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Ecology

Variations in beta diversity among plant types with different water dependence in arid palm groves of the Baja California Peninsula

Variación de la diversidad beta entre tipos de plantas con diferente dependencia del agua en los palmares áridos de la península de Baja California

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Abstract

The palm groves of the Baja California Peninsula constitute a semi-isolated network of arid wetlands spanning over 1,000 kilometers. The plant species within them exhibit varying degrees of water adaptation, including 3 types of hydrophytes (aquatic, subaquatic, and tolerant species), and non-hydrophytic or intolerant species. Our objective was to evaluate the effect of different water dependence among these distinct groups on their floristic similarity change between palm groves, relative to the geographical distance separating them. After reviewing scientific literature, we compiled the floristic lists of 25 palm groves across the region, finding 518 species (27 aquatic, 57 subaquatic, 53 tolerant, and 381 intolerant species). We utilized the Sørensen similarity index to estimate similarity in the 4 plant groups and analyzed how similarity changes with respect to the distance between palm groves. Floristic similarity decreased with increasing distance in the 4 plant groups according to a negative exponential model ($S = S_0 \cdot e^{-\mathrm{b}d}$), with the rate of decrease (b) growing as water dependence of plants decreased ($\mathrm{b}_{\mathrm{Aquatic}} = 0.0010$, $\mathrm{b}_{\mathrm{Subaquatic}} = 0.0016$, $\mathrm{b}_{\mathrm{Tolerant}} = 0.0029$, $\mathrm{b}_{\mathrm{Intolerant}} = 0.0046$). In summary, the aquatic adaptation of plants within the Baja California Peninsula palm groves affects the geographical pattern of beta diversity in these wetlands.

Keywords: Aquatic plants; Arid wetlands; Floristic similarity; Sonoran Desert

Resumen

Los palmares de la península de Baja California conforman una red semi-aislada de humedales áridos por más de 1,000 km. Las plantas de estos palmares muestran distinto grado de adaptación acuática, incluyendo tres tipos de hidrófitas (acuáticas, subacuáticas y tolerantes) y no hidrófitas o intolerantes. Nuestro objetivo fue evaluar el efecto que diferente grado de especialización acuática entre grupos tiene en su cambio de similitud florística entre palmares respecto a la distancia. Después de revisar la literatura científica, compilamos la relación florística de 25 palmares de la región y encontramos 518 especies (27 acuáticas, 57 subacuáticas, 53 tolerantes y 381 intolerantes). Utilizamos el índice de similitud de Sørensen para estimar la similitud en los 4 grupos y analizamos cómo la similitud cambia en función de la distancia entre palamares. La similitud florística disminuyó en los 4 grupos al aumentar la distancia, según un modelo exponencial negativo ($S=S_0 \cdot e^{-bd}$), con tasa de disminución (b) creciente conforme es menor la dependencia del agua ($b_{Acuáticas} = 0.0010$, $b_{Subacuáticas} = 0.0016$, $b_{Tolerantes} = 0.0029$, $b_{Intolerantes} = 0.0046$). En síntesis, la adaptación acuática de las plantas de los palmares de la península de Baja California afecta el patrón geográfico de la diversidad beta en estos humedales.

Palabras clave: Plantas acuáticas; Humedales áridos; Similitud florística; Desierto sonorense

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Introduction

Change of species composition and abundance in time and space, i.e., beta diversity, is a fundamental dimension of community dynamics across spatio-temporal scales (Mori et al., 2018). Ecological differences among species can affect how communities change in time and space. Species present in a community can have different levels of adaptation to local habitats and therefore, respond differently to environmental factors and influence how species composition changes among communities (Leibold et al., 2022; Pandit et al., 2009).

Wetlands can be conceptualized in the broad sense as landscape units that, while not being rivers, lakes or seas, constitute spatio-temporal positive hydric anomalies in comparison to their drier surrounding areas, such as oases, vernal pools or marshes (González Bernáldez & Montes, 1989). Frequently, they are identified and characterized using the presence of hydrophytic plants, i.e., those plants that live in water or on saturated soils, at least periodically saturated soils (Lot et al., 2015; Tiner, 1991). Depending on the level of their water requirement to complete their life cycle, plant species in wetlands can be grouped into 3 different types of hydrophytes: aquatic, subaquatic, and tolerant species (Lot et al., 2015). Aquatic plants are ecologically important elements of wetland ecosystems because they provide habitat and food sources for different organisms (Francechini et al., 2020; Gross et al., 2001; Jeppesen et al., 1998; Martín et al., 2005), as well as participate in carbon and nutrient cycles (Carpenter & Lodge, 1986; Xing et al., 2006).

It has been extensively studied how taxonomic composition changes between wetland communities (i.e., beta diversity) and the role that dispersal limitation (e.g., Boughton et al., 2010; Crow, 1993; Flinn et al., 2010; Hájek et al., 2011; Murphy et al., 2019; Santamaría, 2002) and niche processes, as climatic factors, water quality or habitat heterogeneity play on species assemblages in wetland communities (Alahuhta, 2015; Alahuhta et al., 2021; Alahuhta & Heino, 2013; Capers et al., 2010; Fernández-Aláez et al., 2020). However, it has been less analyzed whether different degrees of water adaptation in wetland taxa can generate differences in their spatial beta diversity patterns in response to various processes acting at different spatial scales (Alahuhta, 2015; Chappuis et al., 2012; Zhou et al., 2022). To address this gap, our study aimed to investigate the role of water adaptation of plant species in spatial patterns of wetland plant communities by using beta diversity dynamics as our analytical framework, and arid palm groves in the Baja California Peninsula, Mexico, as our study system of wetlands.

Nekola and White (1999) proposed a conceptual framework for distance decay of biological similarity, where similarity shows a negative relationship with geographical distance. Since then, the variation in distance decay rate of compositional similarity between sites (communities) has been related to multiple factors as climatic gradients, geographical distance, limits to dispersal or niche width (e.g., Garcillán & Ezcurra, 2003; Graco-Roza et al., 2022; Nekola & White, 1999; Soininen et al., 2007), that are categorized in 2 main processes, dispersal processes and species sorting by niche selection (Gómez-Rodríguez & Baselga, 2018). In the first case, increase in spatial distance between 2 sites would reduce the probability of species reaching both sites. In the second case, greater distance would be associated with an increase in environmental differences (niche), due to the assumed spatial autocorrelation of environmental variables (Gómez-Rodríguez & Baselga, 2018).

Floodable palm groves are one of the woody plant assemblages of wetlands described for Mexico by Lot et al. (2015) and are characterized by having palms as the dominant element. One singular type of these floodable palm groves is the palm groves of semi-arid regions of northern Mexico. These systems do not always have permanent surface water, however, palms (*Brahea* spp., *Sabal uresana* Trel., and *Washingtonia* spp.) constitute indicator species of habitats with water saturation (Lot et al., 2015). Particularly, in the Baja California Peninsula, palm groves can be found along its arid lands, from the tropical dry vegetation of the southern tip of the peninsula, which lies on the Tropic of Cancer (23° N - 24° N), to the Mediterranean-type vegetation of northwestern Baja California (30° N - 32.5° N). The palm groves in this region are home to 2 native genera, *Brahea* and *Washingtonia*, with 4 species, namely *B. armata* S. Watson, *B. brandegeei* (Purpus) H.E. Moore, *W. filifera* (André) Bary, and *W. robusta* H. Wendl.; and in many of them the naturalized non-native species, *Phoenix dactylifera* L.

The plant species composition of any palm grove is mainly driven, as in other wetlands, by dispersal and niche selection processes. However, distinct types of wetland plants could experience these processes differently. More water-dependent plants would need to arrive by long-distance dispersal from other wetlands but would be strongly selected by the wetter conditions of the local palm grove's habitat. In contrast, less water-dependent plants could arrive from the nearby landscape and be dispersed through a more continuous scenario between palm groves but would be less selected by local wetland habitat.

Our objective was to evaluate the effect of different degrees of aquatic specialization among plant species groups in arid palm groves on the spatial variations of beta diversity within these groups. We hypothesized that the level of water specialization in plant groups influences how their beta diversity changes with the distance between palm groves. We expect that, due to the greater ecological similarity between habitats of palm groves across varying distances compared to the surrounding landscapes, more water-dependent species will exhibit a lower rate of compositional similarity decay over extended distances compared to less water-dependent species.

Materials and methods

We selected as our study system a set of palm groves found along the 1,000 km-long strip of land comprising the tropical Cape Region, and the extratropical Sonoran Desert that runs through the Baja California Peninsula in northwestern Mexico (Fig. 1). We reviewed published studies containing floristic data of palm groves of any of the 4 native palm species of Baja California Peninsula (*Brahea armata*, *B. brandegeei*, *Washingtonia filifera*, and *W. robusta*), and compiled a database of plant species associated with them through the region. We also added an unpublished species list from floristic fieldwork conducted in 2018, at the palm grove of the Guadalupe Canyon, in the northern Baja California Peninsula (J.P. Rebman, unpublished data). We standardized all of the plant nomenclature following The Plant List (2013) Version 1.1 (www.theplantlist.org) according to Rebman et al. (2016). We established the level of water association of plant species following the categorization established by Lot et al. (2015) and our field observations as aquatic (A), if they complete their life cycle submerged and cannot survive outside of water; subaquatic (S), if they complete their life cycle on the edge of water bodies or saturated soil and can tolerate dry soil only temporarily; and tolerant (T), if they complete most of their life cycle in a dry environment but can be seasonally submerged. All other plant species were classified as non-hydrophytes or intolerants (I). We found data from a total of 48 palm groves and selected the 25 palm sites (Fig. 1; Appendix) that had at least 10 recorded plant species, with at least 1 aquatic species present, and were separated from each other by at least 5 km. Finally, we created a database of species presence/absence per site for each of the 4 plant categories.

We aimed to investigate whether plant species in palm groves, with different level of water requirement to complete their life cycle, i.e., different positions on a habitat specialization gradient (Pandit et al., 2009) (aquatic - subaquatic - tolerant - and non-hydrophyte plants), exhibit dissimilar beta diversity patterns. For this purpose, we examined in each plant group the relationship between floristic similarity (i.e., 1 - beta diversity) and spatial distance between palm groves. We estimated floristic similarity between pairs of palm groves for each plant category using Sørensen′s similarity, defined as $S_{jk} = 2a/(2a + b + c)$, where a is the number of species shared between communities j and k, and b and c are the unique species of communities j and k, respectively. Beta diversity can be defined as the variation of species composition between communities. It can be decomposed in 2 components: spatial turnover, and nestedness. Spatial turnover results from replacement of some species by others caused by environmental sorting or historical constraints, and nestedness, which occurs when smaller communities are subsets of larger communities and are produced by non-random process of species loss (Baselga, 2010). We also estimated the total beta diversity of each plant category for the set of sites,

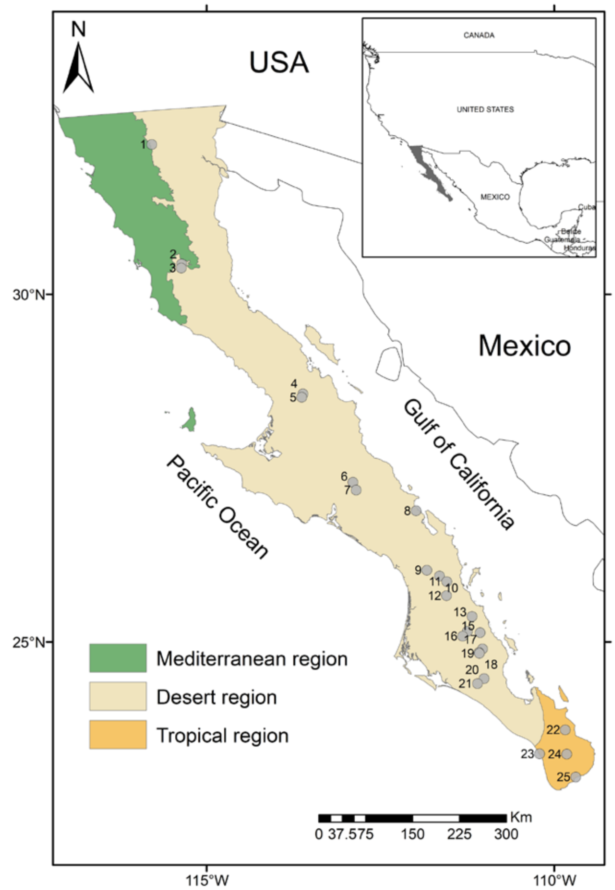

Figure 1. Localization of the 25 palm groves included in this study along the Baja California Peninsula, indicating the 3 main ecoregions of the peninsula: Mediterranean, Tropical, and Desert. Refer to the Appendix for details about the palm groves. Map by Danaee Jiménez Guevara.

measured as Sørensen´s dissimilarity and its partition on species turnover and nestedness components. Both analyses were done using the R package 'betapart' v.1.6 (Baselga et al., 2023). We used the R package 'geosphere' v 1.5-18 (Hijmans, 2022) to calculate the geographical distance between palm groves, based on the geographical coordinates of the 25 sites.

To analyze the relationship between similarity in the different plant groups (A, S, T, and I) and the geographical distance, we used the negative exponential decay model, $S = S_0 \times e^{-bd}$ (Nekola & White, 1999; Whittaker, 1972), where S_0 represents the initial similarity, and b, the rate of distance decay of similarity (Nekola & White, 1999). We did this analysis by using the function "decay.model" included in the R package "betapart" v.1.6 (Baselga et al., 2023). In this function, the nonlinear models are fitted using the Levenberg-Marquardt nonlinear least-squares algorithm (Baselga et al., 2023). In each decay model the goodness of fit is computed as pseudo-r^2, which represents the proportion of the variation in the dependent variable that the model accounts for, and the significance of the model is estimated from a permutation (1,000) test. Finally, we tested if differences between parameters of distance decay models on the 4 plant groups are significant using the function "zdep" included in R package "betapart" v.1.6 (Baselga et al., 2023; Martín-Devasa et al., 2022). This function assesses whether the parameters of 2 models are significantly different via block-site bootstrap. All the analyses were done with R v.4.2.3 (R Core Team, 2023).

Results

We assembled a database consisting of 27 aquatic species, 57 subaquatic species, 53 tolerant species, and 381 non-hydrophytic species. The 4 types of plants showed similar values of Sørensen beta diversity (aquatics: 0.91, subaquatic species: 0.92, tolerant species: 0.94, and non-hydrophytes: 0.97), and also similar high dominance of their turnover components (aquatics: 91%, subaquatic species: 95%, tolerant species: 95%, and non-hydrophytes: 93%; Fig. 2).

The negative exponential model significantly expressed the change in taxonomic similarity over spatial distance in the 4 types of plants (p = 0.001) (Fig. 3). Explained variance was higher in subaquatic species (pseudo-r^2 = 0.38) than in aquatics (pseudo-r^2 = 0.11), tolerant hydrophytes (pseudo-r^2 = 0.17), and non-hydrophytic plants (pseudo-r^2 = 0.19) (Fig. 3). The rate of similarity distance decay increased as water association decreased: aquatics (b = 0.0010), subaquatic species (b = 0.0016), tolerant species (b = 0.0029), and non-hydrophytes (b = 0.0046). If we consider that aquatics, subaquatic species, tolerant species, and non-hydrophytes represent a gradient of water dependence, the rate of similarity distance decay (b) was not significantly different between contiguous groups along this gradient, aquatics vs. subaquatic species (z.dep = 1.59, p = 0.113), subaquatic species vs. tolerant species (z.dep = 1.77, p = 0.077), and tolerant species vs. non-hydrophytes (z.dep = 1.432, p = 0.152) (Fig. 4). However, the rate of distance decay increased significantly between non-contiguous groups along the gradient from more to less water dependency, aquatics vs. tolerant species (z.dep = 2.47, p = 0.013), aquatics vs. non-hydrophytes (z.dep = 3.45, $p < 0.001$), and subaquatic species vs. non-hydrophytes (z.dep = 2.94, p = 0.003) (Fig. 4).

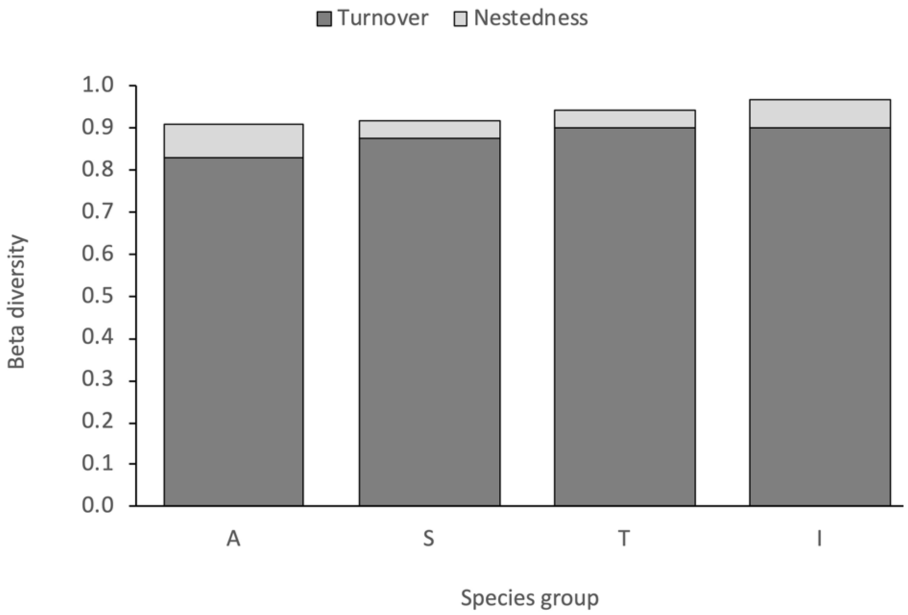

Figure 2. Partitioning of beta diversity, quantified as Sørensen dissimilarity (β_{SOR}), into its turnover and nestedness components for the 4 groups of plants (A: aquatics, S: semiaquatic plants, T: tolerant plants, and I: non-hydrophytes or intolerant plants) within 25 palm groves of the Baja California Peninsula.

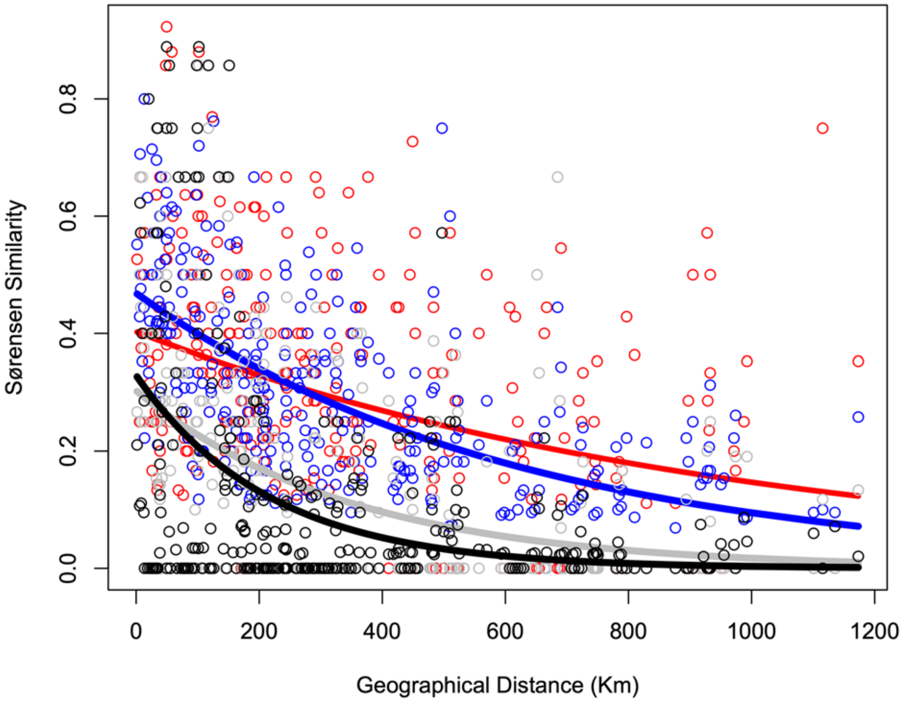

Figure 3. Distance decay of floristic similarity (Sørensen index) among palm groves of the Baja California Peninsula for 4 types of plants: aquatics (red), semiaquatic species (blue), tolerant species (gray), and non-hydrophytes (black). Circles represent observed similarity, and lines depict corresponding fitted exponential model ($S = S_0.e^{-bd}$). All 4 models were significant ($p = 0.001$).

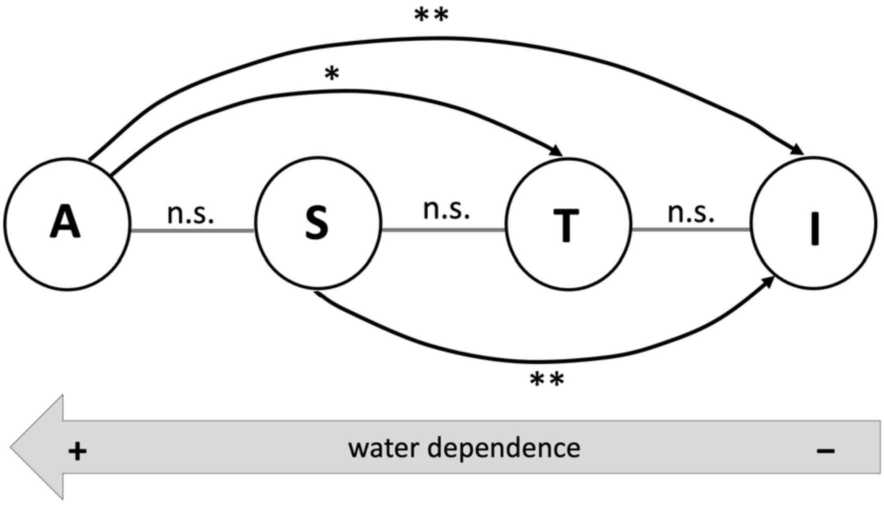

Figure 4. Comparison of distance decay rates (b) for 4 plant groups recorded in palm groves: aquatics (A), subaquatic plants (S), tolerant plants (T), and non-hydrophytes or intolerant plants (I) across spatial distances between palm groves. The arrow points indicate the direction of increasing b. Significance levels of b differences: (**) $p < 0.01$, (*) $p < 0.05$, n.s.: non-significant.

Discussion

Our findings indicate that the 4 plant types of arid palm groves of the Baja California Peninsula (aquatics, subaquatic species, tolerant species, and non-hydrophytes) exhibit a negative relationship between taxonomic similarity and geographical distance, however, this relationship shows differences between plant types. The rate of similarity decay with distance (b) increased as the water dependency of the species group decreased, from aquatics to non-hydrophytes. These results support our hypothesis, that the level of water dependence in different groups of plants of arid palm groves in the Baja California Peninsula affects the change of their beta diversity along the distance.

However, contrary to our expectations the rates of similarity decay between adjacent categories (aquatic - subaquatic, subaquatic - tolerant, and tolerant - non-hydrophyte) were not different, but they did differ between non-adjacent groups (aquatic - tolerant, subaquatic - non-hydrophyte, and aquatic - non-hydrophyte). It appears that spatial variation of beta diversity in different plant groups is related with their level of water dependence. However, it does not occur through 4 differentiated steps, but through an increasing gradient from aquatics to non-hydrophytes.

The increasing rate of decay from aquatics to non-hydrophytic species might be attributed to the varying importance of niche selection within local wetland habitat of palm groves for different types of plants (Alahuhta et al., 2018). Arid palm groves are typically characterized by the presence of water or saturated soils throughout the year, making them an archipelago of wet islands with higher water availability than the sourruonding desertic landscapes (Arriaga et al., 1997; Rodríguez-Estrella, 2004). Consequently, if the wetland environment in palm groves exhibits greater spatio-temporal homogeneity in water availability, plant species that are better adapted to this environment, specifically aquatics and subaquatic species, will likely experience higher positive filtering by this environment than tolerant species and non-hydrophytes. Therefore, this will result in higher similarity in aquatics and subaquatic species between palm groves over longer distances compared to species that are less adapted to wetland habitats (Zhou et al., 2022). In contrast, the composition of tolerant species and non-hydrophytes, being less influenced by local habitat filtering, is likely to owe a higher proportion of their presence to more stochastic processes (e.g., ecological drift; Vellend, 2010), which are associated with shorter dispersal distances from the surrounding landscapes. Tolerant species and non-hydrophytes, contrary to our expectations, showed no significant differences in their rate of beta diversity change across geographic distances. This suggests that, at our scale of analysis, the adaptation of tolerant species to seasonal submergence does not significantly influence their local selection compared to non-hydrophytes. This could be related to the brief duration of seasonal flooding events in our region (Bullock, 2003; Hastings & Turner, 1965). In such a scenario, some level of tolerance to short-term flooding is also present to a certain extent in non-hydrophytic species.

It is widely accepted that low dispersal rates of species can be correlated with low similarity among sites (Mouquet & Loreau, 2003). Consequently, community composition across large geographical regions appears to be driven mainly by dispersal limitation and to a lesser degree by environmental variation (Heino, 2011). Hence, we cannot discount the possibility that aquatic and subaquatic plants may have fewer dispersal limitations compared to more terrestrial plants. This could be attributed to their superior passive dispersal capacity or their dispersal by animals, such as waterbirds, which are strongly associated with wetlands and specifically select for them (Green et al., 2023). Finally, changes in the composition of wetland communities can also result from historical barriers and corridors (Leibold et al., 2010). The complex geological and climatic history of the Baja California region, which has influenced the spatial distribution patterns of numerous species (Dolby et al., 2015), could likewise have affected the spatial distribution of plant taxa among the palm groves.

All 4 categories of palm grove species displayed comparable total beta diversity values, with a notable prevalence of the turnover component. This suggests that beta diversity structure is similar across these groups, primarily driven by species replacement due to environmental selection, competitive interactions, and historical constraints, rather than by substantial loss along an environmental gradient (Baselga, 2010; Leprieur et al., 2011; Qian et al., 2005). Species turnover has been identified as the predominant factor shaping freshwater plant communities (Alahuhta et al., 2017; Murphy et al., 2020). Nonetheless, the prevalence of species turnover compared to nestedness is not confined to wetland communities, as indicated by similar patterns observed in numerous non-hydrophytic species (Soininen et al., 2018).

Our results are consistent with the idea that metacommunities can be composed of 2 general types of species, habitat specialists and habitat generalists, which would be more and less influenced by local environmental processes, respectively (Leibold et al., 2004; Pandit et al., 2009; Szekely & Langenheder, 2014). Hence, patterns of diversity along palm grove communities will differ if we choose water-dependent species (aquatic and subaquatic species), less water-dependent species (tolerant species and non-hydrophytic species), or both. Therefore, design decisions regarding the delimitation criterion of a wetland community under study can influence the outcomes of the community-assembly process and, consequently, affect potential conservation actions (Deane et al., 2016; Fauth et al., 1996).

We are aware that given the importance of niche selection at the local scale of palm groves, the lack of empirical data on habitat heterogeneity among palm groves, especially about temporal water variability (Casanova & Brock, 2000), can be a possible caveat for our results showing aquatics and subaquatics as one "functional" group. However, these results also can be considered a hint in the spatial ecology of these wetlands to initiate further research on these plant groups, which can act as a funtional group. We are certain that including heterogeneity of local wetland habitats could better explain, and maybe differentiate, the beta diversity dynamics of aquatic and subaquatic species (Zhou et al., 2022). It should be noted that our study focuses only on a specific type of wetland, arid palm groves, and not on all wetlands in the region. The palm grove flora compiled in this study contains only 37% of the 56 strictly aquatic plant species reported by Mora-Olivo et al. (2013) for the Baja California Peninsula. Therefore, the patterns we found should be interpreted in the context of palm groves and not necessarily generalized to all other wetland types. Our data come from the compilation of studies conducted to achieve different objectives and employing sampling methods at different spatio-temporal scales. However, we believe that the main geographical patterns captured by these data remain robust enough. Floristic similarity among arid palm groves decreases with increasing distance for all 4 plant groups. The decline is less pronounced in more water-dependent groups, aquatics and subaquatic plants, compared to less water-dependent groups like, tolerant species and non-hydrophytes. Therefore, the aquatic adaptation of plants within the Baja California Peninsula palm groves influences the geographical pattern of beta diversity in these wetlands. It would be interesting to explore if the relation between spatial beta diversity and the level of water dependence of species documented in this study is present in the flora of other types of arid wetlands or in the wetlands of less arid environments.

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Appendix. List of the 25 palm groves analyzed in this study, including their geographical coordinates and native palm species. Site numbers correspond to the numeric IDs shown in Figure 1, while letters in the "Sources" column indicate the references used to compile the plant species database for each site. The source for site 1 (h) refers to a species list recorded during fieldwork in 2018 by the second author (J. Rebman), whereas the sources for the remaining sites (a-g) are indicated in the Appendix footnote. Native palm species include *Washingtonia filifera* (W.f.), *W. robusta* (W.r.), *Brahea armata* (B.a.), and *B. brandegeei* (B.b.).

Sites	Sources	Locality name	Lat	Lon	*W. f.*	*B. a.*	*W. r.*	*B. b.*
1	h	Guadalupe Canyon	32.1553	-115.7879	*	*		
2	a	San Miguel	30.4369	-115.3577		*		
3	a	El Rincón	30.3786	-115.3637		*		
4	b	El Paraíso, upper canyon	28.5681	-113.6145		*		
5	b	El Paraíso, lower canyon	28.5184	-113.6324		*		
6	c, g	San Ignacio	27.2967	-112.8953			*	
7	g	San Joaquín	27.1833	-112.8500			*	
8	e, g	Mulegé	26.8868	-111.9867			*	
9	d, g	San Miguel Comondú	26.0327	-111.8329			*	
10	d	Palmar Las Bebelamas	25.9500	-111.6500			*	
11	g	San Javier	25.8686	-111.5469			*	
12	d	El Edén	25.6667	-111.5500			*	
13	d	Poza del León	25.3667	-111.1833			*	
14	d	El Rosario	25.1500	-111.2500			*	
15	d	La Ensenada	25.1333	-111.0667			*	
16	d	Tepentú	25.0833	-111.3167			*	
17	d	Santa María Toris	24.9000	-111.0333			*	
18	d	Cantarranas	24.8500	-111.0833			*	
19	c, d, g	San Pedro de la Presa	24.8370	-111.0771			*	*
20	c, d	El Pilar	24.4750	-111.0083			*	
21	g	Las Pocitas del Vado	24.4029	-111.1036				*
22	c, g	San Bartolo	23.7361	-109.8417			*	*
23	c, g	Punta San Pedro	23.3913	-110.2112			*	*
24	c	Boca de la Sierra	23.3863	-109.8199			*	*
25	f, g	San José del Cabo	23.0589	-109.6913			*	*

Sources: (a) Franco-Vizcaíno et al. (2007), (b) Wehncke et al. (2012), (c) Arriaga et al. (1997), (d) León-de la Luz & Domínguez-Cadena (2006), (e) Valov (2020), (f) León-de la Luz et al. (1997), (g) Ruiz-Campos et al. (2014).

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