampling was conducted on a 40 × 40 m grid within the 50-ha plot in July 1996. Each sample was taken at the centre of the 40 × 40 m quadrat; each of these quadrats contained four 20 × 20 m quadrats within the plot. At each sampling location, soil colour, texture, depth, drainage class, slope and parent material were recorded. Based on these parameters, soil series were identified according to Paramanathan (1978, 1987). In total, 11 series were identified within the plot. These series were collapsed into three soil types: (1) soils developed on sub-recent alluvium (riverine alluvium), (2) soils developed on sedimentary soils with a shale parent material, and (3) soils developed on reworked material classified as lateritic soils. The riverine alluvium was further divided into two types based on drainage: (1) poorly drained or wet alluvium, and (2) well-drained or dry alluvium (Adzimi and Suhaimi, personal communication). This work resulted in four habitat classes: wet (WA) and dry (DA) alluvium, shale (SH) and laterite (LA). Each of 1250 20 × 20 m quadrats within the plot was classified as one of the above soil habitats based upon the 40 × 40 m quadrat in which it occurred.

As we were interested in testing for performance differences among species occupying portions of the Malay–Thai Peninsula that differ in seasonality of rainfall we classified each species as widespread or southern based upon its distribution with respect to the KPL (i.e. the northern limit of the aseasonal forest in the peninsula). The ranges were based on plant taxonomic records. Primary sources were the *Tree flora of Malaya*, *Flora Malesiana* and the *Flora of Thailand*, all of which list the states or provinces as well as all other countries in which the species has been recorded. Additional range data were collected from other reliable sources (Symington *et al.*, 2004; Van Welzen & Chayamarit, 2005). Certainty of range size in this region is problematic, as Thailand is floristically not as well documented as Malaysia. Many new records of taxa formerly thought to be limited in range to the aseasonal forests of Malaysia have arisen with the ongoing compilation of the *Flora of Thailand*. Thus, despite our best efforts, there are undoubtedly some misclassified species but the use of a binary descriptor of geographical range based on presence or absence above the KPL will reduce such errors in comparison to those associated with quantification of range areas or northern geographical limits which would require much more precise

data than are currently available for many species in this region.

Analyses

Species performance differences

Annual growth and mortality rates were estimated for the most recent census interval (1995–2000) for all species with $n > 10$ and $n > 20$ individuals for growth and mortality, respectively. Locally rare species were excluded from these analyses, as a sufficient number of individuals must be available to calculate accurate growth and mortality rates. Small populations often show no mortality over a given census period and erroneous or unusual growth measurements will have disproportionately large effects in small samples. There is not likely to be any bias in the calculated values due to the exclusion of species that were locally very rare, for two reasons: (1) similar numbers of rare species were excluded for both widespread and southern distributed species, and (2) no apparent relationship existed between vital rates and population size which corresponds with other studies on this topic (Connell *et al.*, 1984). There were strong positive relationships between 1985–2000 and 1995–2000 growth ($r^2 = 0.8933$, $P < 0.0001$) and mortality ($r^2 = 0.8439$, $P < 0.0001$) rates; however, more species could be included using the 1995–2000 data set. Growth was calculated as the change in diameter in millimetres divided by the time between census intervals. Extreme growth rates ($> 75 \text{ mm year}^{-1}$) were excluded as erroneous points (Condit *et al.*, 2004). Annual mortality rates were calculated as $M = [\ln(n) - \ln(S)]/t$ where n is the number of live trees in the initial census, S is the number survivors and t is the mean time interval across all n . Criteria for recording tree death in the field are described in Condit (1998).

Differences in growth rates between widespread and southern distributed species were tested using analysis of variance (ANOVA) on species' log-transformed mean growth rates followed by Tukey's highly significant difference tests. Mortality was approximately Poisson-distributed and could not be normalized using transformations. We therefore used a generalized linear model (GLM) with a quasi-Poisson error distribution with a log link function to determine the contribution of geographical range to variation in mortality rate. Family-level responses were also examined to determine whether observed patterns held across families or if certain taxa were reversing the trends. To do this, we made a reduced data set that included all families with more than 10 genera and at least two representatives of widespread and southern distributions. ANOVA was used to test for differences in log-transformed growth rates as a function of family, distribution and their interaction term.

Habitat association and response to soil type

Each stem was assigned a soil type based upon the classification of the $20 \times 20 \text{ m}$ subplot where it occurred. Species

with more than 50 individuals in the 50-ha plot were classified as edaphic specialists or generalists using torus translation tests of species association with the four soil classes (DA, WA, SH and LA, as described above) following methods described in Harms *et al.* (2001). Very few species showed positive associations with multiple habitats (20 of the 528 tree species with $n > 50$; 3.4%). For analysis, only species showing positive associations with a single habitat were considered true habitat specialists. To test the hypothesis that geographically restricted species are more likely to behave as habitat specialists a chi-square test of independence was employed with two categories for specialization (generalist/specialist) and two for geographical distribution (widespread/southern).

Species mean growth and mortality rates were calculated for all species on each soil type with $n > 10$ and $n > 20$ individuals, respectively. We were interested in determining if species with contrasting geographical ranges performed differently on the four soil types. Performance differences were tested using ANOVA for log-transformed growth rates and GLM (as described above) for mortality rates with soil type and geographical distribution as predictor variables.

To examine differences in species performance between pairs of soil types as a function of geographical range we calculated the absolute differences in species mean growth and mortality rates for each soil type pair. The mean absolute differences in growth or mortality rates were then calculated for each soil type–geographical range combination. A paired *t*-test was conducted in which the mean absolute difference of either growth or mortality for each soil type combination was compared for widespread and southern distributed species. This allowed for assessment of whether widespread and southern distributed species differ in the plasticity of their performance among different habitat types.

RESULTS

Of the 823 species in Pasoh, 487 were found to have distributions restricted to the region south of the KPL and 289 were classified as widespread. The remaining 47 species could not be classified due to a lack of distributional data. Of these, only 419 southern and 229 widespread species had sufficient numbers to conduct growth analyses ($n \geq 10$), 398 and 214 could be included in mortality analyses ($n \geq 20$), and 328 and 175 could be included in habitat association analyses ($n \geq 50$).

Habitat specialization

Of the 525 species with sufficient population sizes to test for habitat associations, 54% showed significant positive associations with a single habitat (Table 1). Of these 525 species, we could estimate geographical distribution for 503 species. Fifty-six per cent of widespread species and 52% of southern species were significantly positively associated with a single habitat in Pasoh (Table 1). There was no significant

Table 1 Counts (% of total) of habitat specialists in each of the four soil-based habitats in Pasoh. Five hundred and twenty-five species were included in the analysis and 503 of these had distributional data (175 species had distributions traversing the Kangar–Pattani Line (KPL; widespread) and 328 species were restricted to the region south of the KPL (southern).

Soil type	All species	Southern	Widespread
Dry alluvium	58 (11.5%)	39 (11.9%)	19 (10.8%)
Wet alluvium	110 (21.9%)	66 (20.1%)	44 (25.1%)
Shale	49 (10.1%)	34 (10.4%)	15 (8.6%)
Laterite	53 (10.3%)	32 (9.8%)	21 (12.0%)

difference in the distribution of habitat associations between southern and widespread species ($\chi^2 = 0.88$, $P = 0.935$, d.f. = 1) (Table 1). Similarly, the proportion of species associated with each soil type did not differ between southern and widespread species ($t = -0.2428$, $P = 0.8176$) or when either was compared with forest-wide proportions (all vs. southern: $t = 0.1079$, $P = 0.9177$; all vs. widespread: $t = -0.1442$, $P = 0.8904$).

Performance differences

Species restricted to the aseasonal climate south of the KPL had significantly higher growth rates than widespread species (Fig. 2a). Mortality rates were marginally higher in widespread than southern-restricted species (Fig. 2b).

The ANOVA results indicated that family contributes most substantially to variation in growth rates ($F_{43,492} = 5.30$, $P < 0.0001$); however, even when family is accounted for, the effect of distribution was marginally significant with widespread species having slower growth rates overall ($F_{43,492} = 3.32$, $P = 0.0690$). The interaction term was not significant ($F_{43,492} = 1.18$, $P = 0.2649$).

Growth rates for all species were slowest on the lateritic soil type and fastest on the dry alluvial soil type (Fig. 3). Similarly, species-wide mortality rates were lowest on the lateritic soils compared with all other soils (Fig. 3). ANOVA indicated that both soil type ($F_{7,1851} = 3.40$, $P = 0.0171$) and geographical range ($F_{7,1851} = 11.54$, $P < 0.001$) contribute to variation in species mean growth rates. The interaction term was not significant ($F_{7,1851} = 0.40$, $P = 0.7519$): species with widespread distributions showed slower growth rates than southern species on all soil types. Soil type contributed marginally to differences in species mean mortality rates ($F_{7,1969} = 2.76$, $P = 0.0993$) as did species distribution ($F_{7,1969} = 2.92$, $P = 0.0986$). Mortality was lowest on the laterite compared with all other soil types and widespread species had marginally higher mortality rates than southern species. The interaction term was not significant ($F_{7,1969} = 0.34$, $P = 0.3731$) indicating a consistent trend toward marginally greater mortality in widespread species across soil types.

Differences in species performance between pairs of soil types as a function of geographical distribution were

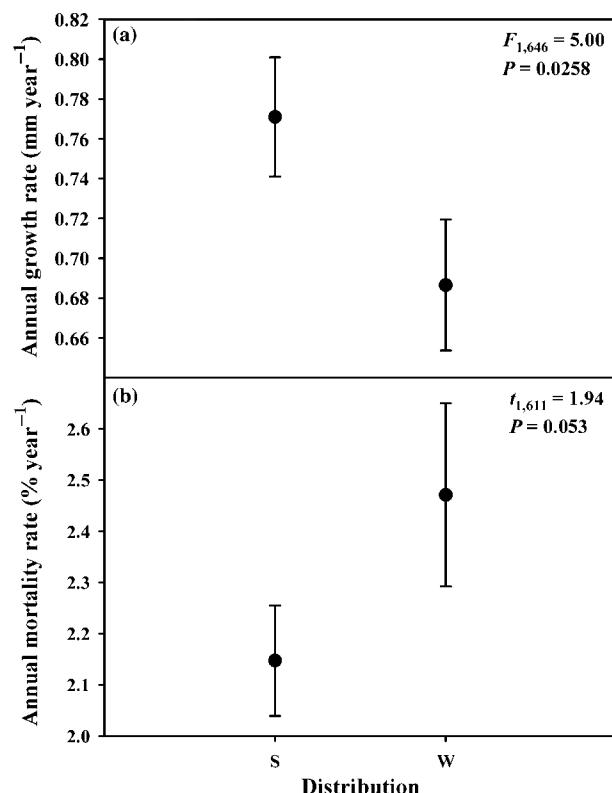


Figure 2 Mean annual growth (a) and mortality (b) rates (\pm SE) across geographical category based upon species mean rates (for species with $n \geq 10$ and 20, respectively). Southern (S) and widespread (W) indicate species restricted to aseasonal forest and those occurring in both aseasonal and seasonally dry forests, respectively.

detected. A paired t -test of the mean absolute difference in growth rate for widespread vs. southern distributed species for each soil type combination revealed that species with widespread distributions were less responsive in their growth rates across soil types ($t = -3.36$, $P > |t| = 0.0200$; Fig. 4). This difference was evident for all soil type combinations with the exception of the wet alluvium–laterite combination, and the difference was most evident in the dry alluvium–shale and laterite–shale comparisons. Overall, a more conservative pattern of growth response was evident in the widespread species (Fig. 4). This was not the case for mortality rates. Although a similar trend was evident in four of the six pairs, differences in mortality rate between pairs of soil types did not differ significantly between widespread and southern distributed species ($t = -1.34$, $P > |t| = 0.2379$; Fig. 4).

DISCUSSION

Environmental tolerances and requirements are one of the primary determinants of a species' geographical range. These tolerances are tied to other aspects of a species' ecology including local distribution pattern (i.e. habitat associations)

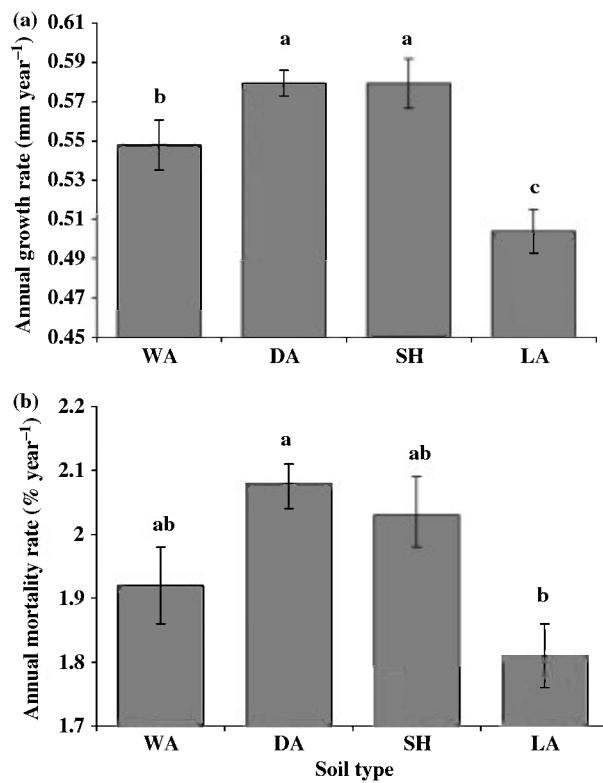


Figure 3 Mean annual growth (a) and mortality (b) rates ($\pm \text{SE}$) across soil type based on species mean rates (for species with $n \geq 10$ and 20, respectively). Soil type abbreviations are: WA, wet alluvium; DA, dry alluvium; LA, laterite; SH, shale. Significant ($P < 0.05$) differences are indicated with letters and are based on Tukey's highly significant difference tests.

and, presumably, performance and/or competitive ability at a given site. Ecological theory predicts that species with wider climatic tolerances will be more generalized in their habitat requirements at the local scale due to the greater trait plasticity necessary to tolerate wider climatic variability (e.g. Brown, 1984). We found no evidence of this pattern for 503 tree species occurring on four soil types in Pasoh, Malaysia, which may indicate that different factors are dictating species distributions at the local and geographical scales (e.g. Hughes, 2000; Hawkins & Porter, 2003). Alternatively, it may be the case that there is greater small-scale variation in a broader range of biotic and abiotic factors, thus making species distributions less predictable at the local than regional scale (e.g. MacNally *et al.*, 2004). Greater trait plasticity necessary for spanning broad climatic ranges may be associated with limitations such that widespread species will not be capable of achieving optimal performance in all environments whereas less plastic species may perform closer to the optimum in their preferred environment (Dewitt *et al.*, 1998). We found evidence for the hypothesized performance trade-offs based upon geographical distribution. Slower growth rates were evident in species whose ranges span both seasonal and aseasonal forests when compared with species restricted to aseasonal forests. Widespread species were also more conser-

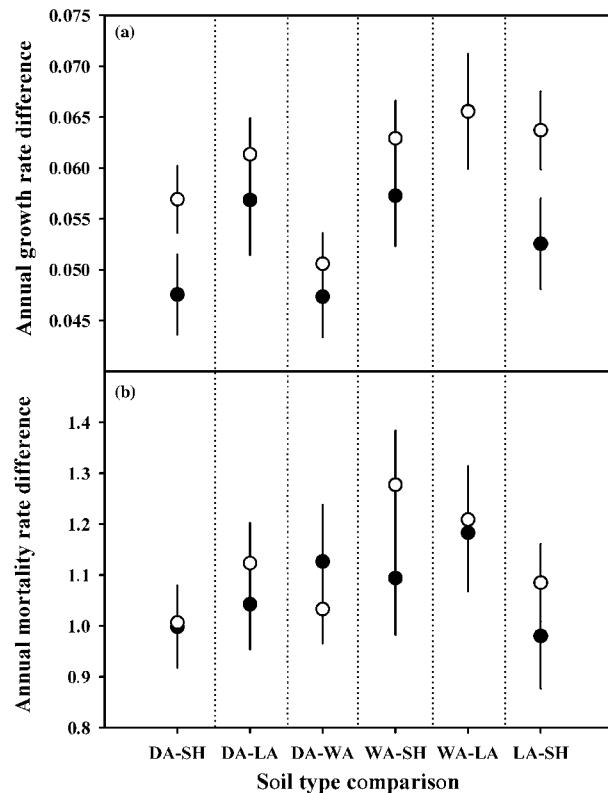


Figure 4 Absolute differences in mean relative growth (a) and mortality (b) rates ($\pm \text{SE}$) between all possible soil type combinations for widespread (closed circles) and southern (open circles) species (for species with $n \geq 10$ and 20, respectively). Classification for southern vs. widespread species follow Fig. 2. Soil type abbreviations follow Fig. 3. A paired t -test indicated that widespread species had smaller absolute differences in growth rates between pairs of soil types ($t = -3.36$, $P > |t| = 0.0200$) but mortality did not differ.

vative than southern species in terms of growth responses to different soil types. Both findings support the notion of greater abiotic stress tolerance in species spanning a wider climatic range (Morin & Chuine, 2006).

Geographical distribution as a predictor of performance

Detectable performance differences existed as a function of species geographical distributions. Overall, species tolerant of both seasonal and aseasonal climates whose ranges include areas north and south of the KPL had slower annual growth rates and marginally higher mortality rates than species restricted to the aseasonal forests south of the KPL. These findings support the hypothesis that tolerance of a wider range of abiotic conditions will trade off against competitive ability (Morin & Chuine, 2006). Slower growth rates have been shown repeatedly to correspond with occurrence in more adverse environments (Grime, 1977; Lambers & Poorter, 1992; Russo *et al.*, 2005) and are thought to be due to conservative plant

traits conducive to persistence under harsher conditions (Reich *et al.*, 1999, 2003; Wright *et al.*, 2004). In addition to having slower growth rates, stress-tolerant species tend to be less responsive to changes (positive or negative) in resource availability (Bazzaz, 1979; Riddoch *et al.*, 1991; Kreuzwieser *et al.*, 2002). In the present study, widespread species were less responsive to the different edaphic environments than were southern species. The findings of lower and less variable growth rates both support the idea that species experiencing wider climatic variation will be more stress tolerant (Morin & Chuine, 2006). Is lower responsiveness to different soil types in terms of growth a function of greater trait plasticity (e.g. high plasticity in resource use efficiency), which compensates for differences in resource availability among soil types? Our data do not address this but it would be an interesting extension of these findings.

Mortality rates did not differ significantly with geographical distribution. Lower mortality rates associated with the more conservative growth rates observed in this group might be expected given the typical growth–mortality trade-off (Davies, 2001; Lusk & Del Pozo, 2002; Russo *et al.*, 2005; Gilbert *et al.*, 2006); however, the opposite trend, albeit marginally significant, was detected. A potential explanation is that biotic factors are differentially affecting species in these more southern locations. Generally, species distributions are limited by increasing physical stress in one direction within their range while increasing number and impact of biological entities will limit distribution in the other direction (reviewed in Brown *et al.*, 1996). For example, Sax (2001) demonstrated that the southern limits (from a Northern Hemisphere perspective) of exotic species distributions are strongly influenced by biotic pressures. Such interactions may include greater competition for resources, differential rates of herbivory and/or higher pathogen loads, all of which can have an effect on mortality rates.

Could differences in performance be helping to maintain the higher diversity of certain taxa in the aseasonal forests south of the KPL? The resource use hypothesis states that geographical generalists (i.e. widespread species) tend to be less susceptible to fluctuations in resource availability and thus will be less prone to vicariant events (fragmentation of geographical distributions) and therefore speciation and extinction (Vrba, 1987; Fernandez & Vrba, 2005). Over long periods this might result in proportional overrepresentation of geographical specialists (i.e. restricted species), assuming heritability in physiological tolerances and requirements, as their populations will be more frequently fragmented providing opportunity for divergence. We demonstrate that, in general, widespread species show more conservative patterns of growth and response to small-scale habitat variation and thus should be less susceptible to fluctuations in resource availability, as predicted by the resource use hypothesis. Forest wide, there are approximately twice the number of southern species when compared with widespread species: in keeping with the hypothesized greater rates of divergence in geographical specialists than generalists.

Clearly, certain taxa are exceptions to this potential mechanism. The Dipterocarpaceae, whose diversity is remarkably lower in seasonally dry forests, showed little differentiation in growth rates between widespread and southern taxa (data not shown). In the Dipterocarpaceae the shift from highly synchronized, supra-annual mass flowering in the aseasonal forests to unsynchronized, annual or supra-annual flowering in the seasonal forests may be an important factor contributing to the diversity differences (Ashton, 1997). Undoubtedly, other taxa have similarly important but less well documented mechanisms that could contribute to diversity differences.

Another issue to consider with respect to maintenance of biodiversity is the role of the climatic niche in maintaining regional biodiversity. In the context of niche theory, trade-offs within the community context represent niche differentiation among species emerging from constraints placed on an individual in the environmental context in which it occurs (Kneitel & Chase, 2004). Our findings demonstrate a trade-off between the ability of species to tolerate broad climatic variation and their competitive ability. At regional scales, such trade-offs could contribute to the maintenance of biodiversity through differentiation along a climatic gradient in the same manner that sorting along abiotic gradients is thought to promote diversity at local scales (*sensu* Grubb, 1977).

Habitat specialization and geographical distribution

The niche breadth hypothesis (Brown, 1984) proposes a relationship between species geographical range sizes and habitat specialization. Brown (1984) argues that generalist species will have wider geographical ranges as a consequence of their ability to tolerate a broader spectrum of resource availabilities or microhabitats. Similarly, specialists will have narrower geographical range sizes. Tests of this generality have shown mixed results with little support for these patterns in plant taxa (Thompson & Ceriani, 2003; Kolb *et al.*, 2006). We classified over 500 tropical tree species as specialists or generalists with regard to four edaphically based habitat categories and as having widespread or southern distributions in relation to the KPL. Contrary to expectations arising from the niche breadth hypothesis, there was no detectable relationship between habitat specialization (based upon edaphic habitats) and geographical distribution in relation to rainfall seasonality. Other studies making use of a similarly fine scale of habitat categorization have found little evidence for the postulated relationship between geographical range and habitat specialization (Anderson *et al.*, 2000; Hughes, 2000). It may be that this relationship is highly scale dependent. There are potential differences in the classification as specialist or generalist when considering local and regional or geographical scales. A species may be specialized on a particular resource at the local scale simply because the remainder of its preferred resources are lacking in the given location, but considered at a regional scale one might conclude the opposite (see Fig. 1 in Hughes, 2000).

Likewise, entirely different factors may dictate species distributions at the local and geographical scales. It is worthwhile considering that habitat association classifications based on species distributions within the Pasoh 50-ha plot may not be representative of species regional or geographical classifications of habitat requirements and thus the anticipated relationship between niche breadth and climatic tolerance or geographical range is not detectable. It is equally plausible that our binary classification of species as widespread or southern distributed in relation to the KPL is too coarse to detect the pattern, if it exists. Specifically, the binary classification does not predict actual areas occupied by the tree species in question; therefore we cannot directly test the niche breadth hypothesis. However, part of the rationale behind the niche breadth hypothesis is that greater range size generally equates to a broader tolerance of environmental variation; our binary measure likewise provides a measure of this. One further caveat of the above conclusion is that in terms of growth the widespread species did exhibit lower responsiveness to different soil types. In other words, they show less preference with respect to performance on different habitats than southern species. Thus, if classification as a specialist or generalist were based upon performance responses to different habitats, we might conclude that widespread species are in fact showing more habitat generalist behaviour than are the southern species.

CONCLUSIONS

Previous work examining biogeographical patterns on the Malay–Thai Peninsula have focused upon historical factors as primary drivers of species distributions (Hughes *et al.*, 2003; Woodruff, 2003). Specifically these studies have proposed vicariant events caused by ancient seaways during periods of high sea levels. We recognize the enormous role that such boundaries would play, particularly with respect to the high regional diversity. However, present tree species distributions in this region are thought to have arisen since the last glacial retreat (10,000–15,000 yr ago), well after the most recent marine highstand suggestive of seaway formation (early Pliocene; Woodruff, 2003). The implications of this are that additional factors are contributing to the present distributions. We present evidence that differences in species performance and response to small-scale edaphic variation are in part determined by their distribution in relation to the KPL, which approximately corresponds with a shift from aseasonal to a seasonal pattern of rainfall. This is consistent with the hypothesis that species tolerant of a wider range of climatic variation perform more poorly in any given environment as a consequence of limitations on plasticity. These performance differences provide the first quantitative evidence, to our knowledge, that tree species distributions in relation to the KPL in the Indo-Sundaic region may in part be determined by the tolerance of species to the climatic transition. However, the proximate factors contributing to the observed distributions have not been determined. Direct tests of the differences in the

ability of species to tolerate drought are required to adequately assess the contribution of seasonality of rainfall to species range limits in the region. Further investigation of the mechanisms driving these performance differences would contribute not only to our understanding of tree species distributions but also to assessing potential responses to climate change in this region.

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