Landscape dynamics and their effect on the functional connectivity of a Mediterranean landscape in Chile

Angela Hernández a,*, Marcelo Miranda a, b, Eduardo C. Arellano a, b, Santiago Saura c, Carlos Ovalle d

a Departamento de Ecosistemas y Medio Ambiente, Pontificia Universidad Católica de Chile, Ave. Vicuña Mackenna 4860, Santiago, Chile
b Center of Applied Ecology & Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile
c E.T.S.I. Montes, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, 28040 Madrid, Spain
d Instituto de Investigaciones Agropecuarias-INIA, Casilla 3, La Cruz, Quillota, Chile

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A B S T R A C T

Land use and cover changes have been identified as a major factor contributing to shape landscape structure and biodiversity patterns, particularly in areas with a long history of human occupation and habitat fragmentation, such as the Mediterranean landscapes. However, the existing studies on landscape change indicators for Mediterranean areas have mostly focused in Europe, while for other Mediterranean zones, and especially for South America, there is a serious lack of knowledge concerning the impact of landscape dynamics on ecological processes. Further research on this topic is urgently needed, given the high biodiversity levels and the rapidly increasing rates of human modification in the Mediterranean landscapes of South America. For this purpose, we investigated the dynamics of a landscape in the semi-arid region of the Mediterranean zone of Chile, and measured the effect of those dynamics on functional connectivity, during a period of about four decades (1975–2011). Landscape connectivity indicators were extracted from a series of Landsat images. The Equivalent Connected Area index (ECA) was used as indicator of connectivity trends, and was evaluated for three representative distances of seed dispersal in the study area (150 m, 500 m and 1000 m). In addition, the patches that most contribute to maintain the present connectivity, and their roles as connectivity providers, were identified through a set of commensurable indicators: betweenness centrality and the fractions (intra, flux connector) of the Integral Index of Connectivity. We found that these indicators were useful to detect and summarize a number of previously unreported trends in these Mediterranean landscapes. First, population growth and economic development were compatible with an increase in functional connectivity for forest habitats, mainly because the abandonment of marginal agricultural lands and their subsequent conversion to espinals (Acacia caven) triggered vegetation succession towards secondary forests. Second, increased forest connectivity was not associated to a decrease in the characteristic heterogeneity of Mediterranean landscapes. Third, many patches of espinal, despite being commonly regarded as of poor conservation value, were crucial to promote connectivity by acting as stepping stones among other patches with higher habitat quality. The approach here presented provides a combined assessment of landscape structure, function and change that should be valuable and applicable to deliver operational indicators in dynamic landscapes in South America and other Mediterranean regions.

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1. Introduction

Land use and cover change (LUCC) has been identified as an important factor determining the structure and functionality of the landscape, especially in regions having a long history of human occupancy (Parcerisas et al., 2012). Socio-economic changes are the main drivers of LUCC and have a strong impact on landscape structural patterns and ecological processes, improving or degrading their capacity to support a variety of species and ecosystem services (Forman, 1995; Stoms et al., 2002; Potschin and Haines-Young, 2006). Recent work has shown the dramatic changes which have taken place during the past few years in South American landscapes (García et al., 2001; Echeverría et al., 2008; Armenteras et al., 2013). In particular, the Mediterranean region of Chile, classified as a biological hotspot due to its high endemism (Myers et al., 2000),

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is being severely affected by LUCC (Aguayo et al., 2009; Schulz et al., 2010).

Habitat fragmentation is one of the main consequences of LUCC, and can result in a loss of connectivity for different species (e.g., Pereira et al., 2011). Connectivity is the degree to which the landscape helps or impedes the movement of organisms and other ecological fluxes between habitat patches (Taylor et al., 1993; Tischendorf and Fahrig, 2000). This definition stresses that connectivity depends not only on the characteristics of the landscape (structural connectivity), but also on the movement abilities of the organism (functional connectivity) (Tischendorf and Fahrig, 2000; Moilanen and Hanski, 2001). Connectivity is considered crucial for the conservation of biodiversity and for mitigating the negative effects of habitat fragmentation and climate change on native biota (Crooks and Sanjayan, 2006). Corridors and stepping stones have been proposed as strategies to foster connectivity and promote the flow of genes and individuals among fragmented populations (Simberloff et al., 1992; Haddad, 2000).

The Mediterranean region furnishes good examples of complex and dynamic landscapes, because the strong human intervention has built a heterogeneous mosaic of agriculture, shrublands and forest patches (Blondel and Aronson, 1999). Research on the ecological consequences of Mediterranean landscape heterogeneity and habitat fragmentation have focused almost exclusively on Europe (Preiss et al., 1997; Bielsa et al., 2005; Geri et al., 2010; Saura et al., 2011a,b), while other Mediterranean zones and especially the Mediterranean Chilean landscape, unique in South America, have received scant attention from researchers, especially considering the high ecological and socioeconomic relevance of these landscapes (Preiss et al., 1997; Rocamora, 1997).

To tackle this lack of knowledge and provide novel insights into the Mediterranean landscape changes in South America, we have evaluated the spatio-temporal dynamics and their effects on functional connectivity in a Mediterranean landscape in the Valparaíso region of Chile during a period of almost four decades (1975–2011). For this purpose, we used a set of recently developed, but so far untested in this continent, indicators of connectivity that can account for both temporal trends (Saura et al., 2011a) and for spatial variability in the contribution of habitat patches to landscape connectivity (Bodin and Saura, 2010; Saura and Rubio, 2010). These indicators were used to identify patches functioning as stepping stones that uphold connectivity between other habitat areas. The temporal trend indicators were extracted from satellite images covering the study area in four different dates along the 36-year period. By combining temporal and spatial indicators of connectivity and LUCC impacts, we were able to integrate the analysis of landscape structure, function and change, which is rarely achieved despite all these three aspects being recognized as fundamental for the analysis of landscape dynamics (Forman and Godron, 1986; Turner, 1989). Our hypothesis was that given the intense LUCC in these Mediterranean landscapes, and the subsequent alteration of their habitats and spatial patterns, connectivity would diminish along time. These changes could therefore have negative impacts on different species of this ecosystem. However, our aim was not to focus on the details of a single specific species, but rather to deliver indicators that could be relevant for a broad spectrum of the forest tree species in these Mediterranean landscapes.

2. Materials and methods

2.1. Study area

The study area is located in the semi-arid Mediterranean zone of Chile, specifically in the rural area of the Catapilco locality (32°34′6.20″S–71°16′31.48″O), Valparaíso Region (Fig. 1). Mediterranean ecosystems are a special type of dry lands, representing less than 5% of the surface of the Earth. However, they hold 20% of the plant species of the world, many of them endemic (Cowling et al., 1996). The Mediterranean landscape of Chile has suffered constant changes, due to the intensive use of the land, mainly for livestock farming and agriculture (Ovalle et al., 2006). The climate is characterized by cold rainy winters and dry hot summers. The average yearly precipitation reaches 548 mm and the average yearly temperature is 15.4°C.

The study area has a surface of approximately 10,000 ha. It shows a vegetation mosaic typical from Mediterranean ecosystems: sclerophyll forests in the mountainous areas, arborescent shrubland on the hill slopes and valleys, with extensive Acacia caven...
espinas, agriculture, livestock farming and urban zones also concentrated in this area.

2.2. Processing and classification of satellite images

A spatio-temporal analysis encompassing 36 years (1975–2011) was carried out to analyze the structural aspect of the landscape. A set of four Landsat satellite images was classified: one MSS image of 1975 and three TM5 images of 1992, 2001 and 2011. All the images were selected from the spring season and in clear sky conditions to allow for adequate comparability. Images were pre-processed by standard methods to minimize errors in the classification process, and were geometrically, atmospherically and topographically corrected (Gautam et al., 2003). As the images had different spatial resolutions (MSS: 80 m and TM5: 30 m), a pixel standardization was applied, all images then having a 30 m spatial resolution, so as to compare ground cover changes quantitatively (Echeverría et al., 2008; Carmona and Nahueltual, 2012).

A supervised classification method was applied, consisting in the selection of representative areas of each cover to obtain their spectral values, using the statistical decision criterion of maximum likelihood, where pixels are assigned to the class with higher probability (Chuvieco, 2002). We used three information sources as references to classify the Landsat images: (1) Aerial photographs of the 1976, 1991 and 2001 years, (2) High resolution images available in Google Earth (http://earth.google.com), and (3) field surveys during 2011 and 2012, to collect control points for those covers showing greater confusion. Additionally, informal interviews were carried out with inhabitants of the different sites, to obtain information about the present and historical LUC.

Nine land cover classes were identified in the classification: (1) Native Forest, (2) Arborescent Shrubland, (3) Dense Espinal, (4) Good Espinal, (5) Very Degraded Espinal, (6) Agriculture, (7) Water, (8) Urban and Barren land and (9) Plantations (Table 1). The different espinal types were determined according to the canopy cover percentage of A. caven (Mol.), following the criterion adopted by Muñoz et al. (2007).

Classification accuracy was evaluated through a confusion matrix between the reference data (approximately 150 verification points on the ground for each image) and the classified data (Chuvieco, 2002). A global accuracy of 93%, 91%, 96% and 79% was obtained for the 1975, 1992, 2001 and 2011 images, respectively. The Kappa Cohen’s coefficient was of 0.91, 0.89, 0.95 and 0.77, respectively for each year. This accuracy is acceptable, taking into account the size of the area analyzed (10,000 ha) (Ellis et al., 2010). The values of lower accuracy occurred in the following classes: Native Forest, Plantations, Arborescent Shrubland and Dense Espinal. Their spectral similarity caused confusion in the classification algorithm (Altamirano and Lara, 2010), which was most evident in the 2011 image because all classes were present in that date. Pre-processing and image classification were carried out using ENVI 4.7 software (Exelis Visual Information Solutions, Boulder, Co.).

The LUC dynamics were evaluated through the changes in the different covers during the 1975–1992, 1992–2001 and 2001–2011 periods. Land cover maps for each year of study were prepared using the data obtained from the classification and ArcMap 10 (ESRI, Redlands, Ca.) software. The analysis of the different periods was carried out using transition matrices on the cover maps, using the IDRISI Selva software (Eastman, 2012). The transition matrices represent the area of the landscape that suffers a transition from class i to class j between two consecutive images (Pontius et al., 2004).

### Table 1

Description of land use and cover types.

<table>
<thead>
<tr>
<th>Class</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native Forest</td>
<td>Advanced succession stage of the sclerophyll forest, with species such as Cryptocarya alba, Peumus boldus, Quillaja saponaria, Lithrea caustica, among others. 80–98% cover.</td>
</tr>
<tr>
<td>Arborescent Shrubland</td>
<td>Intermediate situation between the matorral and the sclerophyll removal Cover by arborescent species such as: Acacia caven, Maytenus boaria, Prosopis chilensis, Trevoa trinervis, Calliandra odorifera and renewables of sclerophyll species. 35–75% woody cover.</td>
</tr>
<tr>
<td>Dense Espinal</td>
<td>Thick A. caven cover in arboreal stage, together with renewals of Quillaja saponaria. 51–80% woody cover</td>
</tr>
<tr>
<td>Good Espinal</td>
<td>Cover showing high density of arbustive A. caven and Trevoa trinervis together with herbaceous cover. 26–50% woody cover</td>
</tr>
<tr>
<td>Very Degraded Espinal</td>
<td>Herbaceous covers with isolated A. caven and Trevoa trinervis shrubs. 0–10% woody cover</td>
</tr>
<tr>
<td>Agriculture</td>
<td>Dry farming and irrigation cultures, vineyards and olive groves</td>
</tr>
<tr>
<td>Urban/Barren land</td>
<td>Urban zones, rocks, barren lake beds, recently cleared lands, roads and highways</td>
</tr>
<tr>
<td>Water</td>
<td>Rivers, lakes and water reservoirs</td>
</tr>
<tr>
<td>Plantations</td>
<td>Ornamental trees and plantations of Pinus radiata and Eucalyptus globulus</td>
</tr>
</tbody>
</table>

2.3. General description of the connectivity indicator analysis

The functional aspect of the landscape was evaluated through a set of recently developed connectivity indicators. The connectivity analysis was carried out in two steps: (1) evaluation of the landscape connectivity change during the 36 years of the study, applying the Equivalent Connected Area (ECA) index (Saura et al., 2011a) calculated as ECA,IIC, i.e. as the square root transformation of the numerator of the Integral Index of Connectivity (IC)) (Pascual-Hortal and Saura, 2006), and (2) Evaluation of the contribution of each habitat patch to the connectivity of the present landscape (2011), applying the three fractions (intra, flux, connector) of the IC index (Saura and Rubio, 2010) and the Betweness Centrality (BC) metric as recently generalized to render it commensurable with IIC and particularly with the connector fraction of that index (Bodin and Saura, 2010). All connectivity indicators were based on graph theory (network analysis) and were calculated using Conefor 2.6 software (Saura and Torné, 2009) available at www.conefor.org. A graph is a set of nodes (representing habitat patches) connected by links; a link between two nodes indicates a functional connection (possibility for movement) between them (Urban et al., 2009). The Native Forest, Arborescent Shrubland, Dense Espinal and Good Espinal covers were considered as habitat, and the remainder of the covers (non habitat) were considered as matrix (Very Degraded Espinal, Urban/Barren land, Agriculture, Water and Plantations). Different dispersal distances (d) were used in the connectivity analysis to cover a range of seed dispersal distances for the forest tree species in the study area, providing indicators that may be relevant to some forest tree species in this ecosyste. This perspective is similar to that adopted, in other study areas and with other objectives, in previous related connectivity studies (Saura et al., 2011b; Bergsten et al., 2013). Due to limited data about seed dispersal in the Chilean Matorral sclerophyll species, we selected three dispersal distances (d = 150 m, d = 500 m and d = 1000 m) based on recent studies summarizing seed dispersal distances under different dispersal syndromes (Thomson et al., 2011) and focusing in the maximum plausible distances given the importance of long-distance dispersal for large-scale...
ecological processes such as species distribution patterns and range shifts (Nathan, 2006).

2.4. Indicators of temporal connectivity trends

We first estimated the habitat availability (reachability) in the landscape using the IIC metric (Pascual-Hortal and Saura, 2006). IIC varies from 0 to 1 and increases as connectivity improves, given by:

\[
IIC = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} \frac{a_i a_j}{A_i}}
\]

Where \(a_i\) is the area of each habitat patch; \(n\) is the number of links on the shortest route (topological distance) between patches \(i\) and \(j\); \(n\) is the total number of habitat patches in the landscape and \(A_i\) is the total landscape area. IIC is sufficiently general to be applied to any landscape, either totally connected or not, and can be used, directly as given by the formula above or with some advantageous variations, to assess both temporal connectivity trends (as described next in this section) and the importance for connectivity of any element or combination of elements of the landscape (as will be described in the next section).

We used the ECA index (Saura et al., 2011a) to evaluate connectivity changes during the 36 years of the study. Differing from IIC, ECA does have area units, allowing to compare directly the changes in habitat connectivity (amount of reachable habitat) with the changes in habitat area. ECA is defined as the area that a hypothetical single continuous habitat patch should have, so that it would provide the same amount of reachable habitat (as measured by the value of IIC) as the set of habitat patches and links in the evaluated landscape (Saura et al., 2011a). ECA is calculated as the square root of the IIC index numerator:

\[
ECA(IIC) = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} \frac{a_i a_j}{1 + n_{ij}}}
\]

ECA was calculated for the four dates, and the relative change (percent) in ECA values (dECA) for the three periods (1975–1992, 1992–2001 and 2001–2011) was compared with the relative variation in habitat area (dA). This comparison between dECA and dA allows to account for the efficiency of the habitat areas being lost or reforested to uphold connectivity among the rest of the patches, and therefore to indicate whether the changes in habitat area translate into amplified or comparatively smaller connectivity variations (Saura et al., 2011a).

2.5. Spatially-explicit indicators of patch-level importance for connectivity

For this analysis the amount of habitat resources in each individual patch was determined considering both the area and the quality of habitat in the patch. To determine the quality of each patch, we employed data about species richness, abundance and arborescent endemism, obtained in the zone by means of vegetation inventories. With those data, we established a quality value in a scale ranging from 0 to 1 depending on the type of cover (Good Espinal = 0.25, Dense Espinal = 0.30, Arborescent Shrubland = 0.39, Native Forest = 0.95).

The decrease in the IIC index that would be caused by the removal of a given habitat patch from the landscape (dIIC) can be used as an indicator of the importance of that patch to sustain connectivity (Pascual-Hortal and Saura, 2006). dIIC can be partitioned in three commensurable fractions: intra, flux and connector (Saura and Rubio, 2010). These fractions indicate the different ways in which a given habitat patch can contribute to habitat connectivity in the landscape. The intra fraction (dIICintra) prioritizes the habitat which is found in a single continuous large patch (intrapatch connectivity). The flux fraction (dIICflux) assesses if the analyzed patch is connected to many other and large habitat patches, therefore making the analyzed patch susceptible of receiving a greater amount of dispersal flux (assuming that the flux increases when the patches are larger and better connected, closer to each other). The connector fraction (dIICconnector) is especially interesting as a connectivity indicator, since it assesses the contribution of a patch to the connectivity among other patches, acting as stepping stone, that is, contributing to maintain functional connectivity among other patches of the landscape (Saura and Rubio, 2010).

Finally, to complement the assessment of the present landscape connectivity, we applied the BC metric corresponding to the IIC index (BCIIC) as presented by Bodin and Saura (2010). BCIIC indicates the degree to which a specific habitat patch \(k\) is found in the paths that need to be followed when moving among all other patches in the landscape. A specific patch with a high BCIIC value will be involved in large-scale dispersal fluxes, coming not only from neighboring patches, but also from patches that might be far away. BCIIC variation takes into account the area and quality of the patches that are connected through a specific patch \(k\), and in this way determine which patches act as stepping stones. The difference between dIICconnector and BCIIC is that the latter metric indicates how much a patch is involved in current dispersal fluxes (in the present landscape), while dIICconnector quantifies how irreplaceable that patch is as a connectivity provider, i.e., how much connectivity between the rest of habitat areas would be lost if that patch was removed from the landscape (Bodin and Saura, 2010).

3. Results and discussion

3.1. Land covers dynamics

Landscapes must be studied integrating their structure, function, and change (Forman and Godron, 1986; Turner, 1989). In this study in a semi-arid region of the Chilean Mediterranean zone, we undertook the study of the landscape integrating these three aspects through the analysis of the spatio-temporal dynamics of the landscape pattern and its effects on functional connectivity.

In our study area, the most prominent changes have occurred in the espinal valleys. Mainly, the area occupied by Very Degraded Espinals largely decreased during the 36-year period, while other forest covers and anthropogenic land uses increased in the same area (Fig. 2 and 3D). Land use intensification was evident by the conversion of Very Degraded Espinal to Agriculture, Urban/Barren Land and Plantation cover classes. Between 1975 and 2001 most of the lost area of Very Degraded Espinal was converted to crops, mainly associated to the rotation between cereal crops and the natural prairies that regenerate after cultivation. Losses of the Very Degraded Espinals from 2001 onwards were largely due to the emergence of Plantation cover in the landscape, although the Agriculture cover also showed a slight increase (Fig. 2) because of the establishment of vineyards and olive groves in the zone.

On the other hand, other forest covers (Good Espinal, Arborescent Shrubland and Dense Espinal) increased their extent by occupying areas formerly covered by Very Degraded Espinal. This was mainly the result of the abandonment of agricultural lands and grazing areas. These changes took place mainly in the espinal valleys from 1992 to 2011, with forests expanding upslope along with the progress of vegetation succession (Fig. 3). The larger losses of Very Degraded Espinal were evident between 1992 and 2001, but at the same time there was a significant increase of the
Arborescent Shrubland and Good Espinal; furthermore in 2011 the Dense Espinal began to appear in the landscape (Fig. 2). Due to this dynamic between forest covers, the decrease of the Very Degraded Espinal is considered, in part, a result of vegetation succession.

These dynamics are mostly due to socioeconomic and environmental factors (Díaz et al., 2011) generated along the whole Mediterranean zone (Aguayo et al., 2009; Schulz et al., 2010).

The increase in antropic land use could be due to an increase of the local demand, as a result of population growth and the open markets policy which began after the economic crisis of Chile at the beginning of the 1970 decade (Schulz et al., 2010). Additionally, the incentives for new crops oriented to exportation, the introduction of new irrigation technologies and also improvements in the highways infrastructure (Valdés and Foster, 2005), have been
a stimulus for companies to establish vineyards and olive groves in the zone. These factors, together with the implementation of new income sources at the family level, such as nurseries and apiculture, have produced an industrial and economic development as well as the growth of the attendant dynamic labor markets. These socio-economic aspects, together with restrictive environmental aspects, such as the inter-annual climate variability, have brought as a consequence, the abandonment of large extensions of agricultural lands and their replacement, mostly by subsistence crops and a few heads of livestock limited to small paddocks. This abandonment of the lands dynamic explains the increase and improvement of the espinals and therefore the increase of some forest covers (Fig. 2).

This use of the land has generated an heterogeneous landscape that is overshadowed in different proportions by the A. caven covers (Muñoz et al., 2007). Therefore, in the central part of the study area where the rotation of grassland/cultivation has been most intense, the espinals are more degraded and the A. caven shrubs present lower cover. As a result, they become the Very Degraded Espinal. By contrast, where the agricultural abandonment has been permanent and the grazing intermittent, the development of a higher cover of A. caven has been possible (Muñoz et al., 2007), causing an expansion of the Good Espinal cover. Finally, in a few areas of the valleys, mainly the more humid zones, where cultivation and livestock have been completely removed, the A. caven cover has become more dense and the establishment of some species of the sclerophyll forest, such as Quillaja Saponaria, has been detected. These conditions have fostered the creation of the Dense Espinal cover (Fig. 3B, C and D). Altamirano and Lara (2010) affirm that the conversion of those lands, mainly into shrubland, suggests they were abandoned after the harvest and their later colonization was done by pioneer species, thus originating these initial succession stages. Additionally, the presence of neighboring woods (forest native patches) facilitates the initial establishment of the species and the ensuing forestry succession (Díaz and Armesto, 2007).

In general, the abandonment of agricultural lands in the study zone, mainly between 1992 and 2001 (Fig. 2), has allowed the improvement of the espinals, leading to the expansion of the Arborescent Shrubland; this is in turn has contributed to the increase of Native Forests. This is reflected over the whole period of the study, where the Native Forest increased at a yearly rate of 2.1% expanding from 617 ha in 1975 to 1307 ha in 2011 (Fig. 2). Several authors have recently reported similar trends of forest increase due to the reduction of cultivation lands in different parts of the world (e.g. Preiss et al., 1997; Bicik et al., 2001; Taillefumier and Piégay, 2003; Díaz et al., 2011; Saura et al., 2011b). However, this is the first time this trend is reported in the Chilean Mediterranean zone.

3.2. Functional connectivity analysis

This analysis provided information that can be helpful to maintain the biological diversity (Taylor et al., 1993; Hannah et al., 2002), taking into account that the methods and indicators employed are sufficiently general to be applied also to other ecosystems with different spatial configurations.

In the first place, we consider it very important to analyze if the new habitat areas that have expanded in the studied landscape along the 36 years of the study were really useful to improve its connectivity. The indicators of landscape configuration and dynamics described above have allowed detecting slight improvements in functional connectivity during the last years. The connectivity results (DECA) indicate landscape changes during the analyzed period have been less beneficial to species with shorter dispersal abilities (d = 150 m), while more mobile species (d = 500 m, d = 1000 m) have experimented comparatively higher increases in connectivity (Fig. 4).

![Fig. 4. Connectivity variation (dECA) compared to the changes in total habitat area (dA) for the different dispersal distances (d = 150 m, d = 500 m and d = 1000 m), for the 1975–1992, 1992–2001 and 2001–2011 periods.](Image)

The only period where we found a greater increase in connectivity (dECA) than in habitat area (dA) for d = 150 m over d = 500 m and d = 1000 m (dECA > dA) was between 1975–1992 (Fig. 4); this is possibly explained as the new habitat areas (Native Forest and Good Espinal) were spatially arranged so that they were able to act as connectivity providers (e.g. stepping stones) among other previously existing habitat patches, particularly for species with short dispersal distances. On the contrary, a loss of connectivity was detected for d = 150 m during the 1992–2001 period and additionally, the dA (dECA < dA > 0) increased. In the same period, an larger increase in habitat area than in connectivity (dA > dECA > 0) was also observed for d = 500 m and d = 1000 m (Fig. 4). This is contrary to what would be at first expected, because it is in this period (1992–2001) that important increases were detected in the habitat areas: Native Forest, Arborescent Shrubland and Good Espinal (Fig. 2). This result can be explained because the habitat areas lost during the previous period (1975–1992), had a more important role as connecting elements than the new habitat zones generated between 1992 and 2001 (Saura et al., 2011b).

The last period (2001–2011) has shown greater dynamism and expansion of the habitat area and its connectivity, with dECA being similar for the three dispersal distances (16.9%, 18.7% and 17.5% respectively for d = 150 m, 500 m and 1000 m), being larger than dA = 13.2% (dECA > dA). These dynamics are mostly attributed to the expansion of the Native Forest and Good Espinal, together with the expansion of the Dense Espinal, mainly due to the abandonment of agricultural lands. This result is similar to that detected in European forests between 1990 and 2000 and is explained by the increase in forest cover and the permeability of the landscape matrix due to the abandonment of agricultural lands, forestation and conservation policies (Saura et al., 2011a). In our case, matrix permeability could have improved, taking into account that the most abundant cover of the matrix is due the Very Degraded Espinal. It is very feasible that in specific occasions and due to succesful seed dispersal and establishment, some plant species germinate mostly in zones in the degraded espinals near to the Good Espinal and Dense Espinal patches. These results are in line with those suggesting that the quantity of habitat is the main determinant for the abundance and persistence of species, prevailing generally over the role of the spatial configuration per se (Fahrig, 2003).

In the second place, and in order to have a more comprehensive connectivity analysis, we were able to determine which
elements (habitat patches) are facilitating dispersal in the present landscape, acting as stepping stones among other habitat patches. Visconti and Elkin (2009) maintain that the incorporation of the quality of the patch is especially important in landscapes where habitat quality is very variable. This situation is present in our study area, where, without doubt the habitats of Good Espinal patches have a quality well below that of the Native Forest.

The BC$_{IIC}$ index was useful to identify the key patches that, by having a stepping stone role, are involved in dispersal among the different patches in the present landscape (Fig. 5). The use of such network centrality metric is important, considering that it allows to prioritize the habitat patches in terms of their importance for global connectivity (Bodin and Saura, 2010; Segurado et al., 2013). This becomes especially relevant considering that the global connectivity between patches suitable for seed establishment is of crucial importance for the persistence of native species present in the landscape (Pereira et al., 2011).

The results of the different metrics reveal that the Good Espinal patches contribute in an important manner to the connectivity of the landscape (Fig. 5), and play a key role as stepping stones for seed dispersal. Therefore, the high values detected for the Good Espinal patches by the BC$_{IIC}$ metrics and the dIICflux fraction, show the importance of those patches as main focus for conservation management or restoration activities.

The dIICintra values were very low and of little relevance in this study. This metric would show high values (compared to the flux and connector fractions) when a patch was severely isolated. The higher dIICintra values would occur when a species is not able to move any distance out of the habitat patches ($d=0$), and the only reachable habitat is that existing within the patches where it is found (Saura and Rubio, 2010). In our case we used long dispersal distances as compared to the distance between patches in the study zone; therefore the contribution of this metrics was very small in all cases. On the contrary, for long distances dIICflux determined almost all the connectivity and availability of habitat in the landscape (Saura and Rubio, 2010). This explains why the results show the highest IICflux proportion for $d=1000$ m, and diminishes for shorter dispersal distances (Fig. 5).

An important contribution of the dIICconnector was undoubt-edly observed for the three dispersal distances. However, it was detected that the proportion decreased slightly as distance increased (Fig. 5). This result suggests that stepping stones are fundamental to facilitate the dispersal of species whose dispersal abilities are more limited. As the species can traverse longer distances, these patches are less necessary to promote successful movement. The efficiency of stepping stones can be significantly improved when they are embedded in a low resistance matrix (which promotes relatively high interpatch movement rates), in comparison with a high resistance matrix (promoting relatively low intrapatch dispersal rates) (Baum et al., 2004; Saura et al., 2011b). In our case the matrix is considered as of low resistance as it is mostly formed by Very Degraded Espinals (see discussion above). Bodin and Saura (2010) demonstrated that patches with high values in the connector fraction are crucial, because their elimination immediately reduces connectivity. Therefore, we recommend that future management activities to be carried out in the study zone, should have as objective, if possible, the preservation of the espinal patches with higher dPCconnector values, to promote the global connectivity of the landscape (Lisa et al., 2001; Pereira et al., 2011), which is possible by means of maintaining the key stepping stone patches.

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**Fig. 5.** Ten key patches with a highest contribution to connectivity by functioning as stepping stones among other habitat areas (as measured by BC$_{IIC}$). The size of the circles is proportional to the BC$_{IIC}$ value. In each circle the proportions of the fractions dIICconnector and dIICflux for the different dispersal distances (150 m, 500 m and 1000 m) are shown. The contribution of fraction dIICintra was very small in all cases and is not shown in the figure. The patches correspond Native Forest, Good Espinal and Dense Espinal classes. Although the Arborescent Shrubland is one of the habitat classes, none of its patches fell within the 10 most important ones as stepping stones.
One of the advantages of using this type of indicators to analyze functional connectivity is that they could be used for the analysis of different plant or animal species, taking into account that a potential great number of species can be present in a landscape and disperse through it, using the different habitat patches and moving among them in different ways (Saura et al., 2011a). However, an important limiting factor is the scarcity of knowledge regarding the dispersal distances of the different species that are present in this ecosystem. For this reason, more generic analysis of potential connectivity, using a range of different dispersal distances, are a good option to balance the need between species-specific information in connectivity analysis and generality in the analyses that intend to be representative of the biodiversity impacts in an entire landscape or ecosystem.

3.3. The contribution of espinals to connectivity and biodiversity

When analyzing the spatio-temporal dynamics of the landscape together with its functional connectivity, we conclude that the espinals are largely contributing to an improvement of the structure and connectivity of the landscape. It was demonstrated that the espinals were the most dynamic and that Denses Espinals was generated during the last period of study. On the connectivity level, it was found that the Good Espinal patches are fundamental to maintain the connectivity in the study area. Although habitat quality in these espinals is not as good a quality as in the Native Forest, but possibly with some forest edge characteristics, which could be enough to promote ecological fluxes and increase biodiversity. Besides, espinals are the habitat of many small mammals and native birds (Iriarte et al., 1989; Lazo and Anabalon, 1992) which could be contributing to seed dispersal. This contribution is very relevant, considering that the espinal cover at present about 45% of the Mediterranean landscape in the center of Chile (Van de Wouw et al., 2011), but data has been lacking on the structure and connectivity of the espinals (Root-Bernstein and Jaksic, 2013). Therefore, in this study we offer an approach to characterize the connectivity of this ecosystem and contribute to the functioning of key ecological processes in the study area. Historically the espinals have been used as grazing zones (Ovvalle et al., 1990); here, we supply evidence that they can render other important ecological services and that, particularly with the help of restoration plans, good quality espinals can be generated and significantly contribute to connectivity in the broader landscape. Recent studies have been proposing different restoration techniques and sustainable exploitation to preserve the espinals (Root-Bernstein and Jaksic, 2013), as it has been found that the A. caven espinals could act as an intermediate successional stage for the recuperation of the sclerophyll forest (Armeteo and Pickett, 1985; Fuentes et al., 1986).

Finally, this evaluation of the dynamics of the structure and connectivity of the landscape is a case study for a specific Mediterranean area. Therefore, it is not a conclusive analysis concerning the trends that could be present in the whole Mediterranean region or in other zones of Chile or South America. In this respect, Turner (1989) affirms that the scale at which the studies are carried out can deeply influence the conclusions, and the processes and parameters important in one scale could be not so important or predictive in another scale.

4. Conclusions

We have obtained a set of evidences, based on indicators of landscape dynamics and connectivity, which lead us to partially reject the proposed hypothesis that “given the permanent LUCC in the Mediterranean landscape and the corresponding alteration of its spatial pattern, it would be expected that connectivity would diminish along time”. The results on the spatio-temporal dynamics provide clear evidence that the changes detected during the analyzed period, largely modified the configuration of the landscape patterns, altering both their structural and functional aspects. However, in spite of the constant changes in the use of the land detected between 1975 and 1992, the abandonment of agricultural lands and their later conversion to espinals observed from 1992 on, allowed the generation of a plant succession dynamics towards secondary forests. This dynamics triggered increases in functional connectivity. These dynamics highlighted the importance of the different espinal types for functional connectivity and for maintaining the heterogeneity of the Mediterranean landscape.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2014.08.010.

References


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