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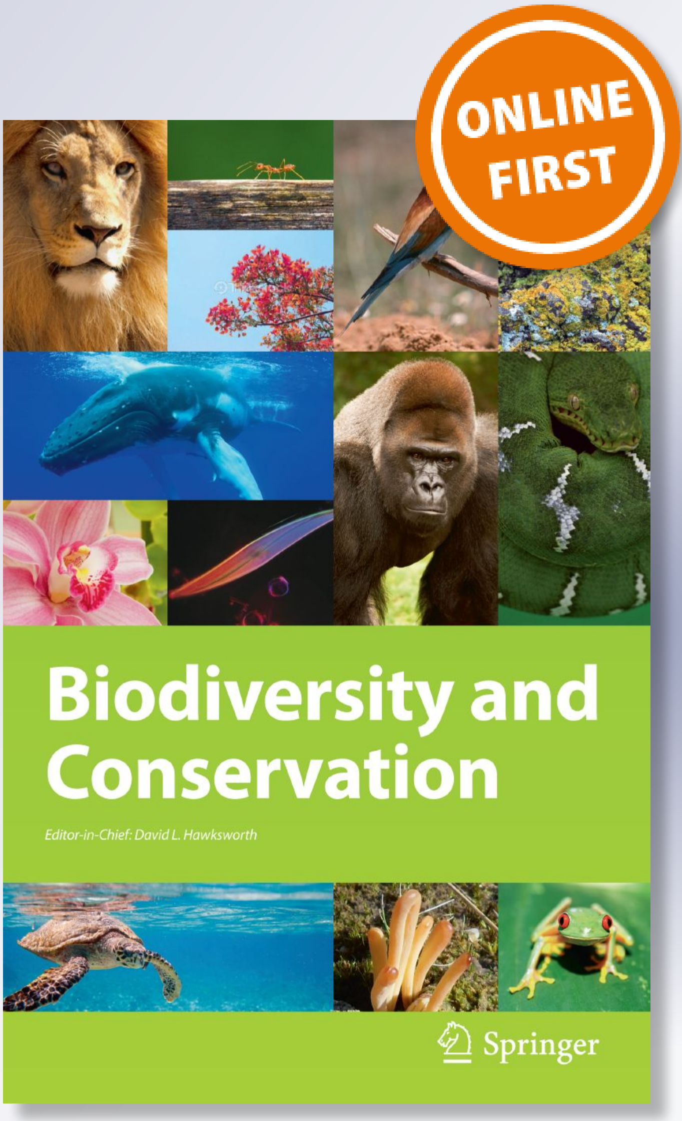

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ORIGINAL PAPER

Landscape connectivity and the role of small habitat patches as stepping stones: an assessment of the grassland biome in South America

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Abstract Connectivity losses lead to a reduction of the amount of habitat resources that can be reached and used by species, and hence to a decline in the ranges and abundance of multiple taxa. Despite the recognized important role of small habitat patches for many species inhabiting fragmented landscapes, their potential contribution as stepping stones for maintaining overall landscape connectivity has received less attention. Using connectivity metrics based on a graph-theoretic approach we (i) quantified the connectivity of grassland patches in a sector of the Pampa region in Argentina, using a range of dispersal distances (from 100 to 10,000 m) representative of the scale of dispersal of different species; (ii) identified the most relevant patches for maintaining overall connectivity; and (iii) studied the importance of small patches (defined for different area thresholds of 5, 20, and 50 ha) as connectivity providers in the landscape. Although grassland patches were in general poorly connected at all distances, some of them were critical for overall connectivity and were found to play different crucial roles in the patch network. The location of small patches in the grassland network allowed them to function as stepping stones, yielding significant connectivity gains for species that move large distances (>5000 m) for

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the three area thresholds considered. Thus, under the spatial pattern of the studied landscape, species that move long distances would benefit from stepping stones, while less mobile organisms would benefit from, and mostly rely on the largest patches. We recommend that future management activities should (i) aim at preserving the grassland patches with the highest potential as stepping stones to promote landscape-level connectivity; and (ii) pay more attention to the conservation of key small patches, particularly given that usually they are those more vulnerable to land clearing for agriculture.

Keywords Threatened ecosystems · Conservation planning · Pampa region · Habitat patch networks

Introduction

The increasing changes in rural landscapes, mainly associated with the expansion of agriculture, have prompted a rapid development of tools to measure and evaluate the fragmentation of natural habitats and its effect on plant and animal populations (Forman and Godron 1986; Forman 1995; Turner et al. 2001). In particular, landscape connectivity, defined as the degree to which the landscape facilitates or impedes the movement of organisms and matter among resource patches (Taylor et al. 1993; Crooks and Sanjayan 2006), is crucial for maintaining landscape health and ecosystem functioning (Forman 1995; Fahrig 2003). Connectivity is critical for biodiversity conservation, since it determines the possibility of exchanging genes and individuals among plant and animal populations. The lack of connectivity can translate into declines in species richness and abundance, loss of genetic diversity, and inbreeding depression, all of which may ultimately hamper metapopulation functioning and species persistence in fragmented landscapes (Levins 1969; Hanski 1999; Burel and Baudry 2005; Baguette et al. 2013). Connectivity depends on the movement abilities of the organism under consideration, on the spatial distribution of suitable habitat, and on the permeability of the landscape matrix through which movement may need to happen (Tischendorf and Fahrig 2000; Rey Benayas et al. 2008; Manning et al. 2009). Graph-theoretic approaches are among the most widely and advocated methods for analyzing landscape connectivity (Pascual-Hortal and Saura 2006; Urban et al. 2009; Galpern et al. 2011). Their relative simplicity and considerable flexibility offer much to land practitioners, such as the opportunity to make decisions based on which patches are most critical to uphold landscape connectivity, allowing the scope and effectiveness of resource management to be increased (Urban et al. 2009; Correa et al. 2014).

In fragmented landscapes, conservation efforts have typically focused on the preservation of remaining large habitat patches that are intact and well connected (Fischer et al. 2009). Large patches can accumulate more species (MacArthur and Wilson 1967), conserve species with large population size (Akçakaya et al. 2007), and provide high quality interior habitat (Laurance 2000). Comparatively, small habitat patches have usually received much less attention in conservation initiatives, even when they may play a significant role in conserving remaining vegetation (e.g. endemic species), being a valuable complement to large patches (Fischer and Lindenmayer 2002), and in maintaining connectivity in the landscapes (Baum et al. 2004; Uezu et al. 2008; Tulloch et al. 2015). According to Fischer and Lindenmayer (2002), it is crucial to examine the value of small habitat patches so they are not removed simply because they are small, and hence implicitly assumed to be of little value. Authors suggest that due to their lower costs, small scale restoration programs using small patches are more likely to be implemented in the short term than large scale projects. This is an important issue since small patches dominate in most current rural landscapes, and they are often the most vulnerable to land clearing (Stickler et al. 2013). In terms of habitat connectivity, small patches can make different contributions and be beneficial in different degrees depending on landscape spatial patterns and on species dispersal abilities. For example, they can make a weak contribution to habitat connectivity and availability if they are isolated or peripheral, they can have a neutral effect in terms of their benefits for connectivity (not larger than the area of habitat they provide), or they can play a more significant role by acting as a key part of a discontinuous corridor or as a stepping stone between other, eventually larger habitat patches (Saura et al. 2011). In addition, small patches can contribute to connect large and distant reserves/patches, making the system more functional and effective for biodiversity conservation than when only large but very isolated reserves/patches exist (SLOSS debate: Single Large Or Several Small patches, Rösch et al. 2015). Saura et al. (2014) demonstrated through a generalized network model of habitat connectivity that stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks, reducing isolation of the largest habitats and hence contributing to species persistence across wide spatial and temporal scales.

The Tandilia System in the Southern Pampa region of Argentina forms an arc of discontinuous elevation of approximately 1,400,000 ha in the Pampean plain (Fig. 1). It is characterized by ancient (lower Paleozoic) eroded hills (sierras) and small rocky outcrops (cerrilladas) surrounding by an undulating relief with deep soils, where agricultural activity takes place (Herrera et al. 2016). Native grasslands that originally dominated the region, together with native shrublands, still persist in sierras and cerrilladas because of steep

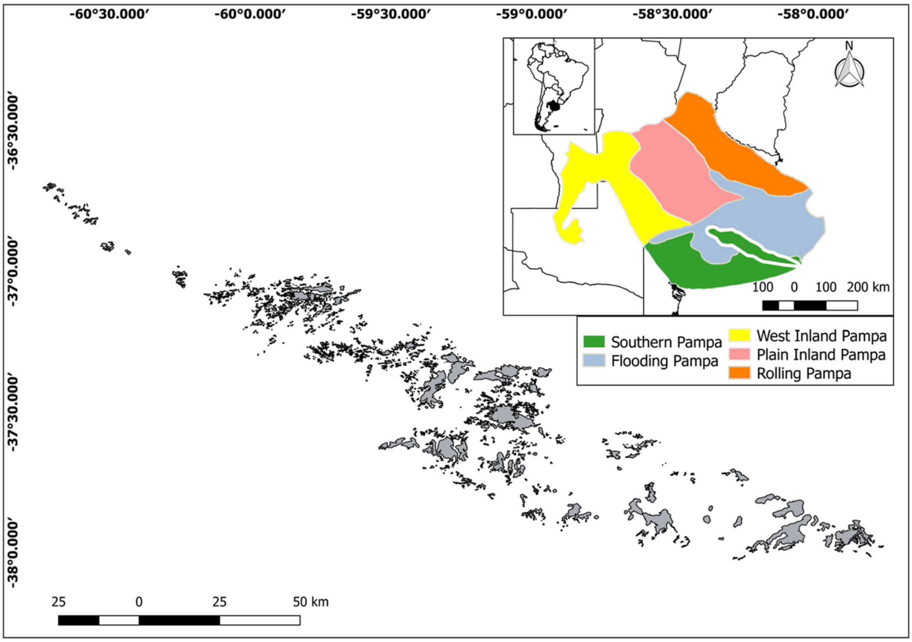


Fig. 1 Distribution of grassland patches in the study area. Figure on the *upper right* shows the Pampa subregions in Argentina; *white* polygon in Southern Pampa shows Tandilia System. (Color figure online)

slopes, shallow soils, and exposed bedrock, which do not allow tillage to be used (Herrera and Laterra 2011). The sierras and cerrilladas (hereafter "grassland patches") range in area from tens to thousands of hectares and differ in their distance to the closest neighbor patch from a few hundred meters to several kilometers. Grassland patches represent important hotspots of biodiversity (Herrera and Laterra 2011) especially of endemic species (Gilarranz et al. 2015; Kristensen et al. 2014), and a source of ecosystem services (Barral and Maceira 2012). Thus, we can consider grassland patches as islands of biodiversity immersed in one of the most intensively used agricultural matrices in South America (Sabatino et al. 2010). For this reason, they are under the increased pressure of different threats (Barral and Maceira 2012), the impacts of which may depend on patch type or size. While smaller patches are usually those most exposed to herbicides used in the agricultural matrix, and hence subject to land clearing, larger patches are usually overgrazed or used for mining or farming on their flat top, where the soils are deep enough for cropping. In addition, a recent study in a sector of the Tandilia System demonstrated that although grassland patches were poorly connected for species with different dispersal distances, some of them were found to be critical for global connectivity (Herrera et al. 2016). These authors evidenced the urgent need of introducing grassland patches conservation and/or restoration efforts, with a particular emphasis on grassland connectivity, into public and private environmental agendas, in agreement with other studies (Logsdon and Chaubey 2013).

For these reasons, it is highly necessary to analyze the connectivity of the grassland in the entire Tandilia System so as to determine and manage the effects of the increased habitat fragmentation in these ecosystems. For this purpose, we here quantified connectivity of grassland patches using graph theoretic approaches. In particular, we (i) investigated overall landscape connectivity; (ii) identified the most relevant patches for maintaining overall connectivity; and (iii) studied the importance of small area size patches for upholding connectivity in the landscape. We intend to contribute with information that will help prioritize conservation and restoration efforts in these increasingly human-dominated landscapes.

Materials and methods

Study area

The study area is located in the Southern Pampa region of Argentina within the Tandilia System (Fig. 1). Approximately 87% of the study area is cultivated by annual crops such as soybean, sunflower, wheat, corn and potato, and, to a lesser extent, perennial pastures (Unpublished data). Vegetation of grassland patches consists of grasslands dominated by species of the genera *Nasella*, *Piptochaetium*, *Bromus*, *Aristida*, *Briza*, *Setaria*, among many others; pajonales (tall grasses) of *Paspalum quadrifarium*; and shrublands of *Eupatorium* spp., *Colletia* spp., and *Bacharis* spp., among others (Frangi 1975; Soriano et al. 1991; Valicenti et al. 2010). The climate of the region is sub-humid–humid mesothermal with no or small water deficiency, with a noticeable seasonal variation in temperature, and a short cold period. Mean annual precipitation is 800 mm (Burgos and Vidal 1951). Soils are typical Argiudoll and Hapludoll developed from loessic deposits over cuarcitic rocks (INTA 1991).

Defining grassland patches

Grassland patches in the study area were delineated from Google Earth images. By grassland patch we mean any area of sierras and cerrilladas that has not been transformed into land for agriculture, plantation forestry or mining by 2015 due to the presence of steep slopes, shallow soils, and exposed bedrock. We made sure that the grassland patches had not been previously cultivated checking images available from 2001 to 2003. The resulting grassland patch layer contained 1786 patches that range in area from 1 ha to 7000 ha, giving a total grassland area of 107,778 ha (Fig. 1).

Quantifying overall landscape connectivity

A graph is a model in which the landscape is represented by a network of spatially explicit *nodes* corresponding to habitat patches (here grassland patches), connected by *links* that capture the capability of focal species to disperse between two patches (Urban and Keitt 2001). We used the Probability Connectivity index (PC), which is based on the habitat availability concept, interpatch dispersal probabilities (probabilistic connection model), and spatial graphs (Saura and Pascual-Hortal 2007). The PC index is defined as the probability that two organisms randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of n habitat patches and the connections (p_{ij}) among them, expressed as follows:

$$PC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p_{ij}^{*}}{A_L^2}$$

where a_i and a_j are the attributes of the habitat patches i and j (here habitat patch area), A_L is the maximum landscape attribute (here the total area of the study region, comprising both habitat and non-habitat patches), and p_{ij}* is the maximum product probability of all possible paths between patches i and j. p_{ij}* accounts for the probabilities of direct dispersal between nodes (p_{ij}) (i.e. the probability that an organism is able to disperse a distance equal to or larger than the distance between these nodes, without using any other intermediate node) and for the role of intermediate stepping stones along the dispersal process that may increase the likelihood of dispersal between i and j ($p_{ij}* \geq p_{ij}$). The p_{ij} values were calculated from a negative exponential function of the Euclidean distance between nodes (Bunn et al. 2000; Urban and Keitt 2001) as follows:

$$p_{ij} = e^{-k \cdot d_{ij}}$$

where d_{ij} is the distance between patches i and j, and k is a constant defined according to the species dispersal distances. We calculated d_{ij} as edge-to-edge Euclidian distances between patches using QGIS 2.4 and the Conefor Inputs plugin (http://www.conefor.org/gisextensions.html). In this case k was set in such a way that $p_{ij} = 0.5$ when the distance between patches was equal to the species median dispersal distance examined. We considered six hypothetical values of the species median dispersal distance: 100, 500, 1000, 2000, 5000, and 10,000 m. These distances cover a wide range of responses of different species of plants and animals to the landscape pattern (Bowman et al. 2002; Smith and Green 2005; Thomson et al. 2011; Stevens et al. 2013), and were used because landscape connectivity depends on specific species dispersal abilities, so that the same landscape has different levels of connectivity for different species (Crooks and Sanjayan 2006; Fourie et al. 2015).

The equivalent connected area (ECA) is defined as the size of a single habitat patch (maximally connected) that would provide the same PC value (same habitat reachability) as the actual habitat pattern in the landscape (Saura et al. 2011; Saura and de la Fuente 2017). ECA is calculated as the square root of the numerator of the PC index. ECA can never be smaller than the size of the largest patch in the landscape and will never be above the total habitat area in the landscape. Here we summarized the relative level of grassland connectivity in the study area as the ratio between ECA and the total area covered by grassland patches (hereafter called normalized ECA). Normalized ECA was calculated for the six median dispersal distances. We also used the number of components (NC) as another measure of overall landscape connectivity. A component is a group of connected nodes. This means that an organism inhabiting any node within the component can potentially move or disperse to any other node in the same component, while by definition two patches are isolated from each other if they belong to different components. A more connected habitat network consists of one big component in which all patches are connected (Saura and Pascual-Hortal 2007). The calculation of NC relies on a binary connection model in which each pair of patches is either connected or not connected through a link; unlike in PC or ECA, different probabilities in the links are not considered when identifying the components of a graph. Therefore, for NC we determined which pairs of nodes had a link by using a set of threshold distances with the same values as those specified above for the median dispersal distances.

Importance of individual grassland patches for overall connectivity

In order to evaluate the contribution of individual grasslands to the maintenance of overall landscape connectivity, each of the 1786 patches was systematically removed from the landscape (one at a time), and the impact of their loss was evaluated through the following equation:

$$dPC(\%) = 100 \times \frac{PC - PC_{\text{remove}}}{PC}$$

where PC is the index value when all nodes are present in the landscape, and PC_{remove} is the index value after the removal of a given habitat patch (Saura and Pascual-Hortal 2007; Saura and de la Fuente 2017). Thus, dPC values represent the percentage of connectivity decrease that would result from the loss of a given patch from the landscape.

The patch-level dPC values can be partitioned into three distinct fractions (intra, flux, and connector) considering the different ways in which a certain landscape element k (here a grassland patch) can contribute to habitat connectivity and availability in the landscape (Saura and Rubio 2010):

$$dPC_k = dPCintra_k + dPCflux_k + dPCconnector_k$$

The intra fraction is the contribution of patch k in terms of intrapatch connectivity (amount of grassland habitat resources that exist within the patch). It is independent of how patch k may be connected to other patches. This fraction is equivalent to the variation in a family of fragmentation indices that take the squared patch area as the basis for their computation, such as the area-weighted mean patch size (Li and Archer 1997). The flux fraction estimates the potential amount of dispersal flux expected to depart from or arrive at a particular habitat patch, i.e. it measures how well connected a particular habitat patch is to the rest of the habitat areas in the landscape. The connector fraction evaluates how important *k* is in maintaining the rest of the patches (different from *k*) connected to each other, i.e. how much the patch contributes to connectivity by functioning as a stepping stone in between other patches. For more details on these fractions see Saura and Rubio (2010).

The dPC index and its fractions were calculated for the six selected median dispersal distances, as well as for several larger distances (up to 100,000 km) outside the expected range of dispersal of species with different dispersal abilities. This was performed in order to illustrate the pattern of variation of dPC fractions in a broader range of hypothetical conditions.

Importance of small patches in maintaining landscape connectivity

ECA was used to determine to what extent small patches contribute to the overall landscape connectivity. When there is a change in the landscape such as an increase or a decrease in the amount of habitat, most likely involving also a variation in the spatial arrangement of habitat in the landscape, we can calculate the relative change in the amount of reachable habitat (ECA). This is given by dECA = (ECAfinal − ECAinitial)/ECAinitial. The relative change in the total amount (area) of habitat in the landscape (A) can also be similarly calculated, given by dA = (Afinal − Ainitial)/Ainitial (with initial and final referring both for dECA and dA to the values of these variables before and after the landscape change). Both magnitudes (dECA and dA) can be directly compared to assess the degree to which a given habitat change is beneficial or detrimental to ecological connectivity, as given by the relative connectivity improvement or loss compared to the change in habitat amount (Saura et al. 2011, 2014). For example, a net decrease in the total amount of habitat ($dA < 0$) may translate into a higher, lower, or equal loss of connectivity as measured by dECA, as given by the cases in which $dECA < dA < 0$ (higher loss in the amount of reachable habitat than in the total habitat area), $dA < dECA < 0$ (higher loss in the total habitat area than in the amount of reachable habitat), and $dECA = dA < 0$ (both magnitudes decrease at the same rate, corresponding to a purely proportional effect of habitat loss). In order to analyze the impact of the loss of small patches, we calculated a series of dECA by comparing a landscape in which all the existing patches (large and small) remained (ECAinitial) with three landscapes in which the grassland patches smaller than 5, 20, and 50 ha were removed (ECAfinal). The dECA calculation was performed for the six median dispersal distances used in this study.

All the connectivity indices considered in this study (PC, dPC, and its fractions, NC, ECA, and dECA) were calculated using Conefor 2.6 (Saura and Torné 2009), available at www.conefor.org.

Results

Quantifying overall connectivity

The graph-based analyses showed that overall landscape connectivity in terms of normalized ECA was relatively low, ranging from 16.41 to 52.61% for the different dispersal distances (Table 1). The high number of components (NC), many of them with only one patch, also indicated a low connectivity in the study system for most of the threshold dispersal distances considered. NC decreased from 1144 to 1 as the threshold dispersal

Table 1 Overall connectivity indices for the study area and for the six selected dispersal distances

	Normalized ECA (%)	NC	Proportion of patch area in the largest component (%)	Percentage of patches in the main component (%)	Number of components with only one patch	Highest dPC (%) for a single patch
100	16.41	1144	7.26	0.62	1537	20.3
500	19.92	277	10.41	8.12	105	18.14
1000	23.26	111	18.45	11.36	41	18.20
2000	28.96	41	23.21	17.19	8	21.93
5000	40.73	12	66.36	91.27	2	24.60
10,000	52.61	1	100	100	0	22.58

Normalized ECA equivalent connected area/total area covered by grassland patches, *NC* number of components, *dPC* delta probability of connectivity

distance increased from 100 to 10,000 m (Table 1). The area size of the largest component (sum of the areas of all the grassland patches it contained) largely increased with dispersal distance (Table 1), but only for very large dispersal distances (5000 and 10,000 m) most of the habitat area was found within the largest component.

Importance of individual grassland patches for overall connectivity

The highest contribution of an individual grassland patch for the maintenance of overall landscape connectivity, as evaluated by dPC at the different dispersal distances, varied from 18.14 to 24.60% (Table 1). These dPC values represent the percentage of connectivity decrease that would result from the loss of a given patch from the landscape. More than 95% of the patches had dPC values below 1%, and very few patches had high importance values for connectivity at all distances (data not shown). The dPC decomposition suggests that grassland patches contribute to connectivity mainly depending on dPCintra, followed by dPCflux at shorter distances; and on dPCflux followed by dPCconnector at larger dispersal distances (Fig. 2). The dPCconnector has its greatest value at about 5000 m dispersal distance. As shown in Fig. 3 for 500 m dispersal distance, the main component includes the grassland patch with the largest dPC value, which is also true for the other, shorter and larger, dispersal distances (data not shown).

Importance of small patches in maintaining connectivity

In the hypothetical case that smaller patches (5, 20, and 50 ha) were removed from the landscape, loss in total habitat area would be larger than the loss in connectivity ($dA < dECA < 0$) at lower dispersal distances (100–1000 m) (Fig. 4). For dispersal distance of nearly 2000 m, the loss in connectivity was rather similar to the loss in area of grassland patches ($dA = dECA < 0$). For larger dispersal distance (>5000 m), the decrease in connectivity was larger than the decrease in the area of grassland patches ($dECA < dA < 0$) (Fig. 4). This means that for species dispersing larger distances across these landscapes, small patches can play a substantial role as connectors or stepping stones.

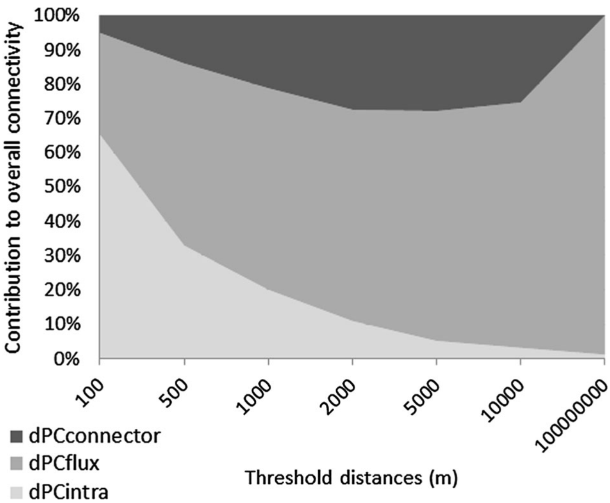


Fig. 2 Relative contribution of each dPC fraction to the total importance of grassland patches for connectivity in the landscape. To illustrate the broader pattern, we used median dispersal distances larger than 10,000 m

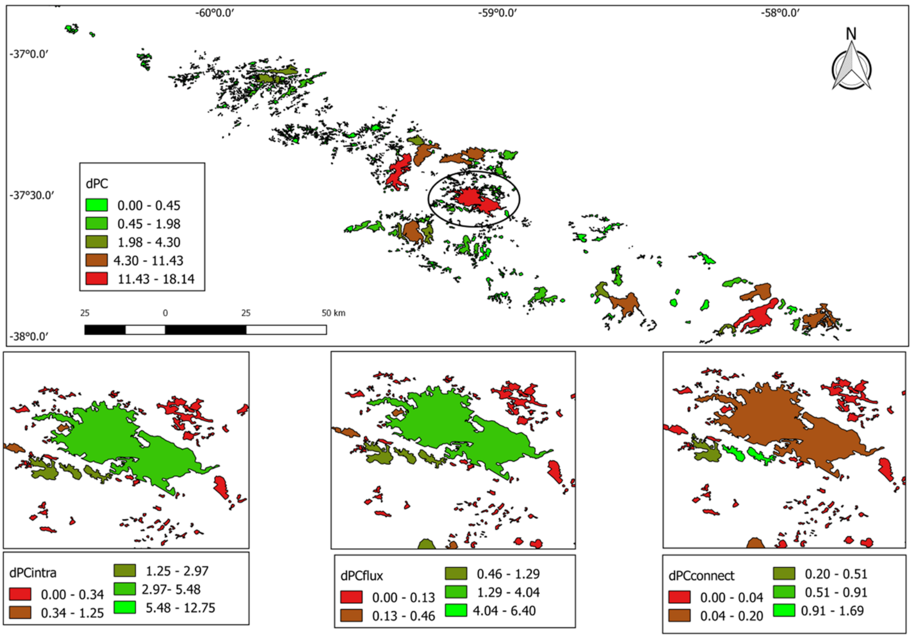
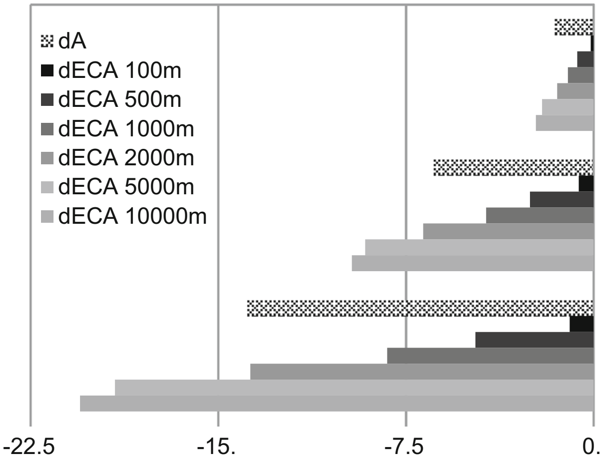


Fig. 3 Figure above shows the contribution of individual grassland patches for the maintenance of overall landscape connectivity at dispersal distance of 500 m as measured by the delta Probability of Connectivity (dPC). The *circle* indicates the main component. Figures below show the main component with the contribution values of individual grassland patches for the maintenance of overall landscape connectivity in terms of the three dPC fractions (intra, flux and connector). In all the figures *green colors* represent grassland patches more important for the maintenance of overall connectivity. (Color figure online)

Fig. 4 Relative (%) changes of habitat area (dA) and connectivity (dECA) given by the effect of removing grassland patches smaller than 5, 20 and 50 ha in the studied landscape. Calculations were performed for six median dispersal distances



Discussion

In this study, we showed evidence of the low overall connectivity of grassland patches in the Tandilia System, identified the most critical grassland patches for the maintenance of landscape connectivity, and highlighted the importance of small patches for species that disperse long distances. This findings significantly advance our understanding of the functioning of, and of the limitations in, the grassland habitat networks in this area, given that previous research only explored the impact of landscape connectivity on different groups of organisms for different sectors of the Tandilia System (Sabatino et al. 2010; Herrera and Laterra 2011; Aizen et al. 2016).

Grassland patches in the study area were poorly connected, especially at shorter dispersal distances. Compared with the results of this study, other grasslands of the world have been reported to be better connected, as is the case of Mpumalanga (South Africa), where 93.6% of the total grassland patch area (27.6% of the number of patches) was connected in a single component for a dispersal distance of 50 m (Fourie et al. 2015). It is worthy to note, however, that of the 14 world's biomes assessed by Saura et al. (2017), the biome of temperate grasslands, savannas and shrublands (in which our study area is located) was found to be by far the one with the lowest connectivity of protected areas (Saura et al. 2017). Here, we did not consider protected areas in this biome, but a specific set of grassland patches regardless of their protection status. There are, however, some inevitable links between the lack of formal protection (and the lack of connectivity between protected sites) and increased rates of habitat loss and fragmentation (Joppa and Pfaff 2011; Laurance et al. 2012; Geldmann et al. 2013). This would lead to poorer habitat connectivity levels, such as those we found in our study, ultimately propagating into potentially increased rates of biodiversity loss. In this context, Newbold et al. (2016) showed that this biome (temperate grasslands, savannas and shrublands) has the lowest biodiversity integrity of all world's biomes, which further calls for increased efforts in protecting and ensuring sufficient connectivity levels for the natural grassland habitat patches that still remain today in the rapidly changing landscapes of this biome.

Individual patches have different roles in the landscape as evaluated by dPC fractions (Fig. 3). For example, grassland patches with high dPCintra also have higher values of dPCflux. This means that large patches (with large dPCintra) can serve as sites for shelter, foraging and breeding, and at the same time produce (or receive) dispersal fluxes to (or from) other patches (large dPCflux) (Saura and Rubio 2010). In addition, a given patch can function as a stepping stone, even when it is not the final destination of the dispersal fluxes, facilitating dispersal between other patches. Thus, within the same landscape and for the same focal species, different patches may play different roles depending on their topological position and intrinsic habitat characteristics (Saura and Rubio 2010). The relative contribution of patches in terms of intra patch connectivity (as evaluated by dPCintra) would be larger for species that are only able to move over short distances (Fig. 2). In our grassland study area, these species could correspond to small mammals such as the emblematic Mulita (*Dasypus hybridus*), or some birds dependent on grasslands such as Perdiz chica (*Nothura maculosa*) (Comparatore et al. 1996). A recent study found that the distribution of entomophilous shrub species in the studied landscape was explained by intra patch connectivity most likely associated with their high dispersal limitation (Herrera et al. 2016). Therefore, for the majority of these short-dispersal species, most of the reachable habitat would be the one that exists within the patches where the individuals are initially found (Saura and Rubio 2010). In this context, maintaining or enhancing the quality of the largest patches is crucial to ensure population persistence. On the other hand, the largest contribution of patches in terms of dPCconnector was found at around 5000 m of dispersal distance (Fig. 2), suggesting that in our study system these patches are more successful as stepping stones and are fundamental to facilitate the movement of the species that can traverse relatively long distances, e.g. some birds such as Pecho amarillo (*Pseudoleistes virescens*), another species that is dependent on grasslands (Comparatore et al. 1996). In other words, as the species can traverse relatively long distances, these patches are able to play a more prominent role as stepping stones promoting movement through the landscape. This is in agreement with the findings by Saura and Rubio (2010), who also reported the highest contribution of dPCconnector fraction at intermediate dispersal distances, and a very low contribution of this fraction for species with poor dispersal abilities. Indeed, when species disperse too little, they can hardly reach any other habitat patch, and hence they have no possibility of accessing and using stepping stones, as these are too far away from their movement range, particularly in highly fragmented landscapes, such as the one here considered. For larger dispersal distances, the species start to be able to access these stepping stone patches and hence to use them as intermediate points for subsequently reaching other habitat patches in a dispersal process that encompasses multiple movement steps through the landscape network.

The location of small patches in the studied grassland network allows them to function as stepping stones with potential benefits for species that move large distances. In fact, these patches play a more prominent role in overall habitat availability than the one that may be expected just from the area they provided (Saura et al. 2011). In agreement with previous discussion, given the low connectivity of the studied landscape, sufficient mobility of species is required for them to benefit from these networks of stepping stones, while species with shorter dispersal distance would profit from and rely more heavily on the few large patches remaining in the landscape. Although it is not the central topic of this work, these results could contribute with the "single large or several small" (SLOSS) debate still in discussion among the biologist community. According to Akçakaya et al. (2007), who analyzed the metapopulation dynamics in the SLOSS context, a mixture of smaller and larger patches could hedge against uncertainty in future impacts, having potential genetic benefits. The authors emphasize that unless the small populations act as sinks, they are likely to send out a greater proportion of emigrants as well as receiving more immigrants, than larger populations. Meanwhile, Rösch et al. (2015) in their revisiting study of the SLOSS debate, showed that both single large and many small fragments are needed to promote landscape-wide biodiversity across taxa. Authors questioned the focus on large fragments only and called for a new diversified habitat fragmentation strategy for biodiversity conservation, which is further reinforced here by our findings on the potential key role of small patches as stepping stones upholding connectivity at wider spatial scales.

Low connectivity found in the studied area could be alleviated, and the potential role of stepping stones could be enhanced, by incorporating elements of the matrix, like different types of land use, successional states and linear landscape elements, such as roadsides. There is interesting evidence of the role of linear elements as connecting elements and of the role of the matrix as potential habitat. For example, Jiménez et al. (2015) found that plantings on roadside acted as selective bird attractors, providing food and perches for frugivorous species. In their grassland connectivity study in South Africa, Fourie et al. (2015) found that the inclusion of abandoned croplands increased the overall connectivity of the landscape. In a sector of our study area, Sáez et al. (2014) investigated the interactive effects of habitat patches at different scales acting as pollinator sources for sunflower and demonstrated that honey bee visitation to crops was strongly affected by proximity to large expanses of natural habitats (sierras). Despite the value of this information, there is a general lack of knowledge for our study system about how the diversity of the matrix and the structure and dynamics of linear elements simultaneously affect spatial landscape structure and organism dispersal, as well as the geographic distribution of ecosystem services and co-evolutionary processes, which should be addressed in further research.

This study identified the most critical grassland patches for the conservation of overall landscape connectivity. This is an important result since not all the habitat patches in a landscape can be protected due to limited conservation resources (Estrada and Bodin 2008). Among conservation efforts, the inclusion of important areas in restoration and/or protected area network would be carried out when some of the municipalities in the region update the land planning policies (Barral and Maceira 2012), ideally leading to better prospects for the connectivity of these grassland ecosystems. The integration of spatial patterns, together with the perception of the landscape by different dispersers, could improve the effectiveness of conservation and land use allocation decisions in terms of the maintenance and enhancement of overall habitat connectivity and availability. However, the main challenge facing public and private environmental agendas is the inclusion of priority areas when most of the land in the study area is private and novel acquisition strategies in the plan-making process are needed (Gerber and Rissman 2012). As suggested by Uezu et al. (2008), stepping stones can be considered an important alternative to corridors to manage fragmented landscapes in order to facilitate the movements of organisms and connect spatially separated populations. Here we recommend that future management activities should aim at preserving the grassland patches with highest dPC-connector values, to promote the connectivity of the landscape with some emphasis in those key small habitat patches that may be in risk from additional land conversion; and at mitigating pressures over large grassland patches in order to maintain habitat quality for different groups of species.

We provided a broad quantification of landscape connectivity over a range of different dispersal distances in one of the most intensively managed areas in the Pampa region in Argentina. The approach under graph-theoretic metrics used in this research demonstrated the low functional connectivity of the study system and made it possible to identify critical areas to be included in conservation planning despite the lack of species-specific dispersal information. The identification of relatively small grassland patches sustaining overall connectivity as stepping stones in the studied area is a significant contribution of this work and should pave the way for prioritization of conservation and restoration efforts in these increasingly human-dominated landscapes.

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