Drivers of lowland rain forest community assembly, species diversity and forest structure on islands in the tropical South Pacific

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Summary

1. Testing the comparative strength and influence of age and area of islands, proximity of source propagules and disturbances on community assembly, species diversity and vegetation structure has proved difficult at large scales. The little-studied rain forests in the Tropical South Pacific (TSP) provide a unique study area to investigate determinants of community dynamics, with islands varying in age, isolation, area and cyclone frequency. We tested the effects of biogeographical factors and cyclone frequency on the species composition, species diversity and forest structure of old-growth rain forest using 1-ha inventory plots on 12 islands between New Guinea and the Solomon Islands.

2. As predicted by the General Dynamic Model of Oceanic Island Biogeography, the biogeographical variables of archipelago age and island area are the most important factors affecting species richness and diversity, with older and larger islands having higher richness and diversity. There is no significant effect of cyclone frequency on species diversity.

3. The theory that diversity drives endemism is not supported in this system as endemism is not correlated with species diversity. Instead, age and isolation of an island best explain patterns of endemism, with the latter suggesting dispersal limitations between archipelagos.

4. Proximity to source area influences species composition of lowland tropical rain forests in the TSP, which is also supported by a strong correlation between geographic distance and floristic similarity. Vector-fitting onto non-metric multidimensional scaling suggests that archipelago age and cyclone frequency may, in addition to proximity to source area, influence species composition. This implies that a species’ tolerance to cyclones affects its abundance at different cyclone frequencies.

5. Synthesis. Both biogeographical variables (island area and isolation) and cyclone frequency appear to affect community assembly in lowland rain forests in the TSP. While species are hence not ecologically equivalent, interspecific ecological differences do not seem to affect the overall patterns of species diversity, which are mostly determined by biogeographical variables, as predicted by the neutral theory.

Key-words: cyclones, disturbance, endemism, hurricanes, island biogeography, neutral theory, species composition

Introduction

There is a rich body of theory in community ecology that predicts how age, area, disturbance frequency and proximity to source propagules affect community composition, diversity and structure. Mainland community assembly is believed to be the result of both, neutral (dispersal limitation and stochastic events) and deterministic (habitat) factors (Svenning et al. 2004; John et al. 2007). Climate (MacDougall, Wilson & Bakker 2008) and disturbance events (Condit, Hubbell & Foster 1995; van Nieuwstadt & Sheil 2005) also play a major role in determining community assembly. Hubbell (2001) proposed that patterns of species diversity and abundance of species can be predicted from neutral processes. His theory has received much criticism (McGill 2003; Dornelas, Connolly & Hughes 2006), especially the assumption that species are ecologically equivalent (Chave 2004; Wootton 2005).

Much of our understanding of the evolution and ecology of lowland tropical rain forest has come from research in Amazonia and Southeast Asia (Condit et al. 2002; ter Steege...
et al. 2006). Although the Tropical South Pacific (TSP) contains several biodiversity hot spots with numerous endemic species (Myers et al. 2000), rain forests in this region (Fig. 1) have received comparatively little attention, possibly with the exception of Tonga (McConkey et al. 2003; Franklin et al. 2006; McConkey & Drake 2006; Franklin 2007) and Samoa (Elmqvist et al. 1994; Webb 1999; Webb & Fa’aamu 1999). There is not only an urgent need to understand the evolution and ecology of the forests in the TSP, but an opportunity to use the inherent variability in island area, age, isolation and cyclone frequency to explain the diversity, structure and composition of rain forests in island systems.

For insular environments, MacArthur & Wilson (1967) proposed the Theory of Island Biogeography (TIB) to explain patterns of species diversity amongst islands. The TIB is based on species turnover on islands caused by colonization and extinction, resulting in a dynamic equilibrium number of species that is determined by the area of an island ($S = cA^{Z}$, where $S$ is the number of species or species diversity, $A$ is the area and $c$ and $Z$ are constants). This model of island biogeography is therefore based on neutral mechanisms. The equilibrium status of islands has been called into question (Heaney 2000; Lomolino 2000) and the species diversity–area model is often considered simplistic because it does not include variables for other important factors, especially island age and isolation (Lomolino 2000; Lomolino & Weiser 2001; Badano et al. 2005). Whittaker et al. (2007) and Whittaker, Triantis & Ladle (2008) suggested that species diversity initially increases after an island emerges, but eventually decreases, as the island erodes and finally submerges. Based on this they proposed the General Dynamic Model of Oceanic Island Biogeography (GDMOIB), which also incorporates time ($t$) since island emergence [$S = a + bt + ct^{2} + d(\log A)$, where $a$, $b$, $c$ and $d$ are constants].

Disturbance also drives diversity in some communities. In addition to anthropogenic disturbances (Bayliss-Smith, Hviding & Whitmore 2003; Franklin et al. 2006; Haberle 2007), tropical cyclones commonly produce disturbances in the TSP (Hastings 1990; Kerr 2000) and have major short- and long-term impacts on lowland rain forests (Lugo 2008). Initial effects of tropical cyclones on forests are usually moderate, ranging from partial or complete defoliation and broken branches to uprooting and snapped trunks (Elmqvist et al. 1994; Franklin et al. 2004; Turton & Siegenthaler 2004). Severe cyclone damage may result in increased mortality rates (Franklin et al. 2004; Pascarella, Aide & Zimmerman 2004). However, forests generally recover quickly from such disturbances, mostly following the expected successional sequence (Kerr 2000; Pascarella, Aide & Zimmerman 2004). In the long-term, high frequency of cyclones has also been shown to result in lower canopies and higher tree densities (de Gouvenain & Silander 2003).

Damage and mortality caused by cyclones is usually non-random. Large trees are more vulnerable (Walker 1991; Basnet et al. 1992; Herbert, Fowkes & Vitousek 1999), as are certain species (Elmqvist et al. 1994; Burslem, Whitmore & Brown 2000). Species- and size-specific mortality of trees means that frequent tropical cyclones could change the composition and
structure of forests, as has been suggested for Carribean and Pacific rain forests (Brokaw & Grear 1991; Basnet et al. 1992; Hjerpe, Hedénas & Elmqvist 2001), especially if the cyclone is followed by fires (Hjerpe, Hedénas & Elmqvist 2001; Franklin 2007).

Here, we used 12 vegetation inventory plots spread throughout several Pacific archipelagos to address three questions about community composition and assembly in lowland rain forests in the TSP. (i) Can current patterns of species diversity, richness and endemism on Pacific islands be explained better by an island size and area model (consistent with island biogeography and neutral factors) or a cyclone frequency model? (ii) What factors drive species composition of old-growth forest? We expect that the biogeographical variable of isolation (different dispersal capabilities of species) and possibly age (some species may take longer to colonize islands) affect species composition; but we also propose cyclone frequency to be an important factor, because species differ in their susceptibility to cyclones (Curran et al. 2008). (iii) Does cyclone frequency affect the structure of lowland rainforests in the TSP? We expect to find higher densities of stems in forests that experience higher cyclone frequencies.

Materials and methods

STUDY SITES

All inventory plots were located in unlogged forests on red-brown clay soils (oxisols) in lowland rain forest (50–450 m a.s.l., precipitation < 3000 mm year⁻¹; WorldClim 2008), located at least 1 km from the coast, on 10 islands in the Pacific (Table 1 and Fig. 1). Plots were located in homogenous (no major tree-fall gaps), mature-stage forest located in homogenous (no major tree-fall gaps), mature-stage forest. Two additional sites were included from published data: a 1.2-ha plot at Vatia on Tutuila in American Samoa (Webb 1999) and a 1-ha plot in the Crater Mountain Wildlife Management Area in Papua New Guinea (Weiblen 1998).

<table>
<thead>
<tr>
<th>Site (abbreviation)</th>
<th>Island (Archipelago)</th>
<th>Location</th>
<th>C</th>
<th>d</th>
<th>b</th>
<th>S</th>
<th>α</th>
<th>E</th>
<th>Tax</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crater Mountain (CM)*</td>
<td>NG (NG)</td>
<td>6°47′ S, 145°02′ E</td>
<td>0.00</td>
<td>602</td>
<td>31.5</td>
<td>167</td>
<td>75.8</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Halowia (HAL)</td>
<td>NG (NG)</td>
<td>16°19′ S, 150°36′ E</td>
<td>0.09</td>
<td>529</td>
<td>40.1</td>
<td>135</td>
<td>58.5</td>
<td>11.4</td>
<td>24/70/85</td>
</tr>
<tr>
<td>Sewa (SEW)</td>
<td>Normanby (NG)</td>
<td>10°03′ S, 15°59′ E</td>
<td>0.09</td>
<td>612</td>
<td>46.3</td>
<td>85</td>
<td>26.4</td>
<td>16.1</td>
<td>32/72/89</td>
</tr>
<tr>
<td>Laura (LAU)</td>
<td>Lauru/Choiseul (SI)</td>
<td>6°59′ S, 150°59′ E</td>
<td>0.00</td>
<td>662</td>
<td>34.4</td>
<td>131</td>
<td>47.8</td>
<td>14.3</td>
<td>66/90/95</td>
</tr>
<tr>
<td>Kolombangara (KOL)</td>
<td>Kolombangara (SI)</td>
<td>8°42′ S, 157°07′ E</td>
<td>0.00</td>
<td>534</td>
<td>43.3</td>
<td>82</td>
<td>27.4</td>
<td>7.5</td>
<td>78/95/98</td>
</tr>
<tr>
<td>Tetepare (TET)</td>
<td>Tetepare (SI)</td>
<td>8°42′ S, 157°27′ E</td>
<td>0.00</td>
<td>409</td>
<td>31.2</td>
<td>85</td>
<td>32.6</td>
<td>7.6</td>
<td>78/96/100</td>
</tr>
<tr>
<td>Erromango (ERR)</td>
<td>Erromango (VA)</td>
<td>18°11′ S, 169°15′ E</td>
<td>0.91</td>
<td>616</td>
<td>37.7</td>
<td>62</td>
<td>15.0</td>
<td>22.4</td>
<td>92/100/100</td>
</tr>
<tr>
<td>Savura (SAY)</td>
<td>Viti Levu (FI)</td>
<td>18°04′ S, 178°26′ E</td>
<td>0.35</td>
<td>905</td>
<td>42.0</td>
<td>124</td>
<td>38.9</td>
<td>11.1</td>
<td>90/98/99</td>
</tr>
<tr>
<td>Gau (GUAU)</td>
<td>Gau (FI)</td>
<td>18°00′ S, 170°16′ E</td>
<td>0.35</td>
<td>840</td>
<td>45.7</td>
<td>85</td>
<td>25.9</td>
<td>56.5</td>
<td>93/100/100</td>
</tr>
<tr>
<td>Tiavea (TIA)</td>
<td>'Upolu (SA)</td>
<td>13°58′ S, 171°29′ W</td>
<td>0.39</td>
<td>712</td>
<td>36.8</td>
<td>41</td>
<td>9.5</td>
<td>18.4</td>
<td>87/100/100</td>
</tr>
<tr>
<td>Vatia (VAT)†</td>
<td>Tutuila (SA)</td>
<td>14°18′ S, 170°41′ W</td>
<td>0.39</td>
<td>580</td>
<td>30.0</td>
<td>35</td>
<td>8.7</td>
<td>17.2</td>
<td>97/97/97</td>
</tr>
</tbody>
</table>

†Webb & Fa’aumu (1999).

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Table 1. Floristic and structural data for twelve 1-ha vegetation plots in the Pacific. α, Fisher’s α; b, basal area (m² ha⁻¹); C, cyclone frequency (cyclones per year); d, density (stems ≥10 cm d.b.h.) ha⁻¹; S, richness (species per hectare); E, percentage endemism; Tax, taxonomic accuracy (percentage of taxa identified to the species, genus or family level); ?, values could not be calculated from published data; FI, Fiji; NG, New Guinea; SA, Samoa; SI, Solomon Islands; VA, Vanuatu.

VARIABLES CALCULATED

For each site, the following variables were calculated using ‘Species Diversity and Richness 3.03’ (Henderson & Seaby 2002): species richness (S; number of species), percentage endemism (E) and Fisher’s α [S = α ln(1 + n/α)], where n is the number of individuals; Fisher, Corbet & Williams (1943)], a reasonable estimator for α-diversity (Condit et al. 1996). The annual frequency of cyclones affecting a study site was calculated by counting every cyclone that had passed within 200 km of the site between 1985 and 2007 (Bath & Deguara 2008). Although this period spans only 23 years (data covering longer time periods would be desirable but are not readily available for the entire study region), we assumed it to be sufficient to determine major trends in cyclone regimes for the study sites. We determined the approximate distances of each study site to other study sites and to the continental islands of New Guinea.

DATA COLLECTION

At each study site four 50 × 50 m inventory plots (total area = 1 ha) were established at least 200 m apart to reduce the influence of chance factors on a single plot. Within each plot species identity (or morphospecies, i.e., species that could not be identified but are defined based on distinct morphological characters) and d.b.h. (measured at 1.4 m height) were recorded for each tree with a d.b.h. ≥10 cm. Trees were identified with the assistance of local experts (P. Ala, S. Chanell and S.Q. Sirikolo) and available literature (Whitmore 1966; Foreman 1971; Smith 1979–1991; Whistler 2004; Conn & Damas 2005; Keppel & Ghazanchian 2006). Specimens of species that could not be identified in the field were collected, where possible, and deposited at the South Pacific Regional Herbarium (SUVA). Nomenclature follows the International Plant Names Index (IPNI 2008). Several taxa, especially in plots in Papua New Guinea (Table 1), could not be identified to the species level. Most analyses, except those involving endemism, in this study should not be affected by this shortcoming, because such taxa could generally be readily assigned to morphospecies. Analyses pertaining to endemism were carried out including and not including the sites in Papua New Guinea, to ensure that the inability to identify taxa to species level did not affect the results, and both always yielded similar results.
(d_{dSG}) and New Caledonia (d_{dSC}), the closest likely source areas of the biota on oceanic islands in the south-west Pacific (Keppel, Lowe & Possingham 2009), using Google Earth. Although the North Australian rain forest is another potential source area, we did not include it in this analysis because the distances to the study sites were similar to those from New Guinea. We used the log of the sum of the distances to New Guinea and New Caledonia as a measure of isolation \( I = \log (d_{dSG} + d_{dSC}) \). Because the ages of individual islands are not definitely known, we used the approximate age of each archipelago (Keppel, Lowe & Possingham 2009) as the age of an island \( t \), hence assuming dispersal within an archipelago occurred readily. In addition, the total number of stems per hectare (density) was calculated.

**DATA ANALYSIS**

The software R 2.9.0 (R Development Core Team 2008) was used for all analyses. Before testing our hypotheses, we tested all the variables for multicollinearity by calculating correlation coefficients among them and the variance inflation factors (VIF; Neter et al. 1996). Although many of the predictor variables that used (log (a), t, C, I) were correlated, cross-correlations did not exceed 0.70 and VIF (log (A) = 2.02, t = 3.78, C = 1.61, I = 2.01) did not exceed 4, which is well below the thresholds of 0.75 and 10, respectively, suggested by Neter et al. (1996).

**Does island biogeography or cyclone frequency explain patterns of species diversity, richness and endemism?**

We extended the GDMOIB, which includes both age \( t \) and area \( A \) of an island, to also include isolation \( I \) and cyclone frequency \( C \) as follows: \( \log S = a + bt + cf^2 + d(log A) + eC + fc^2 + gf \). The term added for isolation is linear because we expect diversity to linearly decrease with increased isolation, whereas the term added for cyclone frequency is nonlinear because cyclones can be classified as disturbances and the intermediate disturbance hypothesis (Grime 1973; Connell 1978) predicts a quadratic relationship between diversity and disturbance. We then simplified this model by removing non-significant terms (at the 5% level using a likelihood ratio test to compare the models), using the log of species richness \( S \), log of Fisher’s \( a \) diversity \( (a) \) and the arcsine-transformed proportion of endemic species \( (E) \) as the dependent variables in three different analyses. In addition, we used the Akaike Information Criterion (AIC; Akaike 1974) to test the performance of the various models. We used a second-order AIC to account for our small sample size: \( AIC_c = AIC + 2(K + 1)/(n - K - 1) \), where \( K \) is the number of parameters in the model and \( n \) is the number of sample points (Burnham & Anderson 1998).

**What factors affect the composition of lowland rainforests?**

To investigate how quickly species turn over, we correlated the floristic similarity between sites (as measured by the Bray–Curtis dissimilarity index, \( B \)) with geographic distance. Because of the quick species turnover (Fig. 2) and the high endemism at the species level in some of the study sites (more than 50% for Fijian sites, Table 1), we conducted analyses at the genus level (in addition to the species level). Genera generally have a wider distribution and more stable taxonomy than species (ter Steege et al. 2006). Because we did not have information about the d.b.h. of individual trees for the two data sets obtained from the literature, we restricted this analysis to the 10 original sites.

We used this reduced data set (10 sites) to conduct Kruskal’s non-metric multidimensional scaling (NMDS) based on the Bray–Curtis dissimilarity coefficient \( (B; \) if \( B = 0 \), sites have equal composition; if \( B = 1 \), sites have no species in common). We then correlated the cyclone frequency \( (C) \), distances to New Guinea \( (d_{dSG}) \) and New Caledonia \( (d_{dSC}) \), island area \( (log(A)) \) and archipelago age \( (t) \) to this data set using vector fitting, which allows quantification of the strength of relationships through the correlation coefficient \( r^2 \); Dargie 1984; Kantvilas & Minchin 1989).
Does cyclone frequency affect the structure of lowland rainforests?

We tested whether cyclone frequency (C), isolation (I) or age (t) had an impact on the stem density (log(d)) or basal area (log(b)) of Pacific lowland tropical rainforest. We used a model similar to the previous model by removing insignificant terms (at the 5% level using an ANOVA). We simplified the aforementioned linear term because its effect on forest structure is likely to be linear (de Gouvenain & Silander 2003). We simplified the aforementioned model by removing insignificant terms (at the 5% level using an ANOVA to compare the models).

**Results**

**FACTORS AFFECTING RICHNESS, DIVERSITY AND ENDEMISM**

Patterns of species richness and endemism are depicted in Fig. 1. New Guinea mainland had the highest species richness (135 and 164 species per hectare), but Lauru (131) in the northern Solomon Islands and Savura (on Viti Levu, Fiji’s largest island) have a species richness that was comparable with New Guinea. Stem densities (stems per hectare) differed between the sites (greatest in Savura, followed by Lauru and New Guinea; Table 1). As a result, sites in New Guinea were clearly more diverse (α = 75.78 and 58.54) compared with Lauru (47.81) and Savura (38.86) (Table 1). Islands in the Solomon Islands and Fiji have similar species richness and species diversity, but about half of the diversity on Fiji is composed of species endemic to the Fiji archipelago, while only c. 15% of the species encountered in the Solomon Islands are endemic to that archipelago.

Diversity (Fisher’s α) and species richness were strongly correlated (adjusted $r^2 = 0.993$, $P = 2.1 \times 10^{-7}$). However, neither variable had a significant correlation with endemism when tested separately. Cyclone frequency did not have a significant impact on any of species richness, species diversity or endemism, when included in a model with the other variables (Table 2). The GDMOIB (including both area and time since island emergence) was the best model explaining species richness and species diversity as estimated by Fisher’s α. A model incorporating time since island emergence and isolation ($E = a + bI + ct + dr^2$) best described the observed patterns of endemism.

Model comparison using the AIC corrected for small sample size (AICc) yields results similar to those obtained using stepwise elimination of non-significant terms (Tables 2 and 3). However, a model including island area, archipelago age and isolation performs marginally better in estimating species diversity using AICc than the model including only island area and archipelago age (Table 3), which was determined to be the best using stepwise elimination of non-significant terms. However, because the AICc difference between the two models is small (0.48) and isolation was not significant at the 5% level, we only considered the best model as determined by stepwise elimination of non-significant terms (Table 2).

**FACTORS AFFECTING SPECIES COMPOSITION**

A strong correlation between the log of geographic distance between the islands and the Bray–Curtis dissimilarity index

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>Species richness [log(number of species ha$^{-1}$)]</th>
<th>Diversity [log(Fisher’s α)]</th>
<th>Endemism (arcsine of proportion of endemic species)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F-value</td>
<td>P-value</td>
<td>Coeff.</td>
</tr>
<tr>
<td>log (t)</td>
<td>12.61, 10</td>
<td>0.0075</td>
<td>0.0838</td>
</tr>
<tr>
<td>Age (t)</td>
<td>36.45, 10</td>
<td>0.0003</td>
<td>0.0312</td>
</tr>
<tr>
<td>$r^2$</td>
<td>26.84, 10</td>
<td>0.0008</td>
<td>−0.0002</td>
</tr>
<tr>
<td>Isolation (d)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Cyclone frequency (C)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>$C^2$</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

**Best model**

<table>
<thead>
<tr>
<th></th>
<th>F-value</th>
<th>P-value</th>
<th>Coeff.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>3.1701</td>
<td></td>
<td>1.5724</td>
</tr>
<tr>
<td>Adjusted $r^2$</td>
<td>0.8751</td>
<td></td>
<td>0.8498</td>
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<tr>
<td>F-value</td>
<td>26.68</td>
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<td>21.75</td>
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<tr>
<td>d.f.</td>
<td>3, 8</td>
<td></td>
<td>3, 8</td>
</tr>
<tr>
<td>P-value</td>
<td>0.0002</td>
<td></td>
<td>0.0003</td>
</tr>
</tbody>
</table>

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Table 3. Akaike Information Criterion corrected for small sample size (AICc) values for the various models. Asterisks (*) indicates the best model determined by stepwise elimination of insignificant variables. \( a, b, c, d, e, f \) and \( g \) are constants; \( A \) is the area of the island (km\(^2\)); \( t \) is the age of the archipelago (my); \( C \) is the cyclone frequency (cyclones per year); \( I \) is isolation \([\log{\text{(distance to New Guinea + distance to New Caledonia)}}]\)

<table>
<thead>
<tr>
<th>Model</th>
<th>Species richness ([\log{\text{(number of species ha}^{-1})]})</th>
<th>Diversity ([\log{\text{(Fisher’s ( \alpha )}}})</th>
<th>Endemism (\text{(proportion of endemic species)})</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a + b(\log A) + c + d r^2 + e C + f C^2 + g I )</td>
<td>20.87</td>
<td>27.17</td>
<td>Model not tested</td>
</tr>
<tr>
<td>( a + b(\log A) + c + d r^2 + g I )</td>
<td>3.00</td>
<td>11.98</td>
<td>−3.50</td>
</tr>
<tr>
<td>( a + b(\log A) + c + d r^2 + e C + f C^2 )</td>
<td>8.88</td>
<td>15.11</td>
<td>Model not tested</td>
</tr>
<tr>
<td>( a + b(\log A) + c + d r^2 )</td>
<td>1.79*</td>
<td>12.46*</td>
<td>6.72</td>
</tr>
<tr>
<td>( a + b(\log A) )</td>
<td>14.38</td>
<td>22.69</td>
<td>0.19</td>
</tr>
<tr>
<td>( a + b(\log A) + g I )</td>
<td>13.38</td>
<td>19.85</td>
<td>−0.11</td>
</tr>
<tr>
<td>( a + c + d r^2 + g I )</td>
<td>12.13</td>
<td>19.51</td>
<td>−4.01*</td>
</tr>
</tbody>
</table>

**Fig. 3.** Non-metric multidimensional scaling (NMDS) for 10 study sites at the genus level with fitted vectors for cyclone frequency \( C \), distances to New Guinea \( d_{NG} \) and to New Caledonia \( d_{NC} \), island area \([\log{\text{(area)}}]\) and archipelago age \( t \). Length of vector indicates strength of correlation between vector and NMDS \((r^2 = 0.1272; P = 0.6532; C: r^2 = 0.7145; P = 0.0053; d_{NC}: r^2 = 0.2557; P = 0.3536; d_{GC}: r^2 = 0.6431; P = 0.0114; I: r^2 = 0.8653, P = 0.0001)\). ERR, Erromango; GAU, Gau; HAL, Halowia; KOL, Kolombangara; KUB, Kubaluu; LAU, Lauru/Choiseul; SAV, Savura; TET, Tetepare; TIA, Tiavea.

was detected, showing that floristic similarity declines with distance. Bray–Curtis dissimilarity \( B \) exceeds 0.9 at a distance of c. 1000 km (Fig. 2), indicating that very few species have ranges that extend over this distance. NMDS based on genus-level data (results of the species-level analysis are available upon request from the authors) shows that geographically close sites cluster together (Fig. 3). The importance of isolation (geographic distance) is supported by the significant role of distance from New Guinea \( d_{GC} \; (P = 0.0114; \text{Fig. 3}); \) when it is fitted as a vector onto the NMDS plot. The vectors for archipelago age \( t \); \( P = 0.0001 \) and cyclone frequency \( C \); \( P = 0.0053 \) were also significant.

**FACTORS AFFECTING FOREST STRUCTURE**

Only cyclone frequency \( C \) was a significant predictor of total stem density per site (adjusted \( R^2 = 0.5462; \text{d.f.} = 1, 10; F = 12.04; P = 0.0060; \text{intercept} = 6.3218; \text{slope} = 0.6426 \)). None of the predictor variables included in the model to explain variations in basal area \( b \) were significant.

**Discussion**

Biogeographical factors such as island size and age appear to be the main correlates of species diversity, and we speculate that they are also drivers of species diversity. No significant relationship between cyclone frequency and diversity was detected, although our samples included a wide range of cyclone frequencies (almost zero on Tetepare, Solomon Islands, to almost one per year on Erromango, Vanuatu), suggesting that cyclone frequency has little long-term impact on species diversity. However, cyclones may temporarily increase the diversity of samples by creating gaps that facilitate establishment of pioneer species that were previously not present within the sample (Burslem, Whitmore & Brown 2000; Van der Meer et al. 2000; Tanner & Bellingham 2006).

The GDMOIB (Whittaker, Triantis & Ladle 2008), which includes age \( t \) and area \( A \) of an island, is the best model for explaining our data on species richness and diversity as determined using model simplification and a critical value of \( P < 0.05 \). Because the area \( A \) of an island is a significant component of the best models for species richness and species diversity, the TIB model (MacArthur & Wilson 1967) is also a reasonable model for our data. However, the addition of archipelago age \( t \) to the model, as in the GDMOIB, greatly improves the model. This supports the calls that the TIB model is too simplistic (Lomolino 2000; Lomolino & Weiser 2001; Badano et al. 2005).
The roles of island or archipelago age and the GDMOIB in island biogeographical theory need to be further investigated. Although the GDMOIB mostly provides a good fit for observed biogeographical data (Whittaker, Triantis & Ladle 2008), the mechanisms responsible for this explanatory power are less clear. Although it is true that any oceanic island will have no species when it emerges, experiences a steady increase in the number of species and eventually begins to lose species until it has no species on submergence, it is doubtful that the quadratic relationship between island age and species diversity adequately describes this. This is especially true for the geologically and tectonically complex islands of the TSP, which are likely to have experienced increases and decreases in area several times through their geological history (Neall & Trewick 2008). Another confounding factor is that, according to the GDMOIB, island age should be correlated with island area.

Biogeographical factors are also the major drivers of endemism. Our results support the role of island age in determining the levels of endemism and suggest that the role of isolation has been neglected in the recent discussion on the forces driving endemism (Cadena et al. 2005; Whittaker et al. 2007; Gruner et al. 2008). A correlation between isolation and endemism in the Pacific has been previously reported for isolated islands (Gillespie, Claridge & Roderick 2008). Islands in the Fiji archipelago have by far the highest endemism, although endemism of the New Guinean plots is probably underestimated because of problems in the identification of tropical trees in highly diverse forests (Table 1; Wilkie et al. 2004).

Because there is no correlation between species diversity and endemism, our results do not support the assertion that diversity drives endemism (Emerson & Kolm 2005). This is possibly because of the opposing effects of isolation on species diversity and endemism. While isolation is positively correlated with endemism (Table 3), it is expected to have a negative correlation with species diversity (MacArthur & Wilson 1967). Therefore, a positive relationship between species diversity and endemism is unlikely to exist, if the effect of isolation is strong.

Biogeographical variables also have a strong affect on species composition. As expected the distance from the most likely source area, New Guinea, correlates significantly with the distribution of study sites based on the total basal area of genera, as represented by an NMDS plot (Fig. 3). Similarly, the age of an archipelago appears to affect species composition. The importance of age and isolation in determining species composition can be explained by the fact that different plant genera have different dispersal abilities (Carlbquist 1966). Efficient dispersers would colonize islands before less-efficient dispersers, whereas poor dispersers may never colonize isolated islands.

In addition to biogeographical factors acting through dispersal limitation, our data suggest that cyclones affect the composition of lowland rain forests in the TSP. The effect of cyclones is likely caused by interspecific (and intergeneric) differences in cyclone resistance, as species have varying susceptibility to cyclone damage (Elmqvist et al. 1994; Burslem, Whitmore & Brown 2000). Higher wood density and smaller leaf size generally seem to confer resistance to cyclone damage (Curran et al. 2008), although species with high wood densities may still suffer high cyclone mortalities (Burslem, Whitmore & Brown 2000). In any case, our results suggest that higher cyclone resistance may confer a competitive advantage in rain forests that are frequently impacted by cyclones.

Therefore, ecological differences between species (and genera) seemingly have an important influence on the composition of rain forest communities in the TSP, showing that species are not ecologically equivalent, as proposed by the unified neutral theory of biodiversity (Hubbell 2001), and that deterministic factors play an important role in community assembly. However, our results further suggest that these interspecific ecological differences are unimportant when species diversity patterns of similar communities are considered. This implies that the assumption of ecological equivalence of species may be permissible at the community level and that neutral processes are the major factors driving species diversity patterns at this level.

Our study corroborates previous findings of forests affected by cyclones having higher stem densities and shorter canopies (although not precisely measured). The forests in Fiji and Vanuatu with 754–916 stems per hectare are among the densest for any rain forests in the world (de Gouvenain & Silander 2003). The general nature of these forests is probably the result of defoliation and tree mortality increasing the amount of solar radiation reaching the forest floor (Bellingham et al. 1996; Hjerpe, Hedenäs & Elmqvist 2001), which enhances regeneration. The repeated and frequent occurrence of cyclones may therefore result in the continuous existence of non-climax vegetation. Such vegetation, characterized by shorter canopies and higher stem densities, has also been reported from Australia (Webb 1958), the Caribbean (Brokaw & Grear 1991; Basnet et al. 1992) and Madagascar (de Gouvenain & Silander 2003).

Although patterns of species diversity were mostly driven by biogeographical factors, disturbance in the form of cyclones must be considered as a major driver of species composition and forest structure in lowland rain forests of the TSP. Cyclones therefore, contrary to earlier assumptions (Brokaw & Walker 1991; Burslem, Whitmore & Brown 2000), have a long-lasting impact on forest structure and composition and are likely to be major drivers of ecological processes and natural selection. Therefore, the predicted changes in cyclone activity (Goldenberg et al. 2001; Donnelly & Woodruff 2007) and increase in cyclone intensity (Emanuel 2005) will permanently alter ecological and natural selection processes in affected forest ecosystems.

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