Journal of Vegetation Science **25** (2014) 1216–1224

Determinants of fern and angiosperm herb community structure in lower montane rainforest in Indonesia

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Keywords
Diversity; Ecological niche; Indicator species; Light; Pteridophytes; Soil factors; Topography

Nomenclature
http://www.ipni.org/ International Plant Names Index

Received 2 September 2013
Accepted 28 February 2014
Co-ordinating Editor: Francisco Pugnaire

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Abstract

Questions: Do ferns, which are physiologically less well adapted to conserve water than angiosperms but have more efficient propagule dispersal, show different vegetation–environment relationships than co-occurring angiosperm herbs? We hypothesized that ferns should show closer relationships to local environmental conditions and might be more closely associated with humid and shady microhabitats.

Location: Pono and Bariri, two sites in lower montane primary tropical forest, Lore Lindu National Park, Central Sulawesi, Indonesia.

Methods: At each site, all terrestrial herbaceous plants were sampled in 200 plots of 5 m × 5 m. Sixteen environmental factors describing soils, topography and canopy openness were recorded. Correlations were calculated to test the degree of similarity in the species richness and turnover of ferns and angiosperms, and their relationships with environmental factors. Species optima were calculated on each environmental axis and compared between plant groups via randomization tests.

Results: In total, 184 herb morphospecies were encountered at Pono and 135 at Bariri, of which almost 60% at each site were ferns. At both sites, fern species turnover showed closer correlations with soil variables than did angiosperm turnover. At the more topographically heterogeneous site (Bariri) fern species turnover was also more closely associated with topographic differences than was angiosperm turnover. Habitat preferences of ferns and angiosperms appeared more similar at Bariri than Pono, with both tending towards lower topographic positions and richer soils, but steeper slopes, than expected at random. At Bariri, neither plant group tended towards shady microsites, whereas at Pono ferns were better represented than angiosperms in microhabitats with open canopies.

Conclusions: As expected, ferns showed closer correlations with environmental factors than angiosperm herbs. Ferns did not, however, consistently favour humid microhabitats at both sites, and were not significantly associated with shady microhabitats at either site. Furthermore, it appears that physiological differences in water use do not lead to marked divergence in fern and angiosperm herb distributions in the humid understorey of this lower montane rainforest.

Introduction

Studies on the determinants of tropical forest floristic diversity have mostly focused on trees and other woody plants (e.g. De Oliveira & Mori 1999; Wright 2002; Ter Steege et al. 2006; Baldeck et al. 2012). However, herbaceous understorey plants comprise a major component of tropical forest diversity that has been relatively little studied. For example, the understorey flora of neotropical forests may represent between 21% and 47% of total species (Croat 1978; Gentry & Dodson 1987).

Previous studies on tropical understorey herbs have found that species richness and composition vary on soil, topographic (Poulsen 1996; Costa et al. 2005; Costa 2006; Poulsen et al. 2006; Both et al. 2011) and microclimatic gradients at local scales (Jones et al. 2011). At regional to

Doi: 10.1111/jvs.12181

continental scales, and along elevational gradients, climatic factors (Willinghöfer et al. 2012; Cicuzza et al. 2013) and soil parameters (Tuomisto et al. 2003; Jones et al. 2013) both shape understorey herb species composition and diversity. Due to their close relationships with environmental factors, terrestrial herbs have been proposed as a possible candidate group to characterize tropical forest types (Ruokolainen et al. 2007). However, terrestrial herbs encompass many plant lineages, which vary in important life history and reproductive traits (Both et al. 2011). Arguably, the most fundamental distinction should be that between ferns and angiosperms. Both are important understorey plant groups (Gentry 1988; Costa et al. 2005; Poulsen et al. 2006; Linares-Palomino et al. 2009), but they differ in physiological and reproductive traits.

Physiologically, ferns are frequently considered to be more drought-sensitive than angiosperms. Passive rather than active stomatal control predominates in ferns, effectively reducing their water-use efficiency (McAdam & Brodribb 2012). Furthermore, fern sporophytes have relatively inefficient water vessel transport (Watkins et al. 2010) and gametophytes require a film of water for cross-fertilization (Watkins et al. 2006). Nonetheless, ferns have developed efficient morphological and physiological strategies to cope with water stress (Kessler et al. 2007; McAdam & Brodribb 2013). Moreover, gametophytes of at least some tropical ferns are desiccation-tolerant, suggesting that this life stage may be less water-dependent than is commonly thought (Watkins et al. 2006). Thus, it is unclear to what degree physiological differences between ferns and angiosperms translate into distributional differences on gradients in water availability, or canopy openness, especially in the tropical rainforest understorey, where air temperatures are moderated and humidity is generally high (Karger et al. 2012). Furthermore, some fern lineages have highly sensitive photoreceptors and hence can tolerate low understorey light levels (Kawai et al. 2003), perhaps to a greater degree than angiosperm herbs. These physiological traits may have triggered the evolutionary diversification of ferns in modern, angiosperm-dominated rainforests (Schneider et al. 2004; Watkins & Cardelús 2011).

Regarding reproductive ecology, ferns are spore-dispersed and unlike most angiosperms are thus independent of biotic pollination and dispersal vectors. This may explain the wide geographical distributions of many fern species (Smith 1972; Tryon 1986). On the other hand, because of their gametophytic life stage, ferns are more sensitive than seed plants to being covered by leaf litter (Rodrigues & Costa 2012).

Globally, fern diversity declines more steeply towards arid and cold regions than angiosperm diversity (Kreft et al. 2010), and contrasting elevational diversity patterns have been reported in these groups (Willinghöfer et al. 2012). However, relatively little is known about how the fundamental physiological and ecological differences between ferns and angiosperms influence their distributions at local scales in the tropical forest understorey. A few studies have shown weak to moderate congruence in the local to mesoscale species turnover patterns of ferns and angiosperm herbs, linked in particular to changes in soil chemistry or elevation (Costa et al. 2005; Poulsen et al. 2006; Landeiro et al. 2012). However, even if species turnover patterns in two taxa are similar, this does not imply that trends in other community attributes, such as species richness, are congruent. At Reserva Ducke in Brazil, ferns appear to include more slope-restricted species than other herbs (Costa et al. 2005), and Poulsen et al. (2006) found a significant relationship between slope angle and fern, but not angiosperm, species richness within 1 ha of forest in Amazonian Ecuador. Costa et al. (2005) also found ferns occur more consistently than angiosperm herbs across several watersheds, and attributed this to efficient spore dispersal.

In the present study, we compare fern and angiosperm herb species richness, turnover and optima on environmental gradients in two lower montane forest sites on the island of Sulawesi. Based on the above considerations, we developed two hypotheses, one of which includes two competing sub-hypotheses:

H1

Because of their lower dispersal limitation, ferns show closer relationships to environmental factors (gradients in soils, topography and canopy openness) than angiosperms.

H2a

Because of their lower drought and higher shade tolerances, ferns favour more humid, shady microhabitats than angiosperms.

H2b

Because the lower drought and higher shade tolerances of ferns are ecologically irrelevant in the tropical rainforest understorey, ferns do not favour more humid, shady microhabitats than angiosperms.

Methods

Study sites

Two old-growth forest study sites were established 22 km apart in Lore Lindu National Park in Indonesia (Appendix S1). The park is mostly covered with upland and montane forests with steep topography, including rocky acidic ridges and narrow valleys (Cannon et al. 2007).

The first site was situated in Pono valley at 857–1273 m (01°29.6′ S, 120°03.4′ E). Here, soils range from nitisols on relatively flat areas to more fertile cambisols or leptosols with a high stone content on steep slopes (FAO 2006). The second site was located near Bariri village at 1354–1503 m (01°39.5′ S, 120°10.4′ E). Soils at Bariri range from nitisols developed on sedimentary substrates on a level plateau to cambisols on steep slopes, caused by river incision, and fluvisols on recent alluvial deposits. Human impact on both sites is slight and limited to hunting and gathering of some forest products, especially rattan (D. Cicuzza pers. obs.).

The study area has a mean annual precipitation from 1900 to 2100 mm (Hijmans et al. 2005; www.worldclim.org), while mean annual temperatures range from 22.5 °C at 850 m to 19.0 °C at 1500 m a.s.l. The climate is perhumid, with no month receiving less than 100 mm rainfall on average. However, in most years a few months are fairly dry (<100 mm rain), but the timing of these dry spells varies between years.

Species data

At each site, field sampling was carried out in 200 plots arranged along intersecting transects covering an area of ca. 0.7 km^2 and located to sample local topographic variation (Fig. 1). Plots were 5 m × 5 m in area and were spaced either 20 m or 40 m apart within transects. Denser sampling, at 20-m intervals, was carried out on the longest transect (>1 km in length) at each site, as well as on a transect intersecting this long axis perpendicularly in the central part of the study area.

All herbaceous plant species rooted in each plot were sampled by recording percentage cover to the nearest 5% through visual estimation. Occasional individuals with percentage cover clearly below 5% were recorded as occurring at 1% cover. Juvenile individuals less than 10-cm tall were excluded. Voucher specimens of all species were collected for identification at the herbaria of Göttingen (GOET) and Leiden (L). Species difficult to determine were sent to specialists. Specimens were also deposited in the Herbarium Celebense (CEB), Herbarium Bogoriense (BO) and the herbaria of Zürich (Z) and Berkeley (UC, ferns only).

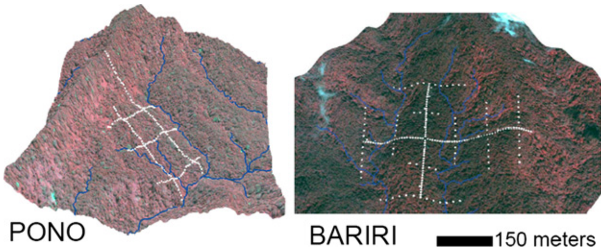

Fig. 1. Spatial arrangement of the sample plots (white dots) at the two study sites, Pono and Bariri, superimposed on false colour composite Quickbird satellite images (bands 1, 2 and 4) overlain on a 30-m resolution digital elevation model.

Environmental variables

Sixteen environmental descriptors of each plot were either measured in the field or derived from field measurements. Canopy openness was calculated as the percentage of open sky measured from a fisheye lens photograph taken with a digital camera mounted 50 cm above the soil surface. The images were converted into black and white using the image processing function in Picasa (picasa.google.com, v. 3.0). A square 100-cell grid was superimposed using the ‘straighten’ function and each cell was classified as predominantly (>50%) black or white. Canopy openness was calculated as the percentage of white cells, after excluding those that did not fully overlap with the image.

Plot elevation (m a.s.l., to an accuracy of ca. 25 m) was measured using a GPS (GPSMAP 96C; Garmin, Olathe, KS, USA) at Pono, the submontane site. Readings were missing for ten plots. However, elevation values were estimated for these by linear interpolation from the values measured in their nearest neighbour plots. At the lower montane site (Bariri), relative elevation among plots was calculated from measures of inclination taken from the centre of each plot to the next plot on the same transect using a clinometer (Wilkie, Kasper & Richter, Uttenreuth, Germany). Elevation values were initially calculated relative to the central plateau. These were then converted into absolute values by adding GPS-measured elevation at the plateau to each value.

Slope inclination (in degrees) was measured using a clinometer. Plot aspect (in degrees) was converted into two variables, northness [cosine(aspect)] and eastness [sine (aspect)]. Stream proximity was noted as a binary variable (stream within 5 m of the plot vs not). Topographic position was recorded on a scale of 1–4, where 1 = depression, 2 = foot slope, 3 = mid- to upper slope and 4 = shoulder or ridge top.

Soil organic layer depth was measured using a ruler at two to three sites within each plot. This was defined as the depth from the leaf litter surface to the start of the mineral soil layer, including organic matter and plant roots. Mineral soil samples were taken from 0 to 10-cm depth for laboratory analysis at the University of Palu. The soil chemical parameters analysed were total C and N (%), pH (in KCl) and the exchangeable cations Al, Ca, K, Mg and Mn (all in $\mu mol \cdot kg^{-1}$). The nutrients Ca, K, Mg, Mn and N were ln-transformed before statistical analysis. This was done

Doi: 10.1111/jvs.12181

under the assumption that small changes in nutrients are more relevant for plant distributions at low than at high overall nutrient availability.

Of the original 200 census plots, 16 were excluded from analysis at lower montane Bariri, and four at submontane Pono, either because of missing environmental data or because some plots lacked either ferns or angiosperms. Thus, 184 plots (total area 0.46 ha) and 196 plots (total area 0.49 ha), respectively, were analysed at the two sites.

Statistical analyses

To reduce co-linearity between the environmental variables, we calculated correlations between all their possible pair-wise combinations and excluded one of each pair with an absolute Pearson correlation >0.7. The variables excluded were soil Al, Mg and N, which correlated strongly with pH, Ca and C, respectively. Thirteen of the original 16 environmental variables were thus retained for analysis (Appendix S2). All statistical analyses were run using species presence–absence data and were replicated for each site.

Species richness and species turnover

To test the degree of congruence between fern and angiosperm herb distributions, we first analysed species richness and turnover patterns. We calculated Pearson correlations between the plot-level species richness of ferns and angiosperms, and Mantel correlations between their inter-plot floristic dissimilarities (henceforth referred to as species turnover), quantified as 1 – Sørensen similarity index.

To assess the role of environmental conditions as drivers of species richness patterns in each plant group, we calculated Pearson correlations between plot-level species richness and environmental gradient values. Mantel tests were run to assess how strongly inter-plot differences in floristic composition in each plant group were correlated with their intervening geographic distances vs environmental differences (Legendre & Legendre 1998). Partial Mantel tests were also run to assess whether correlations between floristic and environmental differences among plots were reduced after controlling for their geographic separation. Floristic differences were calculated as 1 – Sørensen index, and environmental differences and geographic distances were calculated as Euclidean distances. Geographic distances were ln-transformed before analysis. The statistical significance of the correlations was tested by comparing the observed values to the distribution of values obtained after 1000 permutations of the floristic data.

Species optima

We also calculated optimum values for each fern and angiosperm species on each environmental gradient. Species' optima were environmental mean values across those plots in which each species was observed. If sampling plot density along an environmental gradient is uneven, optima will be biased towards the most densely sampled part of a gradient. To avoid this, the environmental mean values were calculated with inverse weighting for sampling density along the gradient following a modification of the approach of Schaffers & Sykora (2000) [details in Appendix S3]. If angiosperms and herbs diverge in their responses to an environmental gradient, their mean species optima should differ. We tested this by permuting the plant group memberships of the observed species optima 10 000 times, and recalculating the difference between mean optima after each permutation.

We also tested whether the mean species optima of angiosperms and ferns on each gradient differed significantly from chance expectation, by comparing observed values to those obtained after randomizing species occurrences across sites. Dispersal limitation is expected to constrain the spatial extent of species ranges, and under these circumstances non-restricted randomizations are excessively liberal tests of habitat association (Harms et al. 2001). Therefore, we ran spatially restricted randomizations that limited randomized species ranges to a similar extent to their observed ranges (see Appendix S3). After each randomization, we recalculated species optima and their plant group means on each environmental gradient. Randomizations were run 2000 times, after which the original mean optima were compared with the distribution of the randomized values to calculate statistical significance.

All analyses were coded in the R language v 2.13.2 (R Foundation for Statistical Computing, Vienna, AT, US). Mantel tests were run using the package vegan. To account for multiple testing, we also calculated Bonferroni-corrected statistical significance in all cases (Legendre & Legendre 1998).

Results

Environmental conditions

Plots at lower montane Bariri were 380 m higher in elevation, on average, than those at submontane Pono (Appendix S2). However, Pono encompassed a larger elevational range than Bariri, and the highest plot at Pono was only 82 m lower than the lowest Bariri plot. Pono was also generally steeper than Bariri, and included one major slope of southeasterly aspect, whereas Bariri was topographically more heterogeneous. Canopy openness and the proportion of plots located close to streams were very similar at the two sites. There was also considerable overlap in their soil properties.

Floristic composition and diversity

In total, 184 herbaceous morphospecies were encountered at submontane Pono and 135 morphospecies at lower montane Bariri, mirroring trends in relative tree species richness at these sites (Culmsee & Pitopang 2009). Due to poor knowledge of the flora of Sulawesi (Cannon et al. 2007), only 50 species at Bariri and 118 at Pono were identified to the species level while the remainder were sorted into morphospecies (all henceforth referred to as species). Ferns comprised an almost identical proportion of the flora at both sites (58% at Pono and 59% at Bariri; Appendix S4).

The most species-rich fern genera at submontane Pono were *Asplenium* (12 species), *Diplazium* (eight) and *Pteris* (seven) and at lower montane Bariri *Asplenium* (seven species), *Lindsaea* (four) and *Diplazium* (three). The most species-rich angiosperm genera at Pono were *Alpinia* (four species), *Elatostema* (four) and *Begonia* (four), and at Bariri *Etlingera* (four species), *Alpinia*, *Elatostema* and *Argostemma* (two species each). Only four angiosperm species and 16 fern species were encountered at both sites. An average plot contained seven fern and six angiosperm species at Pono and five ferns and three angiosperms at Bariri (Appendix S4). Average plot occupancy by fern and angiosperm herb species was similar at both sites, as was the total percentage cover of ferns in the plots. However, many angiosperm species were encountered at a lower percentage cover at Bariri than Pono.

Both plot-level species richness of ferns and angiosperms and their species turnover among plots were significantly correlated (at Bariri $R = 0.37$ and 0.13, respectively, at Pono $R = 0.40$ and 0.21, respectively, $P < 0.001$ in all cases).

Species richness

Fern species richness was positively correlated with canopy openness at submontane Pono, but not at lower montane Bariri (Table 1). At Pono, fern species richness was not related to any soil gradient, and angiosperm richness showed weak relationships with soil C and ln(Mn) alone, which were not significant after Bonferroni correction. In contrast, at Bariri four soil variables were related to angiosperm richness and three to fern richness (or three soil variables and one soil variable, respectively, after Bonferroni correction). Species richness in both plant groups declined with increasing soil C content. At the topographically more heterogeneous Bariri, species richness of both plant groups declined with elevation and topographic position, and increased with slope angle. At Pono, topographic variables were unrelated to herb species richness after Bonferroni correction. Proximity to streams was positively related to angiosperm richness at Pono and to fern richness at Bariri.

Table 1. Pearson correlations between species richness of ferns and angiosperm herbs and canopy openness, soil and topographic parameters in plots at Pono and Bariri.

	Pono		Bariri	
	Ferns	Angiosperms	Ferns	Angiosperms
Canopy Openness	0.23***	n.s.	n.s.	n.s.
Organic Layer Depth	n.s.	n.s.	n.s.	n.s.
Soil C	n.s.	−0.16*	−0.25***	−0.22**
Soil pH	n.s.	n.s.	n.s.	0.23**
ln(Soil Ca)	n.s.	n.s.	0.17*	0.29***
ln(Soil K)	n.s.	n.s.	0.20**	n.s.
ln(Soil Mn)	n.s.	0.17*	n.s.	0.18*
Elevation	n.s.	−0.18*	−0.21**	−0.21**
Stream within 5 m	n.s.	0.24***	0.27***	n.s.
Slope	n.s.	n.s.	0.25**	0.22***
Eastness	−0.15*	n.s.	n.s.	n.s.
Northness	n.s.	n.s.	n.s.	n.s.
Topographic Position	n.s.	−0.14*	−0.27**	−0.17*

Statistical significance in randomization tests is indicated as n.s. (not significant), *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Correlations significant at the Bonferroni-corrected threshold $P < 0.0038$ (13 tests at the $P < 0.05$ level) are underlined.

Species turnover

Mantel correlations between floristic differences and geographic distances were similar in strength at both sites (Table 2). Correlations for ferns were stronger at both sites than those for angiosperms. Correlations between floristic and environmental distances were also generally lower for angiosperms than for ferns. However, the details of these correlations differed between the sites. In particular, topographic differences (in elevation, slope, aspect and topographic position, as well as stream proximity when Bonferroni correction was not applied) were correlated with floristic turnover at lower montane Bariri, whereas at submontane Pono the only significant topography–flora correlation after Bonferroni correction was that with elevation.

In terms of soil parameters, the results at Pono and Bariri were more similar, with floristic turnover in both plant groups associated with gradients in soil Ca and Mn. At Bariri there was also a highly significant correlation between differences in soil pH and floristic turnover in both plant

Table 2. Mantel correlations at Pono and Bariri between floristic dissimilarity (1 – Sørensen index) of terrestrial ferns and angiosperm herbs with the natural logarithm of inter-site distances [ln(GD)] and environmental dissimilarities quantified in terms of canopy openness and soil and topographic parameters.

	Pono		Bariri	
	Ferns	Angiosperms	Ferns	Angiosperms
ln(GD)	0.25***	0.09***	0.20***	0.13***
Canopy Openness	n.s.	0.04*(n.s.)	−0.07*(n.s.)	n.s.
Organic Layer Depth	n.s.	0.06*(0.05*)	0.07*	0.08**(0.07**)
Soil C	0.07**(0.05*)	0.11***(0.10***)	0.05*(n.s.)	n.s.
Soil pH	0.11**(0.08*)	n.s.	0.17***(0.14***)	0.12***(0.10***)
ln(Soil Ca)	0.30***(0.28***)	0.15***(0.14***)	0.22***(0.19***)	0.09***(0.07**)
ln(Soil K)	n.s.	n.s.	n.s.	n.s.
ln(Soil Mn)	0.15***(0.14***)	0.11***	0.16***(0.13***)	0.14***(0.12***)
Elevation	0.21***(0.07*)	0.07**(n.s.)	0.18***(0.11**)	0.16***(0.12***)
Stream within 5 m	n.s.	n.s.	0.07*(0.08*)	n.s.
Slope	n.s.	0.04*	0.14***(0.13***)	0.07***(0.06***)
Eastness	n.s.	n.s.	n.s.	n.s.
Northness	n.s.	n.s.	0.06***(0.04**)	0.03*(n.s.)
Topographic Position	n.s.	n.s.	0.13***(0.12***)	0.06**(0.05*)

Values in parentheses represent partial Mantel correlations between floristic and environmental dissimilarity, controlling for ln(GD). These are presented only when different from the results of the simple Mantel tests. Statistical significance in randomization tests is indicated as n.s. (not significant), *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Correlations significant at the Bonferroni-corrected threshold $P < 0.0038$ (13 tests at the $P < 0.05$ level) are underlined.

groups, whereas at Pono a weaker correlation was observed only in ferns (not significant after Bonferroni correction).

Species optima

The mean species optima of ferns and angiosperms did not diverge significantly, except that ferns at submontane Pono were found under more open canopies than angiosperms, although this tendency was only marginally significant ($P < 0.1$) after Bonferroni correction. At lower montane Bariri, the species optima of both plant groups were biased towards lower topographic positions, steeper slopes and richer, less acidic soils than expected at random (Table 3). At Pono, patterns were less clear, but the optima of both ferns and angiosperms were again located on steeper slopes than expected at random; however, this tendency was not significant after Bonferroni correction.

Discussion

Our first hypothesis stated that ferns, because of their efficient spore dispersal, should more reliably reach suitable microsites and hence show closer relationships between assemblage composition and environmental parameters. The details of vegetation–environment relationships differed between our study sites, being generally weaker at submontane Pono than at the topographically more heterogeneous lower montane Bariri, especially in relation to topographic gradients. Nonetheless, at both sites correlations of species turnover with environmental conditions were generally lower for angiosperm herbs than for ferns, paralleling the results of Poulsen et al. (2006) from Ecuador. This suggests that fern species turnover was indeed more strongly tied to changing local environmental conditions than was that of angiosperm herbs.

Our second hypothesis questioned whether ferns are physiologically restricted to more shady and humid microhabitats than angiosperm herbs. In our study this translates into an expectation that fern distributions would be more strongly biased towards sites under a closed forest canopy, at lower landscape positions, where soil and air humidity are generally higher, and perhaps towards riparian habitats. We did not find support for such patterns, and furthermore the results for the two sites were partly contradictory. Canopy openness was a poor predictor of the species richness or turnover of either plant group at Bariri, and was positively (rather than negatively) related to fern species richness at Pono. Similarly, fern optima tended towards higher rather than lower canopy openness values than expected at random at Pono. At Bariri, the species richness of both plant groups tended to increase towards lower landscape positions, as observed by Poulsen et al. (2006) in Ecuador, and the optima of both plant groups tended towards streams. However, at Pono this pattern was only found for angiosperm herbs.

Overall, our results imply that physiological differences between ferns and angiosperm herbs (Watkins et al. 2010; McAdam & Brodribb 2012, 2013) do not result in significant differences in their microhabitat distributions in the understorey of this lower montane rainforest. Presumably

Table 3. Mean species optima for ferns and angiosperm herbs on environmental gradients at Pono and Bariri.

	Pono		Bariri	
	Ferns	Angiosperms	Ferns	Angiosperms
Canopy Openness (%)	$\underline{\mathbf{65.0{*}{*}{*}}}_{\mathrm{H}}$	60.9	62.7	62.5
Organic Layer Depth (cm)	5.93	5.64	$\mathbf{7.12{*}{*}}_{\mathrm{L}}$	7.54
Soil C (%)	3.25	3.07	$\underline{\mathbf{2.18{*}{*}{*}}}_{\mathrm{L}}$	$\underline{\mathbf{2.19{*}{*}}}_{\mathrm{L}}$
Soil pH	4.31	$\mathbf{4.12{*}}_{\mathrm{L}}$	$\mathbf{4.09{*}}_{\mathrm{H}}$	$\underline{\mathbf{4.18{*}{*}{*}}}_{\mathrm{H}}$
Soil Ca (μmol·kg^{-1})	8.17	9.78	$\underline{\mathbf{21.1{*}{*}{*}}}_{\mathrm{H}}$	$\underline{\mathbf{25.0{*}{*}{*}}}_{\mathrm{H}}$
Soil K (μmol·kg^{-1})	3.22	3.03	$\underline{\mathbf{1.16{*}{*}}}_{\mathrm{H}}$	0.98
Soil Mn (μmol·kg^{-1})	0.49	$\mathbf{0.62{*}}_{\mathrm{H}}$	$\mathbf{1.39{*}}_{\mathrm{H}}$	$\underline{\mathbf{1.84{*}{*}{*}}}_{\mathrm{H}}$
Elevation (m)	1042	1025	1419	1417
Stream within 5 m (1 = yes, 0 = no)	0.20	$\mathbf{0.30{*}{*}}_{\mathrm{H}}$	$\underline{\mathbf{0.39{*}{*}{*}}}_{\mathrm{H}}$	$\mathbf{0.31{*}}_{\mathrm{H}}$
Slope (Degrees)	$\mathbf{27.3{*}}_{\mathrm{H}}$	$\mathbf{27.6{*}}_{\mathrm{H}}$	$\underline{\mathbf{26.8{*}{*}{*}}}_{\mathrm{H}}$	$\underline{\mathbf{26.9{*}{*}{*}}}_{\mathrm{H}}$
Eastness [Sine(Aspect)]	0.19	0.22	$\mathbf{0.04{*}}_{\mathrm{L}}$	0.03
Northness [Cosine(Aspect)]	−0.08	−0.09	−0.04	0.02
Topographic Position (Four Categories: 1 = Depression, 2 = Foot Slope, 3 = mid- to Upper Slope, 4 = Shoulder or Ridge-top)	2.53	2.49	$\underline{\mathbf{2.36{*}{*}{*}}}_{\mathrm{L}}$	$\underline{\mathbf{2.42{*}{*}{*}}}_{\mathrm{L}}$

Values in bold indicate optima lower (subscript L) or higher (subscript H) than expected at random. Statistical significance in a two-tailed test of deviation of optimum values from random expectation is given as ***$P < 0.001$, **$P < 0.01$, *$P < 0.5$. Deviations significant at the Bonferroni-corrected threshold $P < 0.0038$ (13 tests at the $P < 0.05$ level) are underlined.

this is because understorey air humidity is generally so high that drought stress is of limited physiological relevance (Karger et al. 2012).

Interestingly, both plant groups showed significant biases towards sloping rather than flat ground, especially at Bariri. A preference for slope habitats by herbs has also been found in a few earlier studies (Poulsen 1996; Costa 2006). In Amazonia, this has been found to be related to lower litter accumulation on slopes (Rodrigues & Costa 2012). Sloping sites may also provide more favourable drainage conditions, especially at lower landscape positions where there may be periodic waterlogging.

The mean optima of both plant groups in our study area were in fact similar on all environmental gradients except for canopy openness at both sites. Greater divergence might, however, be expected in more seasonal forest environments, where dry season drought stress is a more significant determinant of species sorting. This could explain differences between fern and angiosperm distributions reported in central Amazonia (Costa et al. 2005; Costa 2006). However, further comparative studies are needed before robust conclusions can be drawn.

Two major factors may explain why vegetation–environment relationships at Pono were usually weaker than at Bariri. First, while Bariri was topographically relatively heterogeneous, comprising numerous small valley-to-ridge systems, the site at Pono was dominated by a single long mountain slope, and encompassed a far larger overall range in elevation. Thereby, Bariri, unlike Pono, enabled repeated sampling of herb community composition at various topographic positions in the landscape. Furthermore, relationships with our measured abiotic factors at Pono may have been confounded by elevational species turnover, since sampling covered a >400 m range in elevation. Changes in air temperature and air humidity occur with increasing elevation on mountain slopes, and these are known to correlate with changing plant species richness and composition (Wolf 2003; Crausbay & Hotchkiss 2010; Kessler et al. 2011; Willinghöfer et al. 2012).

Conclusions

We found that ferns showed closer vegetation–environment relationships than angiosperm herbs, presumably due to their relatively efficient spore dispersal. However, ferns were not significantly associated with shady microhabitats at either site, nor did they consistently favour humid microhabitats at both sites. Furthermore, it appears that physiological differences in water use do not lead to marked divergence in fern and angiosperm distributions on soil and topographic gradients in the humid understorey of this lower montane rainforest. Future research should assess the generality of this finding and whether clearer patterns of divergence occur in more seasonal environments.

Acknowledgements

We thank Ramadhanil Pitopang for help during fieldwork and Stefan Köhler and Dr. Stefan Erasmi for cartographic help. Karel Mokany suggested the spatially-restricted randomization approach. The study was principally supported by the German Research Foundation (DFG, SFB 552). M. Jones furthermore acknowledges the German Academic Exchange Service (DAAD), the Academy of Finland and the Jenny and Antti Wihuri Foundation for funding. The identification of herb species was conducted partly at the Herbarium of Leiden, supported by the SYNTHESYS project (NL-TAF-3536).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Location of the study sites in Lore Lindu National Park, Sulawesi, Indonesia.

Appendix S2. Summary statistics for 13 environmental variables measured in plots at the two study sites.

Appendix S3. Detailed description of analyses of mean fern and angiosperm species optima.

Appendix S4. Summary statistics on species richness, frequency of occurrence in plots and percentage cover of understorey ferns and angiosperm herbs encountered in plots at the two study sites.