



ECOSYSTEMS

Disentangling vegetation structure effect on invertebrate communities in contrasting growth periods in subtropical protected wetlands of Argentina

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Abstract: This study assesses the effect of vegetation structure on the subtropical invertebrate communities in contrasting sampling dates of macrophyte populations in the RAMSAR site of Iberá wetlands, South America. Invertebrates associated with the submersed *Egeria najas* and the floating rooted *Pontederia azurea* were chosen to provide a model involving different microhabitat complexity. The results suggest that vegetation structure provided by the two macrophyte species supported significant differences in the density of animals, with invertebrate abundance of *E. najas* twice as high as on *P. azurea*. Abundance showed no significant differences in both contrasting sampling dates, growth and decline. Our result clearly showed invertebrates exclusively associated with each macrophyte species, as well different invertebrate taxa dominating in each sampling date (decline: Cladocera; growth: Aphididae, Belostomatidae and Planorbidae). We also show that working at the taxonomic levels of family could be a sensible trade-off between taxonomic identification effort versus reaching reliable and useful results for environmental monitoring and natural resource management in highly diverse subtropical wetlands. Our results emphasize the role of vegetation structure on invertebrate communities, as well suggest that the growth cycle of macrophyte populations could be a relevant variable influencing these animals in pristine subtropical wetlands.

Key words: Iberá wetlands, invertebrate assemblages, macrophytes, seasonal variation, subtropical wetlands, vegetation structure.

INTRODUCTION

Wetlands are vital ecosystems in providing water for drinking and agriculture, hydroelectric energy, flood regulation and recreation activities. In conjunction with their role in erosion control and sediment transport, wetlands also contribute to land formation and support a high diversity of habitat and organisms (Cherry 2011, Kumari et al. 2020). Such biodiversity provides a wide range of services that are closely related to water, such as nutrient cycling, primary

production, fisheries and tourism (Alcama & Neville 2003, Russi et al. 2012, Batzer & Boix 2016). Despite this, wetlands are being degraded and even disappearing due to the effect of biological invasion, eutrophication, urbanization, intensive and unsustainable agricultural production, and water extraction for domestic and industrial use, among others (Neff 2004, Russi et al. 2012, Gervazoni et al. 2020). The Iberá wetland area is one of the largest inland wetlands, and, also, one of the most pristine subtropical freshwater ecosystems in South America (Neff 2004, Neiff

et al. 2011). From an integrative ecosystemic approach, the development of baseline studies in these natural aquatic ecosystems is fundamental to finding an appropriate balance between conservation, sustainable use of biological diversity and the needs of people who depend on the system (Peteán 2007), including indigene nomadic communities that live exclusively on the resources which the biodiversity provides (<https://www.ramsar.org/wetland/argentina>).

Several biotic and abiotic factors are considered important regulators of the macrophyte community and their associated biota in wetland ecosystems (Bechara 1996, Neiff 2003, Murphy et al. 2003, Trindade et al. 2018, Franceschini et al. 2010, 2020b, de Campos 2021). Amongst these, vegetation structure is of particular interest in subtropical wetland ecosystems in which macrophytes show high diversity values and support plants of various differing growth forms (Chambers et al. 2007, Murphy et al. 2003, 2019).

The vegetation structure of macrophyte species plays an important role in the ecological functioning of freshwater wetlands since they provide different microhabitat quality, resource partitioning, shelter, feeding and reproduction sites to invertebrate and fish, promoting heterogeneity in the structure of aquatic habitats (Batzer & Boix 2016). It has long been known that macrophytes with greater structural complexity support a higher abundance (Karrasowska & Mikulski 1960, Korinkova 1971, O'Hare & Murphy 1999, Thomaz et al. 2008, Dibble & Thomaz 2009, Ferreira et al. 2011, Walker et al. 2013) and richness of macroinvertebrates (Fontanarrosa et al. 2013, Gallardo et al. 2017). In addition, there is evidence that the vegetation structure provided by different macrophytes of different growth forms shows a specific taxonomical and functional composition of invertebrate herbivore

assemblages, with different dominance of "strict aquatics", "semiaquatics" and "landwater interface invertebrates" on the vegetation structure of submersed, floating and emergent macrophyte species (Franceschini et al. 2020a). Fluctuations in macrophyte coverage and composition, could also explain the temporal changes observed in the structure of the macroinvertebrate community in subtropical wetlands (Fontanarrosa et al. 2013).

The typical climate in subtropical wetlands has warm rainy summers and cool winters with few frost days (Köppen 1918). This seasonality influences the vegetation life cycle, resulting in clearly differentiated "growth" and "decline" periods in macrophyte populations present, with high variability in vigor, productivity and biomass across the year (Úbeda et al. 2013, Neiff et al. 2008). This variability on macrophyte populations between growth and decline periods was detected to be also relevant in influencing abundance and richness in the macroinvertebrate community (Bechara 1996, Gallardo et al. 2017) as well in many invertebrate processes at the subtropics (Poi de Neiff & Casco 2003, Franceschini et al. 2010, 2013, Fuentes-Rodríguez et al. 2017).

Among aquatic macrophytes of the subtropical wetlands in South America, the floating-leaf-rooted (FR) *Pontederia azurea* Sw and the submersed (S) *Egeria najas* Planch are abundant in both lentic and lotic systems and both can coexist under the same limnological conditions as monospecific stands. However, there are substantial ecological differences between these two macrophyte species, mainly in terms of plant architecture and biotypes, leaf tissue and microhabitat offered to the invertebrate community. The FR *P. azurea* provide two different spatial microhabitats: a more complex ones dominated by adventive and the main roots and a low complexity microhabitat (above and immediately below the water surface), dominated by flowers, floating leaves and stems (Milne et

al. 2006), plants have one floating or underwater leaf at each node alternately arranged on the stem (Barrett 1978). On the contrary, because their high number of small leaves typically arranged in whorls of 5 leaves at each node and short internode distance between them (Cook & Urmi-Konig 1984), the *S. E. najas* has a complex vegetation structure below the water surface and in the deeper part of the water column, compared with *P. azurea* (Dibble & Thomaz 2006).

These differences raise a question about how abundance and composition of subtropical invertebrate community varies according to vegetation structure in these very different macrophyte populations and in two contrasting sampling dates, growth versus decline period of macrophyte populations. In this context, pristine aquatic ecosystems like the RAMSAR site of Iberá wetlands in South America, has scarce anthropic effects and, as a consequence, represents an ideal scenario to test this question and carry out invertebrate assessment baseline studies for improve environmental monitoring and natural resource management.

In this study, the effect of vegetation structure on the invertebrate community associated with the two macrophytes *E. najas* and *P. azurea* were analyzed sampling in decline and growth periods of plant populations, and the hypothesis that vegetation structure, and potentially macrophyte growth period, are relevant factors influencing abundance, richness and composition of subtropical invertebrate communities were tested.

MATERIALS AND METHODS

Study area

The Iberá wetlands comprise a subtropical freshwater macroecosystem of 13,000 km² located between 27° 36' - 28° 57' S and 58° 00' - 57° 30'

W. Most of the individual wetlands in the area have been under protection as a Natural Reserve since 1983, and in 2002 were incorporated into the RAMSAR protected wetlands. The Iberá basin constitutes the ancient floodplain of the Paraná River, which remained connected to the river until the end of the Pleistocene (Neiff 1999), but currently the wetlands are mainly rain-fed, with water level fluctuations dominated by the local climate. The climate of the study area is classified as humid subtropical (Cfa: according to the Köppen Climate Classification). Winters are mild and short, with absolute minimum temperatures dropping to -2 °C; summers are hot and long, with absolute temperatures that can reach 44 °C. Frosts are rare, with 320 to 360 frost-free days and an average of 0.5 frost-free days in 50 years (Carnevali 1994). Rainfall varies between 1200 and 1700 mm annually, with a dry season occurring during winter (Ferrati et al. 2003).

Sampling was conducted in two wetlands of the Iberá system, each with six sampling points, located on the western margin of the Reserve (Fig. 1). In both wetlands, the *S. Egeria najas* and the FR *Pontederia azurea* clearly predominated in the macrophyte community. The FR *P. azurea* formed dense littoral floating mats throughout, while the *S. E. najas* covered around 40 % of the limnetic area. Other frequent macrophyte species were *Cabomba caroliniana* (S), *Salvinia biloba* (FF: free floating), *Hydrocleys nymphoides* (FR), *Nymphoides indica* (FR), *Oxycaryum cubense* and *Cyperus giganteus* (E: emergent). Due to the homogeneity of the soil in the system and high connectivity of the Iberá wetlands, the physicochemical variables of the study sites were comparable (Table 1).

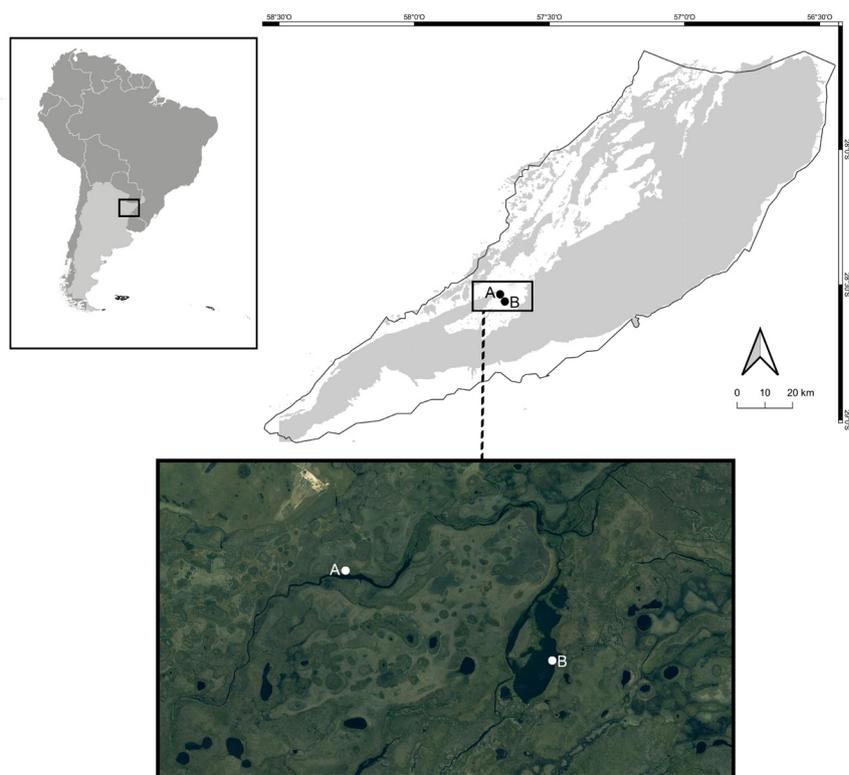


Figure 1. Study area in the Iberá wetlands at the Northeast of Argentina, supporting invertebrate communities associated to the S *Egeria najas* and the FR *Pontederia azurea* macrophytes. Sites are shown with latitude and longitude coordinates. A: Carambolita stream (28° 24' 20.04" S - 57° 39' 32.74" W). B: Datilcito lagoon (28° 25' 52.50" S - 57° 38' 20.22" W). FR: floating-leaf-rooted macrophyte, S: submersed macrophyte.

Table I. Physicochemical variables from the studied wetlands of the Iberá System in growth (G) and decline (D) period of the macrophyte populations. Transparency was measured as Secchi disc depth.

Wetlands/growth period	Datilcito Lagoon		Carambolita Stream	
	G	D	G	D
Water Temperature (°C)	25.3	13.5	24.7	14
pH	6.63	6.8	6.48	6.6
Conductivity ($\mu\text{S cm}^{-1}$)	20.65	21.05	20.34	20.75
Depth (cm)	174	170	200	187
Transparency (cm)	174	140	200	163

Survey design and assessment of invertebrate communities

Sampling of invertebrate communities was carried out in two macrophyte species, the S *E. najas* and the FR *P. azurea*. In order to sample the greatest possible diversity on the invertebrate community, sampling was undertaken in two sampling dates which represented contrasting macrophyte growth periods of plant population cycle: growth (summer) and decline (winter),

in March and August 2016, respectively. At each wetland site, three replicate invertebrate samples per growth form (plant species) and sampling date (plant growth cycle) were collected. Thus, in total 24 samples were gathered for the plant species-sampling date and site combinations. Samples were collected randomly in different parts of the vegetation stands at distances separate enough from each other to maximize the independence of the data.

The collections of macrophytes and their invertebrates were carried out using an invertebrate hand net with an area of 962 cm² and 500 µm mesh size (Poi de Neiff & Carignan 1997). Samples of the S *E. najas* and the FR *P. azurea* and their associated invertebrates were removed from the net and transferred to plastic bags.

Invertebrate and macrophyte samples were preserved with 70% ethanol and immediately transported to the laboratory. There, the aquatic plants were thoroughly washed to separate the associated invertebrates, and the suspensions obtained were filtered through a nest of sieves with 1 mm to 500 µm mesh. Invertebrates were sorted and re-preserved in 70 % ethanol, and the macrophytes were dried at 105 °C for 48 hours, to constant weight.

In tropical and subtropical regions, aquatic invertebrate communities tend to have high diversity and complexity, but descriptions of many taxa are incomplete and specific taxonomic keys are scarce, so taxonomic identification to species or genus level becomes difficult (Clarke et al. 2017, Dallas et al. 2018). Additionally, the dominance of immature forms of many insects with adult aerial life (e.g., Diptera, Odonata, Ephemeroptera, Lepidoptera and Trichoptera) makes identification even more difficult. For these reasons, and following the criteria of Bailey et al. (2001) and Godoy et al. (2019) in this study family level was used in almost all invertebrates as operational taxonomic units, focusing mostly on the insect taxa. First, invertebrate morphospecies were counted and identified to the higher taxonomic level possible using several identification keys (Lopretto & Tell 1995, Trivinho-Strixino & Strixino 1995, Merritt & Cummins 1996, Domínguez & Fernández 2009, Ramírez 2010, Libonatti et al. 2011, Marchese et al. 2014). In Zygoptera, Ostracoda, Cladocera, Oligochaeta, Acari and Aranea, the lack of

regional taxonomic keys and/or revisions for the study area allowed the use of these taxa as operational taxonomic units.

The total number of invertebrates per sample was quantified. Because invertebrate abundance may be affected by aggregation, biomass and life and growth forms of macrophytes, values for invertebrate abundance per sample were used to calculate the number of individuals per 100 g of plant biomass, which allows the comparison between macrophyte species and sampling dates. Individuals of pupal stage impossible to identify to family level were discarded in the data analysis. Among invertebrate community parameters, abundance, Shannon index, evenness and richness, as well as taxonomic composition were chosen to measure variation between vegetation structure and contrasting sampling dates of macrophyte populations due to their worldwide use in invertebrate monitoring (Thomaz et al. 2008, Kubová et al. 2013, Dallas et al. 2018, Epele et al. 2019, Piano et al. 2020).

Statistical analysis

The effects of the vegetation structure (*E. najas* versus *P. azurea*) and the potential effect of macrophyte growth periods (growth versus decline sampling dates) on the total abundance, richness and diversity of invertebrate community were analyzed using 2-way analysis of variance (ANOVA), followed by Tuckey-test mean comparisons after checking Shapiro-Wilk test of normality and Levene's test for homogeneity of variance. To perform statistical analyses on invertebrate community composition, taxa with at least three occurrences were selected and the absolute abundance was Hellinger transformed resulting in a 31 taxa data matrix. To examine the relationship between invertebrate community composition with the vegetation structure and sampling date preference over the studied

cycle, clustering and multivariate ordination techniques were used.

Two statistical approaches have been used to characterize the invertebrate community, an ordination method (RDA) based on two environmental features: vegetation structure and sampling dates and a clustering method based on the relative abundance data (UPGMA). First, to evaluate the relative influence of vegetation structure and sampling dates in the variation of the invertebrate assemblages, redundancy analysis (RDA) was performed (Borcard et al. 1992). This method was selected because the response data are compositional with a gradient length of 2.0 SD (Detrended Correspondence Analysis first run), so a linear method is recommended (Lepš & Šmilauer 2003). The explanatory variables were “*E. najas*” and “*P. azurea*” for vegetation structure and “growth” and “decline” for sampling dates. Second, an Unweighted Pair Group Mean Averages (UPGMA) approach was applied to show the clustering relationship among invertebrate taxa. Analyses of similarity (ANOSIM) were executed using the Bray-Curtis distance procedure, to evaluate the clustering significance level and compare (dis) similarity of the communities between plant microhabitat and sampling date effect (Clarke 1993). The variation explained by each variable group was estimated using adjusted R^2 . Differences were considered significant at $p < 0.05$ values. Statistical analyses were performed using R (version 4.0.2, 2020-06-22; R Core Team 2020), PAST 4.03 (Hammer et al. 2001) and CANOCO 5.0 (Ter Braak & Šmilauer 2012). Hellinger transformations were implemented using the `decostand` function in the package `vegan` (Oksanen et al. 2019), plots were implemented using `ggplot2` (Wickham & Grolemund 2016), `dplyr` (Wickham et al. 2020), and `reshape2` (Wickham 2007) packages.

RESULTS

Vegetation structure effect on invertebrate abundance and richness in two contrasting sampling dates

In total 13655 invertebrates were recorded in the two macrophyte species and sampling dates, with the most abundant group being the Diptera Chironomidae ($n=5261$), followed by Cladocera ($n=1369$) and Ostracoda ($n=1011$).

When invertebrate abundance per plant biomass (ind/100 g plant biomass) were compared (Fig. 2), two different patterns were observed. Significant differences were detected between vegetation structure provided by the two macrophyte species (Two Way ANOVA, $F = 10.362$; $p = 0.004$). Invertebrate abundance values recorded on the S *E. najas* (3866.9 ± 2495) were twice as high as those found on the FR *P. azurea* (1912.0 ± 1615.7). However, no significant differences were found for sampling dates (Two Way ANOVA; $F = 0.0469$; $p = 0.831$), with similar abundance values in both growth and decline sampling dates (Fig. 2). Interactions were significant when comparing vegetation structure and sampling dates (Two Way ANOVA, $F = 6.054$; $p = 0.023$).

Regarding invertebrate richness (S), the FR *P. azurea* tended to have higher taxa richness than the S *E. najas* (40 and 34 taxa, respectively), but the difference between macrophyte species was not significant (Two Way ANOVA $F = 3.438$, $p = 0.079$). Significant differences in taxa richness were observed when sampling dates were compared (Two Way ANOVA $F = 11.139$; $p = 0.003$), with a mean of invertebrate richness higher in growth than in decline (17.83 and 14.08, respectively). Shannon index and Evenness showed no significant differences for the main effects, macrophyte species and sampling dates, although interactions were significant (Two Way ANOVA $F = 12.594$; $p = 0.002$ and $F =$

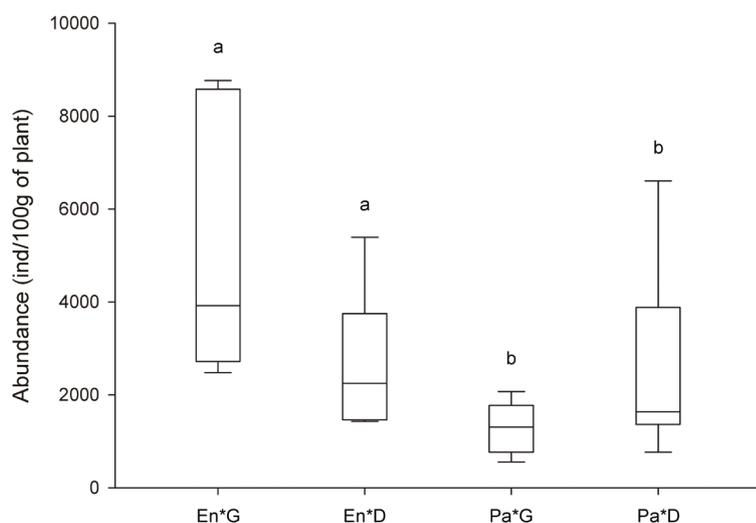
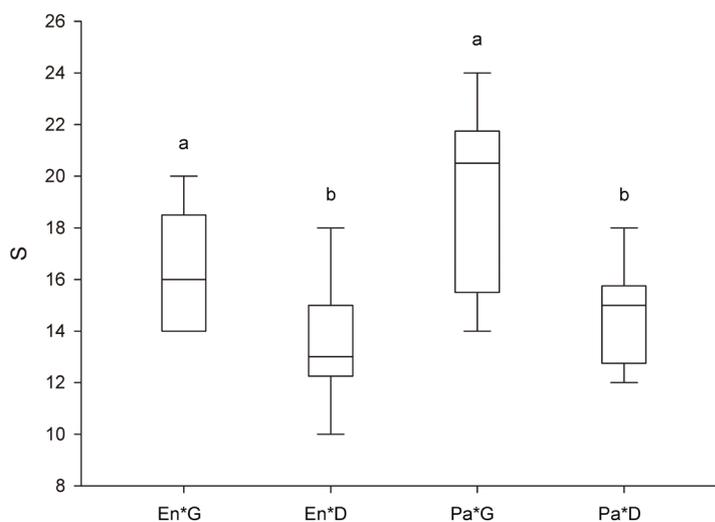


Figure 2. Abundance and richness (S) of invertebrate communities according to the vegetation structure and contrasting sampling dates at the Iberá wetlands. Vegetation structures compared are the *S Egeria najas* (En) and the FR *Pontederia azurea* (Pa). Contrasting sampling dates included growth (G) and decline (D) periods of macrophyte populations. N= 13655 invertebrates, 24 samples. Different letters indicate significant differences with ANOVA test, $p < 0.05$.



15.286; $p = < 0.001$, respectively). Plant biomass did not correlate with invertebrate abundance in different vegetation structures and sampling dates ($r = 0.058$, $p = 0.788$, $n = 24$).

Taxonomic composition of invertebrate communities influenced by vegetation structure and macrophyte growth period

The aquatic invertebrate assemblages from the studied sites were diverse, with 11 orders and 35 families recorded from both vegetation structures and sampling dates (Fig. 3). There was a clear dominance of Chironomidae (with the

subfamilies Chironominae, Tanypodinae and Tanytarsinae), in the two macrophyte species and for both contrasting sampling dates, growth and decline.

The invertebrate community associated with the *S. E. najas* was also dominated by Cyclestheriidae (with a single morphospecies *Cyclestheria hislopi*), Ostracoda and Oligochaeta in the growth sampling date, whereas Ancyliidae, Hydroptilidae (*Oxyethira* sp.) and Ephydriidae (*Hydrellia* sp.) were dominant in the decline sampling date. Ephydriidae, Aeshnidae and

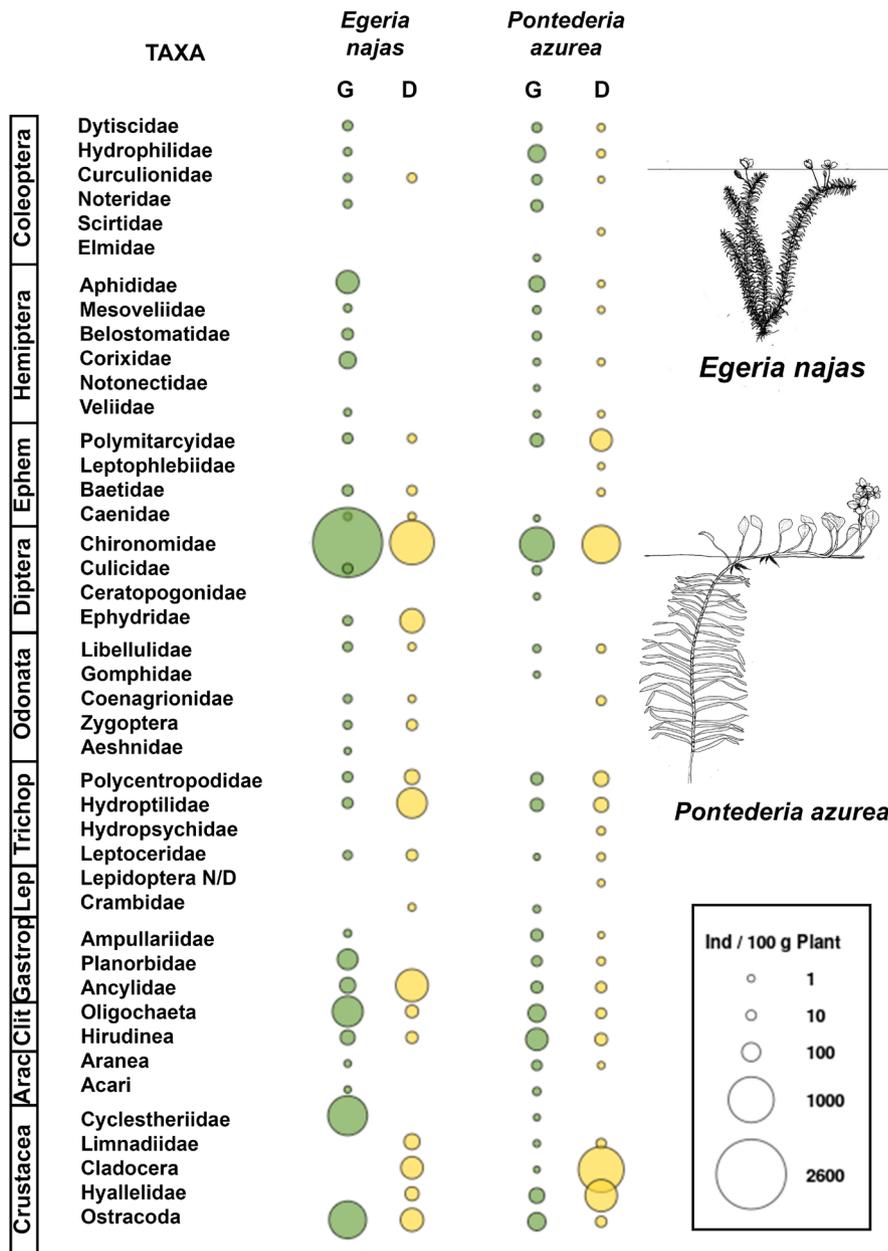


Figure 3. Abundance of invertebrate taxa associated with two vegetation structures, the S *Egeria najas* and the FR *Pontederia azurea*, in growth and decline sampling dates, at the Iberá wetlands. Invertebrates' abundance is indicated proportionally with circle sizes. G: growth sampling date; D: decline sampling date; Ephem: Ephemeroptera; Trichop: Trichoptera; Lep: Lepidoptera; Gastrop: Gastropoda; Clit: Clitellata; Arac: Arachnida.

Zygoptera were found exclusively associated with this macrophyte species.

The invertebrate community associated with the FR *P. azurea* was dominated by Hirudinea (*Helobdella* spp.), Oligochaeta (Naididae), and Hydrophilidae in the growth sampling date. Among Hydrophilidae, morphospecies of the genera *Termonectus*, *Enochrus*, *Helochares* and *Tropisternus* were dominant. During the decline sampling date, Cladocera, the amphipod *Hyalella*

curvispina, and the mayfly *Asthenopus curtus* (Polymitarcyidae) were also dominant members of the invertebrate community. The families Notonectidae (Hemiptera), Ceratopogonidae (Diptera), Gomphidae (Odonata), Hydropsychidae (Trichoptera), Leptophlebiidae (Ephemeroptera), Scirtidae and Elmidae (Coleoptera) were found related to the FR *P. azurea* (Fig. 3).

The RDA organized the occurrence of different taxa constrained by two effects,

vegetation structure and sampling dates (Fig. 4b), with the two components explaining 45% of the invertebrate community variability (adj. 40%; $F=8.6$, $p=0.001$). The first component explained 28.4% of the assemblage variability and separated the taxa occurring in the two sampling dates considered, growth and decline sampling date. Taxa with high scores on Axis 1 were those sampled mainly in the growth sampling date, such as Aphididae, Planorbidae, Belostomatidae, Corixidae, Culicidae and

Noteridae. Taxa such as Cladocera, Hyalellidae, Ancyliidae, Hydroptilidae and Polycentropodidae were negatively associated with Axis 1 and they were primarily recorded in the decline sampling date. The second Axis explained 16.6% of the total variability and separated invertebrate taxa occurring in different vegetation structures. Taxa such as Ephydriidae, Zygoptera and Oligochaeta, occurring on the *S. E. najas*, were positively related to Axis 2, whereas Hyalellidae, Polymitarciidae and Hydrophilidae, related to

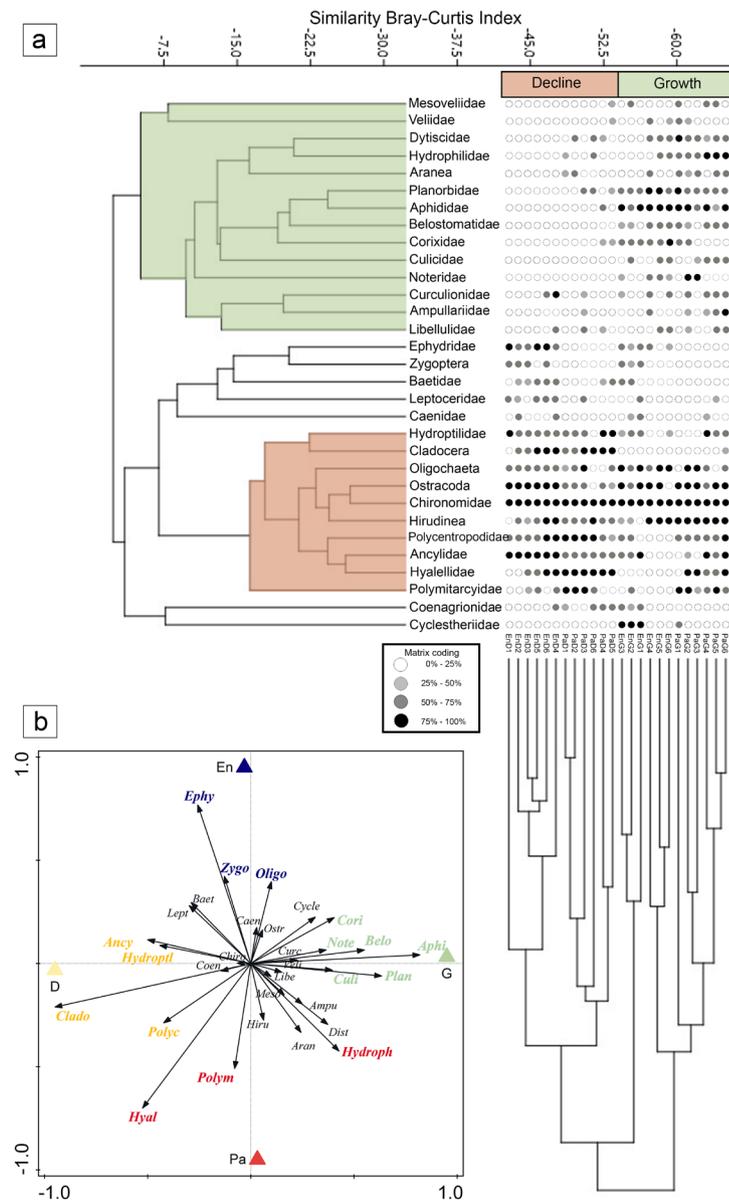


Figure 4. Unweighted Pair Group Mean Averages (UPGMA) (a) and Redundancy analysis (RDAs) (b) of the invertebrate community composition in relation to the selected effects, vegetation structure and contrasting sampling dates. Colored dots indicate abundance proportions represented in ranges. En: *Egeria najas*; Pa: *Pontederia azurea*; G: growth sampling date; D: decline sampling date; Aph: Aphididae, Belo: Belostomatidae, Plan: Planorbidae, Culi: Culicidae, Note: Noteridae, Cori: Corixidae, Cycl: Cyclestheriidae, Curc: Curculionidae, Ostr: Ostracoda, Caen: Caenidae, Veli: Veliidae, Libe: Libellulidae, Meso: Mesoveliidae, Ampu: Ampullariidae, Dit: Dytiscidae, Hydroph: Hydrophilidae, Aran: Aranea, Hiru: Hirudinea, Polym: Polymitarciidae, Hyal: Hyalellidae, Polyc: Polycentropodidae, Clad: Cladocera, Hydroptl: Hydroptilidae, Coen: Coenagrionidae, Ancy: Ancyliidae, Chiro: Chironomidae, Lepto: Leptoceridae, Baet: Baetidae, Zygo: Zygoptera, Ephy: Ephydriidae.

the FR *P. azurea*, were located on the negative side of this axis.

The two-way cluster obtained with the UPGMA, shows the establishment of two well-defined assemblages (Coph. corr. 0.8146). One of these includes samples from the growth sampling date and the other includes the commonly-distributed taxa (Fig. 4a). The first group comprised mainly invertebrate taxa sampling during the growth sampling date, such as Planorbidae, Aphididae, Corixidae, Belostomatidae, Culicidae and Noteridae. This group also included the association of Aranea, Hydrophilidae and Dytiscidae, mainly related to the FR *P. azurea* from the growth sampling date. The second group of the cluster, included invertebrates common to both sampling dates, such as Chironomidae, Oligochaeta, Ostracoda, Hirudinea, Polycentropodidae, Ancyliidae, Polymitarciidae, Hydroptilidae, Leptoceridae and Hyalellidae. The ANOSIM test showed significant differences in invertebrate composition for the two effects considered, vegetation structure ($R = 0.555$; $p = 0.0001$) and potentially sampling dates ($R = 0.748$; $p = 0.0001$).

DISCUSSION

This study shows that vegetation structure provided by aquatic macrophyte species is a relevant factor influencing abundance as well composition of the invertebrate community in subtropical wetlands, which is in agreement with previous results obtained in other warm wetland ecosystems (e.x. Thomaz et al. 2008, Dibble & Thomaz 2009). Also, the data suggest that these invertebrate communities can display substantial differences in the taxonomic composition even when they have similar abundance values in the two contrasting sampling dates, growth and decline. Previous studies were focused mainly on abundance of

invertebrates, and with the exception of the study of Gallardo et al. (2017) in periurban wetlands, all of them assess the effect of the vegetation structure or plant growth periods separately (Balla & Davis 1995, Bechara 1996, Poi de Neiff & Neiff 2006, Thomaz et al. 2008, Dibble & Thomaz 2009, Fontanarroza et al. 2013, Franceschini et al. 2020b). Our study provides evidence that considering the effect of microhabitat structure in contrasting sampling dates of macrophyte growth periods as well as integrating both abundance and composition might contribute to a better understanding of the structure and variation of invertebrate communities in subtropical wetlands. Furthermore, it should be emphasized that this study was undertaken in a large pristine freshwater ecosystem with considerable protection and conservation status, and with little effects of anthropogenic disturbances (CLT 2020). The results hence probably can give an accurate idea of how vegetation structure can influence subtropical plant-associated invertebrate communities in near-pristine aquatic ecosystems, considering also the potential effect of growth periods of macrophyte populations.

Assessment and monitoring of invertebrates in tropical and subtropical wetlands can represent significant time-effort on sampling and taxonomic identifications because animal communities from these systems exhibit high biodiversity and abundance and many taxonomic groups are still not well known (Clarke et al. 2017). However, many relevant aspects about the structure of the invertebrate community and ecosystem functioning are evident only when taxonomic identification of the assemblage's composition is considered (Franceschini et al. 2020a, b). In this sense, our results show that the integration of the composition parameter on invertebrate monitoring, identifying morphospecies at

family level is relevant to appreciate changes in the invertebrate community. In our study, the response of invertebrate community to plant structure and the contrasting sampling dates (growth and decline) was also evident using taxa of Zygoptera, Ostracoda, Cladocera, Oligochaeta, Acari and Aranea as operational taxonomic units (Fig. 3).

Concerning the total abundance of invertebrates inhabiting aquatic macrophytes from the Iberá wetlands, the results suggest that vegetation structure has more influence on abundance than sampling dates. *E. najas*, which has the highest complexity of vegetation structure, supports a greater number of individuals per plant dry weight, that is, two times higher than those found on *P. azurea*, particularly during the growth sampling date. Gallardo et al. (2017) also found that the invertebrate community associated with *E. najas* has higher abundance and taxa richness than those associated with the free-floating (FF) *Salvinia biloba* Raddi in periurban subtropical wetlands. Also, values of invertebrate abundance on *P. azurea* found in this study are broadly in line with those recorded by Poi et al. (2017b) in the same macrophyte species and study area.

Our assessment suggests that invertebrate abundance, which differs according to the vegetation structure, has no variation according to sampling dates considered. Also, results show a group of invertebrate taxa mainly associated with each sampling date (Fig. 4a), which has contrasting conditions mainly according to the macrophyte growth period. It should be noted that our study integrating vegetation structure and plant growth periods on invertebrate communities under pristine conditions is a new contribution for tropical and subtropical wetlands. Also, among several problematic fieldwork issues in these kind of wetlands (Kennedy et al. 2008, Franceschini et al. 2020b,

Poi et al. 2021), our sampling was limited in time and effort mainly due to flooding. Then, future studies incorporating long-term monitoring and taking as a baseline our results could contribute substantially to disentangle the effect of macrophyte growth period on subtropical invertebrate community.

Regarding to the taxonomic composition, our results agree with previous studies showing high taxonomical and functional complexity of invertebrate assemblages associated with subtropical macrophytes (Poi et al. 2017a, 2021, Gallardo et al. 2019, Franceschini et al. 2020a).

Our results obtained in the two contrasting sampling dates agree with those found by other authors in tropical climates, where changes across seasons does not seem to influence abundance levels but it does at the compositional scale (Jacobsen et al. 2008, Babatunde et al. 2018, Marchamalo et al. 2018). In fact, in our study the variability in assemblage composition was first explained by the sampling dates (28.4%) and then by the vegetation structure (16.6%).

Changes on invertebrate composition are also linked to abiotic factors like water level fluctuations, water flow, substrate and nutrient contents of wetlands (da Rocha & Por 1998, Higuti et al. 2007, 2010). As mentioned before, during the study period the Iberá wetlands were experiencing flood conditions. Hence, the low environmental heterogeneity observed among the sampling sites (Table I) is to be expected given previous results mentioning low spatial heterogeneity of these parameters in this macroecosystem when connectivity between flooded individual wetlands is quite high (Lancelle 2003, Cózar et al. 2004, Galassi & Poi 2014, Poi et al. 2017a). Hence, this environmental homogeneity suggests that hydrologic and physic chemical factors are not relevant in determining the differences observed on invertebrate composition.

It is important to consider that there are other biotic factors that could be relevant influencing the abundance and composition of the invertebrate community in subtropical wetlands such as macrophyte coverage, appearance of emergent flowers, allelopathy, palatability of macrophyte tissues, invertebrate life cycle, and predation (Hay & Fenical 1988, Martínez 1993, Corrales de Jacobo & Cannon Veron 1995, Williams et al. 2003, Momo et al. 2006, Higuti et al. 2007, Thomaz et al. 2008, Morrison & Hay 2011, Blanco-Torres et al. 2017, Ceschin et al. 2020, Yofukuji et al. 2021). As a consequence, they should be addressed in future studies to enhance understanding of the structure and functioning of invertebrate communities in subtropical wetland ecosystems.

As mentioned before, the vegetation structure provided by the S E. *najas* and the FR P. *azurea* contributes to explain the observed variability in the invertebrate assemblages' composition (Figure 4b). This might be due to the habitat complexity provided by plant architecture affects the richness and composition, as was observed previously (Taniguchi et al. 2003, Thomaz et al. 2008). *Egeria najas* mostly supports strictly aquatic invertebrates, with semiaquatic taxa restricted to the flower system, which constitute a little part of the total plant structure. However, *P. azurea* supports both semiaquatic and strict aquatic invertebrate fauna (Franceschini et al. 2020a: Multimedia component 1).

Considering that in this study the sampling dates did not affect the invertebrate abundance, but it was important for the taxonomic composition, and, plant structure was a relevant effect determining both, abundance and composition of invertebrate communities, the hypothesis assessed here, that vegetation structure, and potentially macrophyte growth periods, are relevant factors influencing abundance, richness and composition of

subtropical invertebrate communities should be partially accepted.

From the most applicable perspective, our study evidence that working at high taxonomic levels such as family could be a sensible tradeoff between taxonomic identification effort versus reaching reliable and useful results for environmental monitoring and natural resource management in the highly diverse subtropical wetlands. Finally, the macrophyte species included here, have a wide distribution and frequency in South American subtropical wetlands. Many of these systems have been profoundly modified by pollution, eutrophication, biological invasion and habitat modification in past years (Neiff 2003, 2004, da Conceição et al. 2020, Gervazoni et al. 2020). For example, rice fields are considered artificial wetlands, where the existence of a flood phase generates an exchange of water and organisms with the natural wetlands associated with these agroecosystems. This includes *P. azurea* and its associated invertebrates, commonly found in rice fields, as a part of irrigation canals or surrounding wetlands (Barrett 1978). Therefore, the results of this study could contribute as a baseline in monitoring programs for the conservation of protected areas, certifying good agricultural practices and natural resource management in subtropical wetland ecosystems.

Acknowledgments

This study was funded by the PICTO-UNNE 00012, PI 17-Q003 SEGcyT-UNNE, PUE-CONICET 229 2018 0100001 CO, PICT 2019-2408, PIP11220200100224 and UNCo 04/B237. We are grateful to Dr. Kevin J. Murphy for his thoughtful comments that improved the manuscript. We thank Lic. Paula Gervazoni and Lic. Daniela Fuentes-Rodríguez for help with the compilations of figures, Lic. Carolina Giese for helping with statistical analysis and Pedro Cuaranta for drawing the plant species.

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How to cite

SABATER LM, FRANCESCHINI MC, GALLARDO LI, CORONEL JM & PÉREZ AP. 2022. Disentangling vegetation structure effect on invertebrate communities in contrasting growth periods in subtropical protected wetlands of Argentina. *An Acad Bras Cienc* 94: e20210965. DOI 10.1590/0001-3765202220210965.

*Manuscript received on July 2, 2021;
accepted for publication on September 13, 2022*

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Authors contributions

LS, CF and PP designed the research. LS, LG and JMC contributed to the invertebrate sampling. LS and LG contributed to the invertebrate sorting and identification. PP performed the statistical analysis. LS, CF and PP wrote the manuscript and all authors contributed to the final version of the manuscript.

