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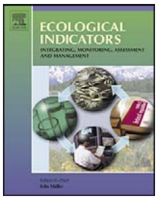

Is species richness congruent among taxa? Surrogacy, complementarity, and environmental correlates among three disparate taxa in geographically isolated wetlands

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ABSTRACT

Globally, there is a growing awareness that geographically isolated wetlands contribute to important landscape functions and ecological services. One of their most important functions is providing habitat to a diverse fauna and flora adapted to variable wet and dry environments. We focus on analysis of similarities among three distinct taxa, vascular plants, aquatic beetles, and amphibians, in isolated wetlands in the southeastern coastal plain of Georgia. Although species richness for these three taxa is quite high in isolated wetlands at a regional scale, we found a low degree of congruence in species richness and species composition among taxa. This finding demonstrates that none of these groups could be used as a surrogate for the overall biodiversity of these wetlands represented by the three taxa. We identified environmental factors influencing the complex patterns of species richness and distribution for the three groups that indicate biotic and abiotic processes operate at different scales for each taxonomic group and for individual species. Our study illustrates the importance of considering structural diversity, hydrologic variation, and landscape position as key elements to understanding overall diversity represented by the three taxa in isolated wetlands and in developing assessment tools of wetland condition.

1. Introduction

Geographically isolated wetlands contribute to important landscape functions and ecological services, sharing many of the structural and functional attributes associated with other wetlands. Even though some governmental agencies have been reluctant to provide regulatory protection for these wetlands that are often not as large, or as permanent as other wetland types, e.g., riverine or coastal ecosystems, there is increasing interest in assessing the effects of changing land use and climate on isolated wetlands (U.S. EPA 2011). Isolated wetlands have some regional differences in their origins or surrounding vegetation yet they share the characteristics of being completely surrounded by uplands and lacking hydrologic connections to other surface waters. While reflecting regional variations, isolated wetlands provide habitat to a unique and diverse fauna and flora adapted to variable wet and dry environments (Semlitsch and Bodie, 1998; Gibbons, 2003; Sharitz, 2003; Nicolet et al., 2004). Even though these habitats are relatively small, they are abundant in some landscapes (Williams, 1997; Leibowitz, 2003; Tiner, 2003). Given their significant contributions to regional biodiversity, an understanding of the need to protect and restore these wetlands is emerging globally (Kirkman et al., 1999; Whigham, 1999; Biggs et al., 2001; Boix et al., 2001; Williams et al., 2003; Nicolet et al., 2004).

Here we focus on assessment of biodiversity and evaluate spatial congruence of species richness, community composition, and the coincidence of rare species among important taxonomic groups in minimally disturbed ecosystems. High congruence across taxa can be useful for developing indicator metrics for rapid assessment methodologies. Such metrics have also been used when maximization of regional biodiversity is a conservation priority (Brown, 1991; Ricketts et al., 1999). Taxa congruence may also be useful in suggesting evolutionary relationships and potential functional regulators of community structure. Alternatively, discordant patterns in taxa diversity may reflect species-specific responses to environmental variability, disturbance frequency and intensity, and habitat fragmentation that limit the usefulness of surrogacy metrics. The

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latter case would emphasize the importance of a better understanding of environmental factors controlling species assemblages and biological diversity among individual taxa.

In the current study, we examine whether vascular plants, aquatic beetles, and amphibians show similar patterns of species richness, i.e., taxon congruence, within geographically isolated wetlands in a reference landscape in the southeastern coastal plain of Georgia, USA. Additionally, we identify environmental factors influencing patterns of species richness and distribution for the three taxa. We selected these particular taxa for study because they have high species richness, include an array of life history strategies, occupy diverse trophic positions, and each group shows potential as indicators of wetland condition (Lopez and Fennessey, 2002; Davis et al., 2003; Bilton et al., 2006; Johnston et al., 2008). Furthermore, these groups contain rare or endangered species; hence, identification of surrogate taxa could be useful in identifying critical habitat for conservation.

Our research focused on the following questions: (1) Are patterns of species richness and community composition congruent across the three taxa?; (2) Does the presence of a particular group of species within a taxon predict high species richness of other taxa?; (3) Does the relationship between species richness or community composition and size, isolation, and/or hydrology differ among taxonomic groups or among wetland types?

2. Methods

2.1. Study area

The study area is located at Ichauway, a 115 km^2 privately owned conservation property of the J.W. Jones Ecological Research Center, located in the coastal plain of southwestern Georgia, USA. Ichauway occurs within the Dougherty Plain physiographic district, a mantled karst landscape characterized by numerous geographically isolated wetlands. These wetlands have been classified into three general types based on vegetation, hydrology, and soils (cypress-gum swamp, cypress savanna and grass-sedge marsh) (Kirkman et al., 2000).

The 29 study wetlands (11 cypress-gum swamps, 8 cypress savannas, and 10 grass-sedge marshes) represent a sub-set of 90 isolated wetlands present on Ichauway and are part of an ongoing, long-term monitoring study. These wetlands were selected for study based on absence of recent timber harvest, drainage ditching, or agricultural activities within the last 60–100 years. Although these wetlands showed no evidence of recent human disturbances, timber was harvested from forested wetlands, presumably prior to 1938, based on earliest available aerial photography. The surrounding upland longleaf pine forests have been managed for 70 years with frequent prescribed fire (return intervals 1–2 years). Some of the study wetlands once had plowed firebreaks adjacent to the uplands; however, all of the wetlands show some evidence of prior fire within the interior, reflective of the fact that they are situated within natural stands of fire-maintained longleaf pine. The relatively undisturbed condition of the study wetlands suggests they can be used to represent potential reference conditions for comparison with more degraded sites in the region (Brinson and Rheinhardt, 1996).

2.2. Data collection

We sampled the three main groups between June 2004 and October 2007. Our goal was to sample each group in a sufficiently exhaustive manner such that the data reflect the potential biodiversity of individual wetlands. The particular dates varied with taxon because inundated conditions were required to detect aquatic fauna, while dry down of the wetlands was preferable for vegetation sampling. Amphibian sampling took place seasonally over nearly 2 years to capture annual and seasonal variation in breeding activity and better represent the overall diversity of this group.

2.2.1. Vegetation

We sampled vegetation within each of 29 wetlands from early September to late October 2006 (9 wetlands; Kaeser and Kirkman, 2009) or 2007 (20 wetlands). Our sampling design consisted of transects spanning each wetland at 30 m intervals. We recorded species presence in 1 m^2 plots spaced 15 m apart along each transect. The total number of transects, length of transects, and number of plots were scaled by wetland size; size of wetlands ranged from 0.1 to 7.0 ha. All taxa present were identified to species, or to genus if they were immature. Nomenclature follows Wunderlin and Hansen (2003). Several vascular plant species area curves within studied wetlands did not reach an asymptote (Kaeser and Kirkman, 2009), thus, the total number of plant species observed may not be an adequate complete estimate of plant richness per wetland in our study. Therefore, we also used three other estimators that are less affected by the number of plots evaluated: the slope and intercept of species area accumulation curves per wetland (by 1 m^2 plots) and a rarefaction estimate of species richness (Colwell, 2006). The intercept is an estimate of the average species richness in a single random 1 m^2 plot per wetland. The slope indicates the rate of species increase as samples accumulate. The rarefaction values estimate the expected number of species for each wetland if all the wetlands were sampled using 15 plots, i.e., the number of plots sampled in the smallest wetland (Gotelli and Colwell, 2001). We examined the correlative relationship among the four different plant species richness estimators.

2.2.2. Amphibians

Amphibian data were collected seasonally at the 29 study wetlands over two sampling periods between June 2004 and April 2006. Sampling methods differed slightly between the first (summer 2004–spring 2005) and second (summer 2005–spring 2006) sampling period, but because methods were consistent among wetlands within each sampling period, and our goal was to estimate overall species richness among wetlands, we combined the two data sets. During the first sampling period, methods included dipnetting, frog call surveys with automated recorders, crayfish and funnel traps, and PVC pipes; effort was scaled to wetland size (see Liner et al., 2008 for details). In the second sampling period, effort was standardized across all wetlands. Methods included crayfish and minnow traps (5 of each per wetland for four nights/season), automated frog call recorders (twice per season), and dipnetting (300 sweeps per wetland per season; Dodd, 2003). We substituted minnow traps for funnel traps in the second sampling period; these two methods would be expected to capture a similar suite of aquatic amphibians (Dodd, 2003; Smith et al., 2006a). We did not use the PVC pipe method, which exclusively targets treefrogs, in the second sampling period because these species can also be detected by dipnetting and frog call recordings.

2.2.3. Aquatic beetles

Larval and adult coleopterans were collected from 25 of the 29 study wetlands in January 2006, April 2006, and February 2007. On some dates, aquatic macroinvertebrates could not be collected from all sites because water was not present. Macroinvertebrates were collected with a 500-μm mesh D-frame sweep net (30.5 cm width). A sample consisted of sweeping the net five times over a transect 1 m in length; the first two sweeps were taken in the water column and the last three were through the benthos and vegetation (Battle and Golladay, 2001). Sweeps were collected at four locations within each wetland and combined to create a composite sample for each site. Habitats sampled varied slightly with wetland type based on preliminary surveys of species detection versus sampling effort. The habitat sampled within each wetland type was as follows (typically in most abundant habitat type): (1) grass-sedge marsh: 3 transects in shallow water with vegetation, and one transect in open, deeper water; (2) cypress-gum swamp: 4 transects in open water, including the area around tree bases; (3) cypress savanna: 4 transects including the perimeter of wetland, in vegetation, and in shallow water. Each sample was then preserved with 70% EtOH and stained with rose Bengal dye to facilitate sorting. Coleoptera larvae and adults were placed in separate containers from other taxonomic groups and identified to genus (most larvae) or species (most adults). Adult coleoptera identified to species were verified (Epler, 2010). We included beetle larvae and adults as separate morphospecies because of their differing ecological characteristics (Epler, 2010).

2.2.4. Hydrologic and landscape measures

Water-level staff gauges were placed at the lowest point of each of the 29 study wetlands and surface water levels were measured twice monthly from 1999 to 2009. To obtain volume and area of each wetland, the perimeter of the basin of each wetland was defined by the hydric soil boundary (USDA Natural Resources Conservation Service, 2006). Based on survey point locations obtained using standard surveying methods, 0.25 m elevation contours, volume, and area were derived for each wetland using a triangulated irregular network (TIN) surface in GIS software (ESRI, ArcGIS version 9.1 2005, Redlands, CA). Percent of area, percent of volume, and length of time inundated were derived from staff gauge readings and contour data using the GIS software (resulting variables analyzed are described below). To evaluate the influence of the surrounding landscape, we calculated the percent forested land cover within a 1 km wide buffer surrounding the perimeter of study wetlands using GIS land cover data that had been photo interpreted from 1:12,000 scale color infrared photography and updated using 1:10,000 scale color infrared digital photography. We also calculated an isolation index (S_i) to characterize the relative distances among wetlands (Hanski and Thomas, 1994):

$$S_i = -\sum_{j}^{n}(exp(-\alpha d_{ij}))$$

where $\alpha = 1$ (constant for strength of distance and area affects); d_{ij} = distance (km) between focal wetland i to j through $n = 124$ (90 on-site wetlands and 34 wetlands within a 250 m buffer around the property). We used 1 as a conservative estimate of α (Quintana-Ascencio and Menges, 1996).

2.3. Analytical methods

2.3.1. Congruence of species richness and community composition

We examined the correlation of patterns of species richness among taxa. We evaluated similarity of plant, amphibian, and beetle species composition among wetlands using Non-Metric Multidimensional Scaling (NMS). We subjected presence-absence data for each taxon to NMS using a distance matrix calculated as 1 minus the Jaccard similarity index. Examination of the badness-of-fit criterion in SAS (SAS Institute Inc., 2004) was used to determine the optimal number of dimensions to retain from the NMS analysis (McCune and Mefford, 2011). We tested for differences between types of wetlands by taxa using Permanova (vegan package; R Development Core Team, 2007) with 1000 permutations. We also examined patterns of species composition among taxa (complementarity) based on Sorensen's similarity index (presence or absence of species). We summarized similarities between pair-wise combinations of wetlands as a matrix for each taxon separately, and we used Mantel tests to test for cross-taxon correlations between the similarity matrices (Legendre and Legendre, 1998; Su et al., 2004). The significance of the correlation was tested with Monte Carlo randomization (10,000 permutations). Taxa that were not identifiable to species were excluded from these analyses. Differences in mean number of non-vegetated plots by wetland type were examined with ANOVA. We performed these analyses using R version 2.10.0 (R Development Core Team, 2007).

2.3.2. Surrogate performance

We used the species accumulation index (SAI) to measure the performance of one taxon as a surrogate of diversity for another taxon (Ferrier, 2002). This approach examines the likelihood that a series of wetlands selected in a step-wise fashion for a surrogate taxon approaches the minimum set producing the fastest accumulation of species for the target taxon. The site selected at each step is the one providing the greatest improvement in representation of diversity within the surrogate taxa; thus, the series of wetlands selected represents the minimum set of wetlands resulting in the fastest accumulation of surrogate species (Ferrier et al., 2000; Moritz et al., 2001; Ferrier, 2002). SAI was calculated as:

$$\text{SAI} = \frac{s-r}{o-r}$$

where s, r, and o are the areas under three species accumulation curves developed by using: (1) the surrogate (s), (2) the target group (o), (3) random addition of sites (r). The SAI can range from 1 for a perfect surrogate to 0 or less for a surrogate that performs no better than a random selection of sites. We also evaluated the performance of the surrogate taxa by defining a confidence interval of the sequence obtained by random selection of wetlands, based on bootstrap resampling of 100 sequences. When several wetlands contributed the same number of additional species, one was chosen randomly. Similarly, wetlands with identical species composition of any given taxa (e.g., beetles) were randomly selected for inclusion in each iteration; thus, optimum and surrogate beetle curves reflected a total of 18 wetlands.

2.3.3. Environmental factors

First, we characterized wetland types by hydrologic and physical parameters with principal components analysis (PCA) via PC-ORD® (MjM Software Design, Gleneden Beach, OR). Variables included: (1) average length of time (days) a wetland was 100% filled in a calendar year (time 100% filled), (2) average volume of water observed in a wetland during a calendar year (volume), (3) number of days a wetland was at least 25% full during a calendar year (time 25% filled), (4) elevation of the wetland at the base of the staff gauge (lowest point above sea level), and (5) wetland area (2-dimensional surface area as viewed from above). For variables 1–3 (above), annual average or average total (each variable averaged over the period of record, 1999–2009) was calculated for each wetland. Years with incomplete records for a particular wetland were not included. We constructed a distance-based joint-plot using a standardized (correlation) cross products matrix (Greig-Smith, 1983). Randomization procedures were used to determine the number of axes to interpret (Peres-Neto et al., 2005). We report correlation coefficients (Pearson's r) between hydrologic and physical parameters and axes in the joint-plot. The r^2 cutoff scores for visualizing correlations between water quality parameters and principal components in the joint plot were set at 0.2, the default setting for the program.

Next, using multiple regression, we built linear models relating environmental variables to each metric of species richness for each taxa. The following environmental variables were examined: wetland type, wetland area (data natural logarithmically transformed), average volume of water observed in a wetland during a calendar year (volume), percent forested area within a 1 km buffer around each wetland, and an isolation index. Wetland types differed in hydrologic and physical characteristics; thus, to avoid collinearity and to simplify interpretation, we only included wetland type as a variable as opposed to a PCA score when assessing species richness variables. We checked for collinearity and variance inflation among the other independent variables (Crawley, 2005). We avoided using independent variables with high correlation (variable inflation factor > 3) in the same model. We used Akaike's Information Criteria (AIC) to identify the most informative models (Burnham and Anderson, 2002) using R version 2.10.0 (R Development Core Team, 2007).

3. Results

3.1. Congruence of species richness and community composition

Across the wetlands, we identified 449 vascular plant species, 26 amphibian species, and 73 beetle morpho-species and found considerable variation in species richness within wetland types (Table 1). We found a significant correlation between beetle richness and the intercept of the plant richness accumulation curve. The slope of the plant species accumulation curve and amphibian richness were weakly correlated. There was no correlation between amphibian and beetle species richness (Table 2). Among wetland types, cypress-gum swamps had a greater percentage of sample plots that were non-vegetated (12.0 ± 1.7%) relative to either savannas (1.0 ± 1.8%) or marshes (1.0 ± 2.0%) (ANOVA, $p < 0.001$). Some estimates of plant species richness were correlated while others were not. Plant species richness was correlated with the intercept of the plant accumulation curve, but not with the slope. Even though the intercept of the curve and the rarefaction estimate were highly correlated, the relationship of each of these metrics with other taxa varied (Table 2).

For all taxa, the NMS solution indicated that swamps differed in species composition from both marshes and savannas (Fig. 1). For plants, we retained 3-dimensions after 14 iterations (badness-of-fit = 0.110) with dimensions 1 and 2 explaining 78% of the variance. For amphibians a 3-dimensional solution was reached after 12 iterations (badness-of-fit = 0.142) with 78% of the variance explained by the first two dimensions. For beetles (Fig. 1) a 3-dimensional solution was reached after 13 iterations (badness-of-fit = 0.151). The first two dimensions explained 73% of the variance. We found significant, but low congruence between amphibian and plant species composition and between amphibian and beetle composition (Mantel Test, $p < 0.05$), but there was incongruence between beetle and plant species composition.

3.2. Performance of surrogates

Selection of wetlands based on potential surrogate taxa did not replicate the species accumulation sequence for any of the target taxa (Fig. 2). All sequences for surrogate species curves were within the confidence interval of the null hypothesis of random selection of wetlands (Fig. 2). Thus, the performance of the surrogates tested was no better than that achieved by random selection of wetlands.

3.3. Environmental correlates

The PCA of hydrologic and physical data indicated that differences between wetland types were related to a combination of hydrologic and physical factors. Cypress-gum swamps generally were larger, held greater volumes of water for longer periods, and

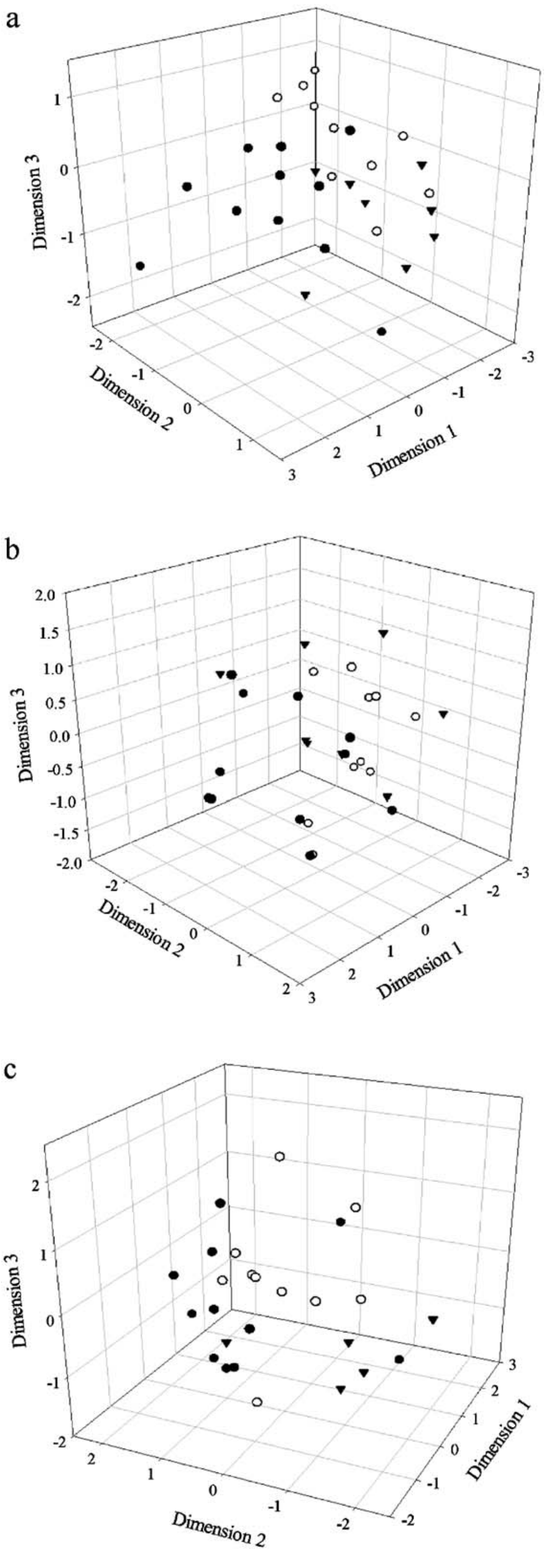

Fig. 1. Non-metric multidimensional scaling three-dimensional solutions for species presence-absence data for: (a) vascular plants; (b) amphibians; (c) coleopterans. Closed circles represent cypress-gum swamps, open circles represent grass-sedge marshes, and triangles represent cypress savannas. Permanova test of differences between types of wetlands, vascular plants, $p < 0.001$; amphibians, $p < 0.001$; coleopterans, $p < 0.01$.

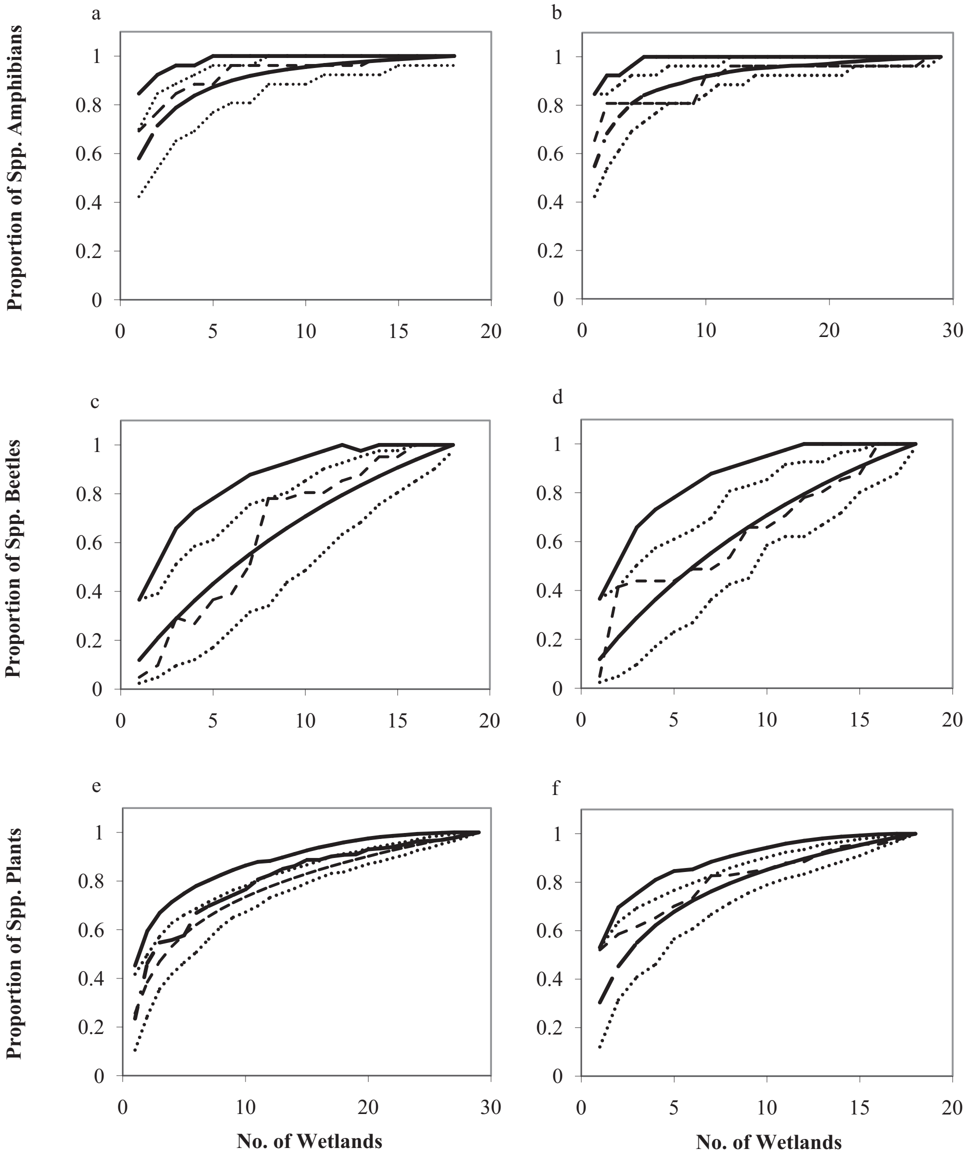

Fig. 2. Species accumulation curves by wetland for amphibians, coleopterans, and vascular plants indicating their efficiency as surrogates for the other taxa as compared to a random accumulation of wetlands. In each graph: bold line = optimum curve for target taxon, dashed line = surrogate curve, dash-dot line = random wetland sequences; and thin dotted lines = 90% confidence intervals. (a) target amphibians and surrogate coleopterans; (b) target amphibians and surrogate plants; (c) target coleopterans and surrogate amphibians; (d) target coleopterans and surrogate plants; (e) target plants and surrogate amphibians; (f) target plants and surrogate coleopterans (SAI values: plants as surrogate of amphibians = 0.02–0.23; amphibians as surrogate of plants = 0.02–0.26; beetles as surrogate of plants = 0.05–0.25; plants as surrogate of beetles = 0.04–0.24; beetles as surrogate of amphibians = 0.06–0.35; amphibians as surrogates of beetles = 0.01–0.31).

were at lower elevations than the other wetland types. Savannas tended to occur at higher elevations, were smaller, and held lower volumes of water for shorter periods than other wetland types. Marshes were intermediate, occurring over a wide range of elevation and were variable in size and hydrologic characteristics (Fig. 3, Table 3).

The association between species richness per wetland and the environmental variables varied by taxon (Table 4). Plant species richness was positively associated with wetland area (ln transformed) and negatively associated with isolation (Fig. 4a), indicating greater species richness in larger and more aggregated wetlands. The average slope of plant species accumulation curves

Table 1
Species richness by taxa and physical characteristics of isolated wetlands in the southeastern coastal plain of southwestern Georgia. Data are summarized by wetland type.

Variable	Grass-sedge marsh		Cypress savanna		Cypress-gum swamp	
	Mean (±SE)	Min/Max	Mean (±SE)	Min/Max	Mean (±SE)	Min/Max
Plant spp. (total)	131 (15)	51/236	114 (14)	50/171	145 (15)	77/243
(per m^2)	10 (1)	0/33	10 (1)	0/39	5 (1)	0/38
Amphibian spp.	15 (1)	11/22	13 (1)	10/16	14 (1)	11/18
Beetle spp.	10 (2)	3/24	6 (2)	0/14	4 (1)	0/9
Isolation index	−9 (1)	−14/−5	−13 (1)	−14/−10	−8 (1)	−12/−4
Area (ha)	1.27 (0.32)	0.24/3.42	0.41 (0.09)	0.86/0.92	3.25 (0.65)	0.58/7.28
Volume (m^3)	4021 (1201)	653/12,150	990 (233)	232/2266	10,610 (2202)	1212/22,043

Table 2
Pearson correlation among species richness or alternative indicators per wetland for various taxa ($n = 29$; except for beetles $n = 25$). Statistical significance ($p < 0.05$) is denoted by asterisks (*). VP = vascular plants.

	Intercept VP	Slope VP	Rarefied VP	Amphibians	Beetles
VP	0.40*	−0.27	0.15	0.36	0.16
Intercept VP		−0.35	0.74 *	0.21	0.48*
Slope VP			0.33	−0.38*	−0.15
Rarefied VP				−0.12	0.27
Amphibians					0.21

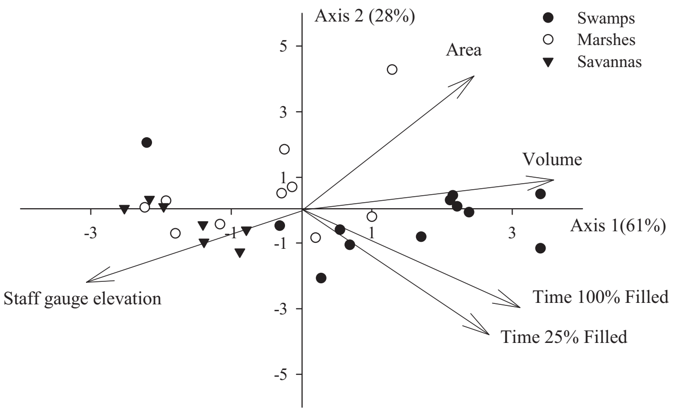

Fig. 3. Principal components analysis (PCA) of hydrologic and physical characteristics of reference wetlands. Hydrologic variables to characterize hydrologic regime were developed from annual means for each wetland from a long-term data set (1999–2009). Physical data are the result of one-time field surveys of wetland perimeters and basin depth (89% of the cumulative variation was explained by axes 1 and 2). Wetland volume (average volume of water) and percent of time filled (100% and >25% full) were strongly correlated with axis 1. Elevation (lowest point above sea level) was negatively correlated with axis 1. Wetland area was positively correlated with axis 2.

Table 3
Correlation coefficients (Pearson's r) of wetland physical and hydrologic characteristics and axes derived from a PCA distanced-based joint-plot using a standardized (correlation) cross products matrix.

	Axis 1	Axis 2
Time 100% filled	0.81	−0.52
Time 25% filled	0.70	−0.67
Volume	0.92	0.16
Elevation	−0.79	−0.38
Area	0.63	0.71

was significantly higher in cypress-gum swamps and cypress savannas than in grass-sedge marshes. The average beetle richness was significantly lower in cypress-gum swamps and cypress savannas than in grass-sedge marshes. The average intercept was lower in cypress-gum swamps than in grass-sedge marshes (Table 4). We found a significant positive association between amphibian richness and the isolation index (Fig. 4b), which indicates that the more isolated wetlands had higher species richness.

4. Discussion

4.1. Species richness and composition among taxa

The low degree of congruence in species richness among taxa demonstrates that none of the groups examined could be used as a surrogate for representing the overall richness of the three taxa within these wetlands. Although beetle species richness and plant accumulation intercept (mean number of species per m^2) were positively correlated, the incongruence in species similarity between beetles and plants and the lack of performance of these taxa as surrogates for one another suggest that factors influencing species presence differ among wetlands. Our finding of low congruence of species richness among taxa is similar to results reported for numerous ecosystems (Prendergast and Eversham, 1997; Oliver et al., 1998; Vessby et al., 2002; Bilton et al., 2006; Wolters et al., 2006; Heino, 2010). In addition to hydrologic and physical factors interacting to determine wetland habitat suitability, congruence of species richness across major taxonomic groups may be a scale-dependent phenomenon (sensu Pickett et al., 1989; Prendergast and Eversham, 1997). Prendergast and Eversham (1997) noted correlation of richness spanning major taxonomic groups across broad geographic regions; but relationships were not consistent at more local scales. The groups we studied may show congruence in species richness at the level of physiographic province because they have a strong tendency to be limited to southeastern isolated wetlands. However, their habitat requirements may be very specific, making congruence of species richness difficult to detect at the scale of individual wetlands (Flather et al., 1997; Prendergast and Eversham, 1997; Vessby et al., 2002).

Our study indicates that for the taxa considered, grass-sedge marshes and cypress savannas are more similar in species composition than cypress-gum swamps. Vegetative structure including open canopy with herbaceous vegetation versus closed canopy forest and little ground cover are known to influence habitat selection by amphibians (Skelly et al., 2005) and beetles (Battle and Golladay, 2001), and may account for taxa distributions we observed. Dense emergent vegetation provides both food and habitat for larval

Table 4
Most informative multiple regression models based on AIC for species richness or alternative richness estimator (rarefied plant richness, and slope and intercept of plant accumulation curves for vascular plants) per wetland for various taxa and environmental variables ($n = 29$; except for beetles $n = 25$). Wetland type (savanna, swamp, marsh), $\log A$ = log of wetland area; I = isolation index (values > 0 indicate more isolated (less aggregated) wetlands, whereas values < 0 indicate less isolated (more aggregated) wetlands. *Note*: Marshes were used as a reference value in the model and are not included. Statistical significance ($p < 0.05$) for wetland types is denoted by asterisks (*). Blanks indicates lack of importance of variable in the AIC analysis. $\beta0$ is the intercept of the models.

Taxa	$\beta0$	Wetland type		$\log A$	I	Ad. r^2
		Cypress savanna	Cypress-gum swamp			
Vascular plants	−316.6			41.19	−7.089	0.443
Raref. VP	26.9				−3.174	0.435
Slope VP	0.47	0.08*	0.09*			0.282
Intercept plants	15.73	−1.7	−5.5*			0.398
Amphibians	17.7				0.384	0.246
Beetles	10.0	−4.5*	−6.4*			0.279

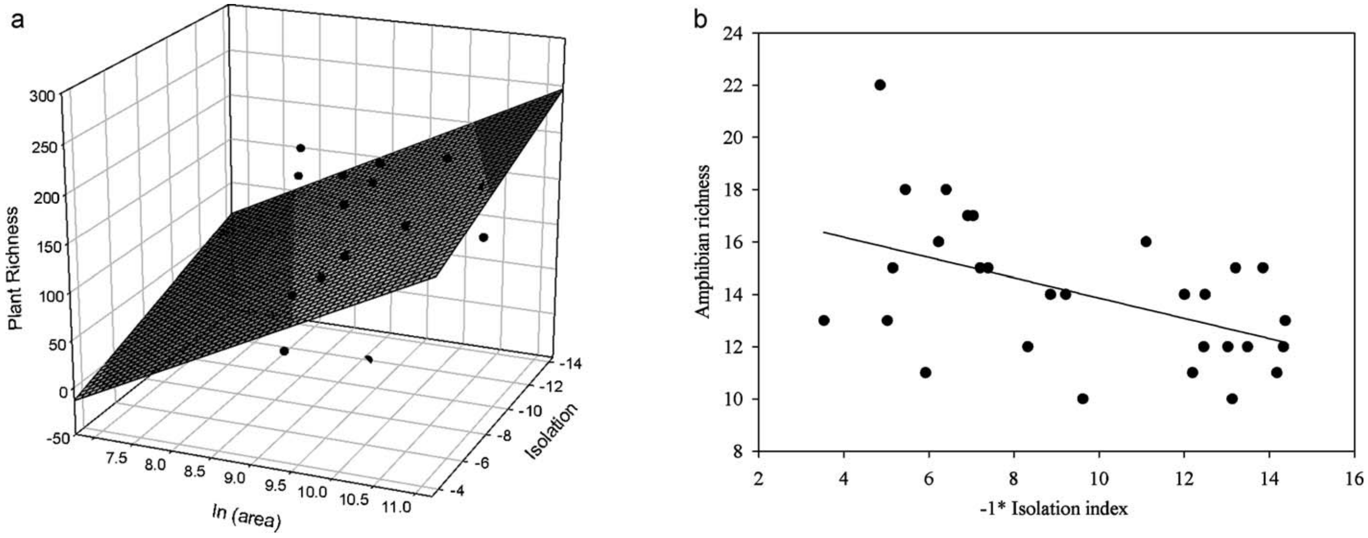

Fig. 4. Plots of significant environmental variables and richness among taxa. (a) Vascular plants with isolation and logarithmic area; (b) amphibian richness with isolation index.

and adult beetles, favoring species that are capable of clinging to plants (Battle and Golladay, 2001). While relatively few aquatic beetles consume live plant material, growth of periphyton and decomposition of senescent plant material provides food resources for both adult and larval beetles and their prey. Although total amphibian species richness did not vary with wetland type, salamander richness was greatest in cypress-gum swamps, whereas larval frog richness was highest in marshes and cypress savannas (Liner et al., 2008). The difference between groups of amphibians is likely related to contrasting hydrology and vegetative structure of the three wetland types. Longer hydroperiods associated with cypress-gum swamps allow fully aquatic salamanders and mole salamanders, which have a longer larval stage than many frogs, to persist in swamps, but not in cypress savannas or marshes. In contrast, larval frogs are largely algal grazers and the open canopy of marshes and savannas stimulates algal production, increasing food availability (Opsahl et al., 2010).

4.2. *Environmental influences on patterns of species assemblages*

The disparate patterns in species richness in our study reflect biotic and abiotic processes operating at different scales for each taxonomic group and for individual species. However, because variables often tend to co-vary in space, factors determining the co-occurrence of species from differing taxa may be confounded. In addition to the strong linkage between wetland type and hydrology, the association among wetland type and several other environmental factors (e.g., area, elevation, isolation) contributes to difficulties in variance partitioning among species assemblages. For example, the larger surface area wetlands tended to have greater variation in percent of time inundated; cypress savannas are smaller and more aggregated than either cypress-gum swamps or grass-sedge marshes (S.W. Golladay, unpublished data). Thus, relationships between wetland size, type, and hydrology in determining habitat suitability appear to be complex in this landscape.

4.2.1. *Vascular plant species*

Our evidence that total plant species richness increases with wetland area is similar to other isolated wetlands in the southeastern USA (Boughton et al., 2010) and elsewhere (Brose, 2001; Matthews, 2004). The positive correlation between total plant species richness and the species accumulation intercept (the average number of species per m^2) and the increasing number of species with area sampled suggests that the high density of species packing at the plot scale is an important factor to be considered. In addition, larger wetlands may be characterized by greater within-site heterogeneity or more likely to receive dispersing propagules. The degree of wetland isolation is also a factor, with total plant species richness per wetland increasing with wetland aggregation. The importance of proximity to other wetlands suggests that dispersal corridors maintain high species diversity (Møller and Rørdam, 1985; Boughton et al., 2010); however, additional variables may be involved and the mechanisms underlying the relationship between isolation and species richness are not understood. Our index of isolation did not account for the type of wetlands, the number of species in neighboring wetlands, the number of neighboring wetlands within a certain distance, or potential surface water connectivity during high precipitation periods. Wetland size may also influence the immigration and extirpation of species (Møller and Rørdam, 1985), where larger wetlands may receive more external propagules than smaller wetlands with similar isolation. Arguably, small wetlands with numerous neighboring wetlands may receive comparable or even greater numbers of external plant propagules than larger more isolated ones. This metapopulation view suggests that greater numbers of propagules arriving in a wetland not only contribute to recruitment of additional plant species, but reduces extirpation rates of existing populations (Dupré and Ehrlén, 2002); however, the role of landscape configuration undoubtedly is dependent on individual species life history characteristics (Quintana-Ascencio and Menges, 1996; Matthews, 2004; Boughton et al., 2010). The role of persistent seedbanks, well documented within isolated wetlands (Kirkman and Sharitz, 1994; Poiani and Dixon, 1995; Mulhouse et al., 2005; Martin and Kirkman, 2009), may also be a factor that off-sets the role of isolation (Brose, 2001).

In contrast to plant species richness, plant species accumulation slope and intercept varied with wetland type. Our observed lower mean species richness per m^2 in most cypress-gum swamps relative to cypress savannas or grass-sedge marshes is similar to observations in Carolina bays by Collins and Battaglia (2001). They noted that bays having greater water level fluctuations and exposed sediment areas lacked zonation in vegetation, with species distributed broadly and continuously across the wetland. Those wetlands also had greater total species richness than wetlands with steep basins and prolonged periods of inundation. Isolated wetlands with steeper gradients also tended to have distinct zones of vegetation (Collins and Battaglia, 2001).

4.2.2. *Amphibian species*

In contrast to a pattern of increasing plant richness with close proximity between wetlands, the most isolated wetlands in our study had the greatest amphibian species richness. Although we did not sample fish, other studies have noted that, during periods of high water, some of the more aggregated wetlands on the study site are connected by ephemeral drains allowing fish to disperse among them (Battle and Golladay, 2002; Liner, 2006; Smith et al., 2006b). Hence, there is a greater likelihood that aggregated wetlands support predatory fish, which may result in reduced amphibian species richness (Hecnar and M'Closkey, 1997; Snodgrass et al., 2000; Baber, 2001; Porej and Hetherington, 2005).

Our focus on factors contributing to overall amphibian richness may obscure the importance of habitat variation among wetlands within a landscape (e.g., wetland type, hydroperiod, and isolation) in supporting local and regional amphibian diversity (Gibbs, 2000; Liner et al., 2008). Wetlands having highest species richness do not necessarily support all species, e.g., greater siren (*Siren lacertina*) occurred only in two cypress-gum swamps having intermediate species richness, whereas striped newts (*Notophthalmus perstriatus*) were found in only one wetland (a marsh). Our data suggest that while individual wetlands may meet the habitat requirements for particular species, a complex of wetlands across the landscape is necessary for persistence of overall biodiversity at a regional scale. Furthermore, amphibian populations in isolated wetlands are exceptionally dynamic, fluctuating drastically with annual variations in climate (Pechmann and Wilbur, 1994; Semlitsch et al., 1996) and likely exist as metapopulations across the larger landscape. Thus, a much longer period of observation is necessary to capture temporal and spatial variation that adequately reflects total species richness within a single isolated wetland or among a complex of wetlands.

4.2.3. *Coleopteran species*

Our finding of greater beetle species richness in marshes and savannas than swamps is consistent with previous studies noting that marshes and savannas have the greatest macroinvertebrate diversity (Battle and Golladay, 2001). Aquatic and semi-aquatic beetles are often the most taxonomically diverse macroinvertebrate group found in our sites and other isolated wetlands (Battle and Golladay, 2001; Bilton et al., 2006). Like other fauna, beetles persist in variable aquatic habitats through a variety of mechanisms and adaptations including wide-dispersing life history stages (colonization), drought tolerant life history stages (resistance), and rapid development times (Wiggins et al., 1980; Zedler, 2004). Dytiscidae, the most diverse and abundant group of beetles found in our wetlands (Battle and Golladay, 2001) are noted for their dispersal abilities as adults. The lack of relationship between beetle species diversity and wetland size and isolation has been noted in other studies (Brose, 2003; Nicolet et al., 2004). For beetles and other widely dispersing faunal groups, dispersal capability may reduce the problem of colonizing relatively small and/or isolated wetland habitats (e.g., Brose, 2003). It has been suggested that for habitat generalists like beetles, a variety of wetlands with varying sizes and hydroperiods ensure metapopulation persistence across variable and unpredictable climate cycles (Briers and Biggs, 2003; Zedler, 2004). Our results, where sampling occurred during normal to below normal rainfall, along with previous studies (Battle and Golladay, 2001) during above average rainfall, are consistent with that suggestion.

4.3. *Implications for developing assessment methods*

Our study underscores the difficulty in describing characteristics of exceptionally diverse ecosystems, and in particular, functionally complex isolated wetlands. Potentially, comparisons of wetlands across a broad gradient of human disturbances may demonstrate greater correlation of species richness among taxa as assemblages of semi-natural environments shift to that of species tolerant to degraded environmental conditions (Briers and Biggs, 2003; Boughton et al., 2010; Menetrey et al., 2011). A combination of plant, amphibian, and macroinvertebrate metrics have proved useful in describing wetland condition in Europe (see Menetrey et al., 2011 and studies cited therein). An understanding of species distributions relative to habitat alterations can help identify whether cross taxonomic indices for quantifying wetland condition are even possible. In this regard, additional study is needed to determine the relative importance of habitat configuration, habitat quality, and land use history on multi-taxa species assemblages and patterns of diversity in isolated wetlands.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolind.2011.10.015.

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