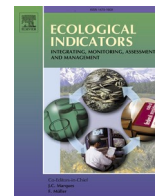


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Aquatic bird communities in Andean lakes of Ecuador are increasingly dissimilar over time

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ABSTRACT

Andean lakes are important for human well-being and biodiversity conservation, yet human-induced environmental changes threaten their biodiversity and the ecosystem services they provide. Knowledge of the relationship between biodiversity and environmental factors can provide insight into how human activity impacts lakes. We report trends of community composition of aquatic bird communities at six Andean lakes in Ecuador based on 15-years of monitoring. Additionally, we explore relationships among the abundance of aquatic bird species and environmental variables, such as elevation, water depth, biochemical demand of oxygen and concentration of phosphates and nitrites. We found a sustained population growth of one species of herbivorous bird, the Andean Coot, *Fulica ardesiaca*, across all lakes. Local trends in community composition show directional changes in four lakes and were likely a result of abundance increases of this species. Environmental factors related to eutrophication explained the abundance of *F. ardesiaca*, indicating that ongoing eutrophication of Andean Ecuadorian lakes, which results in increased submerged vegetation, benefits herbivorous species like this. Management measures that prevent further eutrophication combined with on-going monitoring should be considered in order to maintain ecosystem health and functioning.

1. Introduction

Community dynamics are increasingly influenced by human-induced ecological and environmental factors, such as biotic invasions and land-use and climate change (Collins, 2000; Matthews et al., 2013; Kortz and Magurran, 2019). Species in communities respond to these changes in a variety of ways, including changing their abundance, or even becoming locally extinct, which, in turn, can influence community structure and stability (Moritz and Agudo, 2013). Understanding how and why community structure changes is important in order to mitigate human-induced ecological and environmental stressors. In aquatic systems, birds are particularly appropriate for monitoring human-induced changes because they respond to water quality and land-use changes and are conspicuous and easy to monitor (Cooper et al., 2014).

Andean lakes have been strongly impacted by human induced environmental changes and are of critical conservation concern (Ochoa-Tocachi et al., 2016). These lakes provide important services that

support human well-being and sustain biodiversity (Gandarillas et al., 2016). One of the most important services is freshwater that benefits c 20 million people living in large cities and rural areas in South America and use water for consumption and irrigation (Buytaert et al., 2011; Buytaert and De Bièvre, 2012). Andean lakes also contribute to the maintenance of global biodiversity (Mittermeier et al., 1998). The complex topography of Andean mountains and inter-Andean valleys, along with high precipitation and the presence of mountain glaciers, has resulted in a dense network of wetlands which host endemic biota adapted to local environmental conditions (Fjeldsø, 1985). However, human driven deforestation in lake catchment areas promotes soil erosion and increases sediment load in the water column (Schmeller et al., 2018). The development of urban infrastructure, agricultural land and recreational facilities often take place near lakes, which increases the influx of nutrients into lakes leading to eutrophication and changes in biotic communities (Wittmann et al., 2015; Schmeller et al., 2018). Changes in water level, due to dam construction, affect submerged

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vegetation and nesting sites for aquatic birds (Guevara et al., 2016; Dinesen et al., 2019). In addition, the introduction of exotic species affects the composition of biotic communities and alters trophic interactions. One of the most evident examples is the introduction of the Rainbow Trout *Oncorhynchus mykiss* into temperate freshwater ecosystems in the Andes, which has affected amphibian populations since trout are voracious predators of amphibian eggs and tadpoles (Martín-Torrijos et al., 2016). In the southern Andean lakes of Argentina, trout are suspected to compete for food with native aquatic birds, like the Hooded Grebe, *Podiceps gallardoi* (Roesler et al., 2012).

Given these pressures on Andean lakes, it is important to monitor the dynamics of native fauna. The presence and abundance of aquatic birds is known to be influenced by environmental factors such as nutrients and water level, which influence food resources and nesting sites, respectively (Hanson and Butler, 1994; Noordhuis et al., 2002). For instance, eutrophication often results in the proliferation of green algae and macrophytes that provide food resources for herbivorous birds (Schmeller et al., 2018), thus eutrophication induced fluctuations in aquatic vegetation biomass might influence the population dynamics of herbivorous birds (Perrow et al., 1997; Noordhuis et al., 2002). These dynamics, although occurring locally, could also be reflected at broader spatial scales if mechanisms related to eutrophication operate simultaneously across lakes. Therefore, trends in aquatic birds should be monitored at multiple lakes which will allow the analysis of trends at both local and broader landscape scales.

We studied aquatic bird communities at nine Andean lakes of Ecuador. We examined the relationships among environmental factors and bird abundances for all lakes. For a subset of six lakes we examined trends in common species abundance, as well as directional changes of community composition using counts of aquatic birds taken over 15-year period (2004–2018). We predicted that possible changes in the abundance of common and dominant species could influence community composition, leading to increasing dissimilarity in Andean aquatic bird communities over time.

2. Methods

2.1. Study area and environmental variables

The study region spans 4000 km² in the Andes of Ecuador. We studied bird communities at nine lakes (Table 1) which vary in elevation (2200–4000), water surface (14–700 ha) and water depth (1–150 m).

Table 1

Coordinates, elevation, water surface and maximum depth of the nine lakes studied. ¹Time series refers to whether or not the lake was bird-monitored for the period 2004–2018.

Lake	Coordinates	Elevation (m a.s.l.)	Water surface (ha)	Max depth (m)	Time series ¹
Cuicocha	0°17' N, 78°21' W	3100	700	150	No
San Pablo	0°13' N, 78°14' W	2660	670	35	Yes
Yahuarcocha	0°22' N, 78°06' W	2210	230	7.9	Yes
La Mica	0°32' S, 78°12' W	3900	360	22.5	Yes
Limpiopungo	0°37' S, 78°28' W	4000	15	1	No
Yambo	1°05' S, 78°35' W	2600	16	25	Yes
Pisayambo	1°05' S, 78°19' W	3600	450	70	Yes
Colta	1°44' S, 78°45' W	3420	220	3.5	Yes
Llaviucu	2°50' S, 79°08' W	3100	14	16	No

Environmental information for each lake was obtained from Ecuador's National Wetland Inventory project (Briones et al., 2001) and updated with several recent sources (Gunkel and Beulker, 2009; Labaj et al., 2018; Mouillet et al., 2018). To evaluate the relationship between environmental characteristics of lakes and patterns of aquatic bird richness and abundance, we selected eight variables that are known to influence ecological processes and species abundance in freshwater wetlands (van der Valk, 2012), namely: lake size, maximum depth, elevation, pH, biochemical demand of oxygen, phosphate concentration, nitrate concentration, water turbidity and suspended solids. Environmental data used in analysis are provided in Supplementary Table 1.

2.2. Aquatic bird counts

We performed counts of aquatic birds at nine Andean lakes in Ecuador. We followed the field protocols developed by Wetlands International Neotropical Waterbird Census program, which are based on standardized field monitoring protocols (Bibby et al., 2000). On a typical monitoring day, experienced observers carried out a census, which started in the morning (08:00 h) and lasted for two to three hours. We performed observations either from a boat that toured the lakes perimeter at a constant velocity, remaining at 60–100 m from the shore to avoid massive take-off of birds that congregate, or by walking along the lakes' shores. Whenever a group of birds was encountered we stopped the boat – or paused the hike – and counted all individuals with the aid of binoculars and scopes. We noted movements of single birds or flocks within the lake to avoid double counting individuals. If more than one observer counted birds simultaneously, the highest value was considered. For subsequent analyses, only adult-sized birds were included because our focus was the permanent breeding population. In some cases, immature birds could not be distinguished from adults, in which case we kept the count. For six out of the nine lakes, we performed bird counts in February and July between July 2004 and February 2018, although information obtained at the other three lakes was not sufficient for a time series analysis, we use this information to explore bird-environment relationships (see below). Although census route (i.e., water or land) varied among lakes depending the on logistics of each site, census protocols at each lake were the same across the monitoring period to allow the analysis of temporal trends.

2.3. Trends in single species abundance

We analyzed trends in species counts for the six lakes that were monitored over 2004 – 2018. Because we aimed to analyze landscape-level patterns of species trends, and not only local trends at each lake, we included lake identity as a random effect and analyzed the trends of counts of the four most abundant species in the study region (*Anas andium*, *A. georgica*, *Fulica ardesiaca* and *Oxyura jamaicensis*). These four species are common in most Andean lakes (Fjeldså and Krabbe, 1990) and were present in almost all lakes studied, with the exception of *A. andium* which was absent in Yahuarcocha. After plotting counts against time intervals, we found that most count-time relationships were nonlinear and the variances in the counts differed substantially among species (Fig. 1). Therefore, we applied a generalized additive mixed model of counts against time (Zuur et al., 2009). Our model is as follows:

$$Y \sim \text{gaussian}(\text{counts})$$

$$Y \sim \alpha + \beta[\cos(\text{time} * \pi)] + \beta(\text{time}, \text{byBirdID}) + 1|\text{lakeID} + \varepsilon$$

$$\varepsilon = N(0, \sigma^2)$$

In this model, the parameter $\beta [\cos(\text{time} * \pi)]$ is a cosine function to implement a fixed seasonality effect in the model, since previous work in the region found seasonal patterns of bird abundance (Guevara et al., 2011, 2012). The parameter $\beta(\text{time}, \text{by Bird ID})$ is a thin plate regression spline smoother, one smoother for each level of bird identity. The

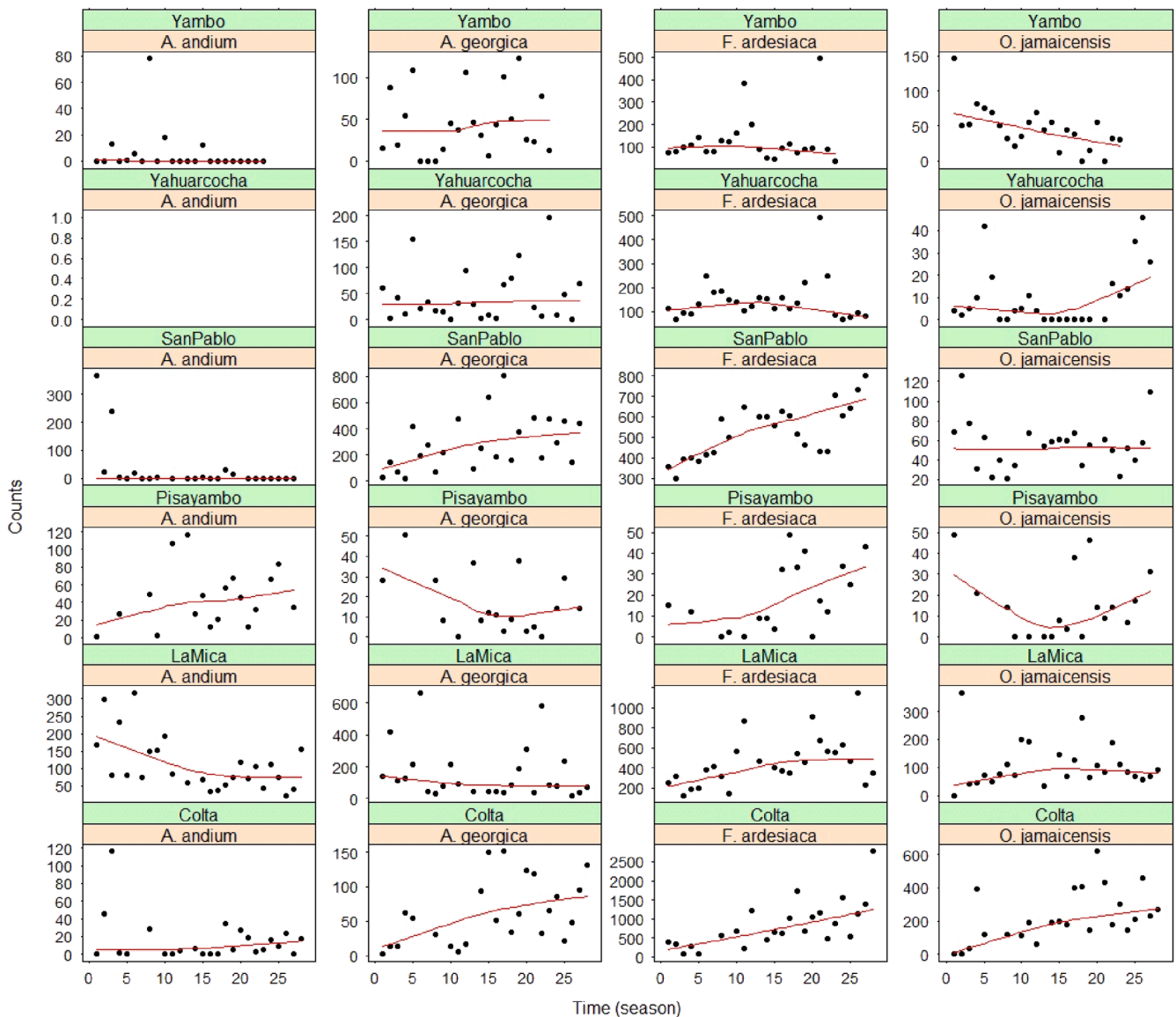


Fig. 1. Temporal trends of semestral counts of four common aquatic bird species and total number of birds recorded at six Andean lakes in Ecuador between year 2004 and 2018. The regression lines indicate the loess smoother (applying a span of 0.9), plots were made with the lattice package in R (Sarkar, 2008).

parameter + 1 | lake ID is the name of each lake which was treated as a random effect. We applied the maximum likelihood method for model fitting and included a weights argument to implement different variances for each level of bird identity. We square root transformed the counts to comply with the assumption of normal distribution of errors in regression analysis. The standardized residuals of the model showed short-term autocorrelation which means that observations along the time series were not completely independent; therefore, we adjusted the model by including a second order auto-regressive moving average correlation structure (ARMA). The new model had substantially lower AIC values, and the autocorrelation of standardized residuals was reduced. Further model validation (residuals against fitted values or against time) did not produce any pattern and visual inspection of quantile-quantile plots per lake showed that residuals did not deviate strongly from normal.

2.4. Trends in community composition

Because our goal was to explore local trends in community composition, we considered each lake as a single community. We justify this

assumption because our study lakes differ substantially in size, depth and elevation (Table1); variables that influence the composition of Andean aquatic bird communities (Servat et al., 2018). We removed species that occurred less than three times at each lake during the whole sampling period in order to reduce the influence of nomadic or vagrant species in community analysis (Donoso, 2017). We analyzed temporal changes in aquatic bird communities for each lake, using three community metrics. First, we analyzed the rate of community change, which provides a measure of the rate and direction of change in a given community (Hallett et al., 2016). The rate of community change was calculated by comparing Euclidean distances in bird community composition among pairwise communities for each time lag interval and for the entire time series (Collins, 2000; Hallett et al., 2016). For instance, to analyze a data series consisting of five yearly intervals we use four one-year time lags (t_1 vs t_2 , t_2 vs t_3 , t_3 vs t_4 , t_4 vs t_5), three two-year time lags (t_1 vs t_3 , t_2 vs t_4 , t_3 vs t_5) and so forth (Hallett et al., 2016). Distance values were then regressed against time intervals reflecting accumulated changes in community composition. We use generalized additive models to test for the effect of time on community composition. Following the species count analysis, we added a second

order correlation structure (ARMA) to account for temporal autocorrelation. The slope of the regression line provides the rate and directionality of changes. A slope of zero indicates stable communities that show no change through time, a positive slope indicates unstable communities that accumulate changes through time, and a negative linear slope also indicates unstable communities, but with a convergent trajectory (Collins, 2000; Hallett et al., 2016). Second, for each lake, we analyzed species turnover across 15 yr. Turnover refers to the proportion of species that are different between two time points (MacArthur and Wilson 1963). We calculated total turnover as a proportion of species richness (lost and gained) in relation to the total species in each year to year comparison (Hallett et al., 2016). The turnover metric varied from 0 (no species gained or lost) to 1 (complete species replacement). Total turnover was decomposed in the proportion of species gained and lost in relation to the total species richness at each time interval (Collins, 2000). Patterns of turnover could be obscured or difficult to interpret because of the high seasonality of aquatic bird communities resulting from both nearctic-neotropical migrants and locally seasonal species, hence for turnover analysis we used data only from the censuses performed in February. Third, we calculated the Shannon community richness index for each time point and for each lake. As our goal was to assess the influence of regional dominant species over patterns of local community composition, we removed species that exhibited a significant and positive trend and repeated the analyses for the three metrics of community dynamics.

2.5. Bird-environment relationships

To explore relationships among environmental variables for the nine lakes and species richness and abundance of the four most common species, we performed a non-metric multidimensional scaling (NMDS; Kruskal, 1964). We used the Bray-Curtis dissimilarity metric to compare compositional similarity among aquatic bird communities and its relationship with environmental variables. We used the scores of species and environmental variables resulting from the ordination to build a bi-plot that illustrates the relationships between environment and bird composition. We set the NMDS analysis to a two-dimension space. The goodness of fit of NMDS was estimated using a stress value which ranged from 0 to 1, with values approaching zero indicating a good fit.

All statistical analyses and figures were done using R 3.5.0 (R Development Core Team, 2018), applying functions in the packages mgcv (Wood, 2006) and nlme (Pinheiro et al., 2011) for additive modelling, codyn (Hallett et al., 2016) for changes of community composition analysis, vegan (Oksanen et al., 2016) for NMDS analysis and ggplot2 (Wickham, 2016) and lattice (Sarkar, 2008) for time series plotting.

3. Results

3.1. Aquatic bird counts

A total of 39 aquatic bird species, belonging to seven families, were recorded during our monitoring period from July 2004 to February 2018. Lake Colta had the highest species richness and abundance with 30 species, and mean counts of 1313 ± 130 SE individuals, whereas Pisayambo had the lowest species richness (15) and mean counts (111 ± 16 SE). *Fulica ardesiaca* was the most abundant species in most lakes with counts as high as 1736 adult individuals recorded in February 2013 in Colta. [Supplementary Table 1](#) provides the list of species recorded at each lake.

3.2. Trends in single species abundance

We visually inspected trends of the four most common species and found that at lake Colta three species, *O. jamaicensis*, *A. georgica* and *F. ardesiaca* were increasing in abundance, whereas *A. andium* remained

stable. Similarly, two species, *A. georgica* and *F. ardesiaca* increased in lake San Pablo. Negative trends are also evident for some species but only at specific lakes; for instance, *A. andium* declined in both San Pablo and La Mica, and *O. jamaicensis* declined in Yambo. Despite these local trends, no significant effect of time on bird counts was detected across multiple lakes, except for *F. ardesiaca* which became more abundant ([Table 2](#)).

3.3. Trends in community composition

The slope of the regression line between Euclidean distance and time, which indicates the rate of community change, revealed positive and significant trends for all sites with the exception of Yahuarcocha and Yambo which remained stable during the monitoring period ($F_{1, 1602} = 184.7$, $p < 0.001$). Positive linear trends indicate that community composition changed over time. Bird communities had high seasonal species turnover, especially when examining the patterns of species gained and lost ([Fig. 2a](#)). Total turnover declined throughout the survey period for all sites ($F_{1, 396} = 70.8$, $p < 0.001$). The mean total turnover throughout the study period was 0.51 ± 0.19 SD. Temporal trends analysis of the Shannon community index showed declines in species richness at four lakes (Colta, La Mica, San Pablo and Yambo), increase at Yahuarcocha and no change in Pisayambo ([Fig. 2a](#)). After the removal of *F. ardesiaca*, which was the most abundant species in bird counts at all lakes, the slope of the regression line of the rate of community change was slightly attenuated for La Mica and San Pablo lakes ([Fig. 2b](#)). The slope of the regression line of Shannon index changed significantly at Colta and La Mica lakes after the removal of *F. ardesiaca*, exhibiting a flat pattern ([Fig. 2b](#)).

3.4. Bird-environment relationships

The stress value of the NMDS analysis was 0.06 based on the 2-axis optimal solution after 20 iterations. Bird richness related positively with lake depth, whereas the abundance of *F. ardesiaca* related positively with intermediate values of biochemical demand of oxygen. The abundance of *A. andium* was mostly explained by high values of elevation, whereas the abundance of *A. georgica* and *O. jamaicensis* was mostly related with phosphates and total suspended solids ([Fig. 3](#)). Colta, San Pablo and Yambo were characterized by a high influence of biochemical demand of oxygen and nitrites suggesting high levels of eutrophication.

4. Discussion

The composition of aquatic bird communities in the high Andes of Ecuador changed over time. These changes can be partially attributed to dramatic increases in the abundance of *F. ardesiaca* in the region. When we removed this species from our analysis, lakes appeared to have a relatively stable species composition over time in all but two lakes. These results suggest that population growth of a single dominant species can influence the structure of aquatic bird communities across

Table 2

Results of generalized additive mixed modelling analysis for the four most abundant species recorded in six Andean lakes in Ecuador, period 2004–2018.

Selected species/seasonality			
Parametric Terms:	Df	F	p-value
cos (time * π)	1	2.05	0.15
ID (selected species)	3	6.33	<0.01
Approximate significance of smooth terms:			
	Estimated df	F	p-value
s(time): <i>A. andium</i>	1	1.78	0.18
s(time): <i>A. georgica</i>	1	0.13	0.72
s(time): <i>F. ardesiaca</i>	1	10.54	<0.01*
s(time): <i>O. jamaicensis</i>	1	1.57	0.23

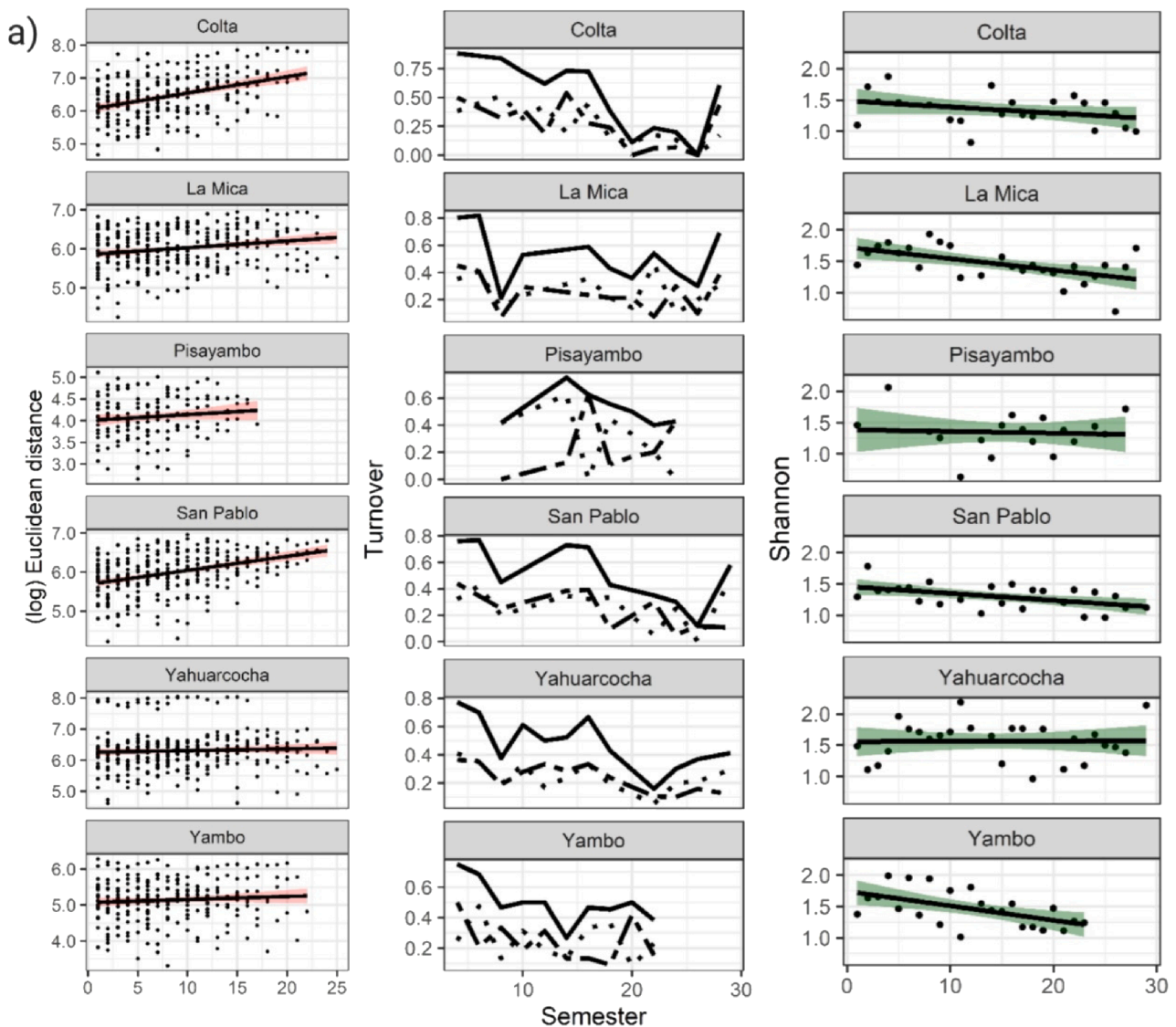


Fig. 2. Analysis of trends of community composition of six Andean aquatic bird communities monitored in northern Ecuador on a semestral basis over the period of 2004–2018. Left boxes illustrate the rate of change of communities estimated as the slope of the relationship between Euclidean distances between pairwise communities and time. Middle boxes illustrate species temporal turnover, where solid line is total turnover, dashed and dotted lines is proportion of species gained and dotted lines is proportion of species lost. Right boxes provide trends of Shannon diversity index. a) All species included, b) dominant species *Fulica ardesiaca* removed.

multiple lakes. Given that this population growth occurred at many lakes, the potential mechanism behind it, likely eutrophication, could be operating simultaneously in multiple Andean lakes.

The population growth of *F. ardesiaca* is particularly high in lakes where human intervention has transformed surrounding habitat and water conditions (Guevara et al., 2016). Specifically, local population growth of *F. ardesiaca* at lake Colta seems to be the major contributor of the observed landscape-level pattern of population growth, since counts at this lake dramatically increased from nearly 500 individuals in 2004 to 2500 individuals in our latest count in 2018. *Fulica ardesiaca* is primarily an herbivorous species that feeds on seeds and aquatic vegetation (*Chara*, *Elodea*, *Myriophyllum*), alternating its diet with arthropods and even small vertebrates (Taylor, 2019). The species is found in a variety of ecosystems including, marshes, lakes, and rivers, and is known to nest in a variety of habitats which include reed beds, beaches or floating vegetation. Due to the species' ability to exploit a wide range of resources for feeding and nesting and its widespread distribution, *F. ardesiaca* could be regarded as a generalist species. Shifts in

abundance of generalist species, at expense of specialists, can result in biotic homogenization (Clavel et al., 2011; Layman and Allgeier, 2012; Gámez-Virués et al., 2015).

At least three out of the six aquatic bird communities studied here exhibit strong directional change (Colta, San Pablo and La Mica, Fig. 2), and these changes are coupled with declines in species richness. The temporal change in bird communities could be attributed to shifts in abundance of dominant species *F. ardesiaca* as once the counts of this species were removed from community analyses, the directional pattern of community change disappeared or were attenuated, especially in lakes where the population growth of *F. ardesiaca* was high (Fig. 2). The observed declines in species richness and compensatory shifts in abundance of dominant species are consistent with other studies conducted on plant communities, which also reported directional changes driven by shifts in dominant species (Collins, 2000; Yang et al., 2017).

In contrast with other studies that have shown that larger wetland area allows for greater aquatic bird richness and abundance (Roselli and Stiles, 2012; Murphy and Dinsmore, 2018), our results show that one of

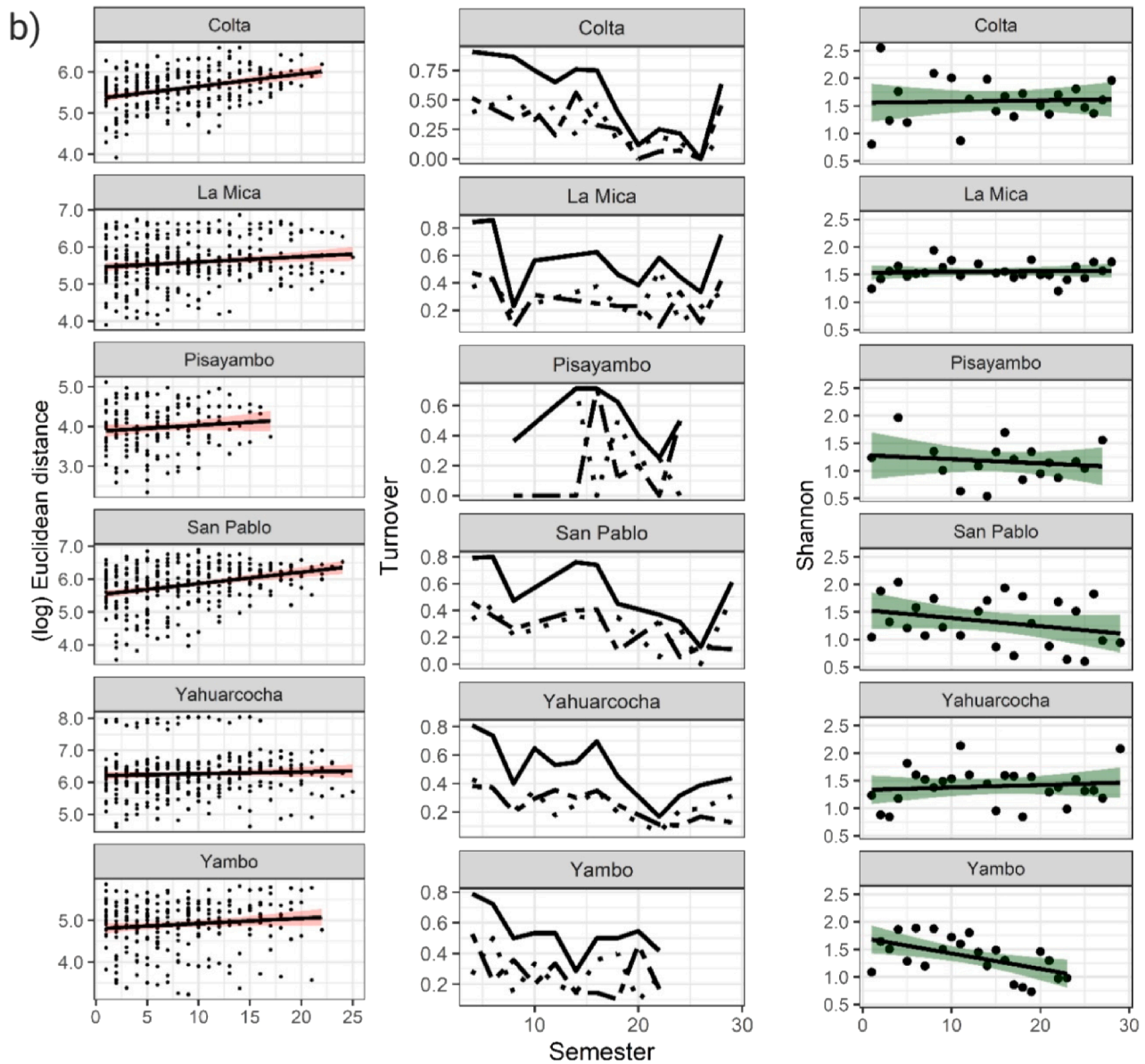


Fig. 2. (continued).

the smallest lakes studied, Colta Lake, has the greatest aquatic bird richness and abundance. We attribute the greater richness and abundance at Colta to high eutrophication levels, expressed as high values of biochemical demand of oxygen and high concentrations of phosphates and nitrites. Eutrophication is often produced by an excess of macronutrients derived from anthropogenic sources, which has been shown to promote growth of aquatic vegetation (O'Hare et al., 2018). Aquatic plants usually exhibit less developed chemical and structural defenses against herbivory as compared to terrestrial plants (Bolser et al., 1998), and thus their proliferation in freshwater systems might represent a readily available resource for herbivorous birds. In contrast to terrestrial bird communities, aquatic bird communities exhibit higher densities of herbivorous species (Fjelds , 1985), therefore intermediate levels of eutrophication might benefit herbivorous species through increase in biomass of aquatic submerged vegetation. Moreover, increases in the abundance and richness of aquatic birds has been associated with shallow lakes where eutrophication promotes food resource availability over larger areas for diving and non-diving species (Noordhuis et al., 2002;  zgen il et al., 2020). In our study region lake Colta is one of the shallowest lakes (maximum depth of 4 m); we believe that the

combination of eutrophication and lake depth make it suitable for sustaining diverse and abundant aquatic bird communities. The abundance of *A. andium* appears to be limited primarily by elevation. This species is known to occur above 3000 m. (Freile and Restall, 2018) and our results confirm this distributional limit, since its abundance is higher at lakes over 3000 m. The abundance of other herbivorous birds, like *O. jamaicensis* and *A. georgica*, was also related to indicators of eutrophication like phosphates and nitrites (Fig. 3).

Although intermediate levels of eutrophication could promote plant growth and benefit some herbivores; high levels of eutrophication may trigger the proliferation of green algae and decline of macrophytes leading to a high-turbidity state of water, in which few species can survive (Scheffer et al., 1993). Therefore, we recommend the implementation of management measures that prevent further eutrophication of lakes in the Andes of Ecuador. The most obvious measure will be the reduction – or elimination – of external sources of organic pollution. This measure could include several actions, such as: 1) implementation of proper systems of waste water disposal in human settlements nearby the lakes, 2) habitat restoration with native flora in the lakes' catchments to prevent the deposition of sediments from rain water drainage

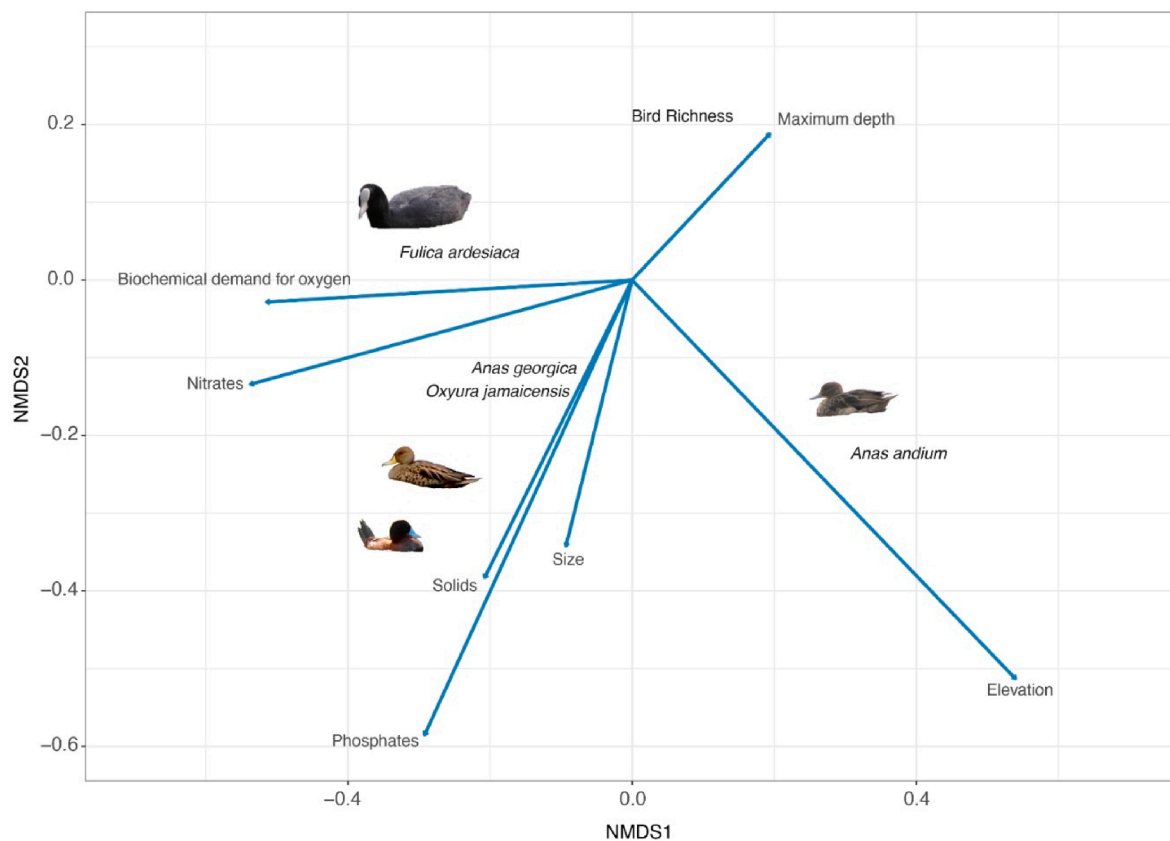


Fig. 3. Bi-plot of the non-metric multidimensional ordination analysis applied to nine aquatic bird communities in the Andes of Ecuador (2-dimensional solution, stress value = 0.06). Relationships among the four most common species in the study region and environmental variables are depicted. Figure created with Bio-Render.com. Photo credits Aves y Conservación, except for *Anas georgica* photo by Carlos Rodriguez.

and increase the capacity of retaining phosphates and nitrites in the catchment (Jørgensen, 2009), and 3) law enforcement to avoid water pollution, especially in lakes located near fertilized agricultural areas.

Our study adds to previous research that stresses the need to consider additional metrics, besides species richness to monitor biodiversity change (Magurran and Henderson, 2010; Cardinale et al., 2018). Species richness often follows a different trajectory than metrics describing community stability or asynchrony (Hillebrand et al., 2017). The results from our study partially support this conclusion. We observed that positive trends in community's composition change were coupled with negative trends of Shannon's diversity index. However, compensatory effects of the increase in species abundance might affect the overall evenness of the community, which in turn might be expressed in lower values of Shannon index.

Understanding the links between aquatic birds and environmental factors, together with continuous monitoring schemes, should help managers detect changes in environmental conditions of Andean wetlands. Specifically, identifying the factors that influence the abundance of dominant species could improve our ability to forecast changes in community composition, which is particularly relevant given the importance of preserving freshwater ecosystems. Aquatic birds are useful and cost-effective indicators of wetland conditions. Thus, in order to improve the predictive power of existing monitoring schemes, like the Neotropical Waterbird Census program, we encourage additional studies aimed at strengthening our knowledge on aquatic bird ecology and natural history.

CRedit authorship contribution statement

Esteban A. Guevara: Conceptualization, Methodology, Writing - review & editing. **G. Tatiana Santander:** Conceptualization, Project

administration, Funding acquisition. **Rodrigo Espinosa:** Methodology. **Catherine H. Graham:** Conceptualization, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.107044>.

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