ORIGINAL ARTICLE

Island biogeography from regional to local scales: evidence for a spatially scaled echo pattern of fern diversity in the Southeast Asian archipelago

Dirk Nikolaus Karger[1][*][†], Patrick Weigelt[2][†], Victor B. Amoroso[3], Dedy Darnaedi[4], Arief Hidayat[4], Holger Kreft[2] and Michael Kessler[1]

[1]*Institute of Systematic Botany, University of Zurich, 8008, Zurich, Switzerland,* [2]*Biodiversity, Macroecology and Conservation Biogeography Group, University of Göttingen, 37077, Göttingen, Germany,* [3]*Department of Biology, Central Mindanao University, Musuan, Bukidnon, Philippines,* [4]*Indonesian Institute of Sciences (LIPI), Botany Division, Cibinong, 16911, Indonesia*

ABSTRACT

Aim The aim of this study was to investigate whether the equilibrium theory of island biogeography (ETIB) is equally applicable at regional and local spatial scales, and whether the 'echo pattern', the correlation between regional species pool and local diversity by which the diversity of the regional species pool 'trickles down' to local scales, influences local diversity equally across a range of sampling scales.

Location Twelve mountain regions on islands having different sizes, degrees of isolation and environmental conditions in Indonesia and the Philippines.

Methods We sampled ferns in standardized field plots within a fixed spatial design at six spatial scales (with the grain size varying from plot to island). Using ordinary least squares regression and relative variable importance, we tested for the predictive power of area and isolation as well as of local and regional environmental factors for explaining diversity at the chosen spatial scales.

Results Consistent with MacArthur and Wilson's ETIB, we found the strongest correlations of area and isolation with diversity at regional scales. The explanatory power of area increased with increasing spatial scale. The strength of the negative relationships among diversity and isolation decreased with increasing spatial scale. We found evidence for an 'echo pattern' at large to intermediate but not at small spatial scales.

Main conclusions Area and isolation are strong predictors of biodiversity at regional scales. The size of the species pool has a scale-dependent influence on diversity at smaller scales but is unimportant at the most local scale, where environmental conditions dominate as predictors of diversity. To make predictions about local diversity on islands it is therefore important to take the scale dependence of the 'echo pattern' into account.

*Correspondence: Dirk Nikolaus Karger, Institute of Systematic Botany, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland.
E-mail: dirk.karger@systbot.uzh.ch
[†]D.N.K. and P.W. contributed equally to this paper.*

INTRODUCTION

Island systems have long played a crucial role in biogeographical and biodiversity research because they provide comparatively simple systems with clearly defined subunits of usually varying sizes and ecological conditions (Whittaker, 1998). The classical equilibrium theory of island biogeography (ETIB) predicts that the number of species that occur on an island is mainly dependent on the balance between species immigration and extinction at rates determined by the surface area of the island and its isolation (MacArthur & Wilson, 1967), although current models also include island age and geological processes (Whittaker *et al.*, 2008).

According to the ETIB, species diversity on islands is positively related to island area and negatively related to isolation. Area is the most fundamental parameter influencing

diversity patterns on islands (Arrhenius, 1921; Connor & McCoy, 1979; Lomolino, 2001; Kreft *et al.*, 2008) and can have different effects on species diversity at different spatial levels (Rosenzweig & Ziv, 1999; Whittaker *et al.*, 2001). A direct effect at the regional scale concerns the number of species that can coexist within a given region (MacArthur & Wilson, 1967). It is still unclear, however, to what degree the increase of species numbers on larger islands is determined by the increase of area per se or by the larger number of habitats (Triantis *et al.*, 2003; Kallimanis *et al.*, 2008) influencing both the maximum number of co-occurring species and the rate of speciation (Losos & Schluter, 2000; Kisel & Barraclough, 2010). In contrast to area, isolation shows inverse relationships with the probability of dispersal to an island and the chance of its colonization. Continuously arriving propagules increase the population viabilities of species present on less isolated islands (the 'rescue effect'; Brown & Kodric-Brown, 1977). On large islands, the effect of isolation may decrease, because large islands receive more immigrants (the 'target area effect'; Whittaker, 1998) and serve as better arenas for *in situ* speciation (Losos & Schluter, 2000; Kisel & Barraclough, 2010). Finally, gene flow to island populations is negatively related to isolation, resulting in a higher chance of speciation on remote islands (Heaney, 2000).

Species diversity is also known to be dependent on spatial scale, with different processes acting at different scales (Levin, 1992; Whittaker, 2000; Whittaker *et al.*, 2001; Triantis *et al.*, 2012). Therefore, the variables explaining species diversity at a local spatial scale may not be the same as those accounting for diversity at regional spatial scales (Willis & Whittaker, 2002; Triantis *et al.*, 2012). While at large scales evolutionary history and energy availability are important factors, at small scales dispersal limitation or random processes might prevail (Triantis *et al.*, 2012). This scale dependence also applies to the effects of area and isolation (Karger *et al.*, 2011; Gillespie *et al.*, 2013; Weigelt & Kreft, 2013).

In addition to the above-mentioned effect of area at the regional scale, at the local scale larger sampling areas typically include more species because they more completely represent the regional species pool (Connor & McCoy, 1979). However, even if sampling area is held constant, regional area will influence local species indirectly through its effects on the regional species pool (the 'echo pattern' *sensu* Rosenzweig & Ziv, 1999). Local communities can be perceived as dynamic samples from the regional species pool (Terborgh, 1973; Graves & Gotelli, 1983; Cornell, 1985; Ricklefs, 1987), with the size of the surrounding area as a surrogate of the regional species pool (Terborgh & Faaborg, 1980; Cornell & Lawton, 1992; Caley & Schluter, 1997; Cornell, 1999; Romdal & Grytnes, 2007).

The 'echo pattern' has a potential impact on island biogeography theory across spatial scales as it shows how local diversity is affected by the regional diversity it emanates from. The ETIB predicts local diversity to increase continuously with an increase of the regional species pool (or regional diversity) owing to higher immigration rates (MacArthur

& Wilson, 1967; Kelly *et al.*, 1989). Therefore, independent of the spatial grain chosen to assess species diversity, a higher regional diversity should always result in a higher local diversity (Fig. 1a). Assuming this relationship between regional and local diversity, species diversity is expected to increase with island area and to decrease with its isolation, independent of the spatial grain at which the species diversity on an island is assessed (Fig. 1b). In contrast, if the spatial grain at which local diversity is assessed influences the way regional diversity translates into local diversity (Fig. 1c), no consistent relationship with island area and isolation is expected at the smallest spatial grain (Fig. 1d). Clearly, a limited regional species pool limits the number of co-occurring species in a local community, but local diversity may not increase continuously with the size of the regional species pool because local communities may become saturated at some point and local diversity may remain constant even if regional diversity increases (Huston, 1999; Srivastava, 1999). Consequently, species diversity at small spatial grains would be more strongly influenced by local environmental conditions that limit the number of individuals that are able to survive in a community than by immigration from the regional species pool.

Islands provide ideal testing grounds for investigating the 'echo pattern' and its scale-dependent influence on the ETIB, as their regional species pools can be defined using island area and island isolation, which are directly related to the number of potential species that can occur within a local sampling site on an island. In contrast, most mainland studies on local species diversity either have a common species pool or have species pools that overlap to unknown degrees (e.g. the Amazonian lowlands; Tuomisto *et al.*, 2003). The species pool contains all those species that could, in theory, disperse to a local community within the study area. On islands, distinguishing the species pool is therefore possible by using the area of the island, representing the 'island' species pool, as well as island isolation, representing the immigration from the 'mainland' species pool. However, while several studies have investigated drivers of species diversity by focusing on the scale dependence of species diversity (Crawley & Harral, 2001; Lennon *et al.*, 2001; Rahbek & Graves, 2001), an investigation into how well the two main factors of the ETIB, area and isolation, predict species diversity at different scales has not yet been conducted. To tackle this, we selected 12 islands of different sizes and degrees of isolation in Indonesia and the Philippines and sampled fern diversity at six spatial grains. We tested whether regional area and isolation are strong predictors of diversity at all grain sizes or whether environmental conditions are more important at a small grain size. We formulated the following two competing hypotheses in accordance with the above-mentioned theoretical assumptions to address the question whether the ETIB is equally applicable from regional (island-level) to local (plot-level) scales.

H₁: Regional area and isolation are strong predictors of species diversity at all grain sizes. The 'echo pattern' will lead

Echo patterns

(a) No spatial scale effect

Diversity patterns

(b)
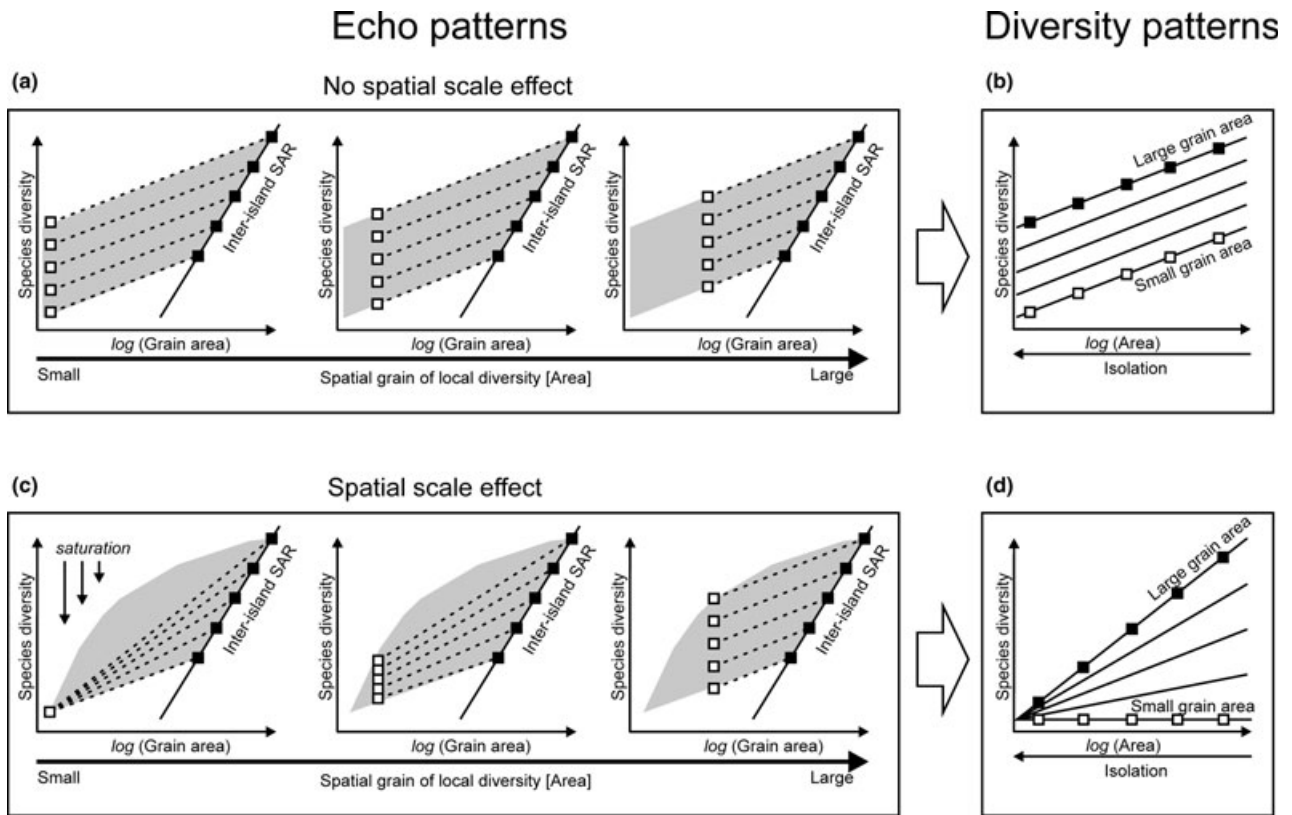

(c) Spatial scale effect

(d)

Figure 1 Schematic representation of how the grain size at which local diversity is assessed changes the way regional diversity (black squares, solid line) translates into local diversity (white squares; modified after Rosenzweig & Ziv, 1999). 'Echo patterns' (a, c) show the relationship between regional diversity and local diversity within islands; diversity patterns (b, d) show the patterns of diversity at different grain sizes across islands. If grain size does not affect how regional diversity translates into local diversity (no spatial scale effect), intra-island species–area relationships (SARs; dashed lines) are parallel lines at all spatial scales (a). This results in parallel species–area relationships when species diversity patterns assessed at different grain sizes are plotted over island area and isolation (b). If grain size affects intra-island SARs (spatial scale effect; c), for example owing to an increase in species saturation at smaller spatial scales, the resulting diversity patterns will show an increase in species diversity for large grain sizes, but not for small grain sizes (d). The grey area shows the potential species diversity that a local sampling site can harbour in relation to regional diversity.

to an equal increase in diversity with regional area at all grain sizes. Therefore, the ETIB is equally applicable at all spatial scales.

H_2: Regional area and isolation are strong predictors of species diversity only at large grain sizes. The species pool affects local diversity in a way that is dependent on the grain size at which local diversity is assessed. The biogeographical effects of regional area and isolation resulting from immigration from the regional species pool are diluted at local scales, where local environmental conditions set an upper limit to species diversity. Therefore, the ETIB is applicable only at regional spatial scales.

MATERIALS AND METHODS

Study sites

We selected 12 mountain regions on islands having different sizes, degrees of isolation and environmental conditions in Indonesia and the Philippines (Fig. 2). On each island,

sampling sites were located at 1100 m a.s.l. and 1200 m a.s.l. in the main mountain range of the island (Table 1). We chose this elevational belt for two reasons. First, it has a high number of fern and lycophyte (henceforth called fern) species (Bhattarai *et al.*, 2004; Carpenter, 2005; Kluge *et al.*, 2006; Kessler *et al.*, 2011), enabling us to collect statistically relevant samples. Second, the human footprint at this elevation is the lowest world-wide (Nogués-Bravo *et al.*, 2008), providing us with mostly undisturbed natural ecosystems.

Ferns as a model group

Ferns are distributed world-wide, and are independent of biotic pollination and animal vectors because of their spore dispersal (Barrington, 1993). The high species diversity of ferns allows statistical inference based on the documented data, and the relatively low dependence on biotic vectors allows linkage of patterns of distribution directly to abiotic factors.
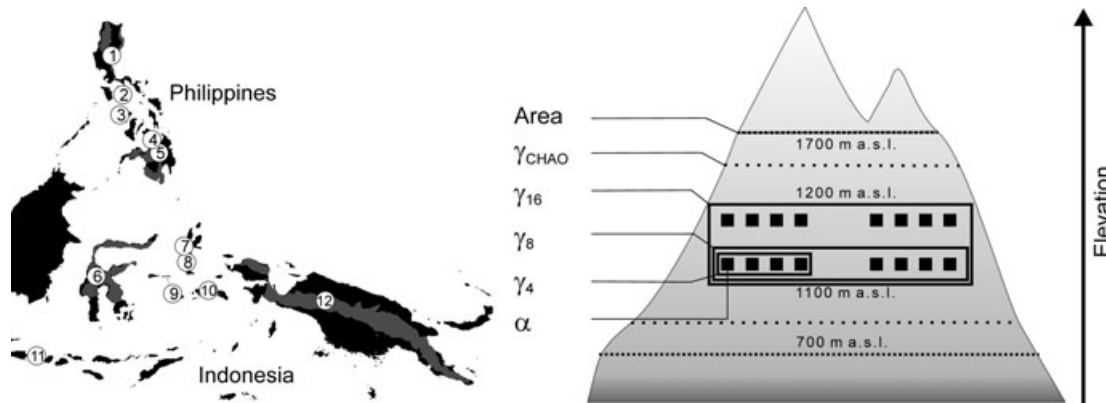
Figure 2 Study locations and sampling design of fern diversity on Southeast Asian islands. Left: sampling locations (white circles with numbers; Table 1) spanning the gradients of habitat area and isolation in the Malesian Archipelago and New Guinea. Right: schematic representation of the sampling design consisting of 16 plots of 20 m × 20 m each (mean richness = α), with one transect consisting of four plots at fixed distances of 20 m (γ_4). Two transects of four plots each were arranged 100 m apart (γ_8), each at both 1100 and 1200 m elevation (γ_{16}). γ_{CHAO} as an approximation of the local species pool was calculated using a species diversity estimator (Chao 2) across all 16 plots. Habitat area was measured as the land surface of each studied mountain range per island between 700 and 1700 m a.s.l. (grey shades on islands, left), corresponding to the mean elevational range amplitude (1000 m) of montane fern species.

Table 1 Locations of the sampling sites of fern diversity in Indonesia and the Philippines. The numbers refer to the locations of the islands in Fig. 2.

No.	Island	Mountain/Site	Latitude	Longitude	Habitat area/site (km²)	Island area (km²)
1	Luzon	Mingan Mountains	15°25′ N	121°24′ E	390	104,688
2	Sibuyan	Mount Guiting Guiting	12°26′ N	122°33′ E	50	445
3	Panay	Mount Madia-as	11°21′ N	122°08′ E	787	12,011
4	Camiguin	Mount Timpoong	09°11′ N	124°42′ E	29	238
5	Mindanao	Mount Kitanglad	08°08′ N	124°55′ E	5854	97,530
6	Sulawesi	Toro, Lore Lindu NP	01°29′ S	120°03′ E	30,557	174,600
7	Tidore	Gunung Kiematubu	00°40′ N	127°24′ E	11	116
8	Bacan	Gunung Sibela	00°42′ S	127°31′ E	110	1900
9	Buru	Wafehai	03°13′ S	126°34′ E	2022	8473
10	Seram	Manusela NP	02°59′ S	129°11′ E	1451	17,100
11	Lombok	Gunung Rinjani	08°20′ S	116°24′ E	799	4725
12	New Guinea	Pass Valley	03°46′ S	139°14′ E	173,416	780,000

Transect design

Samples were taken in standardized plots of 20 m × 20 m. This plot size has previously been used for surveys of local fern diversity (Kessler, 2001; Kluge et al., 2006) and is large enough to be representative but small enough to be ecologically homogeneous and to allow rapid and efficient surveys (Kessler & Bach, 1999). We used a fixed sampling design of transects of four plots separated by a distance of 20 m. In each mountain range, transects were established in pristine forests: two at 1100 m a.s.l. separated by 100 m, and two at 1200 m a.s.l. separated by 100 m (Fig. 2).

Plant sampling

For each plot, we assembled a list of all fern species. Epiphytic species were surveyed by a combination of climbing trees,

cutting selected branches, looking for fallen branches on the ground, and using binoculars. This approach has previously been successfully applied in studies of this kind (Kessler, 2001; Kluge et al., 2006; Kessler et al., 2011). Every fern species in each study region (but not in each plot) was collected for later identification and deposited in the Herbarium Zurich (ZH), the Herbarium of the Central Mindanao University (Central Mindanao University Herbarium), the Herbarium Bogor (BO), or the Herbarium University of California, Berkeley (UC).

Data treatment

We defined α-diversity as the mean diversity of all sixteen 20 m × 20 m plots. γ_4-diversity was defined as the total number of species found in all four plots per transect (calculated as the mean of four transects per site); γ_8-diversity was defined as the total number of species found in two transects

of a total of eight plots at a given elevation (calculated as the mean of two transects per site); and γ_{16}-diversity was defined as the total number of species found in four transects of a total of 16 plots. γ_{CHAO}-diversity was calculated using the Chao 2 estimator (Chao, 1984) based on γ_{16}-diversity and the number of singleton and doubleton species recorded. γ_{reg}-diversity was defined as the total number of fern species on an island, quantified as the total number of species listed in the *Flora Malesiana* (Kalkman & Nooteboom, 1998).

Spatial scale

The term 'scale' in this context refers to the size of the units used in the sampling of the assemblages or *grain size* (Whittaker *et al.*, 2001; Scheiner, 2011) and ranges from 400 m² (α) to the area of the island (γ_{reg}). We considered species numbers at the levels of α to γ_{CHAO} as estimates of local species diversity because they refer to fern assemblages at scales of < 1 km²; that is, at a scale at which direct species interactions are likely to occur. As regional diversity estimates, we used both γ_{reg} and γ_{CHAO}. The latter was included in both the local and regional scales because, while γ_{CHAO} is a subset of γ_{reg} and hence 'local' in this regard, at the same time it represents a narrower 'regional' species pool from which the even more local species assemblages (α to γ_{16}) are recruited.

Explanatory variables

We used area, isolation, habitat heterogeneity and bioclimatic and edaphic characteristics to explain species diversity at the various spatial scales.

Area

We defined area as the total habitat area within the mountain range where the sampling sites were located. For ferns, which have their maximum diversity at mid-elevations and few lowland species (Bhattarai *et al.*, 2004), the lowlands are dispersal barriers for most species, rendering the mountain ranges the actual habitat islands. Using the whole surface area of an island would therefore be misleading. We calculated habitat area based on the total surface area of the elevational belt ranging from 700 to 1700 m a.s.l. This corresponds to the elevational range amplitude of the majority of montane fern species (Bhattarai *et al.*, 2004; Carpenter, 2005; Kluge *et al.*, 2006; Kessler *et al.*, 2011) and allows an approximation of the area that hosts the species pool from which the local assemblages are recruited from. We used ArcGis 10 (ESRI, Redlands, CA, USA) to calculate the surface area of the respective mountain ranges based on Shuttle Radar Topography Mission (SRTM) topographic data at 90-m resolution (Jarvis *et al.*, 2008).

Isolation

Following Weigelt & Kreft (2013), we selected a measure of island isolation empirically by comparing metrics that repre-

sent different isolation concepts and source landmasses (see Appendix S1 in Supporting Information). Because the ETIB had been formulated for entire islands, we selected the isolation metric based on the model fit of γ_{reg} in dependence on area and isolation ($\gamma_{reg} \sim$ area + isolation), considering only models that showed the expected negative relationship among isolation and species diversity. We used the corrected Akaike information criterion (AIC$_c$; Burnham & Anderson, 2002) as the measure of model fit. The distance of a mountain range to the nearest mountain range of at least 100 km² on the mainland (Asia or Australia) received strongest support as an explanatory variable for fern species diversity, and we thus chose this metric for further analyses. Metrics that considered the amount of mountain area in the surrounding mountain ranges did not show consistent relationships to diversity at any spatial scale (see Appendix S1). Distances were measured using azimuthal equidistant map projections using the 'near table' tool in ArcGis 9.31. Mountain ranges were defined as areas above 700 m a.s.l. according to SRTM topographic data at 90-m resolution (Jarvis *et al.*, 2008).

Environmental variables

We used global temperature and precipitation models of 19 climatic variables derived from WorldClim – Bioclim (Hijmans *et al.*, 2005) at a resolution of 30 arcseconds (compare Weigelt *et al.*, 2013). At the local scale (α to γ_{CHAO}), bioclimatic data were extracted for the locations of the sampling plots. At the regional scale (γ_{reg}, γ_{CHAO}), we extracted the bioclimatic variables as the mean over the whole mountain range in which the sampling site was located. γ_{CHAO} has been included as both local and regional, as it has been calculated on the basis of local data but represents a more regional diversity.

Relative air humidity is a crucial environmental factor for ferns because of their relatively poor evaporative control (Kluge *et al.*, 2006; Kessler *et al.*, 2011), but measuring it *in situ* over long periods of time requires considerable effort. Therefore, we used bryophyte cover on trees as a proxy for relative air humidity, a method which has been verified for five sites within the Philippines using data loggers to measure relative humidity (Karger *et al.*, 2012). We also included local environmental factors such as mean inclination of the plot and canopy cover, which were visually estimated in each plot. Soil samples were taken from every plot and analysed for 15 soil parameters (see Appendix S2).

Because the factors potentially co-vary and the use of more explanatory variables than observed variables violates the conditions for regression analysis, we reduced the environmental variables for regional climatic conditions (temperature and precipitation), as well as for local environmental conditions, using principal components analysis (PCA). PCA axes were selected using a threshold of 70% variance explained (see Appendix S3). Where applicable, variables were zero-mean unit-variance standardized to account for different measuring units.

Diversity models

To test the applicability of the ETIB of MacArthur & Wilson (1967) at various spatial scales, we compared regional area and isolation as predictors of fern species diversity assessed at different grain sizes (α to γ_{reg}). In addition, we used regional species diversity (γ_{reg}) as a predictor of species diversity at smaller grain sizes (α to γ_{CHAO}). We used partial residuals to visualize the effect of each factor accounting for the respective co-variable in linear multi-predictor models ($S \sim A + I$), with S = species diversity at a given grain size, A = habitat area, I = island isolation.

To account for regional differences in bioclimate and in microclimatic, edaphic and structural conditions at plot level, we included axes derived from the bioclimate and plot-environment PCAs. The relative importance of each predictor in the multi-predictor framework was assessed using the *pmvd* metric in the R package RELAIMPO (Groemping, 2006).

All statistical analyses were performed using R statistical software version 2.14.2 (R Development Core Team, 2005).

RESULTS

The ETIB of MacArthur & Wilson (1967) applied best at regional scales (Fig. 3, Table 2). Species–area slopes increased with spatial grain, but the relationships were significant only from the γ_{16}-level upwards. These results were consistent both when accounting for the effect of isolation in the multi-predictor models and when disregarding it (Fig. 3). The slopes of the negative relationships between diversity and isolation decreased with increasing spatial grain. However, this relationship was significant only at the island level (γ_{reg}). The explanatory power of the equilibrium model measured as R^2 increased monotonically with the spatial grain from 0.18 (α) to 0.74 (γ_{reg}; Table 2). Similar patterns arose when species diversity at different grain sizes were plotted
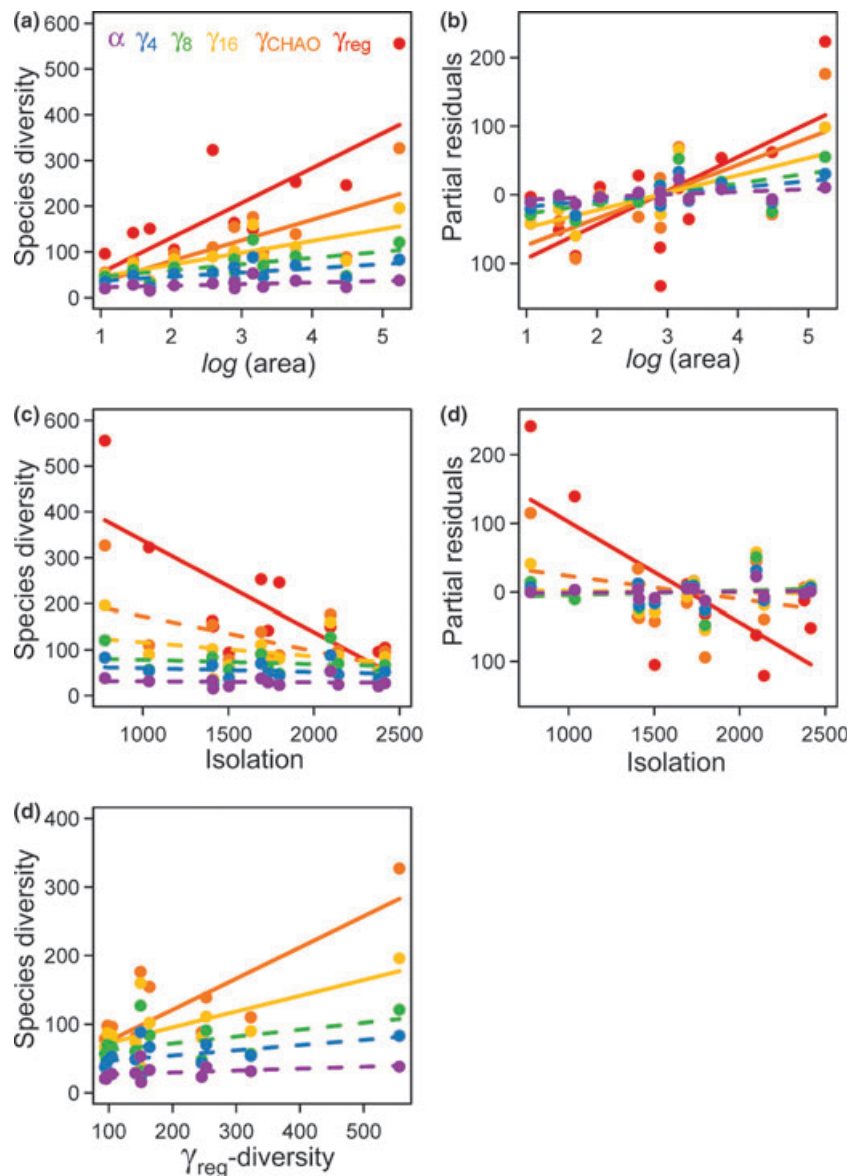

Figure 3 Fern diversity on Southeast Asian islands across various spatial scales plotted over (a) regional habitat area and (c) isolation as well as partial residual plots accounting for the effect of the respective co-variable. Partial residuals are given for area (b) partitioning out the effect of isolation and (d) partitioning out the effect of area. Panel (e) shows the relationship if γ_{reg} is used as the explanatory variable instead of habitat area. Area was measured as the land surface of each studied mountain range per island between 700 and 1700 m a.s.l., and isolation was quantified as the distance to the nearest mountain range on the mainland of Asia or Australia. Spatial grain sizes (see Fig. 2 for definitions) are colour-coded: α, violet; γ_4, blue; γ_8, green; γ_{16}, yellow; γ_{CHAO}, orange; γ_{reg}, red. Regression lines are drawn using ordinary least squares regression. Solid lines, significant ($P < 0.05$); dashed lines, not significant ($P > 0.05$).

Table 2 Model statistics for regional area and isolation (left) and γ_{reg} (right) as descriptors of fern diversity at various spatial scales in mountain ranges on Southeast Asian islands (using ordinary least squares regression). Area was measured as the land surface of each studied mountain range per island between 700 and 1700 m a.s.l. Isolation was quantified as the distance to the nearest mountain range in the mainland of Asia or Australia.

| | Regional area and isolation | | | | | | | | | | | γ_{reg} | | | | | |
| | Intercept | | | Area | | | Isolation | | | | Intercept | | | γ_{reg} | | |
Response	est.	t	P	est.	t	P	est.	t	P	R²	est.	T	P	est.	t	P	R²
γ_{reg}	303.628	2.39	0.041	49.376	2.37	0.042	−0.15	−2.88	0.018	0.74	–	–	–	–	–	–	–
γ_{CHAO}	64.206	0.70	0.503	39.053	2.59	0.029	−0.03	−0.91	0.386	0.57	29.677	0.63	0.541	1.403	4.20	0.002	0.64
γ_{16}	26.557	0.47	0.651	25.399	2.72	0.023	0.00	−0.13	0.903	0.52	−0.895	−0.01	0.990	2.095	3.05	0.012	0.48
γ_{8}	18.264	0.42	0.686	14.706	2.05	0.071	0.01	0.38	0.715	0.34	45.878	0.46	0.655	2.120	1.64	0.132	0.21
γ_{4}	24.243	0.83	0.431	9.388	1.95	0.084	0.00	0.15	0.883	0.33	3.039	0.03	0.978	3.591	1.94	0.082	0.27
α	15.315	0.89	0.395	3.798	1.35	0.210	0.00	0.28	0.783	0.17	56.678	0.47	0.646	4.787	1.25	0.241	0.13

γ_{reg}, total number of fern species on an island; γ_{CHAO}, number of species calculated using the Chao 2 estimator (Chao, 1984) based on γ_{16}-diversity and the number of singleton and doubleton species recorded; γ_{16}, mean number of species found in four transects of a total of sixteen 20 m × 20 m plots; γ_{8}, mean number of species found in two transects of a total of eight plots; γ_{4}, mean number of species found in all four plots per transect; α, mean diversity of sixteen 20 m × 20 m plots. est., estimated values.

Table 3 Relative importance of explanatory variables of fern diversity at various spatial scales in mountain ranges on Southeast Asian islands. Relative importance was quantified using the *pmvd* metric (Groemping, 2006) based on ordinary least squares regression models including all (significant) factors. See Table 2 for a definition of the measures of diversity.

Variable	γ_{reg}	γ_{CHAO}	γ_{16}	γ_{8}	γ_{4}	α
Area	0.26	0.26	0.32	0.28	0.21	0.10
Isolation	0.38	0.10	0.07	0.04	0.04	0.03
$TEMPPC1_{reg}$	0.02	0.03	–	–	–	–
$PRECPC1_{reg}$	0.11	0.07	–	–	–	–
$PRECPC2_{reg}$	0.23	0.15	–	–	–	–
TEMPPC1	–	0.02	0.01	0.01	0.01	0.01
PRECPC1	–	0.02	0.01	0.04	0.05	0.07
ENVPC3	–	0.31	0.46	0.52	0.61	0.67

Area, area of the mountain range between 700 and 1700 m a.s.l.; Isolation, distance to nearest mountain range on the mainland; $TEMPPC1_{reg}$, regional temperature principal components analysis (PCA) axis 1; $PRECPC1_{reg}$, regional precipitation PCA axis 1; $PRECPC2_{reg}$: regional precipitation PCA axis 2; TEMPPC1, local temperature PCA axis 1; PRECPC1, local precipitation PCA axis 1; ENVPC3, local environmental conditions PCA axis 3. ENVPC1 and ENVPC2 are not shown here owing to low predictive power compared with ENVPC3.

over γ_{reg} as an alternative explanatory factor for fern diversity at several smaller spatial grains (Fig. 3e, Table 2).

The relative importance of area decreased with the spatial grain of the units at which diversity was measured (Table 3). Only when diversity was measured as the diversity of the entire island (γ_{reg}) was the relative importance of area lower than expected from a linear decrease. Island isolation showed a significant relationhip with diversity only at the largest grain size (Table 3). However, a decrease of relative importance from γ_{reg}-diversity and γ_{CHAO}-diversity to α-diversity was apparent. Temperature did not explain diversity at any given grain size (Table 3). Precipitation was important only at the regional level but not at grains smaller than γ_{CHAO} ($PRECPC2_{reg}$; Table 3). Local environmental conditions (ENVPC3) showed a clear increase in relative importance with decreasing spatial grain (Table 3). Consequently, the maximum relative importance of environmental conditions was found at the α-level (Table 3).

DISCUSSION

At the regional scale (γ_{reg}), we found the expected relationships of species diversity and habitat area per mountain range and level of isolation, as predicted by the classical theory of island biogeography (MacArthur & Wilson, 1967; Whittaker, 1998). In contrast, the marked decline in importance of area and isolation for diversity measured at smaller spatial scales shows that the ETIB loses its predictive power with decreasing spatial scale from regional to plot level (Fig. 3, Table 2).

At the smallest grain size (α), diversity was correlated neither with regional area nor with isolation. Based on these

results, we have to reject our hypothesis that the ETIB is equally applicable across spatial scales (H_1) in favour of an effect of spatial scale on species diversity on islands (H_2). This leads us to conclude that the influence of the species pool on local diversity is scale-dependent and decreases with decreasing spatial scale. A possible explanation for this pattern could be that local (α) diversity is saturated, limiting the number of species that can migrate into local communities from the regional species pool, so that diversity becomes less saturated at larger scales (Fox & Srivastava, 2006). A local community is considered saturated when the maximum number of species that can disperse into the community, find a suitable niche and keep a viable population size, is reached (Fox & Srivastava, 2006). In addition, a community can be saturated simply because the upper limit of species diversity is reached owing to ecological constraints (Srivastava, 1999). The strong increase in the importance of environmental factors with decreasing spatial scale would favour the hypothesis of environmentally constrained saturation (Table 3). At the α-scale, species diversity thus can be considered to be saturated, as the maximum fern diversity possible under the current environmental conditions appears to have been reached. An increase in the species pool can therefore have no effect on local species diversity, as the maximum number of species that the local assemblages can hold has already been reached.

Isolation did not show the same pronounced patterns as area across spatial scales. Although a decline in the importance of isolation was visible, this was only marginally significant. In fact, only two of the tested isolation metrics showed the expected significant negative effect, and only at the largest scale (γ_{reg}; see Appendix S1). This might be partly a result of the relatively small sampling size of 12 islands, but most likely reflects the fact that the variability of isolation among our study islands (3-fold) was much less than that of area (15,000-fold). Furthermore, isolation in a set of islands as complex as the Southeast Asian archipelago is difficult to quantify, as inter-island connectivity might affect the degree of isolation of small islands more than that of large islands, and a common source pool for all islands is hard to define. In addition, the comparatively low importance of isolation might also be linked to a high degree of speciation, which may counteract the negative effect of isolation on species diversity, especially on large islands such as New Guinea and Mindanao (Kisel & Barraclough, 2010; Weigelt & Kreft, 2013).

Among the regional environmental variables, precipitation appeared to be important for fern diversity at regional and intermediate scales (γ_{reg}, γ_{CHAO}). The influence of precipitation on regional fern diversity has been shown previously at a global scale for ferns (Kreft et al., 2010) and overall for vascular plants (Kreft & Jetz, 2007). Its importance, however, declines towards smaller scales, where local environmental factors become more important. In contrast, temperature did not show any relationship to species diversity at any scale (Table 3). This is not surprising, considering that all of our investigated islands are within the tropics, without a pro-

nounced gradient in mean annual temperature and that water-related variables are more likely drivers of vascular plant diversity in high-energy regions (Kreft & Jetz, 2007). However, the data constraints of WorldClim might be problematic in this context as WorldClim is known to perform especially poorly in tropical mountain regions (Soria-Auza et al., 2010). We therefore caution against an ecological inference from these factors in this case.

Local environmental factors such as soil fertility and microclimatic conditions in contrast varied extensively at the grain size of one study site, and therefore showed a stronger correlation with species diversity at the local scale compared with regional environmental variables. Local environmental factors are also known to increase regional diversity when more environmental conditions are sampled by using a larger number of sampling plots on large islands than on small islands (Sfenthourakis & Panitsa, 2012). We therefore caution against making the inference that local environmental factors do not matter for regional diversity. They can influence regional diversity, however, only when most of their within-island variability is assessed to reflect the regional variation of local environmental conditions (Sfenthourakis & Panitsa, 2012). This, however, contrasts with the equal number of plots per island used in our study, and therefore an influence of local environmental factors on regional diversity might only be a sampling artefact which arises from an uneven number of sampling plots.

By providing evidence for a scale-dependent response of local diversity, our study reveals important insights into how regional diversity translates into local diversity. Translations of regional diversity into local diversity have been thought to be different on islands than on mainlands (Rosenzweig & Ziv, 1999). On the mainland, regional diversity would translate into local diversity, as observed in our data for fern diversity at a larger grain size of local diversity in comparison to islands. On islands, in contrast, regional diversity would translate into local diversity, as observed in our data at small spatial grain sizes. This shows that relationships between regional and local diversity can be altered not only by different geographical settings (mainland versus islands) but also by spatial scale.

CONCLUSIONS

In conclusion, we found that the two main factors of the ETIB, area and isolation, are strong predictors of fern diversity on islands at regional scales. The species pool has a scale-dependent influence on diversity and is unimportant at the local (α) scale, where diversity appears to be saturated. At this scale, local variation in environmental conditions becomes a far stronger predictor of fern diversity. The lack of explanatory power of area and isolation at the local α-scale is most probably a result of the species saturation of communities. More generally, to make predictions about how regional processes may influence local assemblages, it is therefore important to take the scale dependence of species-pool

effects into account and to acknowledge that these effects influence species diversity only down to the scale at which diversity becomes saturated.

REFERENCES

Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

Barrington, D.S. (1993) Ecological and historical factors in fern biogeography. *Journal of Biogeography*, **20**, 275–280.

Bhattarai, K.R., Vetaas, O.R. & Grytnes, J.A. (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, **31**, 389–400.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445–449.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer, New York.

Caley, M.J. & Schluter, D. (1997) The relationship between local and regional diversity. *Ecology*, **78**, 70–80.

Carpenter, C. (2005) The environmental control of plant species density on a Himalayan elevation gradient. *Journal of Biogeography*, **32**, 999–1018.

Chao, A. (1984) Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, **11**, 265–270.

Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species–area relationship. *The American Naturalist*, **113**, 791–833.

Cornell, H.V. (1985) Local and regional richness of cynipine gall wasps on California oaks. *Ecology*, **66**, 1247–1260.

Cornell, H.V. (1999) Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. *Ecoscience*, **6**, 303–315.

Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the diversity of ecological communities – a theoretical perspective. *Journal of Animal Ecology*, **61**, 1–12.

Crawley, M.J. & Harral, J.E. (2001) Scale dependence in plant biodiversity. *Science*, **291**, 864–868.

Fox, J.E. & Srivastava, D.S. (2006) Predicting local–regional richness relationships using island biogeography models. *Oikos*, **113**, 376–382.

Gillespie, T.W., Keppel, G., Pau, S., Price, J.P., Jaffré, T. & O'Neill, K. (2013) Scaling species richness and endemism of tropical dry forests on oceanic islands. *Diversity and Distributions*, **19**, 896–906.

Graves, G.R. & Gotelli, N.J. (1983) Neotropical land-bridge avifaunas: new approaches to null hypotheses in biogeography. *Oikos*, **41**, 322–333.

Groemping, U. (2006) Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software*, **17**, 1–17.

Heaney, L.R. (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, **9**, 59–74.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Huston, M.A. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos*, **86**, 393–401.

Jarvis, A., Reuter, H.I., Nelson, A. & Guevara, E. (2008) *Hole-filled seamless SRTM data, version 4.* International Centre for Tropical Agriculture (CIAT). Available at: http://srtm.csi.cgiar.org (accessed 16 June 2010).

Kalkman, C. & Nooteboom, H.P. (1998) *Flora Malesiana. Series II: Pteridophyta (ferns and fern allies)*, Vols 1–3. Rijksherbarium, Hortus Botanicus, Leiden.

Kallimanis, A.S., Mazaris, A.D., Tzanopoulos, J., Halley, J.M., Pantis, J.D. & Sgardelis, S.P. (2008) How does habitat diversity affect the species–area relationship? *Global Ecology and Biogeography*, **17**, 532–538.

Karger, D.N., Kluge, J., Krömer, T., Hemp, A., Lehnert, M. & Kessler, M. (2011) The effect of area on local and regional elevational patterns of species richness. *Journal of Biogeography*, **38**, 1177–1185.

Karger, D.N., Kluge, J., Abrahamczyk, S., Salazar, L., Homeier, J., Amoroso, V.B., Lehnert, M. & Kessler, M. (2012) Bryophyte cover on trees as proxy for relative air humidity in the tropics. *Ecological Indicators*, **20**, 277–281.

Kelly, B.J., Wilson, J.B. & Mark, A.F. (1989) Causes of the species–area relation: a study of islands in Lake Manapouri, New Zealand. *Journal of Ecology*, **77**, 1021–1028.

Kessler, M. (2001) Pteridophyte species richness in Andean forests in Bolivia. *Biodiversity and Conservation*, **10**, 1473–1495.

Kessler, M. & Bach, K. (1999) Using indicator families for vegetation classification in species-rich Neotropical forests. *Phytocoenologia*, **29**, 485–502.

Kessler, M., Kluge, J., Hemp, A. & Ohlemüller, R. (2011) A global comparative analysis of elevational species richness patterns of ferns. *Global Ecology and Biogeography*, **20**, 868–880.

Kisel, Y. & Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, **175**, 316–334.

Kluge, J., Kessler, M. & Dunn, R.R. (2006) What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography*, **15**, 358–371.

Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences USA*, **104**, 5925–5930.

Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. (2008) Global diversity of island floras from a macroecological perspective. *Ecology Letters*, **11**, 116–127.

Kreft, H., Jetz, W., Mutke, J. & Barthlott, W. (2010) Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. *Ecography*, **33**, 408–419.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, **70**, 966–979.

Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, **73**, 1943–1967.

Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, **10**, 3–13.

Losos, J.B. & Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature*, **408**, 847–850.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Nogués-Bravo, D., Araújo, M.B., Romdal, T. & Rahbek, C. (2008) Scale effects and human impact on the elevational species richness gradients. *Nature*, **453**, 216–220.

R Development Core Team (2005) *R: a language and environment for statistical computing*. Version 2.15.3. R Foundation for Statistical Computing, Vienna. Available at: http://cran.r-project.org/.

Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences USA*, **98**, 4534–4539.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167–171.

Romdal, T.S. & Grytnes, J.-A. (2007) An indirect area effect on elevational species richness patterns. *Ecography*, **30**, 440–448.

Rosenzweig, M.L. & Ziv, Y. (1999) The echo pattern of species diversity: pattern and process. *Ecography*, **22**, 614–628.

Scheiner, S.M. (2011) Musings on the Acropolis: terminology for biogeography. *Frontiers of Biogeography*, **3**, 62–70.

Sfenthourakis, S. & Panitsa, M. (2012) From plots to islands: species diversity at different scales. *Journal of Biogeography*, **39**, 750–759.

Soria-Auza, R.W., Kessler, M., Bach, K., Barajas-Barbosa, P.M., Lehnert, M., Herzog, S.K. & Böhner, J. (2010) Impact of the quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from Bolivia. *Ecological Modelling*, **221**, 1221–1229.

Srivastava, D.S. (1999) Using local–regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology*, **68**, 1–17.

Terborgh, J. (1973) Notion of favorableness in plant ecology. *The American Naturalist*, **107**, 481–501.

Terborgh, J.W. & Faaborg, J. (1980) Saturation of bird communities in the West Indies. *The American Naturalist*, **116**, 178–195.

Triantis, K.A., Mylonas, M., Lika, K. & Vardinoyannis, K. (2003) A model for the species–area–habitat relationship. *Journal of Biogeography*, **30**, 19–27.

Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography*, **39**, 215–231.

Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, **299**, 241–244.

Weigelt, P. & Kreft, H. (2013) Quantifying island isolation – insights from global patterns of insular plant species richness. *Ecography*, **36**, 417–429.

Weigelt, P., Jetz, W. & Kreft, H. (2013) Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences USA*, **110**, 15307–15312.

Whittaker, R.J. (1998) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.

Whittaker, R.J. (2000) Scale, succession and complexity in island biogeography: are we asking the right questions? *Global Ecology and Biogeography*, **9**, 75–85.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977–994.

Willis, K.J. & Whittaker, R.J. (2002) Species diversity – scale matters. *Science*, **295**, 1245–1248.

SUPPORTING INFORMATION

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

Appendix S1 Isolation metrics tested as predictors of regional fern diversity.

Appendix S2 List of explanatory variables.

Appendix S3 Results of the principal components analysis.

BIOSKETCH

Dirk N. Karger is a postdoctoral researcher in the Department of Systematic Botany at the University of Zurich, Switzerland. His current research focuses on patterns of diversity at different spatial scales across Asia and the Pacific.

The authors share a strong research interest in island biogeography. Together, they seek to understand the origin and maintenance of island biodiversity and how local and regional processes drive species diversity.

Author contributions: D.N.K., P.W. and M.K. conceived the ideas; D.N.K., V.B.A., A.H., D.D. and M.K. collected the data; D.N.K. and P.W. analysed the data; and D.N.K., P.W., M.K. and H.K. led the writing.

Editor: Kostas Triantis