



# Diversity of palm communities at different spatial scales in a recently fragmented tropical landscape

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Habitat loss and landscape fragmentation are often associated with changes in biological communities at different spatial scales. Our goal in this study was to identify fragment characteristics and environmental variables linked to palm species richness, abundance and community similarity at local and landscape spatial scales and to contrast these patterns between adults and juveniles. We sampled palm communities in 22 fragments of Chocó rainforest in and around the Mache-Chindul Ecological Reserve in north-western Ecuador, where we recorded 9991 individuals of 23 palm species. At the landscape scale, fragment size and surrounding forest cover were not associated with species richness or abundance for either adults or juveniles. However, community similarity of juveniles was related to surrounding forest cover and the abundance of juveniles and adults increased with elevation. At the local scale, adults and juveniles differed in their relationships to environmental variables and distance to fragment edge: juveniles showed reduced species richness and different community composition near fragment edges compared with interior habitat, but adults did not. These results provide baseline information on palm communities in a poorly studied conservation hotspot and highlight the importance of considering multiple spatial scales and life stages in studies of habitat fragmentation. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, **182**, 451–464

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## INTRODUCTION

Habitat loss and fragmentation are serious threats to global biodiversity, especially in the Tropics (Gardner *et al.*, 2009; Hansen *et al.*, 2013). As formerly continuous forest is reduced to smaller, isolated patches, associated ecological and environmental changes may influence the diversity and composition of organisms that survive the initial wave of deforestation (Saunders, Hobbs & Margules, 1991). Characteristics of remaining forest fragments and the surrounding landscape, for example fragment size and degree of isolation, are thought to influence the number of species a fragment can support, a notion based largely on the theory of island biogeography (MacArthur & Wilson, 1967). Many studies have shown the predicted relationships between fragment characteristics and species richness, with smaller

and more isolated fragments harbouring lower species diversity (Fahrig, 2003; Prugh *et al.*, 2008). However, island biogeography theory does not explicitly address the effects of fragmentation on community composition, a crucial metric of biodiversity, or address effects at local spatial scales, such as edge effects (Laurance, 2008). For this reason, integrating analyses across spatial scales and incorporating biodiversity parameters other than species richness are active goals for scientists seeking to understand and manage biodiversity in fragmented landscapes.

Habitat loss and fragmentation operate at multiple spatial scales. At the landscape scale (1–200 km in extent, following Eiserhardt *et al.*, 2011), habitat loss and fragmentation reduce the total amount of available habitat and isolate remaining habitat, which immediately reduces population sizes and may impede population connectivity, thereby increasing probabilities of local extinction (Saunders *et al.*, 1991; Young, Boyle & Brown, 1996). Deforestation

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can also affect biotic conditions such as hydrology and temperature, which shape environmental niches across the landscape (Saunders *et al.*, 1991; Laurance *et al.*, 2011). At the local scale (< 1 km), edge effects are pervasive and diverse and are among the leading drivers of changes in biological communities in forest fragments (Laurance *et al.*, 2011). Increased tree mortality (Laurance *et al.*, 2000), increased air temperature and reduced humidity (Kapos, 1989; Magnago *et al.*, 2015), among many other effects, can lead to changes in communities at small spatial scales (Yahner, 1988; Gehlhausen, Schwartz & Augspurger, 2000). Identifying the scales at which biological communities vary and the environmental variables linked to this variation in fragmented landscapes will help achieve a holistic understanding of how habitat loss and fragmentation lead to changes in biodiversity.

Not all taxa are equally represented in the literature on habitat fragmentation, leading to a scarcity of information on how some economically and ecologically important groups respond to habitat loss and fragmentation. Palms (Arecaceae), which are among the most abundant and important floristic elements of tropical rain forests (Dransfield *et al.*, 2008), are a case in point. Of the ten most abundant tree species in the Amazon, more than half are palms (Ter Steege *et al.*, 2013). Palms are also widely utilized by humans, with thousands of distinct uses documented in north-western South America alone (Macía *et al.*, 2011). There have been several studies focusing on ecology and evolution of individual palm species in fragmented landscapes, including: demography and growth (e.g. Galetti *et al.*, 2006; Arroyo-Rodríguez *et al.*, 2007; Brum *et al.*, 2008), pollination ecology (e.g. Aguirre & Dirzo, 2008), seed predation and dispersal (e.g. Wright & Duber, 2001; Andreazzi *et al.*, 2012; Zucaratto & dos Santos Pires, 2015), and changes in genetic diversity and structure (e.g. Browne, Ottewell & Karubian, 2015; da Silva Carvalho *et al.*, 2015). However, there has been relatively little research on how palm species respond to habitat loss and fragmentation at the community level. Studies of palm communities in fragmented landscapes suggest that life stages may be differentially affected by habitat fragmentation (Scariot, 1999; Baez & Balslev, 2007; Wang, 2008), but no clear patterns have emerged for this ecologically and economically important group.

Here, we report on palm community diversity in a recently fragmented landscape in north-western Ecuador. Because habitat loss and fragmentation in our study area are relatively recent (beginning 30–40 years ago), it is likely that some adults, especially long-lived canopy palms, would have been established prior to fragmentation, whereas most juveniles

would have been established following fragmentation, potentially leaving them more susceptible to fragmentation effects. Our goals were to: (1) identify environmental variables linked to palm abundance, species richness and community composition at local and landscape scales; and (2) contrast these patterns for adult and juvenile palms. Our working hypothesis was that habitat loss and deforestation would influence diversity at both the landscape and the local scales. Specifically, we predicted that at the landscape scale, fragment size and amount of forest cover surrounding each fragment would be correlated with palm abundance, richness and composition after controlling for differences in elevation. At the local scale, we predicted that distance to the fragment edge would also influence abundance, richness and composition. Due to the relatively recent nature of habitat loss in the study area, we further predicted that juveniles and adults would vary in their relationship to fragmentation-related variables.

## MATERIAL AND METHODS

### STUDY REGION

We sampled palm communities in and around the Mache-Chindul Ecological Reserve (REMACH), Esmeraldas Province, Ecuador, from August to December 2014. We sampled 22 forest fragments along an unpaved road that leads from a main highway to Bilsa Biological Station, one of the most pristine portions of REMACH. This sampling scheme covered a gradient in elevation, precipitation and human disturbance (Fig. 1, Supporting Information, Table S1). The study region covers an area of ca. 75 km<sup>2</sup>, ranges from 250 to 600 m in elevation and receives approximately 2500–3500 mm of rainfall annually (Clark, Neill & Asanza, 2006). In this area agricultural expansion began 30–40 years ago led to extensive deforestation, creating many isolated forest fragments that are surrounded by a matrix of pasture, African oil palm, cacao and other agricultural crops. Less than 5% of the original forest cover remains in western Ecuador (Dodson & Gentry, 1991). Palm species diversity in western Ecuador is generally lower than for the Amazon basin (Borchsenius, 1997), but the Chocó forests are among the most biodiverse and threatened habitats with high rates of endemism (Dodson & Gentry, 1991; Myers *et al.*, 2000; Brooks *et al.*, 2002). The 22 fragments we sampled were selected to minimize any correlation between elevation and fragment size. We chose fragments that contained mostly primary forest, although some fragments did contain portions of selectively logged or regenerating forest. We cannot rule out potential effects of historical harvesting of

palms in study fragments, but we did not observe any contemporary logging or extraction of palm products in the study fragments during the study period. We were also unable to obtain information on the exact time when fragments became isolated. In some cases, fragments were already present when current landowners purchased the land and precise circumstances of fragment formation remain unknown. Due to persistence of cloud cover and low image resolution, there is no available time series of remotely sensed images that could serve to reconstruct the history of each fragment.

#### PALM TRANSECT SAMPLING

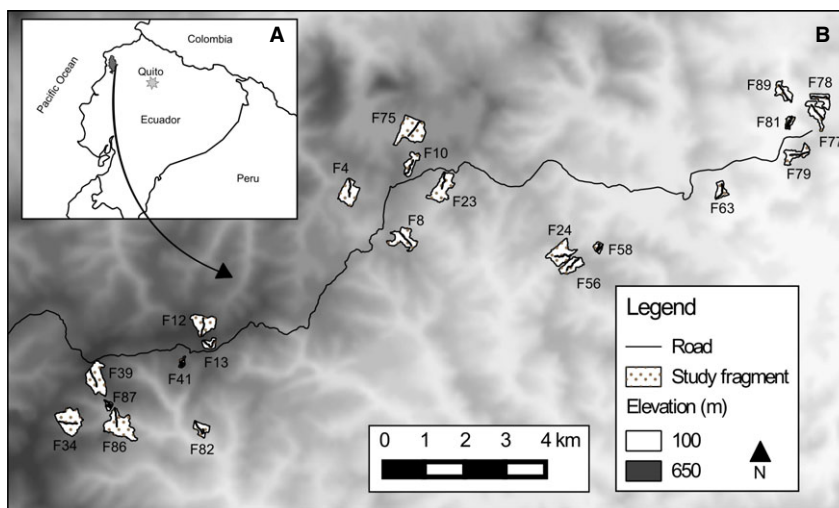
To sample palm communities, we established a  $5 \times 500$ -m transect in each of the 22 forest fragments (Fig. 1). We followed the sampling protocol of Balslev *et al.* (2010), with slight modifications. Transects were started at the edge of the forest fragment and continued inward towards the centre, allowing us to sample both edge and core habitats. For smaller fragments where a straight 500-m transect would not fit, we either split the transect into parallel lines separated by at least 50 m, or reflected the transect line back towards the core area of the fragment upon reaching the opposite edge (Fig. 1). In all cases, the total length of each transect was 500 m and sampling effort (0.25 ha) was equal across fragments.

In each fragment, one observer (L.B.) recorded all individuals of any palm species falling within the transect sampling area, dividing the  $5 \times 500$ -m tran-

sect into 100 separate  $5 \times 5$ -m subunits (Balslev *et al.*, 2010). We classified each individual into one of four age categories: seedlings (leaves undivided), juveniles (leaves divided, no signs of reproduction), subadults (no signs of reproduction, but near size of reproductive adult) and adults (signs of current or past reproduction; Balslev *et al.*, 2010). For clonal species [e.g. species of *Bactris* Jacq., *Prestoea decurrens* (H.Wendl. ex Burret) H.E.Moore], we counted each ramet as an individual (Balslev *et al.*, 2010). Species were identified following Borchsenius, Pedersen & Balslev (1998), comparison with herbarium specimens (QCA) and knowledge of local residents of REMACH. For *Geonoma cuneata* H.Wendl. ex Spruce, individuals were placed into varieties based on the classification of Borchsenius (1999), who found that at the local scale in western Ecuador, varieties of *G. cuneata* could be reliably distinguished based on morphology. For the purposes of this study, we refer to these varieties as species.

#### FRAGMENT CHARACTERISTICS AND ENVIRONMENTAL VARIABLES

We characterized the habitat of each  $5 \times 5$ -m subunit in each transect. We recorded elevation using a handheld GPS and degree of slope along the steepest gradient in the subunit using a clinometer. We estimated canopy openness (an index of light availability) following the methods of Brown *et al.* (2000) and canopy height of the tallest tree over the centre of each subunit using a digital rangefinder. We mapped



**Figure 1.** Map with (A) location the Mache-Chindul Ecological Reserve (grey fill) in Ecuador and (B) the boundaries of the 22 forest fragments sampled for this study, with black lines within fragment boundaries indicating location of  $5 \times 500$ -m transects. Higher elevations are shaded dark grey and lower elevations are white. Characteristics of each fragment are described in Supporting Information (Table S1). Additionally, unsampled fragments occur in the study area but are not included on this map.

fragment boundaries by walking the edge of the fragment with a handheld GPS and used QGIS (QGIS Development Team, 2012) to calculate the area of each fragment. For each subunit we estimated the distance to the edge of the forest fragment by calculating the shortest distance between the centre of each subunit and the nearest fragment edge in QGIS.

We quantified the amount of forest cover and loss in our study area using the Global Forest Change dataset (Hansen *et al.*, 2013). No other comparable set of remote sensing data on forest cover is publicly available for the Mache-Chindul region due to its persistent cloud cover. The Global Forest Change dataset has been criticized for underestimating forest loss and overestimating forest cover by classifying crops such as oil palm as forest (Tropek *et al.*, 2014), which may limit its utility in describing local-scale forest dynamics. To evaluate the degree to which this potential bias may apply to our study area, we compared the Global Forest Change dataset with areas of known land-use type. We confirmed that areas cleared for agriculture 3–5 years ago generally showed up as forest loss and that habitat surrounding fragment boundaries were properly classified as forest or non-forest. Based on these field-based truthing steps, we concluded that the Global Forest Change dataset adequately described fragmentation patterns in our study area and we retained this metric for subsequent analysis. To estimate forest cover and loss, we classified each  $30 \times 30$ -m grid cell across our study area as either forest or non-forest based on whether the estimated proportion of tree canopy cover in 2000 was  $> 95\%$ . We then overlaid data on forest loss for the period 2000–2013, converting each grid cell that was classified as forest in 2000 to non-forest if that forest was altered in the following period. In this way, we were able to obtain a suitable contemporary map of forest cover and forest loss for the region, which we then used to calculate the percentage forest cover in a 1-km radius around the centre point of each fragment. The percentage of forest cover in radii ranging from 500 to 2500 m around each fragment was strongly correlated with forest cover in a 1-km radius ( $R > 0.83$ ,  $P < 0.001$  for all comparisons), so we only present results using a 1-km radius.

#### DATA ANALYSIS

We conducted analyses of palm abundance, species richness and community composition at two spatial scales: landscape and local. At the landscape scale, we used each forest fragment as a sampling unit. We combined data across the entire  $5 \times 500$ -m transect in each fragment and used elevation (m), percentage

forest cover in a 1-km radius and fragment size (ha) as predictor variables. At the local scale, we conducted analyses separately for each transect, treating each  $5 \times 5$ -m subplot as an independent sampling unit and used elevation (m), canopy height (m), canopy openness (scale of 1–25), distance to fragment edge (m) and degree of slope as predictor variables. We conducted each set of analyses separately for ‘adults’, which included adults and subadults pooled together, and ‘juveniles’, which included juveniles and seedlings, following Baez & Balslev (2007). We also performed analyses on seedlings and juveniles separately and found that seedlings and juveniles follow generally consistent trends, although seedlings show stronger responses to ‘distance to edge’ and ‘slope’ in terms of species richness and community composition (Supporting Information, Tables S2–S5). Abundances of juveniles and seedlings in each fragment are presented separately in the Supporting Information (Tables S6, S7).

We modelled species richness and abundance at the landscape and local scales with generalized linear models, using a Poisson and negative binomial distribution, respectively (O’Hara & Kotze, 2010). Because species richness is based on count data, it is often adequately modelled by the Poisson distribution (O’Hara & Kotze, 2010). Abundance data are often over-dispersed and best modelled with the negative binomial distribution (O’Hara & Kotze, 2010). At the local scale, we conducted each regression on each transect separately ( $N = 22$ ), and then assessed whether mean values of the estimated coefficients were different from 0 with a one-sample *t*-test (cf. Normand *et al.*, 2006). We were also interested in variance around the mean estimated coefficients, which would indicate the degree of variation between fragments in local-scale patterns. We quantified this variance using standard deviation. We tested for spatial autocorrelation at the local scale with Mantel tests ( $N = 999$  permutations), assessing the degree of correlation between the geographical distance matrix and the distance matrix of the residuals of each regression model. We performed the one-sample *t*-tests again, excluding transects with significant levels of spatial autocorrelation in model residuals ( $P < 0.05$ ), to test whether our results were robust to the influence of spatial autocorrelation.

To measure community composition at landscape and local scales, we used the Steinhaus coefficient of community similarity, calculated from  $\log + 1$ -transformed abundance data. At the local scale,  $5 \times 5$ -m subunits that contained no palms were removed from the community similarity analyses. To test how community similarity matrices were related to environmental and geographical factors, we used multiple regression on distance matrices, assessing

significance via permutation ( $N = 999$ ; Legendre, Lapointe & Casgrain, 1994; Lichstein, 2007). Environmental distance matrices were calculated using Euclidian distances. We used log-transformed geographical distance to test if community similarity decayed with geographical distance, as dispersal limitation is expected based on neutral models to lead to a linear decay in community similarity on a log-scale of geographical distance (Condit *et al.*, 2002). To assess the relative explanatory power of geographical versus environmental distances, we used a variance partitioning approach (Borcard, Legendre & Drapeau, 1992; Vormisto, Tuomisto & Oksanen, 2004; Normand *et al.*, 2006), which separates the amount of variation ( $R^2$ ) in community similarity contributed by pure environmental factors, pure geographical factors and geographically structured environmental factors. At the local scale, we conducted separate analyses for each transect and assessed whether mean  $R^2$  values and coefficient estimates were different from 0 with a one-sample  $t$ -test (cf. Normand *et al.*, 2006).

All data analyses were performed in R v.3.20 (R Core Development Team, 2015). We centred and scaled predictor variables prior to analyses by subtracting mean values and dividing by one standard deviation (Schielzeth, 2010). Similarity and distance matrices were calculated in the 'vegan' package (Oksanen *et al.*, 2013) and multiple regression on distance matrices analyses were performed with the 'ecodist' package (Goslee & Urban, 2007).

## RESULTS

### SUMMARY OF PALM COMMUNITIES

Across all 22 fragments, including adults and juveniles, we recorded 9991 individuals of 23 palm species. After excluding unidentified individuals ( $N = 22$ ), we found on average  $453.1 \pm 5.6$  (SD) individuals per transect (range: 116–904) and  $12.1 \pm 1.8$  species per transect (range: 10–16; Table 1). Only three species were found in all fragments: *Iriartea deltoidea* Ruiz & Pav., *Socratea exorrhiza* (Mart.) H.Wendl. and *Synechanthus warscewiczianus* H.Wendl. (Table 1). For adults ( $N = 1833$  total), the four most abundant species, which together account for 55% of all individuals, are: *I. deltoidea* (16%), *Geonoma cuneata* var. *gracilis* (H.Wendl. ex Spruce) Skov ex Govaerts & J.Dransf. (14%), *Prestoea decurrens* (13%) and *Geonoma cuneata* var. *cuneata* (13%; Supporting Information, Table S8). For juveniles ( $N = 8136$  in total), the four most abundant species, which together accounted for 58% of all individuals, were: *Socratea exorrhiza* (19%), *Prestoea decurrens* (15%), *Iriartea deltoidea* (14%) and *Phytelephas*

*aequatorialis* Spruce (10%) (Supporting Information, Table S9).

### LANDSCAPE SCALE ABUNDANCE, RICHNESS AND COMMUNITY COMPOSITION

At the landscape scale, abundance of adults and juveniles increased with elevation, but was not significantly related to percentage of surrounding forest cover or fragment size (Table 2). Species richness of adults and juveniles was not significantly related to elevation, forest cover or fragment size (Table 2).

Community similarity of adults and juveniles was related to elevation, indicating that fragments at different elevations harboured different adult and juvenile palm communities (Table 3). Forest cover was also related to community similarity for both adults and juveniles, even after controlling for elevational differences (Table 3). Fragment size was not significantly related to community similarity of either adults or juvenile palms (Table 3).

Community similarity decreased significantly with log-transformed geographical distance, with adults and juveniles showing similar rates of decrease (Table 3). The variance partitioning analysis showed that geographically structured environmental variables accounted for most of the explained variation, with little variation explained by pure geographical effects, and a moderate amount of variation explained by pure environmental effects (Table 3).

### LOCAL SCALE RICHNESS, ABUNDANCE AND COMMUNITY COMPOSITION

At the local scale, adults and juveniles varied in their relationship with environmental factors (Table 4). There was also marked variation from fragment to fragment in these relationships (Table 4). Generally, adult abundance increased with canopy height, while juvenile abundance decreased with canopy openness and slope (Table 4). Adult species richness increased with canopy height, while juvenile species richness increased with elevation and distance to the forest edge and decreased with canopy openness and slope (Table 4). Excluding transects that showed significant patterns of spatial autocorrelation (range 1–5 transects excluded) did not substantially change coefficient estimates, although the relationships between adult abundance and canopy height, and between juvenile species richness and elevation, distance to the forest edge and slope were no longer statistically significant (Supporting Information, Table S10).

Community similarity of adults and juveniles at the local scale was consistently associated with

**Table 1.** Number of individuals (including adults, sub-adults, juveniles and seedlings) of 23 palm species recorded in 22 forest fragments in the Mache Chindul Reserve, north-western Ecuador

| Species  | Site |     |     |     |     |     |     |    |     |     |     |    |     |     |     |     |     |     |     |     |     |     | Occu-<br>pancy |
|--|------|-----|-----|-----|-----|-----|-----|----|-----|-----|-----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----------------|
|  | F81  | F78 | F77 | F89 | F63 | F58 | F79 | F8 | F56 | F24 | F23 | F4 | F10 | F82 | F75 | F86 | F12 | F87 | F13 | F41 | F34 | F39 |                |
| <i>Aiphanes tricuspidata</i><br>Borchs., M.Ruíz &<br>Bernal  | 0    | 0   | 0   | 0   | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 4  | 0   | 7   | 0   | 2   | 3   | 8   | 11  | 8   | 0   | 5   | 8              |
| <i>Astrocaryum standleyanum</i><br>L.H.Bailey  | 19   | 13  | 4   | 1   | 19  | 9   | 6   | 0  | 30  | 0   | 16  | 0  | 3   | 12  | 0   | 16  | 0   | 0   | 0   | 0   | 0   | 0   | 12             |
| <i>Attalea colenda</i><br>(O.F.Cook) Balslev &<br>A.J.Hend.  | 4    | 1   | 79  | 4   | 30  | 6   | 50  | 1  | 0   | 0   | 0   | 0  | 1   | 31  | 6   | 7   | 0   | 0   | 0   | 0   | 0   | 0   | 12             |
| <i>Bactris coloradonis</i><br>L.H.Bailey   | 48   | 0   | 0   | 0   | 0   | 24  | 0   | 19 | 4   | 1   | 27  | 0  | 19  | 67  | 26  | 2   | 6   | 0   | 7   | 0   | 0   | 0   | 12             |
| <i>Bactris gasipaes</i> Kunth  | 5    | 15  | 0   | 2   | 0   | 0   | 3   | 0  | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 0   | 0   | 1   | 0   | 0   | 0   | 0   | 5              |
| <i>Bactris setulosa</i><br>H.Karst.  | 0    | 1   | 11  | 5   | 2   | 0   | 10  | 11 | 6   | 29  | 10  | 22 | 2   | 1   | 12  | 1   | 6   | 23  | 7   | 10  | 16  | 20  | 20             |
| <i>Chamaedorea linearis</i><br>(Ruiz & Pav.) Mart.   | 117  | 0   | 0   | 0   | 140 | 74  | 0   | 0  | 49  | 47  | 0   | 0  | 0   | 1   | 0   | 0   | 0   | 0   | 0   | 2   | 0   | 0   | 7              |
| <i>Chamaedorea pinnatifrons</i> (Jacq.)<br>Oerst.  | 0    | 0   | 0   | 0   | 0   | 0   | 0   | 7  | 5   | 7   | 10  | 15 | 14  | 0   | 3   | 5   | 8   | 7   | 24  | 34  | 1   | 0   | 13             |
| <i>Desmoncus cirrhifer</i><br>A.H.Gentry &<br>Zardini  | 0    | 0   | 0   | 0   | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 2   | 8   | 0   | 2   | 0   | 2   | 0   | 4              |
| <i>Geonoma cuneata</i><br>H.Wendl. ex Spruce<br>var. <i>cuneata</i>                                    | 0    | 0   | 74  | 3   | 8   | 0   | 62  | 0  | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 26  | 22  | 52  | 11  | 29  | 81  | 137 | 11             |
| <i>Geonoma cuneata</i> var.<br><i>gracilis</i> (H.Wendl. ex<br>Spruce) Skov ex<br>Govaerts & J.Dransf. | 0    | 0   | 0   | 0   | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 36  | 84  | 112 | 188 | 85  | 3   | 49  | 7              |
| <i>Geonoma cuneata</i> var.<br><i>irena</i> (Borchs.)<br>A.J.Hend.                                     | 1    | 0   | 0   | 0   | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 1              |
| <i>Geonoma cuneata</i> var.<br><i>sodiroi</i> (Dammer ex<br>Burret) A.J.Hend.                          | 0    | 0   | 0   | 0   | 0   | 9   | 0   | 5  | 28  | 14  | 7   | 74 | 21  | 24  | 44  | 37  | 31  | 6   | 12  | 17  | 0   | 0   | 14             |

Table 1. Continued

| Species  | Site |     |     |     |     |     |     |    |     |     |     |     |     |     |     |     |     | Occupancy |     |     |     |     |     |
|--|------|-----|-----|-----|-----|-----|-----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----------|-----|-----|-----|-----|-----|
|  | F81  | F78 | F77 | F89 | F63 | F58 | F79 | F8 | F56 | F24 | F23 | F4  | F10 | F82 | F75 | F86 | F12 |           | F87 | F13 | F41 | F34 | F39 |
| <i>Iriartea deltoidea</i> Ruiz & Pav.                | 9    | 8   | 45  | 35  | 15  | 41  | 23  | 36 | 64  | 60  | 95  | 148 | 95  | 34  | 225 | 49  | 147 | 41        | 51  | 44  | 129 | 41  | 22  |
| <i>Oenocarpus bataua</i> Mart.                       | 1    | 11  | 16  | 1   | 1   | 0   | 11  | 1  | 0   | 3   | 9   | 14  | 36  | 24  | 8   | 11  | 27  | 12        | 10  | 72  | 13  | 6   | 20  |
| <i>Pholidostachys dactyloides</i> H.E.Moore          | 0    | 0   | 0   | 0   | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 3   | 0         | 9   | 0   | 40  | 36  | 4   |
| <i>Pholidostachys synanthera</i> (Mart.) H.E.Moore   | 9    | 25  | 15  | 13  | 7   | 14  | 16  | 0  | 28  | 3   | 3   | 0   | 13  | 0   | 15  | 0   | 0   | 0         | 0   | 0   | 0   | 0   | 12  |
| <i>Phytelephas aequatorialis</i> Spruce              | 56   | 39  | 9   | 81  | 9   | 77  | 36  | 17 | 51  | 112 | 35  | 45  | 50  | 107 | 3   | 74  | 3   | 0         | 0   | 0   | 3   | 0   | 18  |
| <i>Prestoea decurrens</i> H.E.Moore                  | 0    | 0   | 18  | 0   | 0   | 0   | 11  | 6  | 0   | 0   | 186 | 47  | 84  | 0   | 122 | 23  | 116 | 255       | 225 | 101 | 208 | 69  | 14  |
| <i>Prestoea ensiformis</i> (Ruiz & Pav.) H.E.Moore   | 0    | 0   | 0   | 0   | 0   | 0   | 0   | 0  | 3   | 0   | 0   | 0   | 0   | 28  | 0   | 0   | 0   | 0         | 0   | 0   | 0   | 0   | 2   |
| <i>Socratea exorrhiza</i> (Mart.) H.Wendl.           | 5    | 27  | 543 | 1   | 16  | 28  | 262 | 5  | 48  | 56  | 32  | 96  | 34  | 28  | 24  | 43  | 59  | 24        | 41  | 67  | 107 | 61  | 22  |
| <i>Synechanthus warszewiczianus</i> H.Wendl.         | 35   | 3   | 90  | 4   | 31  | 44  | 86  | 8  | 12  | 56  | 122 | 18  | 72  | 11  | 34  | 14  | 6   | 29        | 16  | 14  | 15  | 3   | 22  |
| <i>Wettinia aequalis</i> (O.F.Cook & Doyle) R.Bernal | 0    | 0   | 0   | 0   | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 79  | 102       | 198 | 107 | 0   | 0   | 4   |

Fragments are ordered left to right from lowest to highest elevation. The last column (Occupancy) is the total number of fragments in which the species was found. Details on the size, elevation and location of each fragment can be found in Supporting Information (Table S1).

**Table 2.** Standardized regression coefficients  $\pm$  SE for landscape-scale adult and juvenile palm abundance and species richness

|               | Adult abundance                        | Juvenile abundance                     | Adult species richness                 | Juvenile species richness              |
|---------------|--|--|--|--|
| Intercept     | <b>4.312 <math>\pm</math> 0.096***</b> | <b>5.894 <math>\pm</math> 0.091***</b> | <b>2.179 <math>\pm</math> 0.072***</b> | <b>2.466 <math>\pm</math> 0.062***</b> |
| Elevation     | <b>0.461 <math>\pm</math> 0.111***</b> | <b>0.227 <math>\pm</math> 0.106*</b>   | 0.142 $\pm$ 0.080                      | 0.088 $\pm$ 0.071                      |
| Forest cover  | 0.083 $\pm$ 0.137                      | -0.138 $\pm$ 0.130                     | 0.071 $\pm$ 0.104                      | -0.007 $\pm$ 0.090                     |
| Fragment size | -0.043 $\pm$ 0.125                     | 0.042 $\pm$ 0.120                      | -0.093 $\pm$ 0.090                     | -0.009 $\pm$ 0.080                     |

Abundance was modelled with a negative binomial regression, and species richness was modelled with a Poisson regression. Statistically significant values of regression coefficients are in bold type.

\* $P < 0.05$ ; \*\*\* $P < 0.001$ .

**Table 3.** Landscape-level community similarity standardized regression coefficients for adults and juveniles estimated with multiple regression on distance matrices for pure environmental and pure geographical models, along with results of a variance partitioning analysis

|   | Adults           | Juveniles        |
|---|------------------|------------------|
| Environmental model                     |                  |                  |
| Intercept                               | <b>0.597***</b>  | <b>0.708***</b>  |
| Elevation                               | <b>-0.117***</b> | <b>-0.121***</b> |
| Forest cover                            | <b>-0.045***</b> | <b>-0.019*</b>   |
| Fragment size                           | 0.032            | 0.013            |
| Geographical model                      |                  |                  |
| Intercept                               | <b>0.633***</b>  | <b>0.739***</b>  |
| Geographical distance                   | <b>-0.202***</b> | <b>-0.194***</b> |
| Variance explained                      |                  |                  |
| $R^2$ – pure environmental              | 0.154            | 0.225            |
| $R^2$ – pure geographical               | 0.0001           | 0.0009           |
| $R^2$ – environmental<br>+ geographical | 0.213            | 0.319            |
| $R^2$ – total                           | 0.367            | 0.545            |
| $R^2$ – unexplained                     | 0.632            | 0.455            |

Geographical distance is log transformed. Statistically significant values of regression coefficients based on  $N = 999$  permutations are in bold type (\* $P < 0.05$ ; \*\*\* $P = 0.001$ ).

differences in elevation (Table 5). For juveniles, community similarity was also significantly related to distance to the fragment edge and slope (Table 5). Overall, environmental variables explained a small but statistically significant amount of variation in community similarity at the local scale (~4%, Table 5).

Community similarity at the local scale decayed with log-transformed geographical distance for both adults and juveniles, although this explained about half as much variation in community similarity compared with environmental variables (Table 5). Variance partitioning revealed that most of the

explainable variation in community similarity at the local scale was due to pure environmental factors, rather than pure geographical factors or geographically structured environmental factors (Table 5).

## DISCUSSION

Contrary to our predictions, at the landscape scale abundance and species richness of adult and juvenile palms were not correlated with either fragment size or amount of surrounding forest cover. However, community composition of adult and juvenile palms was linked to the amount of surrounding forest cover, as well as to elevation. At the local scale, we found evidence that juvenile, but not adult, palms were susceptible to edge effects: community composition was related to distance from edge and species richness generally increased with distance from the forest edge for juveniles, but not for adults. Our results provide baseline data on fragmented palm communities from a relatively poorly explored biogeographical region and highlight the importance of considering forest fragmentation effects at multiple spatial scales and across life stages for future conservation measures.

### LANDSCAPE-SCALE ABUNDANCE, RICHNESS AND COMMUNITY COMPOSITION

Palm species richness was not linked to either size of the forest fragment or amount of surrounding forest cover, contrary to the generally accepted pattern that small, isolated forest fragments harbour fewer species. In fact, the two smallest fragments in this study (2.7 and 3.2 ha) contained 13 species each, which was above average compared with the 20 other fragments. Similarly, in a study of palm diversity in the Brazilian Amazon, Scariot (1999) found that taxa richness across life stages generally did not vary with fragment size. The species richness of palm



**Table 4.** Standardized regression coefficients  $\pm$  SD for local-scale adult and juvenile palm abundance and species richness

|                  | Adult abundance                      | Juvenile abundance                      | Adult species richness                 | Juvenile species richness              |
|------------------|--------------------------------------|---|--|--|
| Intercept        | 0.785 $\pm$ 5.143                    | <b>2.33 <math>\pm</math> 4.928*</b>     | 1.060 $\pm$ 4.216                      | <b>1.510 <math>\pm</math> 3.076*</b>   |
| Elevation        | 0.507 $\pm$ 5.542                    | 1.749 $\pm$ 4.525                       | 0.805 $\pm$ 5.142                      | <b>1.384 <math>\pm</math> 3.013*</b>   |
| Canopy height    | <b>0.112 <math>\pm</math> 0.239*</b> | 0.085 $\pm$ 0.298                       | <b>0.122 <math>\pm</math> 0.146***</b> | 0.043 $\pm$ 0.178                      |
| Canopy openness  | -0.179 $\pm$ 0.507                   | <b>-0.131 <math>\pm</math> 0.139***</b> | -0.147 $\pm$ 0.470                     | <b>-0.097 <math>\pm</math> 0.127**</b> |
| Distance to edge | 0.227 $\pm$ 1.027                    | 0.252 $\pm$ 0.667                       | 0.216 $\pm$ 0.837                      | <b>0.224 <math>\pm</math> 0.436*</b>   |
| Slope            | -0.025 $\pm$ 0.366                   | <b>-0.096 <math>\pm</math> 0.191*</b>   | -0.047 $\pm$ 0.307                     | <b>-0.07 <math>\pm</math> 0.136*</b>   |

Estimates are averaged across models run separately for each transect ( $N = 22$  transects total).  $P$  values come from a one-sided  $t$ -test that the mean coefficient estimate is different from 0. Abundance was modelled with a negative binomial regression, and species richness was modelled with a Poisson regression. Statistically significant values of regression coefficients are in bold type.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P \leq 0.001$ .

**Table 5.** Standardized regression coefficients  $\pm$  SD for local-scale community similarity for adult and juvenile palms for pure environmental and pure geographical models, along with results of variance partitioning analysis

|                                      | Adults                                  | Juveniles                               |
|--------------------------------------|---|---|
| Environmental model                  |   |   |
| Intercept                            | <b>0.248 <math>\pm</math> 0.101***</b>  | <b>0.343 <math>\pm</math> 0.086***</b>  |
| Elevation                            | <b>-0.198 <math>\pm</math> 0.368*</b>   | <b>-0.214 <math>\pm</math> 0.303**</b>  |
| Canopy height                        | 0.008 $\pm$ 0.053                       | -0.008 $\pm$ 0.021                      |
| Canopy openness                      | -0.012 $\pm$ 0.031                      | -0.004 $\pm$ 0.018                      |
| Distance to edge                     | -0.015 $\pm$ 0.064                      | <b>-0.037 <math>\pm</math> 0.039***</b> |
| Slope                                | 0.007 $\pm$ 0.034                       | <b>-0.015 <math>\pm</math> 0.024**</b>  |
| Geographical model                   |   |   |
| Intercept                            | <b>0.252 <math>\pm</math> 0.077***</b>  | <b>0.311 <math>\pm</math> 0.073***</b>  |
| Geographical distance                | <b>-1.379 <math>\pm</math> 1.617***</b> | <b>-1.37 <math>\pm</math> 1.324***</b>  |
| Variance explained                   |   |   |
| $R^2$ – pure environmental           | <b>0.033 <math>\pm</math> 0.041***</b>  | <b>0.027 <math>\pm</math> 0.019***</b>  |
| $R^2$ – pure geographical            | <b>0.013 <math>\pm</math> 0.028*</b>    | <b>0.008 <math>\pm</math> 0.011**</b>   |
| $R^2$ – environmental + geographical | 0.003 $\pm$ 0.036                       | <b>0.013 <math>\pm</math> 0.016***</b>  |
| $R^2$ – total                        | <b>0.049 <math>\pm</math> 0.049***</b>  | <b>0.047 <math>\pm</math> 0.032***</b>  |
| $R^2$ – unexplained                  | <b>0.951 <math>\pm</math> 0.049***</b>  | <b>0.953 <math>\pm</math> 0.032***</b>  |

Geographical distance is log transformed. Estimates are averaged across multiple regression on distance matrices analyses run separately for each transect ( $N = 22$  transects).  $P$  values come from a one-sided  $t$ -test that the mean coefficient estimate is different from 0. Statistically significant values are in bold type.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P \leq 0.001$ .

communities in forest fragments in our study area was comparable to species richness of palms in continuous wet and moist forest across 11 sites in western Ecuador (Borchsenius, 1997), and similar in species richness to two forest fragments near Santa Domingo, Ecuador, *c.* 60 km away from our study site (Baez & Balslev, 2007). The amount of surrounding forest cover may be important for palm richness in some fragmented landscapes (see Wang, 2008), but we did not find an association between forest cover and species richness in this study. These results suggest that other factors beyond simple frag-

ment characteristics, such as size, may play an important role in determining local species richness in fragmented landscapes. Potential factors that may influence local richness include the composition of the surrounding matrix habitat, which can affect the behaviour of pollen and seed dispersers, population connectivity and thus population dynamics in forest fragments (Laurance, 2008; Laurance *et al.*, 2011; Watling *et al.*, 2011). Our metric of forest cover distinguished between forest/non-forest surrounding matrix habitat, but not other land-use types (e.g. pasture, cacao, oil palm) that may influence

disperser/pollinator behaviour. Also, underlying environmental gradients (e.g. hydrology, soil chemistry; Eiserhardt *et al.*, 2011) existing prior to fragmentation could overpower any potential fragmentation effects. Lastly, especially for long-lived canopy palms, it may be that simply not enough generations have passed since deforestation for there to be a detectable impact on species richness at the landscape scale (Kramer *et al.*, 2008).

In terms of community similarity, we found that elevation and forest cover, but not fragment size, were related to differences in community similarity for both adult and juvenile palms. Similarly, elevation had a strong, positive relationship with abundance of juveniles and adults. We were unable to distinguish whether the links between elevation, community similarity and abundance are a result of a pre-existing relationship unrelated to fragmentation. We also do not know if deforestation alters landscape-level environmental conditions that are correlated with elevation (e.g. precipitation, temperature), leading to changes in palm community similarity and abundance. The connection between surrounding forest cover and community similarity suggests that the degree of isolation of a forest fragment may be an indicator of local community composition. Strongly isolated fragments may experience reduced dispersal (see above) or different environmental conditions compared with fragments with large amounts of surrounding forest cover, potentially leading to changes in community composition in each forest fragment. A lack of surrounding forest cover may also be an indicator of high local human impact (e.g. selective harvesting or livestock presence in fragments). We did find evidence of timber extraction in some fragments, but we did not observe any obvious signs of palm trees in particular being harvested. Identifying if and how different land-use types and agricultural activities in areas surrounding forest fragments influence palm diversity and composition in forest fragments is an important area of future research. A complementary study of palm communities across a similar elevational gradient in a continuous landscape might resolve the relative importance of anthropogenic vs. biological factors in determining the relationship between elevation, forest cover and community composition, although in this area it is increasingly difficult to find continuous tracts of forest large enough to make such a study possible (Dodson & Gentry, 1991).

Variance partitioning analyses revealed that geographically structured environmental factors explained more variation in community similarity at the landscape scale than did either pure environmental or geographical factors (Table 3). This high proportion of explained variation, and the corresponding

very low proportion of variation explained by pure geographical factors, is probably due to the fact that our sampling design was located along an elevational gradient. Fragments that were more distantly spaced also had greater elevational differences, confounding geographical and environmental distances. Thus, caution should be taken in interpreting these results in terms of neutral (usually attributed to pure geographical effects) vs. niche processes (pure environmental effects) in assembling communities of palms in this landscape.

Habitat loss and fragmentation could lead to parallel losses of species and genetic diversity. Disruption of dispersal and reduced population sizes typically associated with these forms of disturbance are thought to decrease diversity for both species in communities and genes in species (Vellend, 2003; Vellend & Geber, 2005). A previous study in the same area found no differences in genetic diversity between continuous forest and fragments for either adults or recruits of the canopy palm *Oenocarpus bataua* Mart., but recruits in fragments had increased genetic structure at both landscape and local scales (Browne *et al.*, 2015). These previous results mirror the lack of correlation between landscape-scale species richness and fragmentation effects we report in the current study, along with the observed association between community composition and fragmentation effects. In both cases, a time-lag effect, in which earlier life stages are more susceptible to fragmentation effects than adults (Kramer *et al.*, 2008; Lowe *et al.*, 2015), may explain why we detected stronger differences in juveniles than adults in terms of both genetic and community diversity. Additionally, the results of this study along with those of Browne *et al.* (2015) suggest that the composition of genes and species may be more sensitive to recent deforestation than the richness of genes and species. Assuming these fragments remain intact in the face of rapidly improving roads and infrastructure in the region, a priority for future work would be to resample these fragments along a time series, for comparison with the benchmarks of genetic and species diversity that Browne *et al.* (2015) and the current study provide.

#### LOCAL-SCALE ABUNDANCE, RICHNESS AND COMMUNITY COMPOSITION

In contrast to our landscape-scale analyses, in which adult and juvenile palms exhibited similar patterns, we observed strong differences between life stages at the local scale. Abundance, species richness and community similarity were related to different environmental variables in adults vs. juveniles (Table 4).

Notably, juveniles exhibited stronger responses to the distance from the forest fragment edge compared with adults. This result differs from that of Baez & Balslev (2007), who found that adult, but not juvenile, species richness and abundance were reduced near edges in one of two forest fragments in north-west Ecuador. A longer time since fragment formation [40–50 years in Baez & Balslev (2007) compared with 30–40 years in this study] may partly explain the contrasting results. In our study, variation from fragment to fragment in the relationship between adult species richness and abundance and distance to the forest edge swamped any statistical signal. Juveniles also showed variation from fragment to fragment in the relationship between species richness, abundance and distance to the forest edge, but the overall trend was for richness and abundance to decrease near forest fragment edges, although this pattern was not robust when models containing spatial autocorrelation were excluded. Spatial autocorrelation in transect sampling is a long-standing issue in ecological survey data, leading to a lack of independence in sampling units, a reduction in overall variance in the dataset and an increased probability of type I error. For the purposes of this study, employing a truly random sampling design in each fragment that would reduce spatial autocorrelation between sampling points was not logistically feasible, given the rough terrain and lack of infrastructure. With the potential effects of spatial autocorrelation and ample variation from fragment to fragment, not only for this study but also for that of Baez & Balslev (2007), we urge caution in interpreting the results as general trends in local-scale palm responses to fragmentation. Future studies interested in understanding edge effects in palms should prioritize sampling a large number of fragments in order to adequately capture between-fragment variation, potentially employing stratified random sampling in edge and core habitat and focus on identifying mechanisms of ecological change that lead to edge-related patterns of diversity.

In relation to environmental variables at the local scale, our results add further support to previous studies that indicate palm diversity, abundance and composition are linked to local environmental factors and topography, slope, canopy openness and canopy height (reviewed by Eiserhardt *et al.*, 2011). However, the relatively small amount of overall variation in palm species composition explained by these parameters (Table 5) indicates that additional factors not measured in this study are likely to be important for determining the local densities and distributions of palms, namely soil chemistry, hydrology, species interactions and dispersal. While the community-level analyses employed in this study are important

for revealing trends in palm diversity and abundance as a whole, species-specific responses to fragmentation may be masked by this approach, leaving a need for more detailed studies focusing on one or a few species.

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## SUPPORTING INFORMATION

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

**Table S1.** Coordinates and environmental characteristics of 22 forest fragments sampled for palm diversity and abundance.

**Table S2.** Standardized regression coefficients  $\pm$  SE for landscape-scale seedling and juvenile palm abundance and species richness.

**Table S3.** Landscape-level community similarity standardized regression coefficients for seedlings and juveniles estimated with multiple regression on distance matrices for pure environmental and pure geographical models, along with results of a variance partitioning analysis.

**Table S4.** Standardized regression coefficients  $\pm$  SD for local-scale seedling and juvenile palm abundance and species richness.

**Table S5.** Standardized regression coefficients  $\pm$  SD for local-scale community similarity for seedling and juvenile palms for pure environmental and pure geographical models, along with results of variance partitioning analysis.

**Table S6.** Abundance of juvenile individuals (not including seedlings) in 22 forest fragments.

**Table S7.** Abundance of seedlings in 22 forest fragments.

**Table S8.** Abundance of adult individuals (pooling adult and subadults) in 22 forest fragments.

**Table S9.** Abundance of individuals (pooling juveniles and seedlings) in 22 forest fragments.

**Table S10.** Standardized regression coefficients  $\pm$  SD for local-scale adult and juvenile palm abundance and species richness after removing transects that contained significant ( $P < 0.05$ ) spatial autocorrelation in model residuals, tested via a Mantel test.