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A modularity-based approach for identifying biodiversity management units

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Abstract

Background: Taxon- and/or ecosystem-based definitions of management units typically focus on conspicuous species and physical habitat limits; these definitions implicitly assume that these classification systems are related to the mechanisms that determine biodiversity persistence. However, ecological theory shows that this assumption may not be supported. Herein, we introduce the use of modularity analysis for objectively identifying management units and topological roles that land cover type plays on species movement through the landscape.

Methods: As a case study, we used a coastal system in Uruguay, with 28 land cover types and five taxa (from plants to mammals). A modularity-based approach was used to identify subsets of habitats with biotic affinity, termed modules, across the different taxonomic groups. Modularity detects the tendency of some land cover types to have a higher probability of the mutual interchange of individuals than other land cover types. Based on this approach, pairs of habitats that co-occur in the same module across taxa were considered in the same biodiversity management units (BMU). In addition, the topological role of each habitat was determined based on the occurrence of species through the landscape.

Results: Our approach determined three management units that combine land cover types usually considered independent, but instead are interrelated by an occurrence-based ecological network as proxies of the potential flow of individual and land use. For each selected taxon, the specific topological role of each habitat was determined.

Conclusions: This approach provides an objective way of delineating spatial units for conservation assessment. We showed that land cover types within these spatial units could be identified as refuges for specific types of biodiversity, sources of propagules for neighboring or overall landscapes, or stepping-stones connecting sub-regions. The preservation of these topological roles might help maintain the mechanisms that drive biodiversity in the system. Interestingly, the role of land cover type was strongly contingent on the taxa being considered. The method is comprehensible, applicable to policy and decision-makers, and well-connected with ecological theory. Moreover, this approach complements existing methods, introduces novel quantitative uses of available information, determines criteria for land cover classification and identifies management units that are not evident through other approaches.

Keywords: Biodiversity units, Bipartite networks, Compartmentalization, Conservation prioritization, Metacommunity theory, Topological roles

Background

The identification of management units represents a theoretical challenge of great applied importance considering the increasing modification and alteration of ecosystems [1]. Local biodiversity patterns are frequently used for identifying these management units [2, 3]. This approach may be useful at a large geographic scale but could be limited at smaller scales [4], at which local conditions typically interact with species dispersal to determine biodiversity trends [5–7]. Communities are not isolated entities; the interchange of species within a regional species pool has been identified as a chief determinant of community structure [6, 8–10]. Metacommunity theory put the focus on the interchange of individuals among communities, which further emphasizes the importance of the flow of species and individuals as a key determinant of biodiversity patterns [6, 11–15]. Despite

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increased attention to understanding biodiversity patterns in metacommunity theory, less consideration has been given to potential applications for conservation and management of biological systems [16–19].

Management units for conservation goals have frequently been identified according to the aims and interests of researchers and decision-makers by using discrete land cover boundaries, by identifying dominant or more conspicuous species or by detecting interactions among species in a particular area or time period [20, 21]. Moreover, a trade-off among limited funds and available ecological data often determines the final conservation plan [22–25]. Furthermore, metacommunities are assembled from a broad range of species with contrasting biological attributes and life histories [5, 26]. In this context, a critical challenge is to detect the spatial scale that best reflects the structuring processes underlying biodiversity patterns [5]. Priority strategies for conservation should contribute to preserving the processes that support biodiversity and to balancing local and landscape processes related to species movement [16, 22, 27].

Network-based approaches offer a powerful set of tools for connecting metacommunity theory to conservation and management practices [17, 28–31]. If two habitat patches are connected in a metacommunity, similar species composition could be expected, implying a potential flow of organisms between them [29, 31]. When species-sites occurrences are represented as a graph (e.g. [32, 33]), modularity could be defined as the tendency of a subgroup of sites and species to be linked to another subgroup of sites and species in a network [34, 35]. Specifically, modularity involves the existence of a distinctive set of sites (a module) with a greater number of common species. From a metacommunity perspective, modularity may detect groups of species with different dispersal abilities and biological requirements but with similar responses to the main processes that structure biodiversity [18]. Further, modularity is associated with an intermediate level of metacommunity structure that cannot be detected when the focus is on isolated nodes (species or habitats) or on the entire metacommunity network [35–37]. Once the modular structure is identified, it is possible to determine the potential topological role of each site within the entire set of sites [38] and therefore its relevance for the interchange of species within the module and/or across the entire landscape [39]. In summary, modularity represents an efficient tool to identify meaningful sets of sites, which could be considered conservation units [40–45].

We are responding to the demand for objective approaches to recognize conservation units that account for local and metacommunity processes that support biodiversity [16]. Herein, we use a modular analysis to identify modules of species and land cover types for different taxa. In addition, we estimate the topological role of each land cover type for different taxa. We demonstrate the performance of this method for a coastal system in Uruguay, South America, which includes a wide range of land cover types and species occurrences for five taxa: mammals (55 species), birds (132), amphibians and reptiles (55), butterflies (47) and plants (265).

Methods

Identification of biodiversity management units

Our proposed approach is based on the analysis of modularity in bipartite networks (see [43, 46]). These bipartite networks represent species-areas incidence matrices, where species occurrence in a given area is represented by one and by zero otherwise [40–42]. Areas can represent local communities, land cover types or islands. Modularity analysis attempts to detect areas and species more closely related with each other than with other areas and species [38, 43, 47]. To this aim, we used an algorithm based on simulated annealing—i.e. a stochastic optimization technique that identifies modules in a graph by maximizing a function of modularity (see [38, 47]). Specifically, we used the Barber modularity metric for bipartite networks (see [48]). This algorithm performs well in identifying meaningful levels of species or community aggregations in a wide range of ecological studies (see [18, 39–42, 49, 50]). We ran this analysis with MODULAR software for bipartite networks represented herein by species-land cover types incidence matrices and evaluated the significance of the observed modularity with two null models based on 2000 simulations of random networks (see [46]). Each module involved the detection of an aggregation of land cover types closely interrelated on the basis of species occurrences. Thus, modules represent potential biodiversity management units (BMUs) for the taxa represented in the incidence matrix.

Considering that the same landscape can be perceived in markedly different ways by species with different traits [5, 29, 51], the previous analysis can be improved if it is performed independently for different taxa (e.g., birds, mammals, invertebrates, plants). In addition, the use of different networks for each taxon avoids masking the topological role of land covers for rare or less diverse taxa. In order to combine information from the analysis of modularity among different taxa, we used the frequency at which two land cover types are observed within the same module to construct a land cover type—land cover type similarity matrix. A cluster analysis (or similar method) can be used to identify groups of land cover type that should be considered as a single BMU. These BMUs are hence objectively determined by modularity analysis combined with information from the occurrence of different taxa (Fig. 1).

Topological roles of habitats

A modular structure among habitats (herein land cover types) can be used to identify the potential topological role of each habitat within the entire system. The role of each habitat was determined by two parameters following Guimerà and Amaral [38]. The first parameter is a standardized within-module degree z_i, which represents the number of direct connections of the habitat within its own module [38, 49], and is defined as: $z_i = (k_{is} - \overline{k}_s)/SD_{k_s}$, where k_{is} is the number of links from habitat i to its own module, s, and $\overline{k}_s$ and SD_{k_s} are the average and standard deviation, respectively, of the number of within-module links of all habitats in the module. The second parameter, c_i, corresponds to the connectivity among modules [49]. This parameter is a measure of the number of links in habitat i with other modules normalized by the degree of habitat (k_i) and is estimated as: $c_i = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_i}\right)^2$, where k_{it} is the number of connections from habitat i to species in module t (including module i).

This measure of modular structure defines a parameter-space that is divided into four regions following the criteria of Olesen et al. [49] in setting z_i and c_i, with threshold values corresponding to 2.5 and 0.62, respectively (see [39, 44, 52–54]). Therefore, four types of habitats with different topological roles can be recognized: (1) peripheral habitats with few links that are restricted to their own module ($z_i \leq 2.5$ and $c_i \leq 0.62$), (2) module hubs with many links, most of which are in their own module ($z_i > 2.5$ and $c_i < 0.62$), (3) connectors with few links to species that occur in other modules ($z_i \leq 2.5$ and $c_i > 0.62$) and (4) network hubs that may act as connectors and module hubs simultaneously ($z_i > 2.5$ and $c_i > 0.62$).

Case study

Our study area covers nearly 1350 km^2 of coastal landscape in the eastern region of Uruguay, South America (Fig. 2). Land cover types in the area range from hills in the upper zone to the sandy interface with the Atlantic Ocean and include lagoons and associated wetlands, with native grasslands as the predominant ecosystem. We used an incidence matrix containing 55 species of mammals, 132 species of birds, 55 species of amphibians and reptiles, 47 species of butterflies and 265 species of

a. Matrix M

	Habitat 1	Habitat 2	Habitat 3	Habitat 4	Habitat 5
Taxon A	2	1	2	1	1
Taxon B	3	1	3	2	3
Taxon C	*	4	2	3	1
Taxon D	2	2	2	1	1

* No information about the Taxon C in Habitat 1.

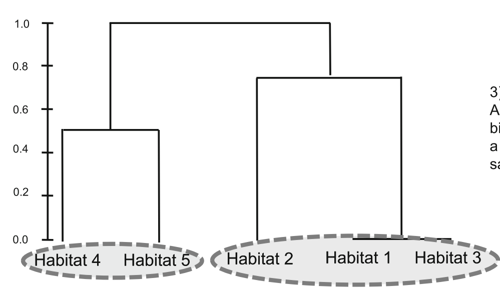
1) **Matrix of habitat membership**
Modularity analysis is applied to the species x habitat matrix of each taxa. A matrix M of taxa x habitat is constructed, wherein each row indicates the habitat membership to the module identified for the row's taxa.

b. Matrix S

	Habitat 1	Habitat 2	Habitat 3	Habitat 4	Habitat 5
Habitat 1	1				
Habitat 2	0.33	1			
Habitat 3	1	0.25	1		
Habitat 4	0	0.25	0	1	
Habitat 5	0.33	0.25	0	0.5	1

2) **Matrix of habitat similarity**
Using the number of times a pair of habitats coincides in the same module a similarity matrix of habitat x habitat, S, is generated. For example, habitat 1 and habitat 3 coincide in all the modules, while habitat 4 and habitat 5 coincide two times from four possible times.

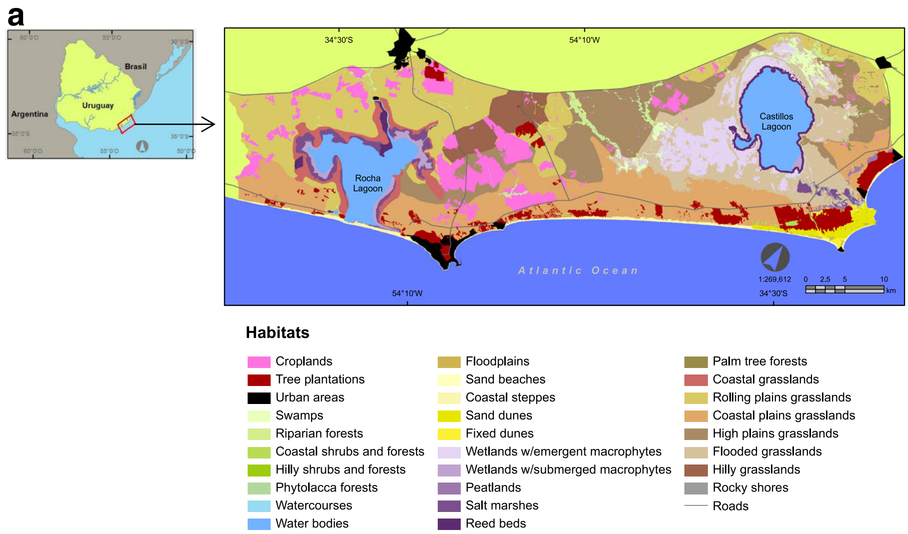
c. Biodiversity management units



3) **Biodiversity Management Units**
A cluster analysis from the S matrix is used to identify biodiversity management units (BMUs). These BMUs involve a set of habitats that are consistently identified as part of the same biodiversity units (modules) among different taxa.

Fig. 1 A modularity-based approach to identify biodiversity management units (BMUs) (see main text for details) including matrices for habitat membership (**a**) and similarity (**b**), and a cluster analysis of BMUs (**c**). In (**a**), a modularity analysis is performed for each taxon and the land cover type memberships for a module are used to generate a new matrix M of taxa x habitats. In (**b**), the number of matches of pairs of habitats in the same module is used to estimate a similarity matrix S. Finally, a cluster analysis applied to matrix S in (**c**) is used to delineate the BMUs

a



b

Habitats	Amphibians and reptiles	Insects	Mammals	Birds	Plants
Croplands	38	15	25	13	-
Fixed dunes	21	-	34	8	4
Swamps	27	41	41	37	10
Riparian forests	27	35	43	45	24
Coastal forests and shrubs	40	19	37	27	133
Hilly forests and shrubs	39	30	38	35	20
Urban areas	34	30	21	14	38
Watercourses	11	43	18	27	-
Floodplains	16	3	34	47	72
Sand dunes	12	-	21	23	8
Water bodies	20	-	16	24	16
Coastal steppes	14	-	32	21	78
Tree plantations	39	21	23	17	31
Wetlands with emergent macrophytes	36	-	21	53	2
Wetlands with submerged macrophytes	37	1	19	27	9
Peatlands	37	-	26	-	9
Salt marshes	-	-	23	42	2
Reed beds	-	-	33	32	8
Phytolacca forests	49	47	45	30	11
Palm tree forests	50	2	29	29	7
Coastal grasslands	-	3	36	44	16
Rolling plain grasslands	46	20	37	44	13
Coastal plain grasslands	48	-	35	42	16
High plain grasslands	47	18	36	40	23
Flooded grasslands	51	7	36	66	17
Hilly grasslands	39	21	36	31	24
Rocky shores	-	4	11	15	-
Sandy beaches	-	-	11	33	-

- data not available.

Fig. 2 a Model system showing the 28 land cover types used in this study (derived from Soutullo et al. 2015). Note that some habitats have a discontinuous spatial distribution. **b** Species richness per taxon and land cover type

plants (total 554 species, see Fig. 2). These species were distributed across 28 land cover types [55]. The land cover classification integrated different classifications available for the study area. Hence it reflects differences in the information available and criteria used by different experts to separate major land cover types (forests, grasslands, wetlands, etc.) into subcategories. The extent of the 28 habitat types ranged from 0.2 to 234 km^2. We performed a separate modular analysis with the species of each of the five major taxon groups and combined the information among taxa as presented in the previous section and in Fig. 1. For each taxon, we analyzed the topological roles of land cover types. We further investigated the congruence of the topological roles played by different land cover types across taxa by combining the observed topological roles across taxa in a single plot.

Results

We detected a significant modular structure higher than expected by chance in the five bipartite taxon networks with three modules for amphibians/reptiles and mammals, four modules for birds, and five modules for butterflies and plants (Fig. 3). Results from the modularity-based approach suggest three BMUs with similar species richness

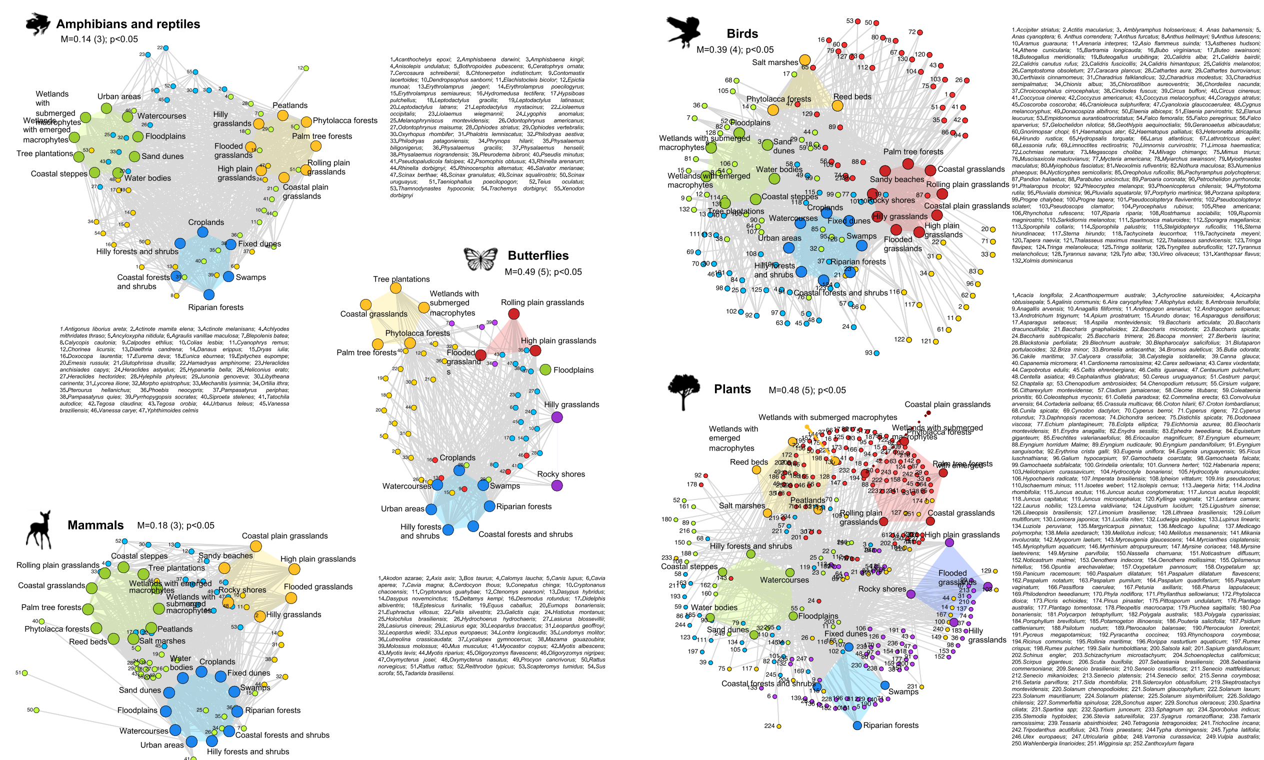


Fig. 3 Bipartite networks of species x land cover types for each taxonomic group considered showing the modules inferred by modularity analysis. We found a significant modular structure for all taxa

and number of land cover types (Fig. 4a, spatial distribution in Fig. 4b). The first BMU represented aquatic habitats (with 314 species and 10 habitat types), which were further subdivided into coastal and wetland habitats. The second BMU contained different types of native forests, forested areas and urban habitats such as villages (with 349 species and 8 habitats types). The third BMU mainly contained grasslands (with 350 species and 10 habitats types). We classified land cover types as peripheral areas or connectors except for the networks for plants and birds, which also had module hubs (Fig. 5). Network hubs were not identified, whereas ultra-peripheral habitats (i.e., habitats with all connections within their own modules: $z_i = 0$) were identified for birds, butterflies, plants and mammals. We observed a large variation among the topological roles of land cover types among taxa (Fig. 5f). For example, land cover types that were ultra-peripheral for mammals were module hubs for birds.

Discussion

The challenge of objectively identifying meaningful limits of biological systems has become a major problem in applied ecology [56–59]. The core of this issue is the determination of the scale that best represents the process that shapes multiple species assemblages [5, 35, 51]. Priority strategies for conservation should preserve processes that support biodiversity. Our modularity-based approach provides objective criteria for identifying management units and ranks land cover types on the basis of their topological role from a metacommunity perspective [16].

There is no magical approach to defining BMUs and ours is no exception. However, our method provides three main relevant contributions for management. First, it highlights the potential connectivity of land cover types that are considered targets for management policies. For example, natural forests, tree plantations, dunes and urban areas are typically considered independently (e.g.[60–63]). However, a network of species and their use of these different land cover types suggests it is more appropriate to consider the network as the management unit. Drivers of system change in one land cover type could indirectly affect other land cover type through for example changes in species composition, thus implying that should not be managed in isolation [64]. This indirect effect identified from modularity analysis would not be evident from alternative approaches. Second, our method ranks land cover types from the perspective of their role in connecting the management units, their role within the entire system (e.g., modules and system hubs), or their role as peripheral habitats. These rankings are based on a metacommunity

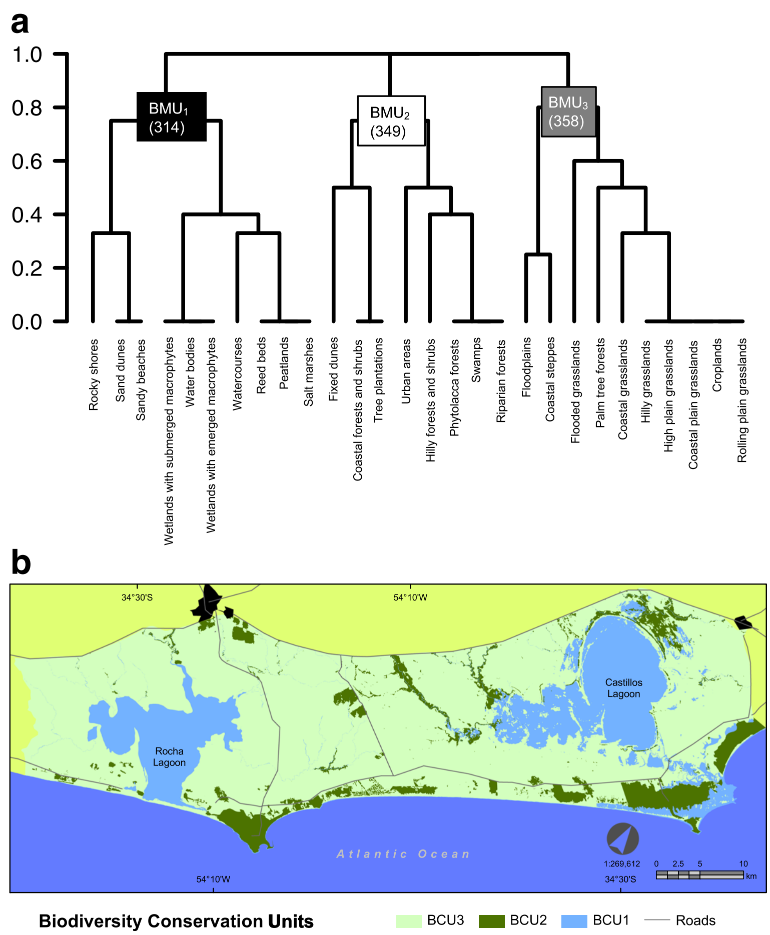


Fig. 4 Biodiversity management units (BMUs) displayed in a dendrogram (**a**) and on a map (**b**). In (**a**), the number in parenthesis corresponds to the number of species in each BMU

perspective that is not normally considered when polices are guided only from local information [16–18]. However, in spite that different land cover types could be merged in a single management unit, they represent an internal heterogeneity of the management unit that should also be preserved. Whereas the focus here was to identify management units and to rank their land cover types, the same analysis could be performed from a species perspective. Third, our method improves our understanding of the spatial structure of the system. Prior to the aggregation of land cover types into BMUs, they had a very patchy and fragmented distribution (Fig. 2a). However, the suggested BMUs included a continuous grasslands system and two fragmented units, aquatic and forested land cover types, with markedly different distributions than the former land cover types (Fig. 4). It should be highlighted that urban areas in the study system were small towns, villages and tourist areas with low human occupancy for most of the year.

The three BMUs we detected using a modularity-based approach did not consist of predetermined taxonomic or ecosystem groups, but were instead defined by their interrelationships within the species-land cover types network. Specifically, the present analysis is focused on land cover types and its potential aggregation on single management units. This is the information that we have for our study system, but further, this is the kind of information generally available for classifying land cover types on conservation units. When additional information is available the analysis could be refined. For example, a spatial explicit consideration of land cover patches could be used to identify the role of particular patches for the conservation of some taxa. However, it should be noted that this requires information about species composition on each patch along the whole study area. This information is not available for any region in Uruguay and in most areas to conserve elsewhere. In a biogeographical context, modularity performs well in identifying groups of interrelated species along environmental gradients [40–44]. In this line, the use of modularity for identifying spatial management units represents a natural extension of current uses of this methodology.

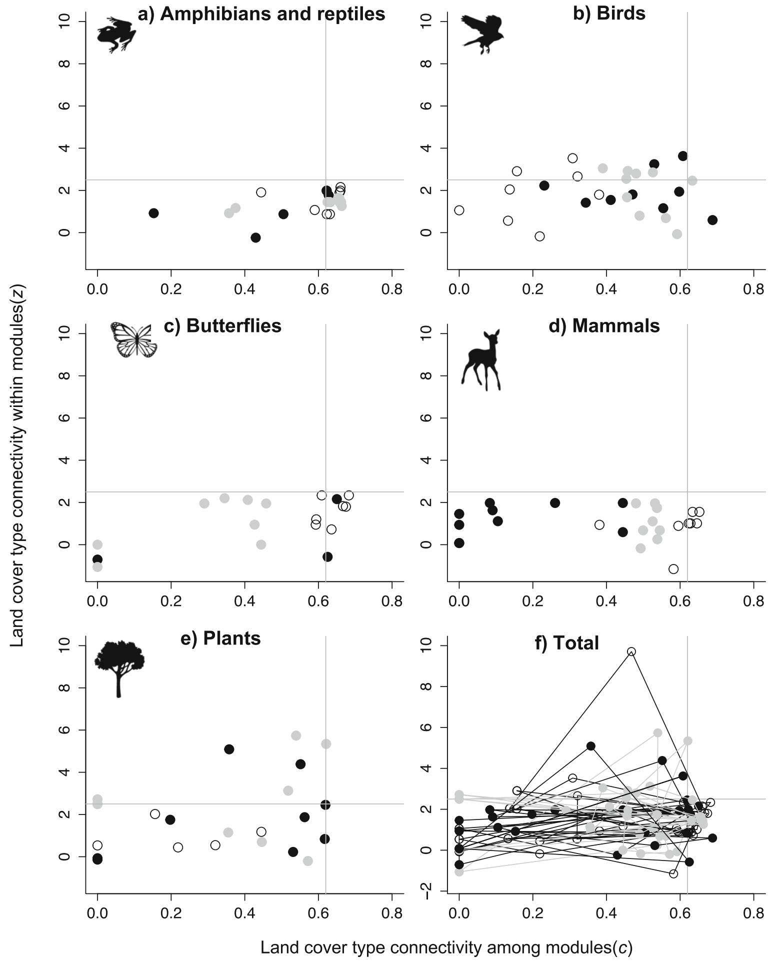


Fig. 5 Topological roles of habitats for different taxa within the same landscape for amphibians and reptiles (**a**), birds (**b**), butterflies (**c**), mammals (**d**), plants (**e**) and total species (**f**). The color of circles in all panels corresponds to the three biodiversity management units identified in this study: aquatic (black), forest (white) and grassland (gray) cover types (see Fig. 4). In (f), each polygon represents the possible role that the same land cover type might play depending on the taxon being considered

An important contribution of the proposed method is the identification of topological roles [38, 49], which suggests the importance of each land cover type for the movement of individuals through the landscape [32, 41, 65, 66]. Following previous approaches, we used occurrence-based ecological network as proxies of the potential flow of individual among local communities [29, 31]. The presence of the same species among different land cover types could result from rare migration events or the continuous flow of individuals. However, in spite of this variation, the existence of a similar species composition is a confident cue about a functional connection among land cover types [29, 31]. Therefore, the conservation of the topological roles might help preserve the mechanisms that drive biodiversity in the system at different scales [10, 39]. In our study, butterflies, amphibians, reptiles and mammals showed congruent patterns of topological roles for land cover types (Fig. 5). For all these taxa, the BMUs associated with "forest" habitats operated as connectors. For butterflies and mammals, BMUs composed of "grasslands" and "wetlands" had more peripheral roles. Interestingly, birds and plants showed the opposite trend of "forests" with peripheral roles, and used grasslands and wetlands as connectors. The three BMUs contained land cover types that were hubs for birds but connectors for plants. Therefore, at least for our study system, the role of a land cover type is strongly contingent on the studied taxa. Moreover, the existence of different roles among land cover types of the same management unit indicates that they are not interchangeable in conservation strategies. These results demonstrate that a cross-taxon approach in the identification of BMUs [18, 67] should be carried out with careful attention. Finally, more or less taxonomic subdivisions may be explored depending on the data in hand and the main question under consideration. With this approach, both robustness and contingency in the topological role of habitat may be used to identified land units that are or not interchangeable in conservation strategies among taxa.

A major advance in metacommunity theory has been the identification of four widely accepted metacommunity mechanisms [51]: species sorting, patch dynamics, mass effect and neutral assembly [68]. The relative importance of these four mechanisms can change with the flow of individuals through local communities [7, 51]. The topological role of land cover types could be related to these mechanisms. Peripheral cover types may enhance biodiversity through species sorting mechanisms, in which species composition changes among habitats in response to local conditions [11]. Similarly, more frequent extinctions of populations using peripheral cover types may lead to enhanced diversity through "patch dynamics," in which the local extinction of stronger competitors enhances their coexistence with species that have high dispersal rates [11, 51]. Alternatively, cover types identified as modules or network hubs are expected to have high species diversity and may operate as sources of propagules for the colonization of peripheral cover types. Finally, connector cover types are expected to operate as stepping-stones for the movement of organisms through the landscape [41]. This movement is crucial to recolonize empty patches and to avoid local extinction from a mass effect [11]. Thus, the preservation of the different topological roles may be a factor to take into account for planning management strategies based on sound ecological processes.

Conclusion

The proposed method represents a general approach towards advancing our understanding about the structure of biodiversity patterns, the interaction of that structure within the landscape and the potential topological roles of single patch habitats [41]. The identification of management units is a primary aim of land-use planning and the conservation of species and ecosystem function [2, 69]. Thus, we anticipate that the method developed here and its possible variants provide an objective, reliable and simple tool for generating such units. Furthermore, this approach complements existing methods and introduces novel quantitative uses of available information and criteria for different types of habitats or land covers classification. Consequently, this approach could be applied to any system, scale or group of taxa.

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Availability of data and materials

We archive our data in the Research Gate database (https://www.researchgate.net/profile/Alvaro_Soutullo).

Authors' contributions

AIB and MA conceived the ideas, analyzed the data, and lead the writing. AS and AC introduced the problem and the study system, and provided the data. All authors contributed comments to the draft versions of the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable.

Competing interests

The authors declare that no conflict of interest exists in the submission of this manuscript, and manuscript is approved by all authors for publication. I declare, on behalf of my co-authors, that the work described is original research that has not, in whole or in part, been previously published and is not under consideration for publication elsewhere. All listed authors have approved the manuscript.

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