# Patch isolation and shape predict plant functional diversity in a naturally fragmented forest

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## Abstract

### Aims

It is known that taxonomic diversity can be predicted by the spatial configuration of the habitat, in particular by its area and degree of isolation. However, taxonomic diversity is a poor predictor of ecosystem functioning. While functional diversity is strongly linked to the functionality and stability of ecosystems, little is known about how changes in the spatial configuration of the habitat affect functional diversity. In this study, we evaluated whether the spatial configuration of forest patches predicts the functional diversity of plants in a fragmented forest.

### Methods

Five functional leaf traits (leaf dry matter content, leaf punch force, specific leaf area, leaf size and leaf thickness) were measured for 23 dominant plant species in 20 forest patches in a naturally fragmented forest on the Yucatan Peninsula. Abundance-weighted multivariate and individual trait metrics of functional diversity were calculated and correlated with size, degree of isolation and the shape of forest patches.

### Important Findings

Patch shape was negatively correlated with multivariate and individual trait (leaf dry matter content and leaf size) metrics of functional diversity. Patch isolation measures were also negatively correlated with individual trait (leaf dry matter content, leaf punch force and leaf size) metrics of functional diversity. In other words, greater patch shape irregularity and isolation degree impoverish plant functional variability. This is the first report of the negative effects of patch shape irregularity and isolation on the functional diversity of plant communities in a forest that has been fragmented for a long time.

*Keywords:* forest fragmentation, functional diversity, habitat spatial configuration, petenes, Yucatan

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## INTRODUCTION

Functional diversity refers to the value, range distribution and relative abundance of the functional traits of the organisms that make up a biotic community (Díaz *et al.* 2007). These traits can be physical, biochemical and phenological, among others, and are the measurable characteristics of an organism that affect or are correlated with its fitness or the functions it carries out in an ecosystem (Cadotte 2011). Functional traits reflect the action of ecological filtering or natural selection under certain environmental conditions and significantly affect the fundamental properties of ecosystems within the framework imposed by the prevailing abiotic conditions (Díaz *et al.* 2004; Lavorel and Garnier 2002). Functional diversity can help to explain how organisms respond to different environmental conditions as well as natural and anthropogenic disturbances, and predicts the impact of these on ecosystem function (Craven *et al.* 2016; Díaz *et al.* 2004; Sonnier *et al.* 2014). The study of the functional diversity of a biotic community highlights the relationship between biodiversity, abiotic factors and ecosystem processes in a way that taxonomic diversity studies cannot (Díaz *et al.* 2002). Functional diversity may also offer better guidance than taxonomic diversity to conservationists and restoration ecologists because, in contrast to species loss,

ecosystem functions can be effectively restored owing to the functional redundancy exhibited by different species in plant communities (Piqueray et al. 2015; Rosenfeld 2002).

Ecologists have long been interested in how species occurrence can be predicted by the spatial configuration of the habitat, and the Theory of Island Biogeography was one of the first to suggest that taxonomic biodiversity (species richness) can be predicted by some of the spatial properties of habitat, particularly size and degree of isolation (MacArthur and Wilson 1963, 1967). This theory was formerly proposed for oceanic islands but, the authors also suggested that similar principles may apply to terrestrial ecosystems where there are analogues of island size and isolation: patch size and isolation between patches or with respect to continuous forest or any source of propagules (MacArthur and Wilson 1963, 1967; but see Laurance 2008, 2009). Nowadays, a great deal of research has not only successfully confirmed that patch size and isolation degree are reliable predictors of plant species richness (and other measures of taxonomic diversity) in terrestrial ecosystems (Bender et al. 1998; Fahrig 2003, 2013; Liira et al. 2014; Munguía-Rosas et al. 2014) but has also identified that other spatial variables of habitat, such as shape and the edge effect are important predictors of taxonomic diversity (Cousins and Aggemyr 2008; De Sanctis et al. 2010; Galanes and Thomlinson 2008; Laurance 2008; Yamura et al. 2008).

Though frequently correlated with patch spatial configuration, taxonomic diversity provides limited information about species because it does not reflect the functional role of species in the ecosystem (Swenson 2011, 2014). Our knowledge about how the spatial configuration of a fragmented habitat can affect components of biodiversity other than taxonomic diversity is still in its early infancy (Sonnier et al. 2014; Swenson 2014). A couple of studies have found that functional diversity tends to be lower in forest fragments than in adjacent continuous forest (Girão et al. 2007; Munguía-Rosas et al. 2014), but only a few studies (Mendes et al. 2016; Sonnier et al. 2014; Ziter et al. 2013) have recently looked at how the spatial configuration of forest fragments affects plant functional diversity. Sonnier et al. (2014) found that patch isolation and age negatively affect the functional diversity, while Ziter et al. (2013) found a positive effect of patch size on functional dispersion. A study conducted in a tropical forest found that patch connectivity was also a reliable predictor of functional divergence (Mendes et al. 2016). Although these results may suggest that in fragmented forests the spatial configuration of patches predicts plant functional diversity and that the effects can increase in the long term, the lack of additional studies makes it impossible to generalize. This is a serious gap in our knowledge because we still do not know whether the previously documented detrimental effects of habitat loss and isolation on species richness (Bender et al. 1998; Duque et al. 2013; Fahrig 2003; Honnay et al. 1999; Liu and Slik 2014; Sun et al. 2007) translates into the loss of functional diversity, the loss of ecosystem productivity and the stability associated with it (Díaz and Cabido 2001; Loreau and De Mazancourt 2013).

In this study, we evaluated whether the spatial configuration of forest patches predicts functional diversity in a naturally fragmented tropical forest on the Yucatan Peninsula. This forest is made up of naturally formed forest patches (locally known as 'petenes', singular: 'peten') that are highly variable in their spatial configuration (Durán 1987a; Mas and Correa 2000; Rico-Gray and Palacios-Ríos 1996). Forest patches in the study area are surrounded by a matrix of contrasting vegetation in terms of composition and structure (Durán 1987b; Rico-Gray 1982). The environmental stressors that prevail in the matrix, such as higher solar radiation, stronger winds, chronic flooding and salinity, may filter those species tolerant to these stressors, not only in the habitat matrix but also near the edges of forest patches (Rico-Gray and Palacios-Ríos 1996). Specifically, we tested whether the multivariate metrics of functional diversity are predicted by patch size, isolation and shape. We predicted that patch area would be positively related to plant functional diversity, and the degree of patch isolation would be negatively related to plant functional diversity. As patch area increases, patches may have greater habitat heterogeneity and may therefore offer more niche opportunities and a greater diversity of ways to exploit the available resources (Boecklen 1986; Tews et al. 2004); likely translating into greater functional diversity in larger patches. Isolation is more related to patch colonization: well-connected patches usually have a similar species composition and, potentially, are similar in functional diversity owing to the high degree of propagule exchange (Dupré and Ehrlén 2002; MacArthur and Wilson 1967). Isolated patches may have lower functional diversity because fewer species have the traits that allow them to arrive and survive in highly isolated patches (Sonnier et al. 2014). Patch shape determines the proportion of edge habitat (i.e. edge perimeter increases with shape irregularity), and plants near the edge typically are subjected to greater environmental stress (Murcia 1995); therefore, we predicted that patches with a more irregular shape would have a relatively lower functional diversity. Additionally, the functional diversity of individual traits along with the dominant trait values of each patch were estimated using leaf metrics related to environmental and biotic stress, biomass allocation and productivity. We expected shade-tolerant plant species that allocate more biomass to tough, durable tissue and the protection of photosynthetic tissue (i.e. forest interior-like species) to dominate large, well connected, nearly circular forest patches, while fast growing, shade-intolerant species, with high productivity (i.e. pioneer-like species) would dominate small, isolated, irregular forest patches.

## MATERIALS AND METHODS

### Study area

The study area is the Petenes-Celestún-El Palmar Biological Corridor (19°53′–21°11′N, 90°28′–90°17′W), located along the northwestern coast of the Yucatan Peninsula (Fig. 1). Its area is approximately 240 000 ha (Costa-Lugo et al. 2010),
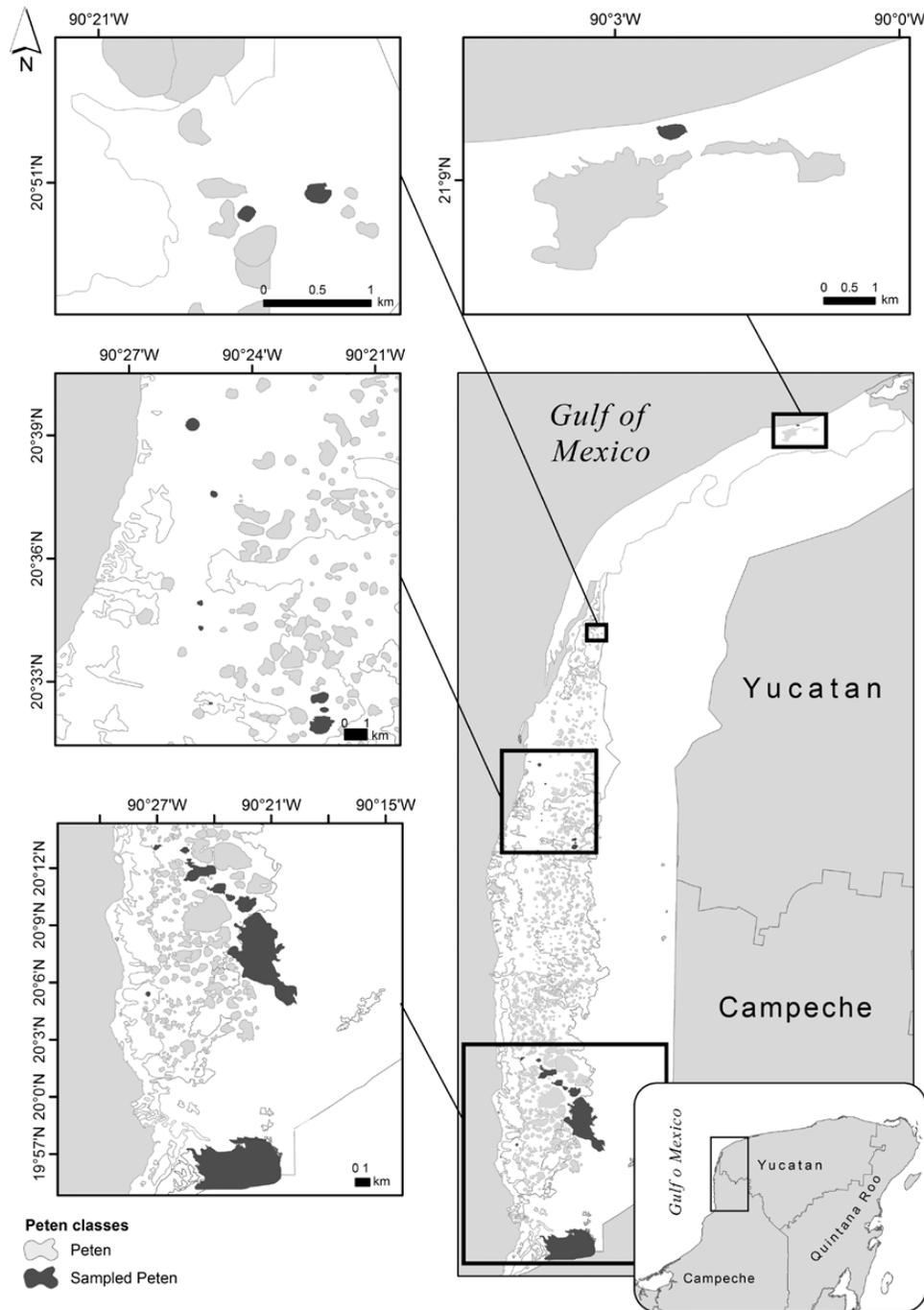
**Figure 1:** map of the study area (Petenes-Celestún-El Palmar Biological Corridor). Forest patches sampled (sampled peten) are shown in black. Patches not sampled are shown in gray (Peten). The white continuous area is the terrestrial portion of the biological corridor dominated by a continuous semi-evergreen forest. The small rectangle in the insert at the bottom right indicates the position of the study area on the Yucatan Peninsula. All bars represent 1 km.

climate is tropical subhumid with a wet season lasting from June to September, precipitation is 1000 to 1200 mm year$^{-1}$ and mean temperature is 26.1 to 27.8°C (Durán 1987a).

The study was done on semi-evergreen tropical forest patches, sometimes mixed with tall mangrove species (Barrera 1982; Rico-Gray 1982). These patches are more abundant on the western part of the peninsula (Durán 1987a, 1987b;

Rico-Gray 1982) where the size of patches is highly variable (mean patch size = 180 ha ± 191; hereafter, mean ± 1 standard error) and the distance from one patch to the next closest one ranges from 20 to 2670 m (Mas and Correa 2000). The shape of forest patches ranges from approximately circular (shape index ≈ 1) to amorphous (shape index ≈ 2.5; Mas and Correa 2000). Two important characteristics of many patches that may at least

partially explain the greater plant diversity observed relative to the matrix are: (i) fresh water is available year-round *via* sink-holes and (ii) patches have a higher elevation relative to the matrix (Barrera 1982; Rico-Gray 1982). The forest patches grow on quaternary geological formations that are about 1.7 my old (CONANP-SEMARNAT 2006; Munguía-Rosas *et al.* 2014).

Plant species richness in the patches tends to be relatively low (6–23 woody species per patch) owing to moderate salinity levels and seasonal flooding, as well as the small size of the patches (Durán 1987b; Munguía-Rosas and Montiel 2014). Patch vegetation is stratified and in each stratum three to five species are strongly dominant (Tun-Dzul 1996). In the canopy, the most abundant species are *Annona glabra* L., different species of *Ficus*, *Manilkara zapota* (L.), *Metopium brownei* (Jacq.), *Swietenia macrophylla* (King.) and *Tabebuia rosea* (Bertol.) Bertero ex A.DC. The shrub layer is characterized by *Acrostichum aureum* (Fée) C. Presl, *Bravaisia berlandieriana* (Nees) T.F. Daniel and *Sabal yapa* C. Wright ex Becc. Because of frequent flooding, the understory is scarce or absent. There are patches that have a mixture of mangrove species (mainly *L. racemosa*) and forest species (Durán 1987b; Tun-Dzul *et al.* 2011), especially on moderately saline patches. Forest patches are discrete units with clearly identifiable edges because the vegetation of the forest patches and that of the surrounding matrix are diametrically different in their species composition and structure (Rico-Gray 1982). The matrix between patches is dominated by shorter salt- and flood-tolerant species such as *Acrostichum danaeifolium* (Fée) C. Presl, *Cladium mariscus jamaicense* (Crantz) Kük, and the mangroves *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* (Rico-Gray 1982). The majority of the plant species that inhabit forest patches cannot tolerate the predominant abiotic conditions of the matrix (Durán 1987a, 1987b; Rico-Gray 1982). Flying vertebrates which disperse seeds of some plants inhabiting forest patches can cross the matrix, a habitat that offers them no feeding resources (Montiel *et al.* 2006).

## DATA COLLECTION

A group of 20 patches of varying sizes, shapes and degree of isolation was selected (Fig. 1). Selection was not random because of limitations imposed by patch accessibility. Only patches with an area greater than one hectare were selected because smaller patches are not permanent as they get totally flooded during the rainy season. From January 2013 to August 2014, vascular plant species were recorded in all 20 forest patches using belt transects. Epiphytes and lianas were not recorded during the vegetation survey owing to the difficulties associated with assessing their presence and abundance. Woody plants with a diameter greater than 1.5 cm and non-woody plants taller than 20 cm were recorded in five parallel transects (50 × 4 m each) per patch (total area sampled per patch = 0.1 ha). Following the advice of previous studies (Arroyo-Rodríguez *et al.* 2008, 2012; Munguía-Rosas and Montiel 2014; Rosati *et al.* 2010), the area sampled was kept constant in all 20 patches to reduce

sample area effects. In each patch, the first transect was placed using a random point and the remaining transects (4) were systematically placed 20 m apart. Plants were identified with the help of field guides (Brokaw *et al.* 2011; Pennington and Sarukhán 2005) and expert advice. An *a posteriori* evaluation of sampling provided evidence that it was representative in all patches (i.e. the species accumulation curve reached an asymptote and species representativeness was greater than 80% in all of the patches).

The species that by abundance represent 90–94% of the vascular plants for each of the 20 patches were selected for leaf functional trait sampling (Pérez-Harguindeguy *et al.* 2013). In total, functional traits were collected for 23 plant species. A list of the species sampled with their respective abundance per forest patch is available as online supplementary Table S1. For each species, five adult plants with no significant signs of herbivory, visually free of pathogens and located in well-illuminated sites (except shade-tolerant species) were selected. From each plant, five true leaves were collected at each site. The leaves were taken to the laboratory in plastic bags with wet paper towels and processed within three days of being collected. For the collected leaves, five functional traits were measured: leaf dry matter content in g g$^{-1}$ (LDMC), leaf punch force in N mm$^{-1}$ (LPF), leaf size in cm$^2$ (LS), specific leaf area in cm$^2$ g$^{-1}$ (SLA) and leaf thickness in mm (LT). All these variables were measured using a standardized protocol for the collection of functional traits in plants (Pérez-Harguindeguy *et al.* 2013).

LDMC was obtained by dividing the weight of the leaves dried in an oven for 48 h at 60°C by the fresh weight of the same leaf. LPF was obtained by measuring the force necessary for a 1 mm cylinder to penetrate the leaf surface, avoiding the main rib. LS was determined as leaf area using a leaf area meter (LI-3000A, Li-COR-Inc., NE, USA). SLA was calculated by dividing leaf area by the dry weight of the same leaf. LT was measured on fresh leaves using a digital caliper (Mitutoyo, Absolute Digimatic, Tokyo, Japan), avoiding the principal veins and for compound leaves a leaflet from a true leaf was measured the same way. Leaves with a high LDMC are more resistant to biotic damage (Cornelissen *et al.* 2003; Pakeman 2014), flooding and salinity (Batriu *et al.* 2015). Additionally, LDMC is inversely related to plant productivity (Cornelissen *et al.* 2003; Pakeman 2014). LPF is a good indicator of the relative investment of carbon in the structural protection of photosynthetic tissues. Leaves with high LPF are physically stronger and have more protection against biotic and abiotic damage; LPF is also negatively correlated with litter decomposition rate (Coley 1983; Cornelissen *et al.* 2003; Ricotta and Moretti 2011). LS has important consequences for the energy of the leaf and water balance. It has been suggested that leaf size decreases in response to heat, drought and other environmental stressors (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013). SLA is positively correlated with growth rate and the rate of photosynthesis; plants growing in highly illuminated places generally have a larger SLA (Cornelissen *et al.*

2003; Pérez-Harguindeguy *et al.* 2013). In coastal marshes, environmental stressors such as flooding and salinity are positively correlated with SLA (Minden *et al.* 2012; Batriu *et al.* 2015). LT is positively correlated with heat regulation and photosynthate content (Niinemets 2001). With this set of functional traits, at least two main ecological strategies of plants can be identified: (i) plant species that allocate more biomass to tough, durable tissue and the protection of photosynthetic tissue (high LDMC, LPF, LS, low SLA and LT); typically, these are forest interior, shade-tolerant species inhabiting relatively undisturbed forest. And (ii) fast growing, shade-intolerant species, with high productivity that inhabit highly illuminated habitats with recurring disturbance such as forest edges (high SLA and LT, low LDMC, LPF, LS; Poorter 2009).

## Patch spatial configuration

For the patches studied, the description of spatial configuration included area (ha), measures of isolation (distance to the nearest patch, distance to the continuous forest and a connectivity index), patch shape (shape index) and elevation (of the patch center in m.a.s.l.). These data were obtained from recent digital cartography (2011) available in Google Earth Pro 7.2. The basic information (areas and distances) needed to calculate patch spatial descriptors was obtained using ArcInfo 9.2 software. Since habitat isolation is a complex variable in terrestrial ecosystems, it was assessed using different complementary isolation metrics (Tischendorf *et al.* 2003): distance to the closest patch (from edge to edge in km), distance to the continuous forest (edge to edge in km), along with a connectivity index based on area weighted by the distance between a focal patch and the three patches closest to it. The connectivity index increases as patch isolation decreases (all values > 0; see Munguía-Rosas and Montiel, 2014, for the details of the calculation). Patch shape was measured with an index of shape complexity ($shape\ index = perimeter/(2\sqrt{\pi} \times area)$) that is independent of area and describes the deviation of each patch from circularity. The shape index of a circular patch is 1, as patch shape irregularity increases, the index becomes progressively >1 (Laurance and Yensen 1991; Mas and Correa 2000; Yamura *et al.* 2008). Some of the spatial data obtained from the digital cartography (elevation, position and patch limits) were corroborated in the field for 4 randomly selected patches, confirming that the spatial configuration data obtained from the digital cartography for the patches were reliable.

Mean patch size was 180.15 ± 191.18 ha, distance to nearest patch was 0.36 ± 0.09 km, distance to the continuous forest was 14.88 ± 4.12 km, patch connectivity was 1749 ± 1308.57, elevation was 8.58 ± 1.29 m.a.s.l and shape index was 1.26 ± 0.06.

## Statistical analyses

Prior to calculating the metrics of functional diversity, a correlation matrix between all pairs of functional traits was constructed. Only functional traits with weak ($r < 0.2$) or non-significant correlations were used to calculate two multivariate metrics (details below). The weak correlation suggests that each character contributes complementary information for understanding the functionality of the community. Multivariate metrics were calculated weighted by abundance (mean pairwise functional distance between species [MPFD] and mean nearest functional distance between species [MNFD]). MPFD was also calculated as a metric of functional diversity of individual traits. Community means weighted by abundance (CWM) were also calculated to assess the dominant trait value in each patch, which indicates the main functional strategy selected by environmental filters and is directly linked to the mass ratio hypothesis that states that the characteristics of dominant species broadly determine ecosystem processes (Grime 1998). Prior to calculating the multivariate and individual trait functional diversity metrics, all functional traits were standardized (mean = 0 and standard error = 1) while CWMs were calculated using the original scale (Pla *et al.* 2012; Swenson 2014). The multivariate metrics reflect functional diversity taking into account all functional traits together, while the individual metric per functional trait gives a more precise idea of how spatial configuration affects each functional trait and the identity of environmental filter or function associated with it (Ricotta and Moretti 2011; Swenson 2014).

Using either all the traits (multivariate metrics: MPFD and MNFD) or a single trait (individual trait metric: MPFD), a matrix of Euclidean functional distances among species was built. The abundance-weighted version of these metrics was used. In contrast to other variables used to weight functional diversity metrics (such as biomass), plant abundance can be recorded in the field quickly and with a high degree of accuracy. Abundance is also the most common weighting variable, so, by using it, comparability with other studies is maximized. Following the advice of de Bello *et al.* (2016), the matrix diagonal was disregarded and distances between pair of species were calculated without replacement. MPFD and MNFD give complementary information, while MNFD indicates functional redundancy (i.e. the distance between species that are functionally more similar in the community), MPFD indicates the average degree of difference between species in the community (i.e. mean functional distance between the species of a community; Swenson 2014). CWM was calculated using the mean of the values of a functional trait weighted by the abundance of each species in each patch (Pla *et al.* 2012).

To assess the relationship between multivariate and individual trait functional diversity metrics with patch spatial configuration, multiple regression models were generated using multivariate (MPFD and MNFD) or individual trait metrics (CMW and MPFD for each functional trait: LDMC, LPF, LS, SLA, LT) as the response variables (a different model per metric) and the spatial configuration descriptors of forest patches (patch size, distance to the nearest patch, distance to the continuous forest, connectivity index, patch elevation and shape index) as the explanatory variables. To improve linearity, patch size, distance to the nearest patch and distance to the continuous forest were log transformed. For each functional metric, and following Crawley (2013), a minimal

adequate model was obtained using stepwise model selection by AIC (the model with the lowest AIC was selected), which is implemented in the step function in the software R 2.14. (R Development Core Team, 2011). Explanatory variables in minimal adequate models were not significantly correlated ($P > 0.05$ in all cases), which suggests little or no multi-col-linearity. Examination of the residuals suggested a good fit to normality in all cases (Crawley 2013). All of the analyses were run in R 2.14. Multivariate and individual MPFD were calculated using the Melodic package (de Bello *et al*. 2016) and CWM and MNFD were calculated using a modification of the script written by Swenson (2014).

## RESULTS

### Multivariate metrics

After model simplification, the minimal adequate model for MPFD retained distance to the nearest patch, patch connectivity, patch elevation and shape as predictors, while for MNFD none of the variables considered in the complete model was retained in the minimal adequate model (see online supplementary Table S2).

Of the variables used in the minimal adequate models, patch shape significantly predicted MPFD and the relationship between these variables was negative. Patch shape explained more than 21% of the among-patch variance in MPFD (Table 1). Also, MPFD tended to decrease as distance to the nearest patch increased; however, this relationship was only marginally significant ($P = 0.07$; Table 1).

### Metrics of individual traits

#### Community weighted means

After model simplification, the explanatory variables retained in the LDMC minimal adequate model were: patch size, distance

**Table 1:** results of linear multiple regression run to assess the relationship between multivariate mean pairwise functional distance (MPFD) and some descriptors of spatial configuration of forest patches (patch size [size], a connectivity index [connectivity], patch elevation [elevation] and a shape index [shape])

| Response | Source of variation | Statistics | Coefficient (SE) | Explained variance (%) |
|---|---|---|---|---|
| MPFD | D nearest P | $F_{1,15} = 3.41^+$ | −0.18 (0.12) | 11.74 |
| | Connectivity | $F_{1,15} = 2.71$ | 0.00005 (0.00003) | 9.21 |
| | Elevation | $F_{1,15} = 1.83$ | 0.006 (0.002) | 6.25 |
| | Shape | $F_{1,15} = 6.38*$ | −1.21 (0.47) | 21.74 |

The statistics, partial regression coefficients (and standard error) and explained variance per source of variation are shown. Only the explanatory variables included in the minimal adequate models are presented (see online supplementary Table S2). *$P < 0.05$; +$P = 0.07$. Abbreviation: SE = standard error.

to the continuous forest and patch shape. The SLA minimal adequate model included: patch size, distance to the continuous forest, distance to the nearest patch, patch elevation and patch shape. For LPF, the minimal adequate model included: patch size and shape. For LS, the explanatory variables in the minimal adequate model were: distance to the continuous forest, patch connectivity, patch elevation and shape. Finally, for LT, the variables included in minimal adequate model were: patch elevation and connectivity (see online supplementary Table S3).

Of the set of explanatory variables included in the minimal adequate models, shape was negatively correlated to SLA and LS (Table 2). Shape also explained among-patch variation in LDMC, but in this case, the coefficient was positive (Table 2). Variance explained by shape was 23% for LDMC, 45% for SLA and 28% for LS (Table 2). Finally, distance to the continuous forest also explained a significant amount of among-patch variance in LS (25%), and the relationship between these variables was negative (Table 2).

### Mean pairwise functional distance

After model simplification, the explanatory variables retained in the minimal adequate model for LDMC were: patch size, distance to the continuous forest, distance to the nearest

**Table 2:** results of a linear multiple regression model run to assess the relationship between community weighted means (CWM) for some functional leaf traits (leaf dry matter content [LDMC], leaf punch force [LPF], specific leaf area [SLA], leaf size [LS] and leaf thickness [LT]) with some descriptors of spatial configuration of forest patches (patch size [size], a connectivity index [connectivity], patch elevation [elevation] and a shape index [shape])

| Trait | Source of variation | Statistics | Coefficient (SE) | % Explained variance |
|---|---|---|---|---|
| LDMC | Size | $F_{1,16} = 0.86$ | −0.19 (0.006) | 3.18 |
| | D continuous | $F_{1,16} = 3.86$ | −0.02 (0.01) | 14.31 |
| | Shape | $F_{1,16} = 6.25*$ | 0.12 (0.05) | 23.18 |
| LPF | Size | $F_{1,17} = 0.55$ | −0.6 (0.03) | 2.72 |
| | Shape | $F_{1,17} = 2.83$ | 0.4 (0.26) | 13.89 |
| SLA | Size | $F_{1,14} = 0.21$ | 8.04 (2.59) | 0.74 |
| | D continuous | $F_{1,14} = 0.76$ | 4.56 (3.36) | 2.65 |
| | Elevation | $F_{1,14} = 0.001$ | −0.91 (0.56) | 0.03 |
| | D nearest P | $F_{1,14} = 0.85$ | −4.75 (2.44) | 2.95 |
| | Shape | $F_{1,14} = 13.09**$ | −66.52 (18.38) | 45.26 |
| LS | D continuous | $F_{1,15} = 9.79**$ | −4.1 (1.67) | 25.18 |
| | Connectivity | $F_{1,15} = 0.27$ | 5.04 (2.93) | 0.70 |
| | Elevation | $F_{1,15} = 3.04$ | −7.93 (2.52) | 7.80 |
| | Shape | $F_{1,15} = 10.79**$ | −1.46 (4.47) | 27.75 |
| LT | Connectivity | $F_{1,17} = 3.86$ | 0.0004 (0.00002) | 17.40 |
| | Elevation | $F_{1,17} = 1.33$ | 0.004 (0.002) | 6.00 |

A separate model was fitted per functional trait. The statistics, partial regression coefficients (and standard error) and explained variance per source of variation are shown. Only the explanatory variables included in the minimal adequate models are presented (see online supplementary Table S3). *$P < 0.05$; **$P < 0.001$. Abbreviation: SE = standard error.

patch, patch elevation and shape. For LPF, the minimal adequate model included: patch connectivity and elevation. The minimal adequate model for LS retained distance to the continuous forest, distance to the nearest patch, patch connectivity, patch elevation and shape. For SLA and LT none of the original set of explanatory variables was retained in the minimal adequate models (see online supplementary Table S3).

Of the variables retained in the minimal adequate models, shape was a significant predictor of LDMC and LS (Table 3). Patch shape accounted for more than 30% of the variance in these two functional traits (Table 3). Distance to the nearest patch (explained variance: 15.6%), connectivity (explained variance: 24.7%) and distance to the continuous forest (explained variance: 20%) were significant predictors of LDMC, LPF and LS, respectively (Table 3). All of the statistically significant relationships described above had a negative coefficient except the patch connectivity of LPF (Table 3).

## DISCUSSION

In this study, we tested the prediction that functional diversity decreases with patch isolation and patch shape complexity because isolated and/or irregularly shaped patches are more heavily influenced by the stressful environmental conditions that prevail in the habitat matrix. We also predicted a positive relationship between functional diversity and patch size because larger patches usually have greater habitat heterogeneity and a

**Table 3:** results of a linear multiple regression model run to assess the relationship between by-trait mean pairwise functional distance (MPFD) for some functional leaf traits (leaf dry mater content [LDMC], leaf punch force [LPF], specific leaf area [SLA], leaf size [LS] and leaf thickness [LT]) with some descriptors of spatial configuration of forest patches (patch size [size], a connectivity index [connectivity], patch elevation [elevation] and a shape index [shape])

| Trait | Source of variation | Statistics | Coefficient (SE) | % Explained variance |
|---|---|---|---|---|
| LDMC | Size | $F_{1,14} = 0.07$ | 0.11 (0.04) | 0.22 |
| | D continuous | $F_{1,14} = 1.18$ | 0.13 (0.06) | 3.88 |
| | D nearest P | $F_{1,14} = 4.77^*$ | −0.13 (0.04) | 15.64 |
| | Elevation | $F_{1,14} = 0.57$ | −0.01 (0.01) | 1.89 |
| | Shape | $F_{1,14} = 9.95^{**}$ | −1.04 (0.32) | 32.62 |
| LPF | Connectivity | $F_{1,17} = 6.02^*$ | 0.0004 (0.00002) | 24.71 |
| | Elevation | $F_{1,17} = 1.31$ | −0.04 (0.002) | 5.41 |
| LS | D continuous | $F_{1,14} = 10.64^{**}$ | −0.22 (0.17) | 19.97 |
| | D nearest P | $F_{1,14} = 0.11$ | −0.186 (0.13) | 0.21 |
| | Connectivity | $F_{1,14} = 3.74$ | 0.00008 (0.00003) | 7.12 |
| | Shape | $F_{1,14} = 21.01^{**}$ | −2.18 (0.47) | 39.44 |

A separate model was fitted for each functional trait. The statistics, partial regression coefficients (and standard error) and explained variance per source of variation are shown. Only the explanatory variables included in the minimal adequate models are presented (see online supplementary Table S3). $^*P < 0.05$; $^{**}P < 0.001$. Abbreviation: SE = standard error.

smaller portion of their habitat is in contact with the matrix. However, our results only partially supported these predictions. We found that as patch shape becomes more irregular, multivariate (MPFD) and individual trait (MPFD for LDMC and LS) metrics of functional diversity decrease. In fact, of all the independent variables evaluated in this study, patch shape had the greatest explanatory value (22–34%). Also, all spatial variables associated with patch isolation, i.e. distance to the nearest patch, the inverse of connectivity and distance to the continuous forest, were negatively correlated with some functional diversity metrics of individual traits. That is, while nearly circular patches may sustain plants with a wide variety of leaf sizes and leaf dry matter content, variability in these traits was dramatically lower in irregularly shaped patches. The shape with lowest edge:area ratio is the circle and the amount of edge increases as patch shape becomes more complex; therefore, environmental stressors associated with edge effect (increased irradiance, temperature, flooding, salinity, herbivory) may be stronger in irregular patches (e.g. Murcia 1995). We suggest that these environmental stressors filter plant species with small leaves and high dry matter content and that are typically stress tolerant (Cornelissen et al. 2003). To our knowledge, no previous study has addressed the effect of patch shape on functional diversity.

Contrary to the predictions, patch size did not explain among-patch variation in functional diversity. Similarly, a previous study (Sonnier et al. 2014) reported a negative correlation between functional diversity and isolation and no significant relationship between patch size and functional diversity. Although Ziter et al. (2013) reported a correlation between patch size and functional diversity, this trend was only significant for patches under intensive management. It was hypothesized that patch area was correlated with environmental heterogeneity and this, in turn, would allow for the occurrence of a wider variety of plant functional strategies (i.e. greater functional diversity). Sonnier et al. (2014) tested this hypothesis using structural equation models and found a direct, positive association between patch area and heterogeneity. However, while heterogeneity has a direct and positive correlation with species richness, there was not a direct link between heterogeneity and functional diversity (Sonnier et al. 2014). The results of their study suggest that the effect of the spatial configuration of habitat on functional diversity may be independent of its effect on species richness. This notion is supported by a recent study in plant communities carried out in a different ecological context (Li et al. 2015). Also, a previous study in the same area (Munguía-Rosas and Montiel 2014) showed that other descriptors of patch spatial configuration predict plant species richness. In the study area, patch size is a good predictor of species richness (Munguía-Rosas and Montiel 2014) but, as evidenced in this study, patch size does not predict plant functional diversity.

To date, there has been a lack of agreement regarding the relationship between patch size and functional diversity (Ziter et al. 2013; Sonnier et al. 2014; this study). While the simplest explanation for this may be that the studies used different

metrics of functional diversity (functional dispersion [Ziter *et al.* 2013], functional richness [Sonnier *et al.* 2014] and MPFD [this study]), we cannot rule out the possibility that different drivers of fragmentation are also involved. Ziter *et al.* (2013) and Sonnier *et al.* (2014) studied forests fragmented by different human activities. In contrast, we studied a naturally fragmented forest where anthropogenic disturbance is limited but flooding and salinity are likely to be important environmental filters. Different fragmentation drivers in different studies may, at least partially, explain the observed variability in results among studies.

We also predicted that shade-tolerant plant species that allocate more biomass to tough, durable tissue and the protection of photosynthetic tissue (i.e. plants with high LDMC, LPF, LS, low SLA and LT) would dominate the larger, well connected, nearly circular forest patches while fast growing, shade-intolerant species, with high productivity (high SLA and LT, low LDMC, LPF, LS) would dominate smaller, isolated, irregularly shaped forest patches. The results only partially support our predictions. As predicted, the results for CWM show that dominant plant species in more isolated patches and those with a more irregular shape tend to have smaller leaves, which is indicative of the more stressful environmental conditions in these patches (Cornelissen *et al.* 2003). However, contrary to our predictions it seems that dominant plants in more irregularly shaped patches allocate more biomass to durable tissue and protection against physical damage (high DMC and low LSA). Although previous studies have shown that a larger proportion of the species inhabiting irregular patches is likely to have a pioneer-like ecological strategy (i.e. high SLA and low LDMC) and allocate more resources to growth than to protection (e.g. Laurance *et al.* 2006; Tabarelli *et al.* 2008), these studies were conducted in forests with human-driven fragmentation and an agricultural habitat matrix. Therefore, it is possible that the peculiarities of the habitat matrix in our study system account for our different results. High salt content and flooding in the matrix have been identified as major environmental filters for plants in the study area (Rico-Gray and Palacios-Ríos 1996), and to cope with this, plants may use a strategy that differs from that used by plants in forest remnants in an anthropogenic matrix where salinity is not an important environmental filter (e.g. Laurance *et al.* 2006; Tabarelli *et al.* 2008). Flooding and salt-tolerant plants such as mangroves and sedges, which frequently inhabit the patch edges in the study area, have a low SLA (50–70 cm$^2$ g$^{-1}$) and a moderately high LDCM (0.3–0.4 g g$^{-1}$). The fact that the frequency of salt-tolerant plants increases with patch shape irregularity (Spearman Rho = 0.52, $S$ = 2023, $P$ = 0.02) also supports the idea that flooding and salinity are important environmental filters in the study area. Another study in coastal marshes has reported similar results (Minden and Kleyer 2011). Additionally, low SLA and high LDMC are correlated with biomass allocation to durable tissues which may also help the plants to cope with the physical hazards typical of forest edges (Poorter 2009).

Regarding the effect of patch isolation, our results suggest that distance to the nearest patch and distance to the continuous forest reduced variability in LDMC and LS respectively, while better connectivity increases variability in LPF. These functional traits are associated with biotic and abiotic stressors (e.g. mechanical damage [LDMC, LPF], herbivory [LPF], heat, solar radiation and water stress [LS]; Cornelissen *et al.* 2003; Niinemets *et al.* 2007). Thus, we infer that environmental stress is harsher in the more isolated patches. Sonnier *et al.* (2014) and Mendes *et al.* (2016) suggested that patch isolation affects functional diversity because it filters out plant species with a limited colonization capacity (i.e. plants with heavy seeds or those dispersed by abiotic vectors). However, in the study area, nearly 70% of plant species are dispersed long distances by vertebrates or water regardless of their degree of isolation. Therefore, mechanisms other than dispersal capacity may also explain the observed effect of patch isolation on functional diversity. Contiguous patches may offer some protection to each other reducing wind velocity and the impact of flooding and salinity (Kapos 1989; Pinto *et al.* 2010). The latter is also supported by an observed increase in the frequency of salt- and flood-tolerant plants with patch isolation in the study area (i.e. the frequency of salt- and flood-tolerant species is positively correlated with distance to the nearest patch; Spearman Rho = 0.51, $S$ = 651, $P$ = 0.02). Therefore, the harsher environmental conditions prevailing in isolated patches may explain the reduced by-trait functional diversity (Table 3) and the smaller leaf size observed in the plants of these patches (Table 2).

An important characteristic of the study system is the fact that this forest has been fragmented for millions of years (Munguía-Rosas and Montiel 2014; Munguía-Rosas *et al.* 2014) and this may help us understand the long-term effects of changes in the spatial configuration of forest remnants on functional diversity. Thus, our results suggest that negative effects resulting from patch isolation and changes in patch shape on functional diversity will be maintained in the long term as long as forest patches remain disconnected. On the other hand, restoration strategies that promote patch connectivity and approximately circular forest shapes may lead to the increased resilience of plants community functioning in fragmented forests.

In conclusion, patch isolation and patch shape have the potential to individually reduce the functional variability of plant communities. As for the ecological strategy of plants, it seems that dominant plant species in irregularly shaped patches allocate more biomass to durable tissue and protection against physical damage. Because the functional traits used in this study are correlated with important ecosystem functions (growth rate, primary productivity and litter decomposition rate), patch spatial configuration may affect not only functional diversity but also ecosystem functioning.

The detrimental effects of shape and degree of isolation on functional variability may be amplified in patches exhibiting both conditions simultaneously, i.e. an irregular shape and heavy isolation, because both variables increase

environmental stress (as suggested by the negative correlation of these variables with leaf size). A non-additive effect of isolation and shape variables cannot be completely ruled out, but was not tested explicitly in this study because the degrees of freedom were insufficient. It should therefore be tested explicitly in a future study.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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