

# Patterns of phylogenetic community structure of sand dune plant communities in the Yucatan Peninsula: the role of deterministic and stochastic processes in community assembly

Diego F. Angulo, Juan Tun-Garrido, Gerardo Arceo-Gómez, Miguel A. Munguía-Rosas & Victor Parra-Tabla

To cite this article: Diego F. Angulo, Juan Tun-Garrido, Gerardo Arceo-Gómez, Miguel A. Munguía-Rosas & Victor Parra-Tabla (2018): Patterns of phylogenetic community structure of sand dune plant communities in the Yucatan Peninsula: the role of deterministic and stochastic processes in community assembly, *Plant Ecology & Diversity*, DOI: [10.1080/17550874.2018.1534289](https://doi.org/10.1080/17550874.2018.1534289)

To link to this article: <https://doi.org/10.1080/17550874.2018.1534289>

 View supplementary material 

 Published online: 08 Nov 2018.

 Submit your article to this journal 

 View Crossmark data 

ARTICLE



## Patterns of phylogenetic community structure of sand dune plant communities in the Yucatan Peninsula: the role of deterministic and stochastic processes in community assembly

Diego F. Angulo <sup>a</sup>, Juan Tun-Garrido<sup>b</sup>, Gerardo Arceo-Gómez<sup>c</sup>, Miguel A. Munguía-Rosas<sup>d</sup> and Victor Parra-Tabla <sup>a</sup>

<sup>a</sup>Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Mérida, México; <sup>b</sup>Departamento de Botánica, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Mérida, México; <sup>c</sup>Department of Biological Sciences, East Tennessee State University, Johnson City, TN, USA; <sup>d</sup>Laboratorio de Ecología Terrestre, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Mérida, México

### ABSTRACT

**Background:** Tropical sand dunes are ideal systems for understanding drivers of community assembly as dunes are subject to both deterministic and stochastic processes. However, studies that evaluate the factors that mediate plant community assembly in these ecosystems are few.

**Aims:** We evaluated phylogenetic community structure to elucidate the role of deterministic and stochastic processes in mediating the assembly of plant communities along the north of the Yucatan Peninsula, Mexico.

**Methods:** We used plastid genetic markers to evaluate phylogenetic relationships in 16 sand-dune communities. To evaluate the role of climate in shaping plant community structure we carried out linear regressions between climatic variables and mean phylogenetic distance. We estimated the Net Relatedness Index and Nearest Taxon Index to identify ecological processes mediating community assembly.

**Results:** Observed phylogenetic structure was not different from random, suggesting that stochastic processes are the major determinants of community assembly. Climate was slightly correlated with phylogenetic diversity suggesting that abiotic environment plays a minimal role in community assembly.

**Conclusions:** Random assembly appears to be the primary factor structuring the studied sand dune plant communities. Environmental filters may represent a secondary factor contributing to the observed phylogenetic structure. Thus, both processes may act simultaneously to mediate the assembly of sand-dune plant communities.

### ARTICLE HISTORY

Received 2 October 2017  
Accepted 6 October 2018

### KEYWORDS

Biotic interactions; climatic filtering; community assembly; phylogenetic structure; plant diversity; sand-dune communities; Yucatan Peninsula

## Introduction

Understanding the processes and mechanisms that mediate the assembly of plant communities has been a long-standing goal in ecology (Götzenberger et al. 2012; Kamilar et al. 2015; Silva et al. 2015). To date, two main hypotheses regarding the drivers of plant species assemblages in natural communities prevail. The deterministic hypothesis, which predicts that biotic (e.g. competition, facilitation) and/or abiotic factors (e.g. temperature, precipitation) are the main forces that determine species composition in a community. On the other hand, stochastic hypothesis emphasise the role of random events (e.g. random dispersal or disturbance events) as the main factors shaping species assemblages (Palmer 1994; Cavender-Bares et al. 2009; Chase and Myers 2011; Vellend et al. 2014). However, to date, the relative importance of deterministic versus stochastic

processes in mediating the assembly of species in natural communities remains controversial (Cavender-Bares et al. 2009; Wang et al. 2013).

The deterministic scenario suggests that abiotic factors may play an important role filtering out species that do not have the morphological and/or physiological adaptations to withstand (i.e. establish and reproduce) the existing abiotic conditions in a given area (Webb et al. 2002). For example, families in the order Caryophyllales (e.g. Aizoaceae, Cactaceae, Didieraceae and Portulacaceae) have been shown to have evolved a variety of adaptations to prevail in xeric conditions (Landrum 2002). Under this hypothesis, it is thus possible to expect that climatic filters favour the co-occurrence of phylogenetically related species because they often share physiological and morphological attributes owing to their shared evolutionary history (Webb et al. 2002;

Cavender-Bares et al. 2004). However, biotic and abiotic factors could act simultaneously to determine the final composition of species in a community. For instance, variation in climatic conditions can influence the frequency and intensity of species interactions (i.e. competition and facilitation), which, in turn, can influence final species assemblage in a community (Bertness and Callaway 1994; Kikvidze and Callaway 2009).

Bertness and Callaway (1994), for instance, have shown that the strength of interspecific competition can vary along stress gradients (e.g. from high to low water availability). Low stress can result in increased competition between closely related species (due to their high niche overlap), and result in competitive exclusion, thus leading to high phylogenetic diversity (Webb et al. 2002; Kembel and Hubbell 2006; Pausas and Verdú 2010; Kamilar et al. 2015; Martins et al. 2015). It is also possible that under stressful conditions facilitative interactions among species (e.g. plants providing shade and improving soil physical and chemical properties that enhance the establishment and survival of other plants) could be more frequent, thus again resulting in high phylogenetic diversity (e.g. Valiente-Banuet and Verdú 2007). There is growing evidence that facilitation is frequent among plant species in stressful environments, such as deserts (Tewksbury and Lloyd 2001; Flores and Jurado 2003; Tirado and Pugnaire 2003), salt marshes (Bertness and Ewanchuk 2002), savannas (Archer 1995), alpine sedge heaths (Choler et al. 2001; Callaway et al. 2002) and sand dunes (Shumway 2000; Franks 2003).

Conversely, the stochastic hypothesis dismisses the importance of biotic and abiotic factors and emphasises the role of random events in structuring natural communities. It proposes that local community assembly is largely the outcome of chance events, and that deterministic processes play a weak or unimportant role (Ricklefs 2009). According to this hypothesis, the species composition of local communities can be determined by random extinction and random colonisation and dispersal events (Hubbell 2001; Rosindell et al. 2011, 2012), as well as by unpredictable disturbance events (Reice et al. 1990). However, most of the evidence supporting the stochastic hypothesis has come from productive environments such as tropical rainforests and coral reefs (Condit et al. 2002; Latimer et al. 2005; Volkov et al. 2007). As a result, little is known about the potential importance of stochastic events in mediating community

assembly in environments with more limited resource availability and subjected to frequent physical disturbances (e.g. deserts, sand dunes; hereafter stressful environment), where biotic and abiotic filters may play a larger role (e.g. Barbour 1992; Ripley and Pammenter 2004).

It has also been shown that both, deterministic and stochastic mechanisms, can act together in mediating community assembly, and that their relative importance can depend on the intrinsic dynamics of local communities (Leibold and McPeck 2006; Adler et al. 2007; Ellwood et al. 2009; Yang et al. 2013). For instance, plant communities that are subjected to recurrent successional processes that lead to random and continuous loss and recovery of vegetation (e.g. sand-dune communities) can also be found in unfavourable environments where facilitative interactions are predicted to be strong. In this case, random and deterministic mechanisms can be predicted to be strong and act together to mediate community assembly (e.g. Forey et al. 2009; Maltez-Mouro et al. 2010; Gallego-Fernández and Martínez 2011).

Plant communities found in stressful environments, such as coastal sand dunes, where biotic and abiotic filters can be strong determinants of community structure (Valiente-Banuet and Verdú 2007; Forey et al. 2009) are ideal systems to evaluate the relative importance of deterministic versus random mechanisms in shaping community assembly. Tropical sand-dune communities are often characterised by low and unpredictable rainfall, high incidence of solar radiation, high soil temperature, high levels of erosion by water and wind, high salt content in air and soil and low nutrient availability (Shreve 1942; Maun 2004; Miller et al. 2010). Indeed, many plant traits such as thick leaf cuticles and a leathery texture, dense layers of pubescence, small leaves and nutrient storage organs have been shown to be important for species to succeed in these environments (Noy-Meir 1973; Marin and Medina 1981; Gallego-Fernández and Martínez 2011). Thus the environment is expected to play an important role in the assembly of these communities. However, sand-dune communities are also characterised by a cyclic succession (i.e. frequent changes in plant species abundance and composition as a result of a high frequency of extreme climatic events; Chapman 1976; Lugo 1980), in which floods, high tides, strong winds and sand movement impact the

composition of species in these plant communities (Martínez et al. 2001; Álvarez-Molina et al. 2012). Thus, in sand-dune ecosystems, stochastic processes such as the incidence of storms and hurricanes can result in the removal of existing vegetation and the opening new niches that can be readily occupied by pioneer species and/or randomly arrived propagules (Guevara 1982; Moreno-Casasola 1985; Maun 2009). However, in spite of their importance, few studies have evaluated the relative role of stochastic and deterministic process in mediating the assembly of sand dune plant communities.

Here, we quantified the processes that mediate phylogenetic structure of pioneer sand dune plant communities along the entire north coast of the Yucatan Peninsula. These sand dune plant communities are located along a noticeable climatic gradient with variation in annual mean precipitation (AMP) and seasonal temperature (White and Hood 2004; Orellana et al. 2009; Torrescano-Valle and Folan 2015). In addition, this region is subjected to frequent and intense tropical storms, such as hurricanes (Sánchez-Sánchez et al. 2015), which has the potential to affect local plant communities on the coast (see Álvarez-Molina et al. 2012). However, the potential role of extreme weather phenomena in mediating patterns of plant community assembly has not been explored in these communities. Overall, we expect that in relatively low stressful environments (high precipitation and low temperature) plant phylogenetic diversity will be high, whereas in stressful environments (low precipitation and high temperature) low levels of phylogenetic diversity will be observed. The finding of a significant relationship between climatic variables and phylogenetic diversity would be indicative that climate is an important filter mediating plant community assembly (Moreno-Casasola and Espejel 1986; Espejel 1987; White and Hood 2004). However, to our knowledge, this has not been tested. Conversely, a continuous successional dynamic could lead to random assembly of local plant communities. In this case, random assembly may result from continuous niche openings due to clearing of existing vegetation by extreme climatic events. These new niches would then be occupied, in a random manner, by plants from the pool of available species. Thus, changes in vegetation cover would be highly dependent on the frequency and intensity of extreme climatic events.

Thus, in this study we asked the following specific questions (1) does the variation in climate

along the north coast of the Yucatan Peninsula affects patterns of phylogenetic diversity in sand dune plant communities; and (2) are local plant communities phylogenetic clustered or over-dispersed compared to expected patterns of random community assembly.

## Materials and methods

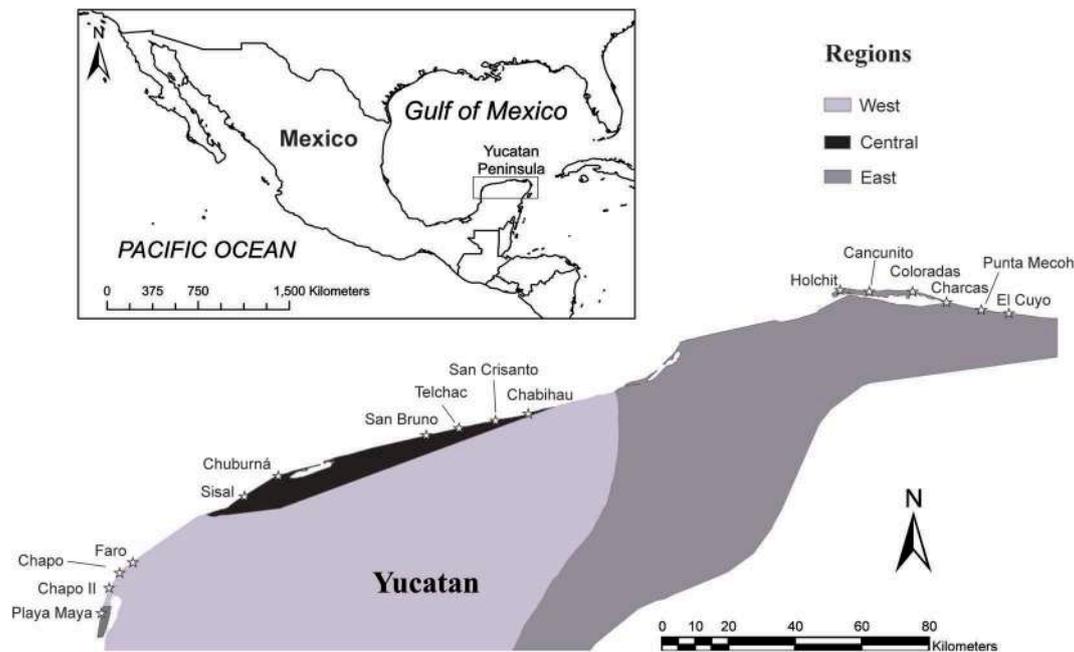
### Study area

The study was conducted in the sand dune plant communities along the north coast of the Yucatan Peninsula, Mexico (Figure 1). The coast of the Yucatan Peninsula represents a transition zone between the Gulf of Mexico and the Caribbean (Mendoza-González et al. 2016). The vegetation of the Gulf of Mexico contains species typical of the western Yucatan Peninsula, while the east of the Peninsula has been influenced by Caribbean plant elements (Moreno-Casasola and Espejel 1986; Espejel 1987; Chiappy et al. 2001). The sand dune plant community is composed of annuals and perennial herbs and shrubs such as *Cakile edentula*, *Sesuvium portulacastrum*, *Licium carollinianum*, *Scaevola plumieri*, *Suriana maritima* and *Ipomoea pes-caprae* which are the most representative species (Miranda 1978; Espejel 1984, 1987; Flores and Espejel 1994).

Within the climatic gradient recognised in the Yucatan Peninsula, the predominant climate in the eastern part is a warm sub-humid tropical environment (mean annual precipitation: 800 mm; Espejel 1987; Orellana et al. 2009; Parra-Tabla et al. 2018), while in the north-westernmost portion of the Peninsula it is arid tropical (ca. 600 pp annual; White and Hood 2004, Parra-Tabla et al. 2018). For this study we selected 16 sites distributed along a coastline of 296 km, encompassing the entire climatic gradient of the Yucatan Peninsula. The average distance among sites was 18.5 km (range: 4–106 km; Figure 1).

### Vegetation sampling

We recorded the identity of each plant species (trees, shrubs, herbs and grasses) present at each site within the fore dune by using the line intercept method (Canfield 1941) between January and March 2016. For this, we established two 100 m linear transects at each site parallel to the coastline and further laid 10 m perpendicular sub-transects on alternate sides of the main transect. The identity



**Figure 1.** Map of Mexico with a zoom on the location of the 16 study sites along the climatic gradient in the north of the Yucatan Peninsula.

of every plant species in each sub-transect was recorded. The two main transects were separated by 50 m. This sampling effort has been previously shown to accurately capture plant species abundance and diversity in these sites (Parra-Tabla et al. 2018; Espejel 1984; Torres et al. 2010). For this study, we only considered presence-absence data because sand dune communities are characterised by low species abundance and cyclic succession (Chapman 1976; Acosta et al. 2009) which could bias results based on abundance.

### **Community phylogenetic reconstruction**

We reconstructed phylogenetic relationships among all the species recorded across all 16 sites by creating a DNA matrix, using two plastid genetic markers (*matK* and *rbcL*). The sequences were obtained from the GenBank database (GenBank accessions are listed in Table S1). Where we were unable to obtain precise sequence data for a species (15 species; 20% of the total), we used data from a sister species (Table S1). The gene regions were concatenated and analysed as a single matrix that was proofed, edited and assembled using PhyDE v.0.99 (Müller et al. 2010). The CpDNA matrix resulted in an aligned matrix of 1912 bp.

To assess the phylogenetic structure, we used a cladogram based on a time-calibrated tree, which was estimated by using a Bayesian approach implemented in BEAST v.1.8.0 (Drummond et al. 2012). The GTR

+ G model was selected based on the AICc values from jModelTest 0.1.1 (Posada 2008). The dataset included gymnosperm species as the out-group (Table S1). We calibrated the genetic tree with three calibration points in the Monocotyledoneae, Eudicotyledoneae and Mesangiospermae following Magallón et al. (2015). The Markov chain Monte Carlo (MCMC) was run simultaneously in four independent runs for 50 million generations and sampling every 2000 generations. TRACER v.1.5 (Rambaut and Drummond 2009) was used to assess convergence and to estimate the effective sample sizes for all parameters. Based on these results, 25% of the stored trees were discarded as burn-in, and the remaining samples were summarised as a maximum clade credibility tree in TREEANNOTATOR 1.6.1, displaying the mean divergence times and 95% highest posterior density (HPD) intervals of each age estimate (Drummond and Rambaut 2007). These results were summarised on a single tree visualised in FIGTREE v. 1.5.4 (<http://tree.bio.ed.ac.uk/software/figtree/>) (Figure S1).

### **Community phylogenetic structure**

The environmental variables included AMP, annual mean temperature (AMT) and temperature seasonality (TS) for each site. All these variables have been shown to strongly influence plant species distribution in studies that evaluate community structure (e.g. Walter 1971; Zaniwski et al. 2002). These were obtained from the WorldClim-

Bioclim database ([www.worldclim.org](http://www.worldclim.org); Hijmans et al. 2005). To test for potential spatial autocorrelation among the plant communities sampled, we conducted a Moran's eigenvector map (MEM's; formerly PCNM [Principal Coordinates of Neighbour Matrices]) and a redundancy analysis (RDA; Dray et al. 2006; Borcard et al. 2011; Legendre and Gauthier 2014). For this, we used the geographical coordinates (i.e. latitude and longitude) of each site. The MEM's and RDA analyses were implemented using 'vegan 2.4' (Oksanen et al. 2017) and the 'packfor' packages in R (Dray et al. 2011, R Core Team 2015).

#### ***Climatic influence on phylogenetic diversity***

We related AMP, AMT and TS with mean pairwise phylogenetic distance (MPD). MPD estimates phylogenetic diversity by calculating the average phylogenetic relatedness between all possible pairs of taxa in a community. We used MPD because this metric is more sensitive than mean nearest taxon phylogenetic distance (MNTD) in deciphering climate – plant distribution relationships (Kraft et al. 2007; Kamilar et al. 2015). Temperature seasonality measures temperature variation over a given year (or averaged years) based on the standard deviation (variation) of monthly temperature averages (O'Donnell and Ignizio 2012). Thus, high variation would indicate high temperature seasonality, while low variation would indicate more stable climatic conditions throughout the year (low temperature seasonality). Temperature seasonality has been proposed as an important variable related to the assembly of the regional forest of the Yucatan Peninsula (e.g. Becerra 2005).

As climatic variables tend to be highly correlated (Wellenreuther et al. 2012; Angulo et al. 2014), we collapsed them into a single variable, using Principal Component Analysis (PCA). We then carried out linear univariate regressions between MPD and the first axis produced by PCA, which explained the largest amount of variation (see results below). Principal Component Analysis and linear regression analyses were carried out in SAS v.9.2 (SAS Institute 2009, Cary, North Carolina, USA).

#### ***Community phylogenetic metrics***

We identify the processes driving sand dune plant community assembly based on phylogenetic patterns (random, clustered or over-dispersed) within each community by estimating Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) (Webb 2000; Webb et al. 2002). These two metrics

provide distinct and evolutionarily relevant information about the phylogenetic structure of each community studied. Specifically, NRI measures the standardised effect size of MPD, which estimates the average phylogenetic relatedness between all possible pairs of taxa in a community. NTI, on the other hand, measures the standardised effect size of the MNTD, which quantifies the phylogenetic distance among the most closely related species in a community (Webb et al. 2002; Vamosi et al. 2009). Significant positive values of NTI and NRI (NRI and NTI > 0; phylogenetic clustering trend) indicate that communities are phylogenetically more clustered than expected by chance, thus suggesting that climatic filtering may be influencing community composition. Conversely, significant negative values of NRI and NTI (NRI and NTI < 0; Phylogenetic evenness trend) indicate that plant communities are phylogenetically more over-dispersed than expected by chance, perhaps due to competitive exclusion among related species.

Communities assembled by stochastic events are expected to exhibit a phylogenetic structure that is not significantly different from that of randomly assembled communities.

We reported MPD and MNTD in millions of years and NRI and NTI in units of standard deviation. Analyses were made using a presence-absence matrix and the metrics were estimated using the 'picante' package (Kembel et al. 2010) for R v. 2.14.0 (R Development Core Team 2015).

## **Results**

### ***Community phylogenetic structure***

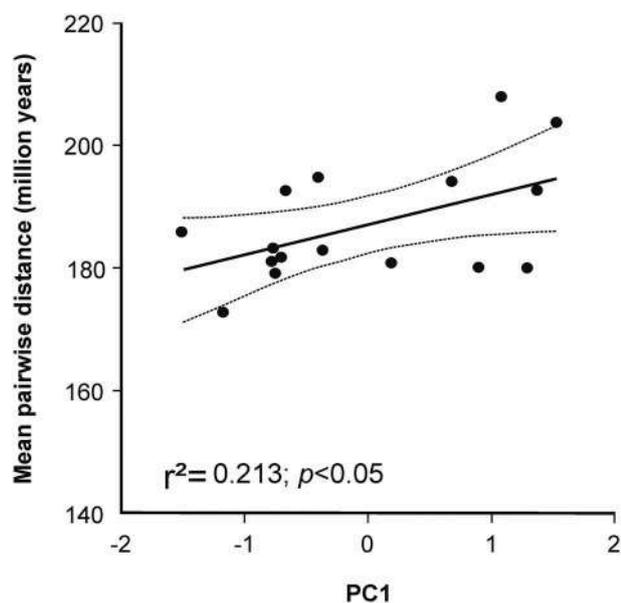
We found a total of 72 angiosperm species belonging to 37 families across the 16 sites sampled. Poaceae (11 species), Fabaceae, Asteraceae and Amaranthaceae (five species each) were the most representative families found at the study sites. The majority of the species were herbaceous (40), followed by shrubs (18), vines (7), trees (5) and palms (2). Sixty-two percent of the families were represented by a single genus and a single species each (Table S1).

Multivariate analyses (MEM and RDA) showed no spatial autocorrelation among sites with respect to plant species composition ( $P > 0.05$  in both cases).

### ***Climatic and phylogenetic diversity***

Principal components analyses showed that 66% of the climatic variation was explained by the first component (PC1). Therefore, this axis was used

to make correlations with phylogenetic estimates of the community in subsequent analyses (see below). TS and AMP showed a strongly positive correlation with PC1 (factor loading = 0.959, and 0.775, respectively), while AMT had a negative correlation (factor loading =  $-0.680$ ). Climate (represented by PC1) significantly affected the degree of phylogenetic diversity (MPD) ( $R^2 = 0.26$ ,  $P < 0.05$ ; Figure 2; see all regression results in Table S2). Localities such as Sisal, Telchac and Faro had low PC1 values, which indicates that these are sites with greater climatic stress (i.e. high AMT and low AMP) and low TS (i.e. more climatic stability).



**Figure 2.** Relationships between mean pairwise distance (MPD) and the first PCA component (PC1). The regression line is depicted by a solid line and the 95% confidence intervals by a dashed line.

These localities also showed low values of phylogenetic diversity (Table 1). In contrast, sites such as Coloradas, El Cuyo and Playa Maya had high values of PC1 indicating less stressful habitats (i.e. low AMT and high AMP) with high TS (i.e. less climatic stability). These sites had high phylogenetic diversity (Table 1). Some localities like San Bruno, Chuburná and Punta Mecó had intermediate PC1 values and intermediate values of phylogenetic diversity.

### Community phylogenetic metrics

Average phylogenetic diversity ranged from  $-0.42$  to  $+1.47$  for NTI and of  $-1.38$  to  $+1.17$  for NRI. Holchit, Punta Mecó and Sisal were localities with high values of NTI, while Telchac, Playa Maya and San Bruno had low values (Figure 3). High values of NRI were observed for Sisal, Chapo 1 and Telchac, and low values for Playa Maya, El Cuyo and Coloradas (Figure 3).

At the community level we did not observe differences between observed phylogenetic structures and those expected under random assembly at any site (Table 1).

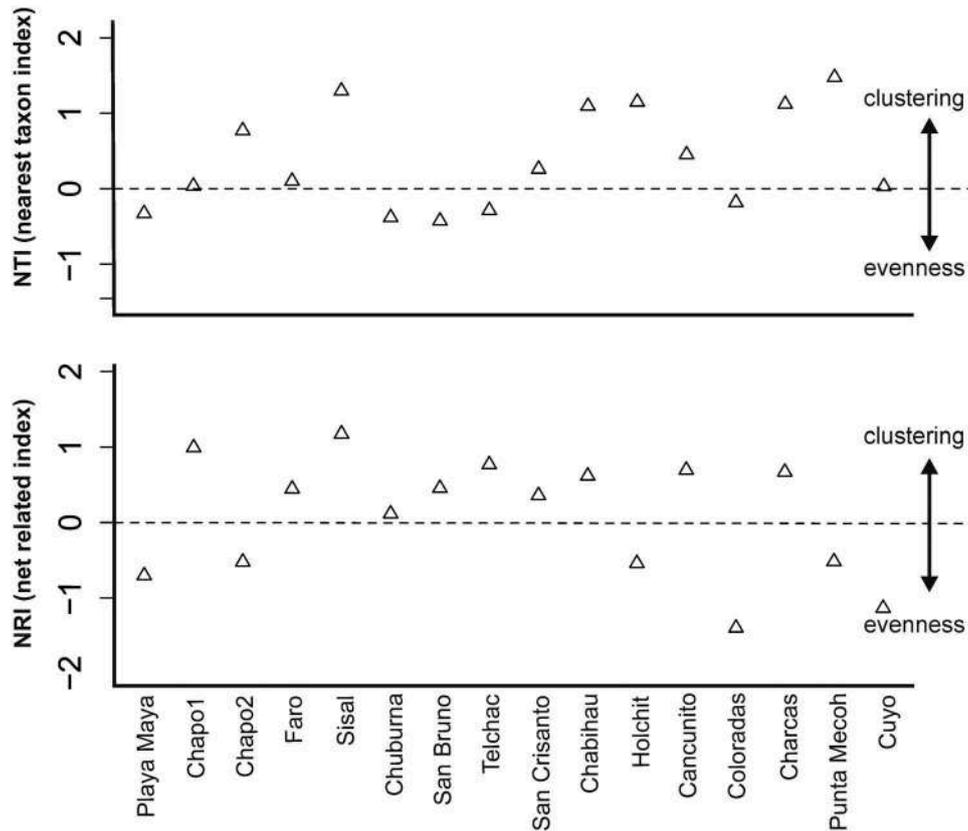
### Discussion

Overall, our results suggest that climatic conditions play a minor role in determining phylogenetic diversity in the plant communities studied even though climate has been largely suggested as a strong driver of community assembly of sand dune communities (Espejel 1987). On the other hand, stochastic processes, likely driven by extreme climatic events, seem to be the major underlying

**Table 1.** Climatic variables and results of the community phylogenetic structure from the 16 coastal sand dune plant communities.

Species	Longitude	Latitude	NTI	<i>p</i> -value	NRI	<i>p</i> -value	MPD	Climatic variables			
								Temperature (standard deviation*100)	Seasonality	Annual mean precipitation	Annual mean temperature
Cancunito	-88.04921952	21.61090035	0.45	0.34	0.71	0.25	179.91	21.22	20.99	646	25.4
Holchit	-88.10398426	21.62039547	1.15	0.12	-0.53	0.67	193.97	20.74	20.95	624	25.4
Cuyo	-87.65956036	21.51403298	0.03	0.49	-1.12	0.86	203.64	20.95	20.95	759	25.2
Punta Mecóh	-87.73949843	21.53033966	1.48	0.07	-0.50	0.66	192.62	21.05	20.95	733	25.3
Charcas	-87.83830432	21.56191733	1.12	0.13	0.68	0.26	179.92	21.05	20.95	713	25.3
Coloradas	-87.94938797	21.60277215	-0.13	0.58	-1.39	0.93	207.92	21.05	20.95	674	25.3
Chuburna	-89.82900262	21.24844443	-0.38	0.66	0.12	0.38	185.78	17.92	18.29	490	25.6
Sisal	-89.955681	21.197769	1.30	0.09	1.18	0.11	172.77	18.14	18.29	548	25.7
Chabihau	-89.0659788	21.36756005	1.10	0.13	0.63	0.25	180.79	19.65	19.03	683	25.7
San Crisanto	-89.18632409	21.3531579	0.26	0.41	0.37	0.31	182.92	19.03	18.29	629	25.7
Telchac	-89.29660491	21.3406644	-0.29	0.59	0.78	0.18	179.23	18.29	18.29	598	25.6
San Bruno	-89.39250295	21.33104139	-0.43	0.64	0.46	0.35	183.11	18.47	19.04	581	25.6
Chapo1	-90.32437109	21.01432538	0.04	0.48	1.00	0.16	181.69	19.04	18.93	651	26.2
Chapo2	-90.35518985	20.97710473	0.77	0.21	-0.52	0.67	192.52	18.93	19.21	665	26.2
Playa Maya	-90.36644675	20.92008166	-0.33	0.62	-0.70	0.74	194.73	19.21	19.04	708	26.3
Faro	-90.294092	21.038076	0.10	0.47	0.45	0.34	180.95	19.04	19.04	637	26.2

NRI: Net relatedness index and NTI: nearest taxa index are shown. Climatic data was obtained from WorldClim (Hijmans et al. 2005; available at <http://www.worldclim.org>) database



**Figure 3.** Differences in the Nearest Taxon Index (NTI) and Net Relatedness Index (NRI) among the studied communities in the north of the Yucatan Peninsula. The open triangles correspond to the values of NTI/NRI found in the Table 1. Positive values indicate phylogenetic clustering and negative values indicate phylogenetic evenness.

factor that structure sand dune plant communities in the Yucatan.

### Community phylogenetic structure

#### Climatic influence on phylogenetic diversity

Our results suggest that climatic variation plays a minor role influencing the phylogenetic diversity observed at each site. Specifically, localities in the east of the Peninsula with less stressful and less stable habitats such as Coloradas, El Cuyo and Holchit (Figure 1) seem to favour the establishment of distantly related species (i.e. greater phylogenetic diversity). However, as climatic conditions become more stressful and more stable, the establishment of more closely related species is favoured (i.e. lower phylogenetic diversity) as is the case in western-central locations such as Sisal, El Faro and Telchac. In all these sites, climatic stress is high and phylogenetic diversity is low. Thus, stressful environments may impose a strong filter where only species with a specific set of traits that help to tolerate such conditions may survive (Espejel 1987; Maun 2004; Gómez et al. 2010). For example, some of the derivate clades that

are lost in stressful areas are the *Dicliptera sexangularis* and *Bravaisia berlandieriana* (Acanthaceae) clade and species such as *Lycium carolinianum* (Solanaceae), and *Maytenus phyllanthoides* (Celastraceae) which grow in the coastal scrubland with less saline soils and more humid and/or shaded areas (authors' pers. obs.). Thus, if the traits that help to tolerate stressful environments are evolutionarily conserved this could then lead to a pattern of low phylogenetic diversity (Webb 2000; Cavender-Bares et al. 2004) such as the one observed here. Patterns of low phylogenetic diversity in harsh environments and high phylogenetic diversity in less stressful environment conditions have been observed in both plant (e.g. Culmsee and Leuschner 2013; González-Caro et al. 2014) and animal communities (e.g. Kamilar et al. 2015). Interestingly, some of our communities showed climatic conditions that do not correspond with the climate of the broader regional areas where they are located (Espejel 1987; Figure1). However, they still followed the overall environment-phylogenetic diversity pattern observed. For example, Chapo 2 is geographically located in the driest part of the Yucatan Peninsula (Figure 1), but

local precipitation and temperature data indicated low levels of climatic stress. In contrast, Playa Maya, located near the driest region, lies parallel to the isoclimatic line of precipitation that influences the eastern region (wettest) (Orellana et al. 2009). Both Chapo 2 and Playa Maya had high levels of phylogenetic diversity (Table 1). On the other hand, Cancunito and Charcas are geographically located in the less dry part of Yucatan Peninsula and they both had low levels of phylogenetic diversity (Table 1) as predicted by climatic filtering. It is possible that phylogenetic diversity at these sites could be associated with other unmeasured environmental factors. For instance, Espejel (1987) has reported an important variation in physical and chemical properties of the soil in the north of the Yucatan Peninsula which could influence plant species distribution (see also Espejel 1984; Valverde et al. 1997).

Overall, our results suggest that even though individual communities share similar local environmental characteristics (e.g. high radiation, low availability of nutrients, high salt concentrations in air and soil), broader differences in temperature seasonality and precipitation along the coastal communities may play a role in influencing phylogenetic structure in these communities. It is important to note that previous studies have shown no relationship between taxonomic and phylogenetic diversity at the study sites (Parra-Tabla et al. 2018) suggesting that the increase in phylogenetic diversity is not driven by an increase in the number of species at a site.

### **Community phylogenetic metrics**

All the plant communities studied showed a random pattern of species assembly since NTI and NRI values were not significantly different from those obtained from null models. Random species assembly in these communities could be the result of constant and dynamic natural successional processes in sand dune coastal systems (Guevara 1982; Moreno-Casasola 1985). Furthermore, rainfall, dew, fog, floods, waves, tides, winds and sand movement (Martínez et al. 2001; Álvarez-Molina et al. 2012) are not uniform along the Yucatan coast and could also contribute to the random patterns of plant community assembly observed in this region. It is also possible that the constant influx of storms and hurricanes to the area (Boose et al. 2003; Islebe et al. 2015) could lead to reduced stability and a constant opening of vegetation gaps that could then be occupied by the random arrival

on new propagules (Guevara 1982; Moreno-Casasola 1985; Martínez et al. 2001; Álvarez-Molina et al. 2012). Furthermore, random storms and/or hurricanes could also alter the strength of biotic and abiotic filters thus weakening their potential effect on community assembly. For instance, hurricanes may alter the result of species competition by limiting the complete establishment of dominant species and thus permit the occurrence of less competitive species that otherwise would be excluded (Gornish and Miller 2010; Ciccarelli et al. 2012). Such an effect could thus weaken the role of long-term interspecific competition or facilitation processes in the assembly of these communities (Hubbell 2001; Ricklefs 2008, 2009). However, we do not necessarily expect that these major climatic events would impact all communities evenly and with the same intensity. For example, in the last 30 years three major hurricanes (Gilberto, 1988; Isidoro, 2004; and Wilma, 2005) have hit the Yucatan Peninsula from the northeast (Islebe et al. 2015) while have also crossed the entire Peninsula and increased in strength when entering the Gulf of Mexico thus affecting the western plant communities (Boose et al. 2003; Islebe et al. 2015). These differences in the trajectory and intensity of extreme climatic events could help explain the random phylogenetic structure of sand dune plant communities in the Yucatan Peninsula. In this sense, local communities would largely be the outcome of random extinction, colonisation and dispersal events (Hubbell 2001; Vellend et al. 2014) and phylogenetic diversity (most species belonging to different botanical families) would be explained by the stochastic arrivals of species. It is important to note, however, that several studies have questioned the usefulness of phylogenetic analysis in inferring community assembly mechanisms, mainly due to the spatial and temporal scale-dependency of phylogenetic patterns (Emerson and Gillespie 2008; Cavender-Bares et al. 2009; Gerhold et al. 2015; Cadotte et al. 2017). Other studies have suggested that the detection of assembly processes may be constrained by the number of species in each community and that a large number of species (> 80) are needed in order to detect significant ecological assembly patterns (Tucker and Cadotte 2013). It is also important to note that in this study we grouped species with very different physiological strategies (e.g. trees and agaves) and these may respond differently to stressful climatic conditions as well as observed differences in the intensity of

human impacts across our study sites. Thus, we suggest that future studies should consider physiological differences as well as human disturbances when evaluating the mechanisms that drive plant community assembly. Notwithstanding, our results represent a first approximation to understanding the mechanisms that mediate the assembly of coastal plant communities in the Yucatan.

### **Patterns of phylogenetic diversity drive community assembly in coastal communities**

To date, there is limited knowledge on the phylogenetic diversity of plant communities in general, and of coastal sand dunes communities in particular. Furthermore, Studies that have aimed to elucidate the mechanisms that structure the assembly of plant communities in coastal dunes have been mostly conducted in temperate systems and thus limited evidence exist for plant communities in the tropics (e.g. Gallego-Fernández and Martínez 2011; Chozas et al. 2017). Our results in a tropical system are partially in line with studies that have suggested that environmental filters drive species composition of sand dunes in temperate areas of America and Europe (Gallego-Fernández and Martínez 2011; Brunbjerg et al. 2012; Chozas et al. 2017). Likewise, Forey et al. (2008) have demonstrated that physical disturbance in the dunes of the French coast is an important factor driving the composition of plant communities. In sand dune plant communities of tropical islands, it has been suggested that distance to the mainland and stochastic events are mainly responsible for differences in species composition and diversity among islands (Da Silva et al. 2018).

### **Conclusions**

Our results suggest that species assemblage in sand dune plant communities in the north coast of the Yucatan Peninsula is primarily affected by stochastic processes and to a lesser degree by the climatic environment. Overall, our results suggest that stochastic processes and environment filters are not mutually exclusive and could act in concert to shape the assembly of plant communities.

### **Acknowledgements**

We thank to Cristopher Albor, Rigel Silveira for field assistance. This study was founded by a grant from CONACyT (248406) to VP-T.

### **Disclosure statement**

No potential conflict of interest was reported by the authors.

### **Funding**

This work was supported by the Consejo Nacional de Ciencia y Tecnología [248406].

### **Notes on contributors**

*Diego F. Angulo* is a post-doctoral researcher and is interested in phylogeography, ecology and evolutionary biology of flowering plants.

*Juan Tun-Garrido* is a plant taxonomist. His research interests are focused in the systematic, floristic and biogeography of the Yucatan flora.

*Gerardo Arceo-Gómez* is a plant ecologist. His research interest is focused in ecology and evolution of plant-animal interactions and community ecology.

*Miguel A. Munguía-Rosas* is a plant ecologist. His research interests include community ecology mainly related to anthropogenic impacts on vegetation.

*Victor Parra-Tabla* is a plant ecologist. His research interest is focused in plant ecology and especially on single and multiple plant-insect interactions.

### **ORCID**

Diego F. Angulo  <http://orcid.org/0000-0002-5678-4946>  
Victor Parra-Tabla  <http://orcid.org/0000-0001-5920-0881>

### **References**

- Álvarez-Molina LL, Martínez ML, Pérez-Maqueo O, Gallego-Fernández JB, Flores P. 2012. Richness, diversity, and rate of primary succession over 20 years in tropical coastal dunes. *Plant Ecol.* 213:1597–1608.
- Acosta A, Carranza ML, Izzi CF. 2009. Are there habitats that contribute best to plant species diversity in coastal dunes? *Biodivers Conserv.* 18:1087–1098.
- Adler PB, HilleRisLambers J, Levine JM. 2007. A niche for neutrality. *Ecol Lett.* 10:95–104.
- Angulo DF, Amarilla LD, Sosa V. 2014. Incipient speciation in the Chihuahuan Desert shrub *Berberis trifoliolata* under divergent climate scenarios. *Botany-Botanique.* 92:195–201.
- Archer S. 1995. Tree-grass dynamics in a *Prosopis* e thornscrub Savanna parkland: reconstructing the past and predicting the future. *Ecoscience.* 2:83–99.
- Barbour MG. 1992. Life at the leading edge: the beach plant syndrome. In: Seeliger V, Editor. *Coastal plant communities of Latin America*, pp 291–307. New York: Academic Press Inc.

- Becerra JX. 2005. Timing the origin and expansion of the Mexican tropical dry forest. *Proc Natl Acad Sci*. 102:10919–10923.
- Bertness MD, Callaway R. 1994. Positive interactions in communities. *Trends Ecol Evol*. 9:191–193.
- Bertness MDEwanchuk PJ. 2002. Latitudinal and climate-driven variation in the strength and nature of biological interactions in new england salt marshes. *Oecologia*. 132:392–401.
- Boose ER, Foster DR, Barker Plotkin A, Hall B. 2003. Geographical and historical variation in hurricanes across the Yucatan Peninsula. In: Gómez-Pompa A, Allen MF, Fedick S, Jiménez-Osornio JJ, editors. *Lowland Maya area: three millennia at the human-wildland interface*. New York (New York, USA): Haworth Press; p. 193–213.
- Borcard D, Gillet F, Legendre P. 2011. *Numerical Ecology with R*. New York: Springer Verlag; p. 1–319.
- Brunbjerg AK, Ejrnæs R, Svenning JC. 2012. Species sorting dominates plant metacommunity structure in coastal dunes. *Acta Oecologica*. 39:33–42.
- Cadotte MW, Davies TJ, Peres-Neto PR. 2017. Why phylogenies do not always predict ecological differences. *Ecol Monogr*. 87:535–551.
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, et al. 2002. Positive interactions among alpine plants increase with stress. *Nature*. 417:844–848.
- Canfield RH. 1941. Application of the line interception method in sampling range vegetation. *J For*. 38:388–394.
- Cavender-Bares J, Ackerly DD, Baum DA, Bazzaz FA. 2004. Phylogenetic overdispersion in Floridian oak communities. *Am Nat*. 163:823–843.
- Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW. 2009. The merging of community ecology and phylogenetic biology. *Ecol Lett*. 12:693–715.
- Chapman VJ. 1976. *Mangrove vegetation*. Germany: J. Cramer Verlag.
- Chase JM, Myers JA. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Trans Royal Soc London B Biol Sci*. 366:2351–2363.
- Chiappy C, Rico-Gray V, Gama L, Giddings L. 2001. Floristic affinities between the Yucatan Peninsula and some karstic areas of Cuba. *J Biogeogr*. 28:535–542.
- Choler P, Michelet R, Callaway RM. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology*. 82:3295–3308.
- Chozas S, Correia O, Santos AMC, Hortal J. 2017. Trait dynamics of Mediterranean xerophytic shrub communities growing on stabilised inland dunes respond to nutrient and aridity gradients. *Plant Ecol Divers*. 10:115–126.
- Ciccarelli D, Bacaro G, Chiarucci A. 2012. Coastline dune vegetation dynamics: evidence of no stability. *Folia Geobotanica*. 47:263–275.
- Condit R, Pitman N, Leigh Jr EG, Chave J, Terborgh J, Foster RB, Núñez P, Aguilar S, Valencia R, Villa G, et al. 2002. Beta-diversity in tropical forest trees. *Science*. 295:666–669.
- Culmsee H, Leuschner C. 2013. Consistent patterns of elevational change in tree taxonomic and phylogenetic diversity across Malaysian mountain forests. *J Biogeogr*. 40:1997–2010.
- da Silva RM, Âca R, Mehlig U. 2018. Diversity and dominance patterns in Amazon coast dune forest island tree communities. *Plant Ecol*. 219:343–357.
- Dray S, Legendre P, Blanchet G. 2011. Packfor: forward selection with permutation. R package version 0.0-8/r100. Available at: <http://R-Forge.R-project.org/projects/sedar/>
- Dray S, Legendre P, Peres-Neto PR. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol Modell*. 196:483–493.
- Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol Biol*. 7:214.
- Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol Biol Evol*. 29:1969–1973.
- Ellwood MDF, Manica A, Foster WA. 2009. Stochastic and deterministic processes jointly structure tropical arthropod communities. *Ecol Lett*. 12:277–284.
- Emerson BC, Gillespie RG. 2008. Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol Evol*. 23:619–630.
- Espejel I. 1984. La vegetación de las dunas costeras de la Península de Yucatán. I. Análisis florístico del estado de Yucatán. *Biotica*. 9:183–210.
- Espejel I. 1987. A phytogeographical analysis of coastal vegetation in the Yucatan Peninsula. *J Biogeogr*. 14:499–519.
- Flores J, Jurado E. 2003. Are nurse–protégé interactions more common among plants from arid environments? *J Vegetation Sci*. 14:911–916.
- Flores JS, Espejel I. 1994. Tipos de vegetación de la Península de Yucatán. *Etnoflora Yucatanense*, Fascículo 3. Mérida (Yucatán).
- Forey E, Chapelet B, Vitasse Y, Tilquin M, Touzard B, Michalet R. 2008. The relative importance of disturbance and environmental stress at local and regional scales in French coastal sand dunes. *J Vegetation Sci*. 19:493–502.
- Forey E, Lortie CJ, Michalet R. 2009. Spatial patterns of association at local and regional scales in coastal sand dune communities. *J Vegetation Sci*. 20:916–925.
- Franks SJ. 2003. Facilitation in multiple life-history stages: evidence for nucleated succession in coastal dunes. *Plant Ecol*. 168:1–11.
- Gallego-Fernández JB, Martínez ML. 2011. Environmental filtering and plant functional types on Mexican fore-dunes along the Gulf of Mexico. *Ecoscience*. 18:52–62.
- Gerhold P, Cahill JF, Winter M, Bartish IV, Prinzing A. 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Funct Ecol*. 29:600–614.
- Gómez JM, Verdu M, Perfectti F. 2010. Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature*. 465:918–921.
- González-Caro S, Umaña MN, Álvarez E, Stevenson PR, Swenson NG. 2014. Phylogenetic alpha and beta diversity in tropical tree assemblages along regional-scale environmental gradients in northwest South America. *J Plant Ecol*. 7:145–153.
- Gornish ES, Miller TE. 2010. Effects of storm frequency on dune vegetation. *Glob Chang Biol*. 16:2668–2675.

- Götzenberger L, De Bello F, Bråthen KA, Davison J, Dubuis A, Guisan A, Lepš J, Lindborg R, Moora M, Pärtel M, et al. 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biol Rev.* 87:111–127.
- Guevara S. 1982. Ecología de la vegetación de dunas costeras: esquema de investigación. *Biotica.* 7:603–610.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol.* 25:1965–1978.
- Hubbell SP. 2001. The unified neutral theory of biodiversity and biogeography. Princeton (New Jersey, USA): Princeton University Press.
- Islebe GA, Calmé S, León Cortés J, Schmook B. 2015. Biodiversity and conservation of the Yucatan Peninsula. Suiza: Springer.
- Kamilar JM, Beaudrot L, Reed KE. 2015. Climate and species richness predict the phylogenetic structure of African mammal communities. *PLoS ONE.* 10(4):e0121808.
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomber SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics.* 26:1463–1464.
- Kembel SW, Hubbell SP. 2006. The phylogenetic structure of a neo-tropical forest tree community. *Ecology.* 87:S86–S99.
- Kikvidze Z, Callaway RM. 2009. Ecological facilitation may drive major evolutionary transitions. *BioScience.* 59:399–404.
- Kraft NJB, Cornwell WK, Webb CO, Ackerly DD. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *Am Naturalist.* 170:271–283.
- Landrum JV. 2002. Four succulent families and 40 million years of evolution and adaptation to xeric environments: what can stem and leaf anatomical characters tell us about their phylogeny? *Taxon.* 51:463–473.
- Latimer AM, Silander JA, Cowling RM. 2005. Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. *Science.* 309:1722–1725.
- Legendre P, Gauthier O. 2014. Statistical methods for temporal and space–time analysis of community composition data. *Proc Royal Society. B.* 281:20132728.
- Leibold MA, McPeck MA. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology.* 87:1399–1410.
- Lugo AE. 1980. Mangrove ecosystems: successional or steady state? *Biotropica.* 12:65–72.
- Magallón S, Gómez-Acevedo S, Sánchez-Reyes LL, Hernández-Hernández T. 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist.* 207:437–453.
- Maltez-Mouro S, Maestre FT, Freitas H. 2010. Co-occurrence patterns and abiotic stress in sand-dune communities: their relationship varies with spatial scale and the stress estimator. *Acta Oecologica.* 36:80–84.
- Marin D, Medina E. 1981. Duracion foliar, contenido de nutrientes y esclerofilia en arboles de un bosque muy seco tropical. *Acta Cient Venez.* 32:508–514.
- Martínez ML, Vázquez G, Sánchez-Colon S. 2001. Spatial and temporal variability during primary succession on tropical coastal sand dunes. *J Vegetation Sci.* 12:361–372.
- Martins CA, Roque FO, Santos BA, Ferreira VL, Strüssmann C, Tomas WM. 2015. What shapes the phylogenetic structure of anuran communities in a seasonal environment? The influence of determinism at regional scale to stochasticity or antagonistic forces at local scale. *PLoS ONE.* 10(6):e0130075.
- Maun MA. 2004. Burial of plants as a selective force in sand dunes. In: Martínez ML, Psuty NP, editors. *Coastal Dunes: ecology and Conservation.* Berlin: Springer-Verlag; p. 119–135.
- Maun MA. 2009. The biology of coastal sand dunes. Oxford: Oxford University Press; p. 265.
- Mendoza-González G, Martínez ML, Rojas-Soto O, Téllez-Valdéz O, Arias-Del Razo I. 2016. Priority areas for conservation of beach and dune vegetation of the Mexican Atlantic coast. *J Nat Conservation.* 33:25–34.
- Miller TE, Gornish ES, Buckley H. 2010. Weather and coastal dune vegetation: effects of storms and drought. *Plant Ecol.* 206:97–104.
- Miranda F. 1978. Vegetación de la Península Yucateca. Chapingo México: Colegio de Postgraduados; p. 271.
- Moreno-Casasola P. 1985. Ecological studies of sand dune vegetation along the Mexican Gulf coast. Ph.D. thesis, Uppsala University.
- Moreno-Casasola P, Espejel I. 1986. Classification and ordination of coastal sand dune vegetation along the Gulf and Caribbean Sea of Mexico. *Vegetation.* 66:147–182.
- Müller J, Müller K, Neinhuis C, Quandt D. 2010. Phylogenetic data editor. <http://www.phyde.de/>.
- Noy-Meir I. 1973. Desert Ecosystems: environment and producers. *Annu Rev Ecol Syst.* 4:25–51.
- O'Donnell MS, Ignizio DA. 2012. Bioclimatic predictors for supporting ecological applications in the conterminous United States. In: US geological survey data series 691. Reston: US Geological Survey.
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, et al. 2017. *Vegan: community ecology package.* R package version 2.4-2. <https://CRAN.R-project.org/package=vegan>
- Orellana R, Espadas C, Conde C, Gay C. 2009. Atlas: escenarios de Cambio Climático en la Península de Yucatán. México: CICY.
- Palmer AR. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica et Phytotaxonomica.* 29:511–530.
- Parra-Tabla V, Albor-Pinto C, Tun-Garrido J, Angulo DF, Barajas C, Silveira R, Ortíz-Díaz JJ, Arceo-Gómez G. 2018. Spatial patterns of species diversity in sand dune plant communities in Yucatan, Mexico: importance of invasive species for species dominance patterns. *Plant Ecol Divers.* 11:157–172.
- Pausas JG, Verdu M. 2010. The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *Bioscience.* 60:614–625.
- Posada D. 2008. jModelTest: phylogenetic model averaging. *Mol Biol Evol.* 25:1253–1256.
- R Development Core Team. 2015. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

- Rambaut A, Drummond AJ. 2009. Tracer, version 1.5. <http://beast.bio.ed.ac.uk/Tracer>.
- Reice ST, Wissmar RC, Naiman RJ. 1990. Disturbance regimes, resilience and recovery of animal communities and habitats in lotic ecosystems. *Environmental Management*. 14:647–659.
- Ricklefs RE. 2008. Disintegration of the ecological community. *Am Nat*. 172:741–750.
- Ricklefs RE. 2009. A brief response to Brooker et al.'s comment. *Am Nat*. 174:928–931.
- Ripley BS, Pammenter NW. 2004. Physiological characteristics of coastal dune pioneer species from the Eastern Cape, South Africa, in relation to stress and disturbance. In: Martínez ML, Psuty NP, editors. *Coastal dunes, ecology and conservation Ecological Studies*, Vol. 171.
- Rosindell J, Hubbell S, Etienne RS. 2011. The unified neutral theory of biodiversity and biogeography at age ten. *Trends Ecol Evol*. 26:340–348.
- Rosindell J, Hubbell SP, He F, Harmon LJ, Etienne RS. 2012. The case for ecological neutral theory. *Trends Ecol Evol*. 27:203–208.
- Sánchez-Sánchez O, Islebe GA, Ramírez-Barajas PJ, Torrescano-Valle N. 2015. Natural and human induced disturbance in vegetation. In: Islebe GA, Calmé S, León-Cortés JL, Schmook B, editors. *Biodiversity and conservation of the Yucatan Peninsula*. Cham: Springer International Publishing; p. 153–167.
- SAS. 2009. SAS, version 9.2. Carey (North Carolina): SAS Institute Inc.
- Shreve F. 1942. The desert vegetation of North America. *Bot Rev*. 8:195–246.
- Shumway SW. 2000. Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. *Oecologia*. 124:138–148.
- Silva JLA, Souza AF, Jardim JG, Goto BT. 2015. Community assembly in harsh environments: the prevalence of ecological drift in the heath vegetation of South America. *Ecosphere*. 6:1–18.
- Tewksbury JJ, Lloyd JD. 2001. Positive interactions under nurse plants: spatial scale, stress gradients and benefactor size. *Oecologia*. 127:425–434.
- Tirado R, Pugnaire FI. 2003. Shrub spatial aggregation and consequences for reproductive success. *Oecologia*. 136:296–301.
- Torres W, Méndez M, Dorantes A, Durán R. 2010. Estructura, composición y diversidad del matorral de duna costera en el litoral yucateco. *Boletín de la Sociedad Botánica de México*. 86:37–51.
- Torrescano-Valle N, Folan WJ. 2015. Physical settings, environmental history with an outlook on global change. In: Islebe GA, Calmé S, León-Cortés JL, Schmook B, editors. *Biodiversity and conservation of the Yucatan Peninsula*. Switzerland: Springer International Publishing; p. 9–37.
- Tucker CM, Cadotte MW. 2013. Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. *Divers Distributions*. 19:845–854.
- Valiente-Banuet A, Verdú M. 2007. Facilitation can increase the phylogenetic diversity of plant communities. *Ecol Lett*. 10:1029–1036.
- Valverde T, Pisanty I, Rincón E. 1997. Growth response of six tropical dune plant species to different nutrient regimes. *J Coastal Res*. 13:497–505.
- Vamosi SM, Heard SB, Vamosi JC, Webb CO. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Mol Ecol*. 18:572–592.
- Vellend M, Srivastava DS, Anderson KM, Brown CD, Jankowski JE, Kleynhans EJ, Kraft NJB, Letaw AD, Macdonald AAM, Maclean JE, et al. 2014. Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos*. 123:1420–1430.
- Volkov I, Banavar JR, Hubbell SP, Maritan A. 2007. Patterns of relative species abundance in rainforests and coral reefs. *Nature*. 450:45–49.
- Walter H. 1971. *Ecology of tropical and subtropical vegetation*. Edinburgh: Oliver and Boyd.
- Wang JJ, Shen J, Wu YC, Tu C, Soininen J, Stegen JC, He J, Liu X, Zhang L, Zhang E. 2013. Phylogenetic beta diversity in bacterial assemblages across ecosystems: deterministic versus stochastic processes. *ISME J*. 7:1310–1321.
- Webb CO. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am Naturalist*. 156:145–155.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ. 2002. Phylogenies and community ecology. *Annu Rev Ecol Syst*. 33:475–505.
- Wellenreuther M, Larson KW, Svensson EI. 2012. Climatic niche divergence or conservatism? Environmental niches and range limits in ecologically similar damselflies. *Ecology*. 93:1353–1366.
- White DA, Hood CS. 2004. Vegetation patterns and environmental gradients in tropical dry forest of the northern Yucatan Peninsula. *J Vegetation Sci*. 15:151–160.
- Yang WJ, Ma KP, Kreft H. 2013. Geographical sampling bias in a large distributional database and its effects on species richness-environment models. *J Biogeogr*. 40:1415–1426.
- Zaniewski AE, Lehmann A, Overton JM. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecol Modell*. 157:261–280.