Foraging guild structure and niche characteristics of waterbirds in an epicontinental lake in Mexico

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Abstract

Background: It was suggested that ecological patterns can be used to infer the nature of ecological processes (i.e., competition) that structure communities. Analysis of patterns of resource partitioning under the classical niche paradigm (competitive niche differentiation in exploiting limited resources) has traditionally been used to understand the structure of communities. On the contrary, neutral theory states that patterns result from neutral processes such as stochasticity and dispersal abilities. Thus, if any ecological process gives rise to a characteristic ecological pattern, the comparative study of patterns with appropriate neutral models may reveal the magnitude of that process. In this study, we analyzed patterns of resource utilization of a waterbird community in Lake Acuitlapilco, an epicontinental lake in central Mexico. In February 2011 to January 2012, we recorded foraging behaviors of waterbird species in two niche dimensions or axes: feeding technique and foraging habitat. The pattern of resource utilization was characterized by niche breath and niche overlap.

Results: Results showed that waterbird species in Lake Acuitlapilco were specialists in resource utilization patterns and therefore were vulnerable to fluctuations in resources, particularly feeding habitat. Niche overlaps were generally largest among species belonging to the same guild. To test competition as an ecological process that plays a role in the community structure, observed niche overlaps were compared with niche overlaps generated with null models of communities in the absence of competition using the RA4 randomization algorithm. Habitat and observed bidimensional overlaps were higher than those of randomly generated communities.

Conclusions: Our study suggested that other processes can be used to predict resource utilization patterns instead of competition alone, as suggested by neutral theory. Future studies analyzing the mechanisms that structure waterbird communities should include the use of null models to support their conclusions.

Keywords: Communities; Feeding behavior; Habitat use; Niche overlap; Null models; Neutral theory

Background

Bird communities that inhabit aquatic environments usually have a complex structure driven by the large number of variables that influence species interactions (Winemiller and Pianka 1990; Weller 1999; Palmer et al. 2003). Thus far, approaches generally used to understand processes organizing waterbird communities have focused on analyzing patterns of resource partitioning (Schoener 1974; Wiens 1977; Pianka 1980; Winemiller and Pianka 1990; López de Casenave et al. 2008). Research generally concluded that species with similar patterns of resource utilization (i.e.,

species of the same guild) are susceptible to competitive interactions that affect the community structure.

Patterns of resource utilization (either food or habitat resources) are usually analyzed in the framework of niche theory, i.e., members of the same guild similarly exploit similar resources and may be potential competitors (Root 1967; Albrecht and Gotelli 2001; Palmer et al. 2003). Thus, species of the same guild are susceptible to competitive interactions over shared resources, and in order to coexist, they should show some mechanism to reduce, but not necessarily eliminate, negative competitive interactions (Cody 1974; Simberloff and Dayan 1991).

Most studies searching for patterns of resource utilization evaluated niche breadth and niche overlap. Spatial models of niches were formalized by Hutchinson (1959) who defined niche breadth as the distance through a niche along

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some particular line in the niche space. In terms of particular resources, niche breadth is the range of resources used by species. Niche overlap refers to the joint use of resources by two or more species (Colwell and Futuyma 1971). Both niche breadth and niche overlap provide indirect ways to explore ecological processes such as competition over shared resources (MacNally 1983).

Schoener (1974) suggested three niche dimensions where species tend to segregate to minimize niche overlap: habitat, food type, and time of habitat occupancy. Thus, characterization of guilds through these dimensions provides information about possible interactions caused by inter- and intraspecific resource partitioning. Studies of waterbird communities have primarily focused on two of the three niche dimensions proposed by Schoener, namely habitat use and food type (Pöysä 1983; Zárate-Ovando et al. 2008; Gatto et al. 2008; López de Casenave et al. 2008), and assume that these two dimensions together suggest resource differentiation (Wiens 1989) and that both dimensions have an effect on the distribution, abundance, and species richness in wetlands (Weller 1999).

Therefore, Robinson and Holmes (1982) proposed an analogy between feeding technique (feeding behavior) and food consumed which was applied in several studies to explain the guild structure and resource partitioning of waterbird communities (Pöysä 1983; Sarrías et al. 1996; Gatto et al. 2008). The advantage of this method is that no dietary study is required for the analysis.

Whether the pattern of resource utilization detected arises from an ecological process, such as competition, is unclear until a comparative study of patterns is carried out to understand processes that underlie the community structure (MacNally 1983; Bell 2001). Under the classical niche paradigm, i.e., competitive niche differentiation resulting from exploitation of limited resources, interspecific competition over shared resources will drive the community structure (MacNally 1983; Hubbell 2006). Alternatively, neutral theory states that patterns can be the result of neutral processes such as stochasticity and dispersal ability rather than competition and niche partitioning (Bell 2001; Hubbell 2001, Hubbell 2006). Where competition results in characteristic ecological patterns, the comparative study of patterns with appropriate neutral models (null models) may reveal the degree of influence of competition on the community structure (Connor and Simberloff 1979; Strong et al. 1979; MacNally 1983; Bell 2001).

The null model is 'a pattern-generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution' (Gotelli and Graves 1996). The null model tests if observed data are non-random with respect to the null hypothesis (Gotelli 2001). Thus, in the context of niche overlap and competition, null modeling allows determination of how much niche overlap could be expected in the absence of competition.

In Mexico, studies of waterbird communities are insufficient and were mostly conducted in coastal wetlands, particularly in the northwestern portion of the country. Those studies analyzed diversity, habitat use, guild structure, and migratory species (see Mellink 2005). However, studies focused on waterbird assemblies in epicontinental lakes are scarce (Ramírez-Bastida 2000; Pineda-López and Arellano-Sanaphre 2010) and largely focused on a single species (Sartor 1989; Munguía et al. 2005; Mellink and Riojas-López 2009; Luevano et al. 2010; Villamagna et al. 2010). Additionally, studies on the community structure of waterbird communities are almost non-existent (see Hernández-Vázquez 2005), and the only study that tested patterns of resource utilization with null models failed in its interpretation (Núñez et al. 2008). Additional studies of waterbirds are needed.

In this study, we evaluated guild patterns of resource utilization within waterbird communities in an epicontinental lake in central Mexico. Three niche dimensions or axes were documented: habitat use, feeding technique, and time. To assess the statistical significance of the observed patterns, we compared observed patterns to those expected under the null hypothesis. Additionally, we discuss ecological mechanisms that structure the waterbird community.

Methods
Study site
This study was conducted at Lake Acuitlapilco, in the southern part of the state of Tlaxcala (at 2,300 m in elevation), 4.5 km to the southeast of Tlaxcala de Xicohténcatl, the capital city of the state. It is located at $19°44' \sim 19°06'$N and $97°38' \sim 98°43'$W (Figure 1; INEGI 2000). The lake has a catchment basin of 10.3 km^2. Average annual precipitation was 839.3 mm over a 40-year period (1967 ~ 2006; Meteorological Observatory of Tlaxcala City). The annual average volume of water drained by the catchment is 1.97×10^6 m^3. The lake volume varies throughout the year because the hydrological input comes exclusively from rainfall (CONAGUA 2010). In October to May (the dry season), the lake's depth reaches a maximum of 0.80 m and a minimum area of 20 ha. In June to September (the rainy season), the lake's depth reaches a maximum of 1.80 m and a maximum area of 75 ha.

Precipitation has an effect on the composition, height, and cover of vegetation within the lake and perimeter zones, and the vegetation undergoes large variations throughout the year. *Cynodon dactylon* (L.) Pers., *Cyperus hermaphroditus* (Jacq.) Standl., *Gnaphalium luteo-album* L., *Paspalum distichum* L., and *Pennisetum clandestinum* Hochst. ex Chiov border areas adjacent to wetlands. Uplands surrounding the lake are cultivated with corn (*Zea mays* L.). In the transition zone between cultivated
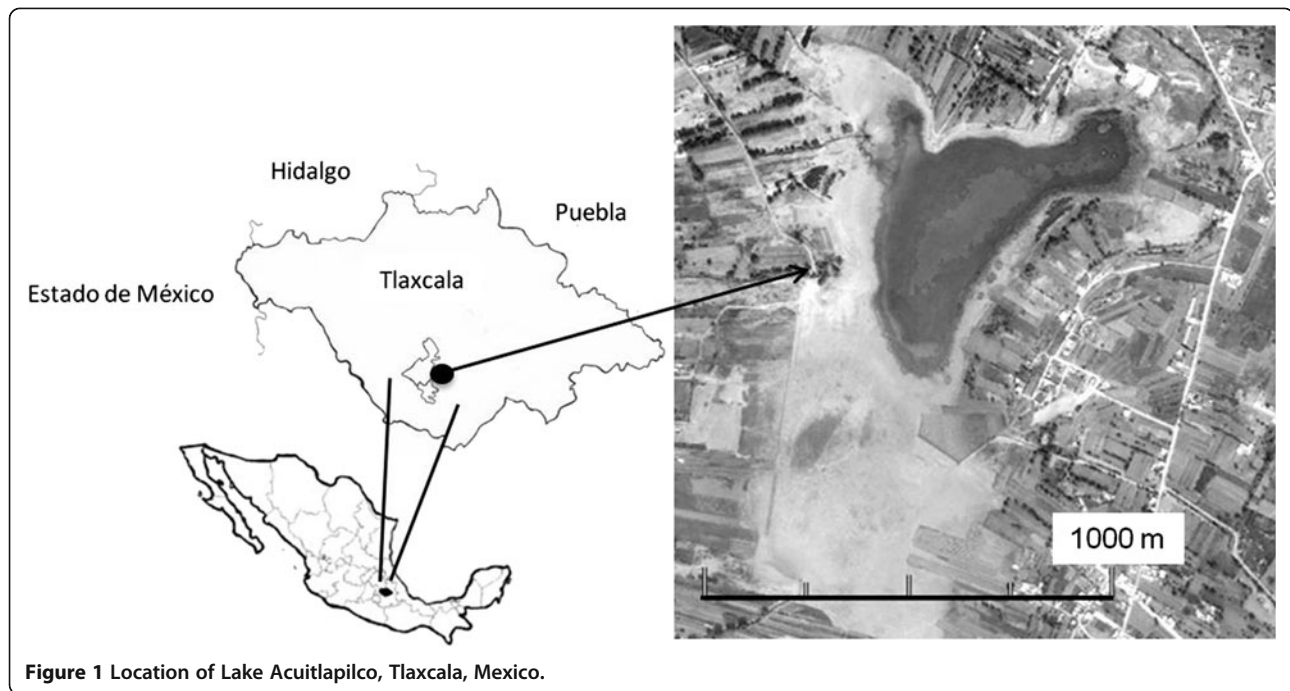
Figure 1 Location of Lake Acuitlapilco, Tlaxcala, Mexico.

areas and the lake, *Echinochloa holciformis* (Kunth) Chase and *Polygonum punctatum* Ell. were found. Finally, *Juncus arcticus* Willd. and *P. punctatum* Ell. were the two main floating species within the lake.

A previous study by Fonseca et al. (2012) reported a total of 36 waterbird species in Lake Acuitlapilco. Twelve were residents, 10 were migratory, and 14 were transient species or accidental records. The highest species richness and abundance were observed in winter (September to January), when most migratory species arrived. Additionally, Pérez-Crespo et al. (2013) studied temporal variations in abundances of birds in this water body. They established three seasons from matrices of the abundance and richness of species, taking into account fluctuations in the size and depth of the lake. Results from both studies showed that the lake is a highly dynamic environment and an important area for resident and migratory waterbirds.

Waterbird monitoring
A waterbird census was conducted every 15 days from February 2011 to January 2012 (24 counts in total). We used the point count method at points every 300 m along the perimeter of the lake. We counted individuals at each point within a radius of 150 m. Censuses began at 7:30 a.m., initiating from a different point count and a different direction to avoid order effects. Binoculars (10 × 50 mm) were used, and species were identified using field guides (Sibley 2003; van Perlo 2006). Observers recorded data at each point count for 10 min and recorded individuals by species feeding behavior (the first and single observation

from an individual) and feeding habitat (water depth and vegetation type) according to categories described in the next section. The number of points at which we found individuals feeding varied from the dry season to the rainy season (9 ~ 13 points, Fonseca et al. 2012). In the dry season, we recorded no individuals feeding at four points.

Feeding behavior
Feeding behavior was characterized by the use of feeding techniques, following categories previously used by Pöysä (1983) and Sarrías et al. (1996): (D) diving in which a bird is completely immersed in water and is lost from sight of the observer; (PM) picking from mud in which the bird's bill is submerged in the mud and balanced from side to side; (HS) head submerged; (BS) bill submerged; (NS) neck submerged (in HS, BS, and NS, the bird might or might not be in motion); (FL) filtering in which a bird is in motion and its bill is partially submerged; (PC) picking in which a bird uses intermittent pecking movements in water, mud, or vegetation; and (UP) up-ending in which a bird is not completely submerged, in a vertical position, with its tail and legs above the water.

Feeding habitat
The feeding habitat was categorized according to Pöysä (1983), by taking into account the water depth and the presence or absence of vegetation. Water depth was measured every 3 months using a marked rope. Additionally, the depth at the shoreline and beyond was monitored monthly to follow changes in water level. Eleven habitat types were defined: the central part of open deep water

of >30 cm deep with (DWV) or without (DW) emerging vegetation; the edge part of open waters, i.e., middle water, of depths >10 cm and <30 cm with (MWV) or without (MW) emerging vegetation; shoreline, i.e., shallow waters, of depths <10 cm with (SWV) or without (SW) emerging vegetation; mud with (MUV) or without (MU) emerging vegetation; dry areas with (DRVN) or without (DR) vegetation next to the shoreline; and dry areas with vegetation (DRVA) inside the lake. Each point count sample contained all of these habitat types within the radius of data observation.

Time dimension

A third dimension, time, was also evaluated. For this purpose, three seasons were established through a cluster analysis from a matrix of species and abundances (Pérez-Crespo et al. 2013). Seasons ranged from February to May (T1), May to September (T2), and September to February 2012 (T3). Data were subdivided by season, and uni- and bidimensional matrices were generated (nine seasonal matrices in total). These matrices were used to perform the overlap analysis and null models.

Data analysis

Data of species observed in at least 15 foraging records (Gatto et al. 2008) were included in the matrices (21 species of a total of 36, Fonseca et al. 2012). We also only used the first feeding behavior recorded per individual. Data were grouped into three matrices: habitat (21 species × 11 habitat variables), feeding technique (21 species × 9 feeding technique variables), and both dimensions simultaneously (21 species × 55 possible combinations of feeding technique and habitat variables). Each row of the matrix represented a different species. Each column represented a different variable (resource or niche). Entries in each cell represented counts of feeding individuals. Then, matrix entries were calculated as proportional values of observed utilization of any particular resource by a species. These proportional values were calculated by summing up counts (rows) of all resources and then dividing each resource count (an entry in the original matrix) by its total (row total). Therefore, entries in a row of final matrices would add up to 1.0 for each species. These unidimensional (habitat and feeding technique) and bidimensional matrices were used to establish guild, niche breadth, niche overlap, and null models.

Guild establishment

A cluster analysis was used to establish the guilds. Original matrices (all data) were transformed (angular transformation $y = \arcsin x^{0.5}$) to reduce the kurtosis of a variable's distribution. Three dendograms were constructed (habitat, foraging technique, and both dimensions together) using the unweighted pair group method with arithmetic mean

(UPGMA) (Sarrías et al. 1996; Gatto et al. 2008) linked to a Euclidean distance matrix (Sarrías et al. 1996; Legendre and Legendre 1998; López de Casenave et al. 2008). The average Euclidean distance between all species pairs was used to determine the level of similarity defining groups (guilds) in both the uni- and bidimensional dendograms (Pöysä 1983; Holmes and Recher 1986; Sarrías et al. 1996; Gatto et al. 2008; López de Casenave et al. 2008). The cluster analysis and dendograms were calculated with R project package, vers. 2.15.0 (Project 2012) and the Vegan package, vers. 2.0-3 (Oksanen et al. 2012).

Niche breadth and niche overlap

Niche breadth (for each species) and niche overlap (between all pairs of species) were calculated using the aforementioned uni- and bidimensional matrices (with untransformed data). The niche breadth of a species was estimated with the index of Levins (1968)): $B = (1 \ / \ \Sigma P_i^2)$, where P is proportional to each resource of a particular species. B is maximal when there is at least a count in each column and is minimal when all counts are in a column. As this index places species along a continuum from generalist to specialist, data were not subdivided by season in this calculation. Niche overlaps were calculated for all data (three matrices), and then niche overlaps were explored by season (nine matrices). The two results were compared.

Niche overlap was calculated with the index of Pianka (1973)): $O_{jk} = (\Sigma p_{ij} \ p_{ik}) \ (\Sigma p_{ij}^2 \ p_{ik}^2)^{-1/2}$, where p_{ij} and p_{ik} are proportional values of utilization of resource i by species j and k, respectively. Pianka's index is symmetrical and assumes values ranging from 0 (no resources used in common between two species) to 1 (complete overlap in resource use).

Null models

To assess whether the observed patterns in niche overlap differed from patterns of random communities, we compared the mean of observed niche overlap with the mean of niche overlap of communities in the absence of competition. Null models (1,000 iterations) of communities were generated. Null models were calculated with the software EcoSim Professional, vers. 1 (Entsminger 2012), using the RA4 randomization algorithm. As waterbird morphology limits the habitat and feeding techniques used, the RA4 algorithm was chosen to preserve the observed niche. The RA4 algorithm retains the niche breadth (values of rows) of each species and fixes zero states to their observed values. Thus, only non-zero values are reshuffled within each row. Therefore, any differences between the observed data and the null model are above and beyond those imposed by morphological constraints. This algorithm is very conservative as it maintains the structure of the original matrix and produces niche overlap values closer to those of the actual data (Jaksic and Medel 1990; Winemiller and

Pianka 1990; Albrecht and Gotelli 2001, 1990). Consequently, if the observed mean statistically differs (higher or lower) from the expected mean, the results reveal significant overlap patterns (Albrecht and Gotelli 2001). Observed niche overlap that is higher than the expected level of overlap further implies either that species are sharing a niche (i.e., flocking behavior or clumped resources), a lack of competition, or a strong competition that has not yet led to divergence in resource use. Conversely, observed niche overlap lower than expected implies interspecific competition and resource partitioning (i.e., dispersed resources; Gotelli and Graves 1996).

Results

Guilds

Results of the cluster analysis of feeding techniques suggested that an average Euclidean distance of 1.112 reliably defined species groups. This resulted in three guilds: (T1) divers, (T2) pickers, and (T3) generalists (Figure 2a). Furthermore, the habitat use matrix analysis suggested that an average Euclidean distance of 1.058 split species into four guilds: (H1) deep-water birds, (H2) medium-water birds, (H3) shallow-water birds, and (H4) generalist birds in waters with vegetation of both the peripheral and interior zones (Figure 2b). Guild characteristics were determined using a table of frequency of habitat use and feeding technique for each bird species (Figures 3 and 4).

When we examined both niche dimensions combined (feeding technique and habitat use) and an average Euclidean distance of 1.314, four guilds were established (Figure 5): (G1) divers; (G2) pickers in water, mud, and vegetation; (G3) pickers with neck submerged; and (G4) generalists.

Composition of guilds

The guild of divers (G1) was comprised of *Oxyura jamaicensis* and *Podiceps nigricollis*. To obtain food, these
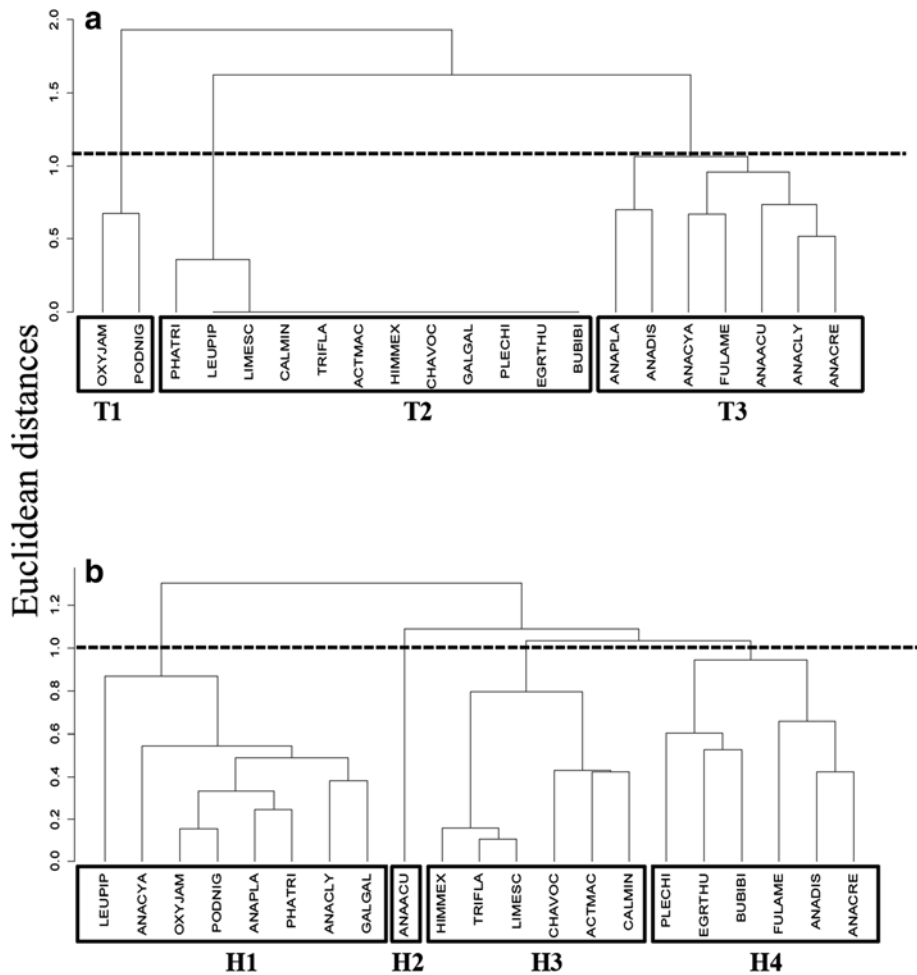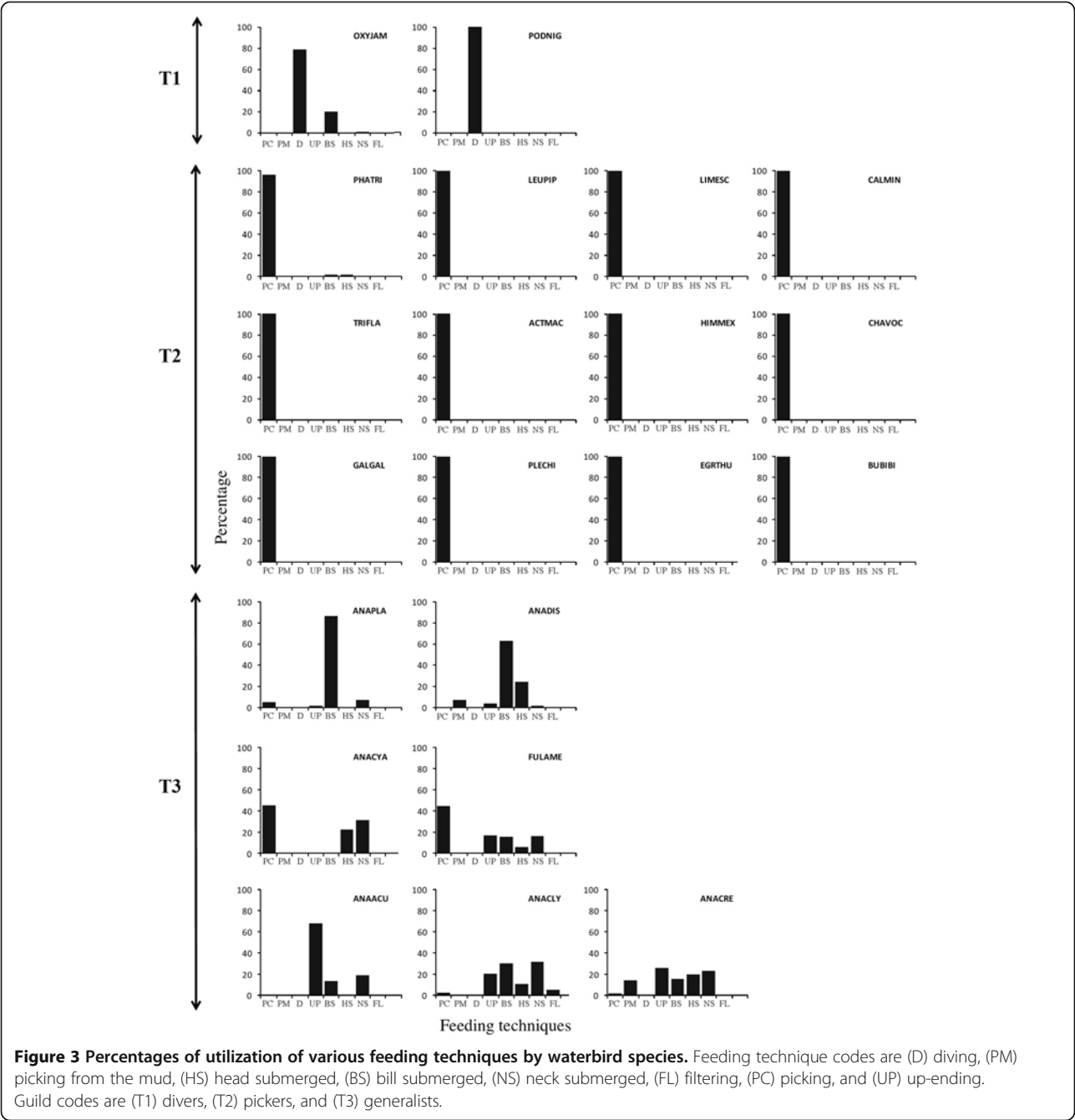

Figure 2 Cluster analysis of waterbird species by niche dimension: (a) feeding technique and (b) habitat use. The average Euclidean distances between all species pairs are marked with a dashed line (feeding technique = 1.112; habitat use = 1.058). Guild codes for feeding technique are (T1) divers, (T2) pickers, and (T3) generalists, and codes for habitat use are (H1) deep-water birds, (H2) medium-water birds, (H3) shallow-water birds, and (H4) generalist birds in waters with vegetation in both peripheral and interior zones.

Figure 3 Percentages of utilization of various feeding techniques by waterbird species. Feeding technique codes are (D) diving, (PM) picking from the mud, (HS) head submerged, (BS) bill submerged, (NS) neck submerged, (FL) filtering, (PC) picking, and (UP) up-ending. Guild codes are (T1) divers, (T2) pickers, and (T3) generalists.

bird species dive in deep water without emergent vegetation. Both species show great specialization in using deep waters to feed. Pickers in water, mud, and vegetation comprised guild G2 and were egrets, ibises (*Bubulcus ibis*, *Egretta thula*, and *Plegadis chihi*), and shorebirds (*Himantopus mexicanus*, *Tringa flavipes*, *Limnodromus scolopaceus*, *Charadrius vociferus*, *Actitis macularius*, and *Calidris minutilla*). These wading species particularly fed in areas of shallow water with vegetation and occasionally in cultivated areas adjacent to the lake.

Guild G3 was comprised of bird species that made intermittent peak movements in water, mud, or vegetation to seek prey but, in deep waters, typically caught prey by submerging their necks. These birds were *Leucophaeus pipixcan*, *Phalaropus tricolor*, *Gallinula galeata*, *Fulica americana*, and *Anas cyanoptera*.

Finally, G4 included five generalist duck species that captured prey by submerging their bill, head, and neck in deep and shallow waters. These generalist birds were *Anas acuta*, *Anas discors*, *Anas clypeata*, *Anas crecca*, and *Anas platyrhynchos*.
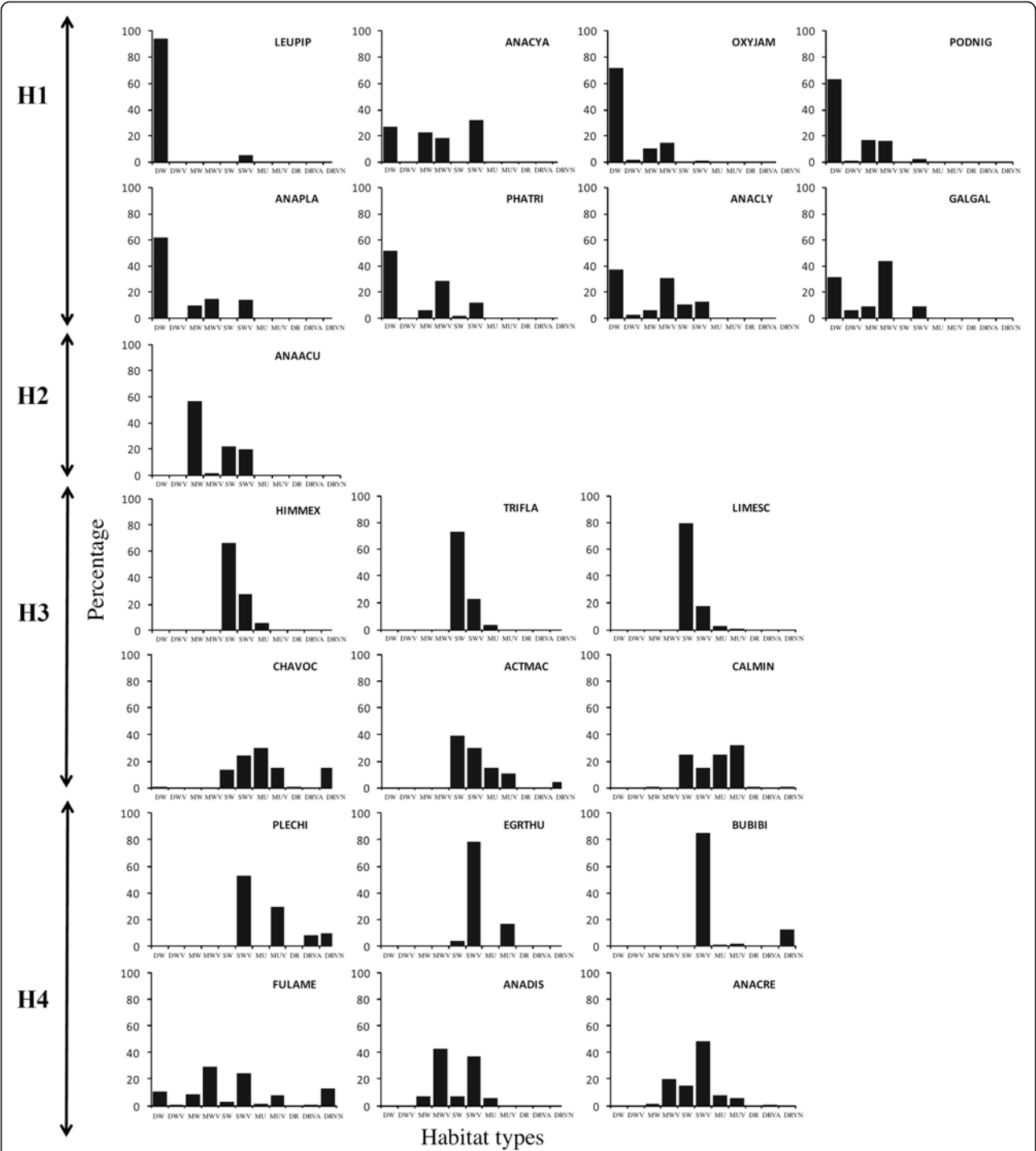
Figure 4 Percentages of utilization of various habitats by waterbird species. Habitat use codes are (DW) deep waters of >30 cm deep without emerging vegetation, (DWV) deep waters of >30 cm deep with emerging vegetation, (MW) medium waters of >10 cm and <30 cm deep without emerging vegetation, (MWV) medium waters of >10 cm and <30 cm deep with emerging vegetation, (SW) waters of <10 cm deep without emerging vegetation, (SWV) waters of <10 cm deep with emerging vegetation, (MU) mud without emerging vegetation, (MUV) mud with emerging vegetation, (DR) dry areas without vegetation, (DRVA) dry areas with vegetation away from the periphery of the lake, and (DRVN) dry areas with vegetation near the periphery of the lake. Guild codes are (H1) deep-water birds, (H2) medium-water birds, (H3) shallow-water birds, and (H4) generalist birds in waters with vegetation in both peripheral and interior zones.
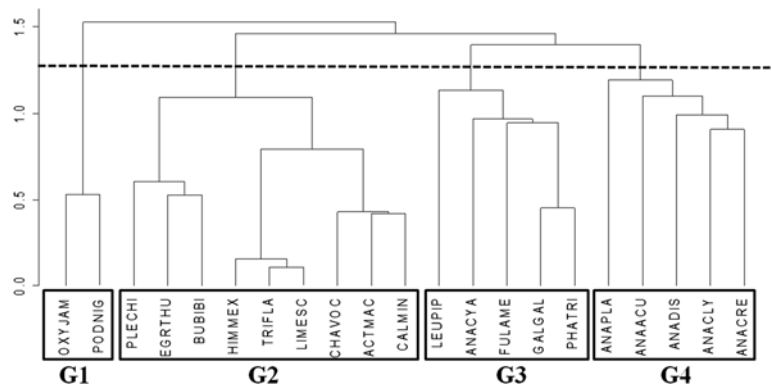
Figure 5 Cluster analysis of waterbird species by both niche dimensions (feeding technique and habitat use). The average Euclidean distance between all species pairs is indicated by a dashed line (mean = 1.314). Guild codes for the obtained guilds are (G1) divers; (G2) pickers in water, mud, and vegetation; (G3) pickers with neck submerged; and (G4) generalists.

Table 1 Niche breadth (Levins' index) of waterbird species calculated from the three niche dimensions used

Guild	Scientific name	Common name	Code	Feeding technique (n = 9)	Habitat use (n = 11)	Both dimensions (n = 55)
	Oxyura jamaicensis	Ruddy duck	OXYJAM	1.51	1.82	2.96
	Podiceps nigricollis	Eared grebe	PODNIG	1.00	2.20	2.20
G1	Mean			1.26	2.01	2.58
	Plegadis chihi	White-faced ibis	PLECHI	1.00	2.61	2.61
	Egretta thula	Snowy egret	EGRTHU	1.00	1.54	1.54
	Bubulcus ibis	Cattle egret	BUBIBI	1.00	1.36	1.36
	Himantopus Mexicanus	Black-necked stilt	HIMMEX	1.00	1.92	1.92
	Tringa flavipes	Lesser yellowlegs	TRIFLA	1.00	1.68	1.68
	Limnodromus scolopaceus	Long-billed dowitcher	LIMSCO	1.00	1.51	1.51
	Charadrius vociferus	Killdeer	CHAVOC	1.00	4.69	4.69
	Actitis macularius	Spotted sandpiper	ACTMAC	1.00	3.53	3.53
	Calidris minutilla	Least sandpiper	CALMIN	1.00	3.96	3.96
G2	Mean			1.00	2.53	2.53
	Leucophaeus pipixcan	Franklin's gull	LEUPIP	1.00	1.12	1.12
	Anas cyanoptera	Cinnamon teal	ANACYA	2.78	3.84	5.15
	Fulica americana	American coot	FULAME	3.53	5.35	12.79
	Gallinula galeata	Common moorhen	GALGAL	1.00	3.22	3.22
	Phalaropus tricolor	Wilson's phalarope	PHATRI	1.14	2.71	3.06
G3	Mean			1.89	3.25	5.07
	Anas platyrhynchos	Mallard	ANAPLA	1.34	2.32	2.86
	Anas acuta	Northern pintail	ANAACU	1.95	2.44	4.13
	Anas discors	Blue-winged teal	ANADIS	2.17	3.01	5.32
	Anas clypeata	Northern shoveler	ANACLY	4.10	3.80	14.57
	Anas crecca	Green-winged teal	ANACRE	4.90	3.25	12.01
G4	Mean			2.89	2.96	7.78
	Total mean			1.76	2.69	4.49

The guild codes correspond to those shown in Figure 5.

Niche measurements

Niche breadth by species for each of the niche dimensions (feeding technique and habitat) and for the bidimensional niche was calculated (Table 1). In general, the niche breadth was lower for feeding technique than for habitat use. Guilds G3 and G4 showed higher niche breadths for the three dimensions than the community. These two guilds showed great flexibility in habitat use and feeding technique.

Niche overlaps for matrices (uni- and bidimensional) were calculated to assess the similarity in yearly patterns of resource utilization among species (Tables 2 and 3). Mean niche overlaps for all pairs of species were 0.48 for feeding technique, 0.42 for habitat use, and 0.19 for both dimensions. Niche overlaps between species of a particular guild were higher than those between other species (Table 4). Species belonging to guild G4 overlapped less than the remaining species in other guilds in all dimensions. The overall pattern in the community was higher niche overlap between species of a guild and also reduced values of bidimensional niche overlap with respect to unidimensional overlap.

Afterward, seasonality patterns were explored (Table 4, see Additional file 1). The composition of guilds was not constant between seasons (Additional file 1), and mean niches by guild overlap changed between seasons. Guild 4 overlapped less than species of other guilds. A similar annual pattern was observed in seasonality overlaps. First, overlaps between species of a guild were higher than the mean overlap of the entire community (Figure 6). Second, bidimensional overlaps tended to be lower than unidimensional overlaps.

Null models

Yearly and seasonality patterns were compared to simulated communities. Yearly overlaps for habitat ($p = 0.01$) and for both dimensions ($p = 0.02$) were significantly higher than the expected niche overlaps. Seasonality overlaps followed a similar pattern. Habitat overlaps were higher than the expected in T1 ($p = 0.01$), T2 ($p = 0.01$), and T3 ($p = 0.05$). Additionally, bidimensional overlaps were higher in T2 ($p = 0.01$) and T3 ($p = 0.01$), but did not significantly differ in T1. Feeding technique overlaps in T2 ($p = 0.04$) differed from those expected in communities without competition.

Discussion

Our study describes the guild structure of a waterbird community in central Mexico and analyzes resource utilization patterns through three niche dimensions: habitat use, feeding technique, and time. Patterns characterized from niche breadth and niche overlap of species showed that species were specialists in feeding technique and more flexible in terms of feeding habitat. To detect if the observed pattern

arose from competition between species, null models were used. Niche overlaps of the waterbird community were higher than expected in a community without competition, suggesting a lack of competition. Processes such as morphological differences, different abundances of species, migration, resource fluctuations, and clumped resources could explain the observed patterns.

The bidimensional niche (under the assumption that it reflects differences in resource exploitation; *sensu* Holmes and Recher 1986) structured the waterbird community into four feeding guilds (Wiens 1989; Sarrías et al. 1996). However, species belonging to the same guild mostly differed in bill and leg morphologies. For instance, guild G2 could be subdivided into subgroups according to morphological characteristics, such as bill or leg size. Morphological differences may explain why members of the same guild feed in different areas using the same techniques or in the same area (apparently exploiting the same resource) but catching different prey (Schoener 1974; Simberloff and Boecklen 1981; Gotelli and Ellison 2002; Zeffer et al. 2003). To provide an accurate description of feeding guilds, more dimensions should be added to the analysis. Data on diet (stomach contents) and availability of prey would be informative (Sarrías et al. 1996).

Important patterns in the waterbird community structure at Lake Acuitlapilco were characterized through niche breadths and niche overlaps. The calculated niche breadths were narrow, suggesting that guilds were mainly specialists in feeding techniques. Only three species (*F. americana*, *A. clypeata*, and *A. crecca*) showed niche breadths wider than the other species. The first two were the most abundant species in the community (Fonseca et al. 2012) and also had the largest values of niche breadth. These species appeared to be unaffected by high abundances of individuals of the same species (*A. clypeata*) or by changes in food habitat availability (*F. americana*). The flocking feeding behavior of *A. clypeata* and *F. americana* and the wide niche breadths in all dimensions suggest that competition for resources or interspecific competition did not play a major role in structuring their populations.

Additionally, narrow niches suggest that changes in resource availability may also affect the composition of the community (Pöysä 1983). Under this scenario, a fluctuation in resources (habitat) would affect species with a narrow niche breadth, such as wading species (of the Scolopacidae and Charadriidae) from guild G2. These guilds use pecking to opportunistically exploit resources in areas with particular characteristics such as muddy areas and shallow water (Skagen and Knopf 1994). Their presence and abundance were restricted to months of water withdrawal (Pérez-Crespo et al. 2013). In contrast, guilds G4 (*A. acuta*, *A. discors*, *A. clypeata*, *A. crecca*, and *A. platyrhynchos*) and G3 (*A. cyanoptera*, *F. americana*, *G. galeata*, *L. pipixcan*, and *P. tricolor*) had wider niche

Table 2 Niche overlap values of waterbird species calculated from feeding technique and habitat use as niche dimensions

	OXYJAM	PODNIG	PLECHI	EGRTHU	BUBIBI	HIMMEX	TRIFLA	LIMSCO	CHAVOC	ACTMAC	CALMIN
OXYJAM	-	0.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PODNIG	0.99	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PLECHI	0.01	0.04	-	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
EGRTHU	0.01	0.04	0.94	-	1.00	1.00	1.00	1.00	1.00	1.00	1.00
BUBIBI	0.02	0.04	0.88	0.97	-	1.00	1.00	1.00	1.00	1.00	1.00
HIMMEX	0.01	0.02	0.33	0.42	0.38	-	1.00	1.00	1.00	1.00	1.00
TRIFLA	0.00	0.01	0.25	0.34	0.29	1.00	-	1.00	1.00	1.00	1.00
LIMSCO	0.00	0.01	0.19	0.26	0.22	0.98	1.00	-	1.00	1.00	1.00
CHAVOC	0.03	0.04	0.65	0.59	0.58	0.52	0.46	0.42	-	1.00	1.00
ACTMAC	0.01	0.02	0.59	0.63	0.58	0.92	0.89	0.86	0.79	-	1.00
CALMIN	0.01	0.01	0.57	0.46	0.32	0.62	0.59	0.57	0.85	0.81	-
LEUPIP	0.97	0.94	0.05	0.06	0.06	0.02	0.02	0.01	0.05	0.03	0.02
ANACYA	0.66	0.73	0.53	0.61	0.62	0.24	0.19	0.14	0.33	0.35	0.19
FULAME	0.41	0.47	0.62	0.59	0.61	0.28	0.24	0.19	0.50	0.44	0.35
GALGAL	0.73	0.77	0.14	0.16	0.17	0.06	0.05	0.04	0.10	0.10	0.05
PHATRI	0.94	0.95	0.16	0.19	0.19	0.10	0.09	0.07	0.13	0.13	0.07
ANAPLA	0.98	0.98	0.18	0.21	0.21	0.08	0.06	0.05	0.13	0.12	0.07
ANAACU	0.14	0.24	0.27	0.32	0.31	0.43	0.42	0.40	0.26	0.43	0.27
ANADIS	0.18	0.24	0.55	0.63	0.64	0.37	0.32	0.27	0.43	0.49	0.31
ANACLY	0.84	0.86	0.21	0.25	0.25	0.28	0.27	0.25	0.20	0.29	0.18
ANACRE	0.09	0.13	0.79	0.89	0.87	0.60	0.53	0.46	0.66	0.76	0.53

Table 2 Niche overlap values of waterbird species calculated from feeding technique and habitat use as niche dimensions (Continued)

	LEUPIP	ANACYA	FULAME	GALGAL	PHATRI	ANAPLA	ANAACU	ANADIS	ANACLY	ANACRE
OXYJAM	0.00	0.01	0.05	0.00	0.01	0.25	0.06	0.23	0.16	0.10
PODNIG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PLECHI	1.00	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
EGRTHU	1.00	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
BUBIBI	1.00	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
HIMMEX	1.00	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
TRIFLA	1.00	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
LIMSCO	1.00	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
CHAVOC	1.00	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
ACTMAC	1.00	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
CALMIN	1.00	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
LEUPIP	-	0.76	0.95	1.00	1.00	0.06	0.00	0.00	0.06	0.03
ANACYA	0.57	-	0.84	0.76	0.76	0.09	0.14	0.15	0.47	0.45
FULAME	0.28	0.81	-	0.95	0.96	0.23	0.25	0.18	0.35	0.30
GALGAL	0.57	0.76	0.80	-	1.00	0.06	0.00	0.00	0.06	0.03
PHATRI	0.87	0.79	0.66	0.90	-	0.08	0.00	0.02	0.08	0.04
ANAPLA	0.95	0.78	0.53	0.76	0.97	-	0.26	0.93	0.67	0.41
ANAACU	0.02	0.60	0.39	0.22	0.17	0.20	-	0.26	0.68	0.75
ANADIS	0.04	0.72	0.89	0.71	0.48	0.32	0.37	-	0.68	0.57
ANACLY	0.74	0.81	0.76	0.94	0.96	0.88	0.27	0.64	-	0.87
ANACRE	0.05	0.69	0.78	0.43	0.35	0.27	0.40	0.88	0.49	-

Above the diagonal line, feeding technique; below the diagonal line, habitat use. The nomenclature of bird species corresponds to the first three letters of the generic and specific names as defined in Table 1.

Table 3 Niche overlap values of waterbird species calculated by considering both niche dimensions together

	OXYJAM	PODNIG	PLECHI	EGRTHU	BUBIBI	HIMMEX	TRIFLA	LIMSCO	CHAVOC	ACTMAC	CALMIN
OXYJAM	-	0.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PODNIG		-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PLECHI			-	0.94	0.88	0.33	0.25	0.19	0.65	0.59	0.57
EGRTHU				-	0.97	0.42	0.34	0.26	0.59	0.63	0.46
BUBIBI					-	0.38	0.29	0.22	0.58	0.58	0.32
HIMMEX						-	1.00	0.98	0.52	0.92	0.62
TRIFLA							-	1.00	0.46	0.89	0.59
LIMSCO								-	0.42	0.86	0.57
CHAVOC									-	0.79	0.85
ACTMAC										-	0.81
CALMIN											-
LEUPIP											
ANACYA											
FULAME											
GALGAL											
PHATRI											
ANAPLA											
ANAACU											
ANADIS											
ANACLY											
ANACRE											

Table 3 Niche overlap values of waterbird species calculated by considering both niche dimensions together *(Continued)*

	LEUPIP	ANACYA	FULAME	GALGAL	PHATRI	ANAPLA	ANAACU	ANADIS	ANACLY	ANACRE
OXYJAM	0.01	0.01	0.02	0.00	0.02	0.32	0.00	0.00	0.19	0.01
PODNIG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PLECHI	0.05	0.00	0.56	0.14	0.16	0.08	0.00	0.00	0.01	0.01
EGRTHU	0.06	0.00	0.45	0.16	0.18	0.09	0.00	0.00	0.01	0.01
BUBIBI	0.06	0.00	0.47	0.17	0.18	0.09	0.00	0.00	0.01	0.00
HIMMEX	0.02	0.00	0.16	0.06	0.09	0.03	0.00	0.00	0.00	0.01
TRIFLA	0.02	0.00	0.13	0.05	0.07	0.03	0.00	0.00	0.00	0.01
LIMSCO	0.01	0.00	0.10	0.04	0.06	0.02	0.00	0.00	0.00	0.01
CHAVOC	0.05	0.01	0.50	0.10	0.12	0.05	0.00	0.00	0.01	0.02
ACTMAC	0.03	0.00	0.34	0.10	0.12	0.05	0.00	0.00	0.01	0.02
CALMIN	0.02	0.00	0.35	0.05	0.07	0.03	0.00	0.00	0.00	0.02
LEUPIP	-	0.62	0.38	0.57	0.86	0.01	0.00	0.00	0.09	0.00
ANACYA		-	0.51	0.67	0.72	0.00	0.06	0.04	0.24	0.27
FULAME			-	0.66	0.61	0.12	0.12	0.22	0.32	0.32
GALGAL				-	0.90	0.01	0.00	0.00	0.07	0.00
PHATRI					-	0.04	0.00	0.00	0.11	0.00
ANAPLA						-	0.07	0.24	0.64	0.08
ANAACU							-	0.22	0.18	0.25
ANADIS								-	0.33	0.46
ANACLY									-	0.44
ANACRE										-

The nomenclature of bird species corresponds to the first three letters of the generic and specific names as defined in Table 1.

Table 4 Total and mean overlap values for species within guilds, for each guild, and for all species

		Feeding technique				Habitat use				Both dimensions			
		T	T1	T2	T3	T	T1	T2	T3	T	T1	T2	T3
Guild													
G1	Mean observed	0.97	0.17	1.00	1.00	0.99	0.86	0.89	0.96	0.94	0.08	0.89	0.96
G2	Mean observed	1.00	1.00	1.00	1.00	0.60	0.56	0.45	0.51	0.60	0.56	0.57	0.51
G3	Mean observed	0.90	0.96	0.98	0.49	0.70	0.82	0.52	0.30	0.65	0.81	0.54	0.27
G4	Mean observed	0.61	0.31	1.00	0.58	0.47	0.23	0.27	0.64	0.29	0.12	0.23	0.40
Null models (all species)													
	Mean observed	0.48	0.47	0.57	0.40	0.42	0.33	0.35	0.41	0.19	0.16	0.22	0.17
	Mean expected	0.45	0.41	0.47	0.41	0.32	0.26	0.26	0.34	0.15	0.13	0.14	0.15
	p	0.26	0.11	0.04	0.58	0.01	0.01	0.01	0.05	0.02	0.11	0.01	0.01

Guilds formed by only one bird species were not considered in this analysis. G1, divers; G2, pickers in water, mud, and vegetation; G3, pickers with neck submerged; G4, generalist; T, total; T1, February to May; T2, May to September; T3, September to February.

breadths in both dimensions and would have been less affected. The ability of these guilds to exploit resources in several habitats of the lake using diverse techniques allowed segregation, thus decreasing potential inter- and intraspecific interactions.

The general pattern of niche overlap found in the Acuitlapilco waterbird community was larger among species of the same guild than between other species in the community. Several authors suggested that competitive interactions are more likely among species of the same guild (Pianka 1980; MacNally 1983; Jaksic and Medel 1990), and they usually occur in guilds with a moderate to small number of species (MacNally 1983). Liordos (2010) found a similar pattern of niche overlap of foraging guilds of waterbirds wintering in a Mediterranean coastal wetland. He concluded that a small niche overlap between species of different guilds suggested a relatively high degree of specialization within the waterbird assemblage. Overlaps of species of the same guild were high, but habitat partitioning was observed. No conclusions about the existence of ecological processes underlying the pattern observed were provided by Liordos. In contrast, the use of null models in our study allowed us to discriminate between ecological phenomena such as competition and species sharing niches.

Results from the null models showed that the observed overlaps were higher than expected, particularly in habitat use and both dimensions together. When data were seasonally subdivided, the same pattern was observed. Therefore, species share habitat more than randomly expected, thus denoting a lack of competition (Gotelli and Graves 1996). Several mechanisms could explain this pattern.

First, seasonal variability of resources allows the addition or removal of species in each guild, reducing competitive interactions (Wiens 1977). Second, clumped resources attract more species and individuals. Studies suggested that shallow waters have greater organic matter and submerged plant beds, providing a rich foraging habitat and protection

from predators (Rozas and Odum 1988; Minello et al. 1994; Rozas and Zimmerman 2000; Castellanos and Rozas 2001; Gossman 2005; Cannaday 2006). Other studies also suggested that shallow waters can accommodate more species than deep waters (Williams 1996; Colwell and Taft 2000), which suggests that clumped and rich resources in shallow waters increase bird density there and reduce competition. Third, rather than simply forming in areas of existing high prey density, social flocks may actively enhance their foraging success through herding or confusing escape reactions of prey (Saino et al. 1995; Battley et al. 2003). Guild G2, pickers in water, mud, and vegetation (egrets, ibises, and shorebirds), feed in groups in shallow waters with high prey availability, and aggressive interactions were not noted between individuals when foraging at our study site. Fourth, the existence of differences in morphology between members of the same guild, as mentioned above (Wiens 1989), allows species to coexist. Fifth, the arrival of migrating species in winter coincides with an increased availability of resources and habitats (Aguilar 2003). Finally, differences in species abundances could be a mechanism explaining coexistence. For example, *O. jamaicensis* (5,300 records, Fonseca et al. 2012) and *P. nigricollis* (280 records) had almost total niche overlap (all dimensions) and narrow niche breadths. In contrast, *A. clypeata* and *A. platyrhynchos* had high niche overlap, but niche breadths and abundances were not equal. Asymmetries in abundance and niche breadth could potentially be acting as mechanisms for coexistence.

Conclusions

In short, our results showed that waterbird species in Lake Acuitlapilco were specialists in resource utilization patterns and therefore vulnerable to fluctuations in resources, particularly feeding habitats. Niche overlaps were generally largest among species belonging to the same guild. The use of null models showed that habitat and observed bidimensional overlaps were higher than those of
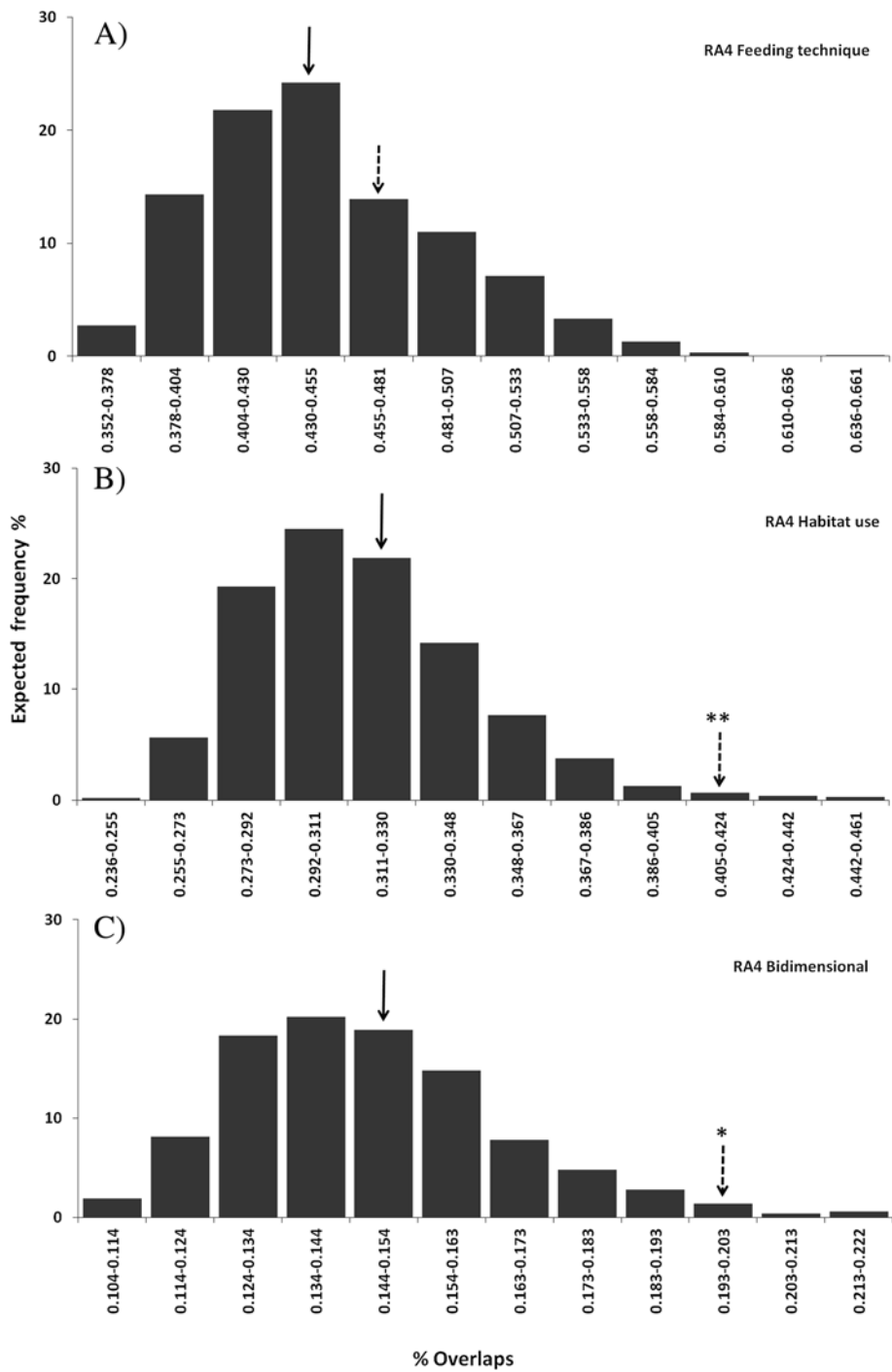
Figure 6 Histogram comparing the mean overlaps from the observed (dashed arrows) and generated communities (solid arrows). With the RA4 algorithm and Pianka index with 1,000 iterations. **(A)** Feeding technique overlaps, **(B)** habitat use overlaps, and **(C)** bidimensional niche overlaps. *$p < 0.05$, **$p < 0.01$.

randomly generated communities, suggesting a lack of competition or species sharing niches. Thus, our study suggested that other processes can be used to predict resource utilization patterns instead of competition alone, as

suggested by neutral theory (Hubbell 2001). Future studies analyzing the mechanisms that structure waterbird communities should include the use of null models to support their conclusions.

Additional file

Additional file 1: Seasonality patterns. Table S1. Seasonal niche overlaps for T1 (February 2011 to May 2011) calculated from feeding technique (above the diagonal line) and habitat use (below the diagonal line). **Table S2.** Seasonal bidimensional (feeding technique and habitat use) niche overlaps for T1 (February 2011 to May 2011). **Table S3.** Seasonal niche overlaps for T2 (May 2011 to September 2011) calculated from feeding technique (above the diagonal line) and habitat use (below the diagonal line). **Table S4.** Seasonal bidimensional (feeding technique and habitat use) niche overlaps for T2 (May 2011 to September 2011). **Table S5.** Seasonal niche overlaps for T3 (September 2011 to February 2012) calculated from feeding technique (above the diagonal line) and habitat use (below the diagonal line). **Table S6.** Seasonal bidimensional (feeding technique and habitat use) niche overlaps for T3 (September 2011 to February 2012).

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