

## Original article

# Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000)

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## ABSTRACT

Landscape networks and ecosystems worldwide are undergoing changes that may impact in different ways relevant ecological processes such as gene flow, pollination, or wildlife dispersal. A myriad of indices have been developed to characterize landscape patterns, but not all of them are equally suited to evaluate temporal changes in landscape connectivity as is increasingly needed for biodiversity monitoring and operational indicator delivery. Relevant advancements in this direction have been recently proposed based on graph theoretical methods to analyze landscape network connectivity and on the measurement of habitat availability at the landscape scale. Building from these developments, we modify a recent index and present the equivalent connected area (ECA) index, defined as the size of a single patch (maximally connected) that would provide the same probability of connectivity than the actual habitat pattern in the landscape. The temporal changes in ECA can be directly compared with the changes in total habitat area. This allows for additional and straightforward insights on the degree to which the gains or losses in habitat amount can be beneficial or deleterious by affecting landscape elements that uphold connectivity in a wider landscape context. We provide a demonstrative example of application and interpretation of this index and approach to monitor changes in functional landscape connectivity. We focus on the trends in European forests at the province level in the period 1990–2000 from Corine land cover data, considering both changes in the forest spatial pattern and in the average permeability of the landscape matrix. The degree of connectivity was rather stable over most of the study area, with a slight overall increase in forest connectivity in Europe. However, a few countries and regions concentrated remarkably high changes in the analyzed period, particularly those with a low forest cover. The species traits also affected the responses to landscape pattern changes, which were more prominent for those species with limited dispersal abilities. We conclude discussing the potential of this approach for consistent indicator delivery, as well as the limitations and possibilities of application to a variety of situations, for which the required quantitative tools are freely available as open source projects.

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## 1. Introduction

Landscape connectivity can be defined as the degree to which the landscape facilitates or impedes movement among the existing resources (modified from Taylor et al., 1993). It determines which proportion of the total habitat area can be reached and is available for an organism located in a particular point in the landscape. Structural connectivity approaches focus on habitat contiguity and on the analysis of landscape patterns without any reference to a particular species or ecological process. However, an ecologically realistic assessment of the actual flows and use of the landscape by differ-

ent organisms requires from a functional connectivity perspective in which the ability of species to move through non-habitat areas is considered (Tischendorf and Fahrig, 2000). Functional connectivity may be ensured not only when the existing habitat units are physically contiguous but also when a permeable matrix, a series of stepping stones or other connecting elements allow for the movement of a particular organism between habitat areas that might be physically distant (With et al., 1997; Adriaensen et al., 2003; Manning et al., 2009; Rey Benayas et al., 2008).

The lack of landscape connectivity and the subsequent isolation of habitat patches can interfere with pollination, seed dispersal, gene flow and wildlife migration and breeding, among other ecological processes (e.g. Crooks and Sanjayan, 2006). Enhancing landscape connectivity is a key part of modern biodiversity conservation strategies worldwide, and may be one of the best responses

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to counteract the potentially adverse effects of habitat fragmentation and facilitate the shifts in the natural ranges of species due to climate change (Taylor et al., 1993; Hannah et al., 2002). However, the importance of the spatial configuration of habitats for biodiversity should not be overemphasized. Connectivity should not be viewed as the only possible response to landscape change but just as a part of a broader set of available conservation management options (Bennett et al., 2006; Hodgson et al., 2009; Saura and Rubio, 2010). In particular, the amount of habitat has been recognized as the major determinant of species abundance and persistence, usually outweighing the role of spatial configuration per se (Fahrig, 2003), although depending on the cases the effects of habitat loss may be exacerbated to different degrees by the fragmentation of the remnant habitat network (Andr en, 1994; Radford et al., 2005; Betts et al., 2006).

Since 2003, several parallel processes at global, European and national levels have been running to develop biodiversity indicators in order to measure progress towards the global biodiversity 2010 target (<http://www.countdown2010.net/>, accessed May 2010) agreed at the Convention on Biological Diversity (<http://www.cbd.int/>, accessed May 2010) conference of the parties (April 2002, decision VI/2006). For the European level implementation (EC Biodiversity Communication, 2006), 26 headline indicators were defined, among which the indicator 13 “fragmentation and connectivity of ecosystem”. However, resources and data availability for indicator design and delivery in this respect are extremely limited (Mace and Baillie, 2007). Further efforts are required towards appropriate and operational ways to assess the magnitude and potential ecological impacts of ongoing landscape pattern changes.

A large number of indices with different characteristics and degrees of complexity have been developed in the last years, intending to capture the status and trends of landscape connectivity and the ecological processes related to it (e.g. Hanski and Ovaskainen, 2000; Moilanen and Nieminen, 2002; Calabrese and Fagan, 2004; Saura and Pascual-Hortal, 2007; Urban et al., 2009). In particular, a network (graph-based) representation of the landscape is being recently but increasingly applied to analyze landscape connectivity (e.g. Bunn et al., 2000; Urban and Keitt, 2001; Jord an et al., 2003; O’Brien et al., 2006; Bodin and Norberg, 2007; Vasas et al., 2009; Saura and Rubio, 2010). In this approach the landscape is represented as a set of nodes (usually habitat patches or other spatial units of interest) and links or connections (representing the potential ability of an organism to directly disperse between two habitat nodes). While some of the available indices and approaches may fail to be used in practice for operational indicator delivery because they rely on biologically detailed information that is hardly available for broad-scale assessments (this may be the case of many metapopulation or spatially explicit population models (Dunning et al., 1995; Hanski, 1998)), graph-based indices have been suggested to possess a good balance between the amount of information they require as an input and the degree of detail in the characterization of connectivity and in the results they provide (Calabrese and Fagan, 2004). Graph indices are adaptable to different degrees of detail in the available information and are still operational with sparse data (Saura and Rubio, 2010), which makes them particularly suited for operational reporting of ecosystem pattern trends at regional scales. In addition, recent studies have shown that the practical outcomes resulting from the application of some network indices to ecological problems are very similar to those provided by considerably more complex and data-hungry spatially explicit population models (Minor and Urban, 2007; Visconti and Elkin, 2009).

On the other hand, various indices have been shown to provide misleading results and to lack of an adequate response to relevant spatial changes related to connectivity (Pascual-Hortal and

Saura, 2006; Saura and Pascual-Hortal, 2007). These problems and limitations are not present when landscape connectivity is analyzed within the concept of habitat availability (reachability) at the landscape scale through indices like the integral index of connectivity (IIC) or the probability of connectivity (PC) (Pascual-Hortal and Saura, 2006; Saura and Rubio, 2010). The habitat availability concept is based on considering a patch itself as a space where connectivity exists. Habitat availability indices integrate, in a single measure, the area existing within the habitat patches (intrapatch connectivity) and the area made available (reachable) through the connections with other habitat patches in the landscape (interpatch connectivity) (Pascual-Hortal and Saura, 2006). From a landscape or ecosystem monitoring perspective, interpatch connectivity cannot be evaluated separately from habitat amount if the resultant indicators are intended to represent a property of the landscape that can be interpreted as beneficial for the ecological processes and flows to be conserved. For instance, for the connections between patches to become frequent at least a certain degree of fragmentation needs to have already degraded the habitat pattern that originally stood as a single large and continuous (maximally connected) piece of habitat. IIC and PC have been applied in many conservation planning case studies (e.g. Neel, 2008; Pascual-Hortal and Saura, 2008; Perotto-Baldivieso et al., 2009; Fu et al., 2010; Laita et al., 2010) but they have not been so far used for landscape monitoring purposes, even when they are well suited to evaluate the impact of spatial changes on functional landscape connectivity.

Here we describe and apply for the first time a network-based and habitat availability approach for the analysis of landscape changes and their potential impact on ecological connectivity. We present the equivalent connected area (ECA) index, as a modification of the PC index more adequate to quantify and interpret changes in connectivity and relate them in a meaningful way to the ongoing and related changes in the amount of habitat within the landscape. We demonstrate the use of this ECA index to monitor changes in functional landscape connectivity by focusing on the trends in European forests at the province level in the period 1990–2000 from Corine land cover data (Bossard et al., 2000). This application has the objective of providing (1) a broad-scale snapshot and European-wide assessment of forest connectivity trends, and (2) a demonstrative example of how the results provided by the ECA index and the proposed methodology can be interpreted and of how the same approach can be applied to other study areas and spatial and temporal scales as it may be needed for ecosystem trends assessment and indicator delivery in a variety of situations.

## 2. Material and methods

### 2.1. The probability of connectivity (PC) and the equivalent connected area (ECA)

The probability of connectivity (PC) is a network-based habitat availability index that quantifies functional connectivity. It is defined as the probability that two points 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 links (direct connections) among them (Saura and Pascual-Hortal, 2007; Saura and Rubio, 2010). PC varies with the spatial arrangement and attributes of the habitat patches, and with the dispersal abilities of the species, and has a bounded range of variation from 0 to 1. It is given by:

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

where  $a_i$  and  $a_j$  are the areas of habitat patches  $i$  and  $j$ , or any other attribute considered relevant for the analysis (such as habitat quality, population size, etc.).  $A_L$  is the maximum landscape attribute; when the patch attribute is habitat area (as we will assume hereafter),  $A_L$  corresponds to the total landscape area (i.e. area of the study region, comprising both habitat and non-habitat patches). The strength of each link is characterized by  $p_{ij}$ , which is the probability of direct dispersal between patches  $i$  and  $j$  (without passing through any other intermediate habitat patch). The product probability of a path (where a path is a sequence of patches in which no patch is visited more than once) is the product of all the values of  $p_{ij}$  for all the links in that path.  $p_{ij}^*$  is the maximum product probability of all the possible paths between patches  $i$  and  $j$  (including direct dispersal between the two patches). If patches  $i$  and  $j$  are close enough or have a strong direct connection, the maximum probability path will simply be the direct movement between patches  $i$  and  $j$  ( $p_{ij}^* = p_{ij}$ ). If patches  $i$  and  $j$  are more distant or have a weak direct connection, the 'best' (maximum probability) path will probably consist of several steps through intermediate stepping stone patches yielding  $p_{ij}^* > p_{ij}$ . When two patches are completely isolated from each other, then  $p_{ij}^* = 0$ . When  $i=j$  then  $p_{ij}^* = 1$  (a patch can always be reached from itself); this relates to the habitat availability concept that applies to PC, in which a patch itself is considered as a space where connectivity exists.

Despite the good properties and behaviour of this index described in Saura and Pascual-Hortal (2007), the use of the PC values may be limited because (1) they are dependent on the definition of the boundaries of the study area ( $A_L$ ), which in some cases may be set arbitrarily around the focal habitat patches, and because (2) very low PC values may be obtained in practice when the habitat patches are small compared to the total landscape area, as reported for example by Neel (2008), who found PC values under 0.00001. To overcome these limitations, we propose an alternative index that is directly derived from PC, the equivalent connected area (ECA). Unlike PC, ECA presents the advantages of having area units, a more reasonable and usable range of variation, and, more importantly, an easier and straightforward interpretation especially when directly compared with the temporal changes in habitat area (as will be described below). ECA is defined as the size of a single habitat patch (maximally connected) that would provide the same value of the probability of connectivity than the actual habitat pattern in the landscape. It is calculated as the square root of the numerator of the PC index as follows:

$$ECA = \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*} \quad (2)$$

The ECA value will not be smaller than the area of the largest patch in the landscape, avoiding the very low values that may be attained with PC. The value of ECA will coincide with the habitat area existing in the landscape when all the habitat is confined in a single habitat patch (no fragmentation) or when the habitat is dissected into different patches but there is a maximal interpatch connectivity such that  $p_{ij}^* = 1$  for each pair of patches.

ECA is a network-based index that takes into account the connected area existing within the habitat patches, the estimated dispersal flux between different habitat patches in the landscape (corresponding to the product  $a_i a_j p_{ij}^*$  when  $i \neq j$  and  $i$  and  $j$  are the starting or ending points of those fluxes), and the contribution of patches and links as stepping stones or connecting elements that uphold the connectivity between other habitat areas (Saura and Rubio, 2010).

In more general terms, ECA can be named as EC (equivalent connectivity) whenever the patch attributes correspond to other

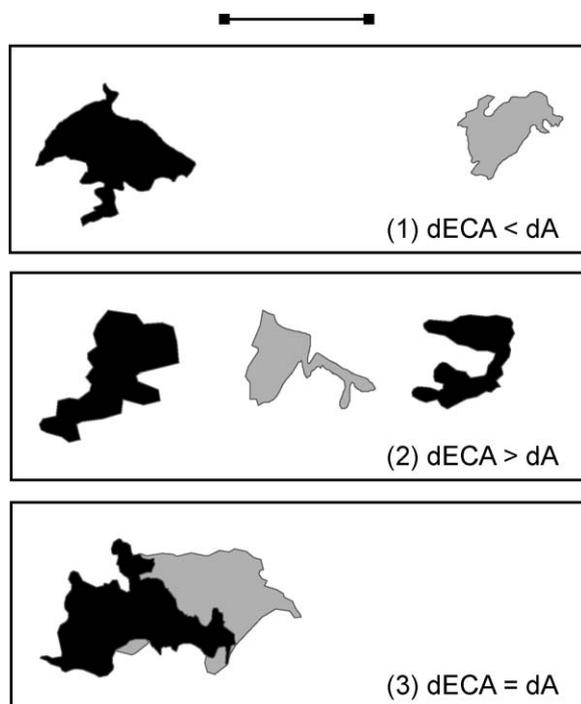
habitat characteristics different from area, such as habitat quality, probability of occurrence of a particular species, population sizes, etc. However, for simplicity and matching to the example of application we will later show for European forests, we will hereafter focus on ECA and habitat area as the patch attribute. In addition, an analogous version of the ECA or EC indices could be as well calculated from the IIC index, although here we will focus in ECA as related to PC since this latter index provides a more detailed characterization of the connections between habitat patches than IIC (Saura and Pascual-Hortal, 2007).

## 2.2. Changes in ECA versus changes in habitat area

The ECA index has area units while at the same time it maintains the good properties and appropriate reaction to spatial changes that it inherits from PC and the habitat availability indices in general (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007; Saura and Rubio, 2010). In addition, the relative variation in ECA after a particular spatial change (or set of changes) in the landscape (dECA, defined as the difference between the ECA value after and before the spatial change, divided by the ECA value before that change) can be directly compared with the variation in the total amount of habitat area in the landscape after the same change (dA), with an easy interpretation and additional insights that can be gained from that comparison.

In what refers to changes directly affecting the habitat areas (assuming at this point that there are no changes in the landscape matrix), an increase in connectivity can obviously only occur if some new habitat area appears in the landscape through natural regeneration or restoration. In the same way, a connectivity decrease would require the loss of some habitat in the landscape. However, the new habitat areas (or habitat losses) in the landscape can have very different impacts in terms of habitat connectivity and availability, and be beneficial (or deleterious) to a different degree (Fig. 1). New isolated pieces of habitat will make a modest contribution to an increased habitat connectivity and availability (dECA < dA, case 1 in Fig. 1). The reverse will occur when the new habitat patches are connected to previously existing habitat areas and act as a part of a discontinuous (or continuous) corridor or stepping stone between them (dECA > dA, case 2 in Fig. 1). Finally, if the new habitat area is established adjacent to the (eventually unique) habitat patch (case 3 in Fig. 1), the entire habitat is fully connected and concentrated in a single patch before and after the spatial change (ECA = A), which corresponds to a neutral area gain in terms of its benefit for connectivity (dECA = dA). In this way dECA is valuable to interpret how spatial changes are occurring in terms of their impact and efficiency for improving landscape connectivity (gain of connectivity per unit of new habitat area). In a given situation dECA will be maximized when the new areas bring up together and provide the maximum connectivity ( $p_{ij}^* = 1$ ) between all the habitat pieces that were previously more weakly connected. This maximum attainable dECA would be higher in those situations where the habitat is initially distributed in a larger number of functionally isolated components each of them comprising a low proportion of total habitat area. Analogous considerations apply for spatial changes involving the loss of habitat in the landscape.

Changes in ECA can also occur even with no variations in the habitat pattern when the landscape matrix is made more permeable (e.g. defragmentation measures, recovery of natural vegetation after agricultural land abandonment, etc.) or more resistant to species movement (e.g. land use intensification, road construction, etc.). When the non-habitat matrix characteristics are considered, the variations in ECA due to the changes in the habitat patches themselves (dECA) will be combined with the changes in the intermediate landscape to produce the final dECA<sub>matrix</sub> value.



**Fig. 1.** Three simple cases to illustrate the different ways and degrees to which an increase in habitat area ( $dA$ ) can improve habitat connectivity and availability at the landscape scale as measured by  $dECA$  (see Section 2.2). The initially existing habitat area is shown in black, the new habitat area is shown in gray color, and the dispersal distance of a hypothetical species dwelling in the landscape is indicated by the line at the top (in this illustrative example we assume that  $p_{ij} = 0$  for patches separated above that distance and  $p_{ij} = 1$  otherwise).

### 2.3. Study area, dataset and processing

The study area covered 21 European countries for which Corine land cover (CLC) data were available in 1990 and 2000. The nomenclature of territorial units for statistics (NUTS, [http://ec.europa.eu/eurostat/ramon/nuts/home\\_regions.en.html](http://ec.europa.eu/eurostat/ramon/nuts/home_regions.en.html), accessed May 2010), official framework for statistical purposes in Europe, was used as reference to define the provinces (NUTS level 3 and 2). To reduce the variability in the size of the reporting units, NUTS 2 was chosen instead of NUTS 3 for a few countries (Austria, Belgium, Germany and Netherlands) as already done in other studies over Europe (Haines-Young and Weber, 2006). This resulted in a total of 564 provincial units over the 21 European countries (Figs. 2 and 3), with an average province size of 5560 km<sup>2</sup>. The analyses described hereafter were performed at this province level.

CLC is the only harmonized land cover database available over the European territory at two different dates (CLC1990 and CLC2000) and has been used in various studies reporting changes in European land cover types (e.g. Haines-Young and Weber, 2006; Weber, 2007; Feranec et al., 2010). CLC provides 44 land cover classes that are mapped at a 1:100,000 scale and with a minimum mapping unit of 25 ha (Bossard et al., 2000). Within the current study, we reclassified the land cover data into forest (broadleaves, coniferous and mixed forest) and non-forest, and identified each individual forest patch (polygon) in the resultant dataset. Forests are defined in CLC as areas with trees higher than 5 m and with a canopy closure of at least 30%. Forest class includes young plantations with at least 500 stems/ha, but not other wooded lands, young plantations when below 500 stems/ha, clear cuts, burnt areas, or forest nurseries. CLC1990 was developed from Landsat 4/5 TM images (with a geometric accuracy of at least 50 m) and other ancillary information, while the satellite data used for CLC2000 were

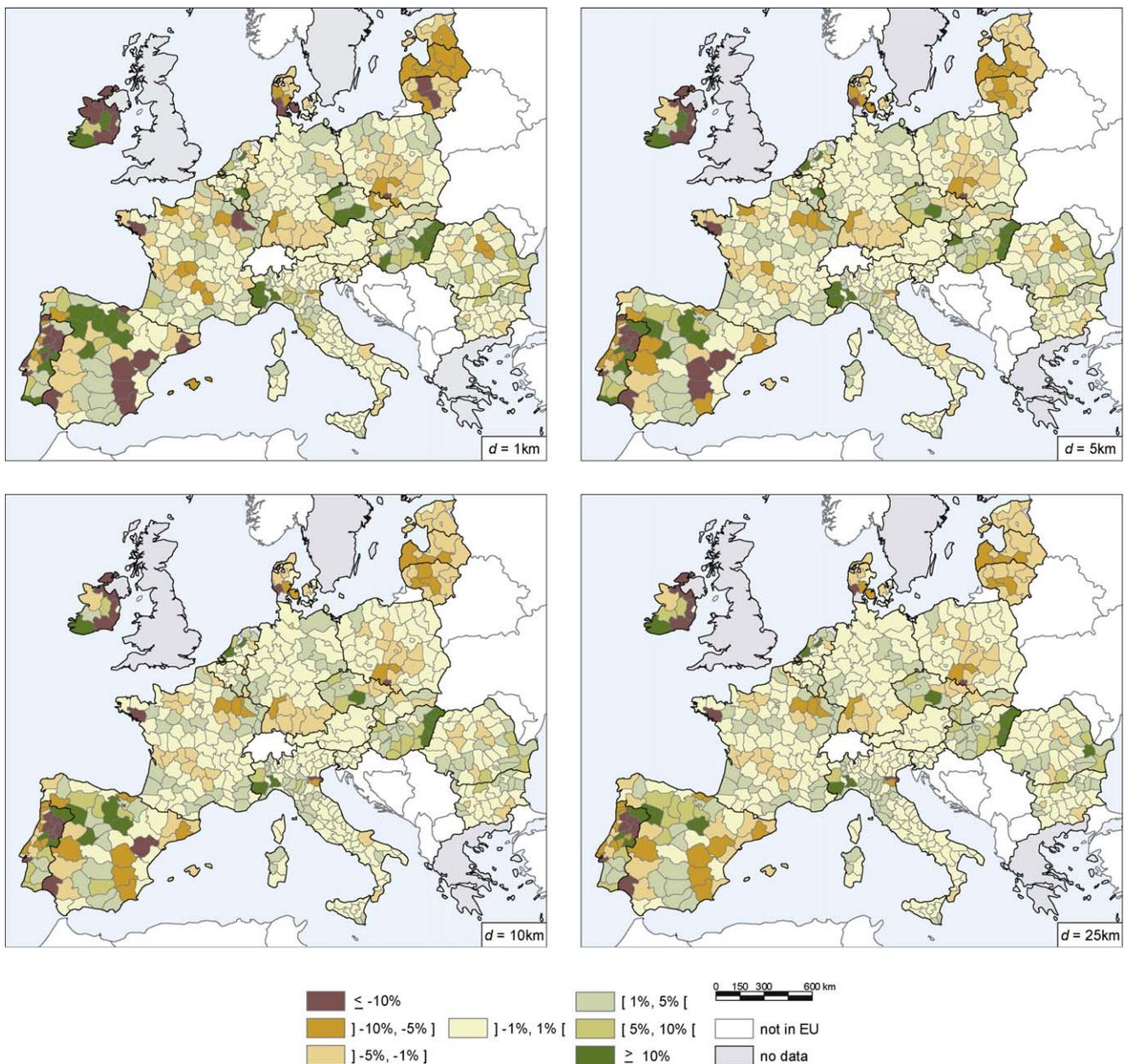
Landsat 7 ETM images with a geometric accuracy of 25 m. The final geometric accuracy of both CLC1990 and CLC2000 data is estimated at 100 m and the thematic accuracy at 85% (Büttner and Maucha, 2006). All the processing described below was performed in the original vector format of the CLC data, with the exception of the resistance surfaces.

We built four graphs for each province and date (1990 and 2000), each corresponding to a different median dispersal distance ( $d = 1, 5, 10$  and 25 km) broadly representative of different generic groups of forest-dwelling species with variable dispersal capabilities (see some examples in Section 4) that may be impacted to different extents by the landscape pattern changes related to connectivity. In all the graphs a node corresponded to one of the forest patches in the reclassified land cover data. The  $p_{ij}$  values (probability of direct dispersal) in the links were characterized by a negative exponential function of the Euclidean (straight line) edge-to-edge distance between forest patches, in which  $p_{ij} = 0.5$  when that distance was equal to  $d$ . This allowed assessing connectivity on a binary habitat map (forest/non-forest) and implied that we assumed that the landscape matrix (non-forest areas) was homogeneous or that the potential changes in its permeability through time were not important to further limit or facilitate the dispersal in the province.

In order to incorporate the effect of the matrix in the assessed temporal trends ( $dECA_{matrix}$ ), we built four additional graphs for each province and date (and for the same  $d$  values and set of nodes as above), but considering a friction or resistance surface throughout the landscape matrix to obtain the  $p_{ij}$  values. Such a resistance surface intends to take into account the variable movement abilities and mortality risk of a species through different portions of the landscape (Adriaensen et al., 2003; Theobald, 2006). The typical approach is to compute the least-cost path between each pair of patches through that resistance surface, and use the accumulated cost along that path to characterize the feasibility of movement between the habitat areas. However, the least-cost approach is computationally very intensive and it remains largely infeasible to implement in landscapes with several thousand nodes (Urban et al., 2009), as required for the needs of this case study. In addition, the need to perform a detailed analysis to identify each possible individual least-cost path may be questionable when the purpose is to deliver indicators that report connectivity changes over relatively large regions, as we intended here.

For these reasons, we used a more simplified approach suited to the needs of this analysis that did not rely in the identification of an individual least-cost path between every pair of patches. We built a resistance surface with a spatial resolution of 100 m (as described below) and computed the cost of movement (effective distance) to every cell in the landscape matrix through a least-cost path starting from the edge of the forest (without differentiating the particular forest patches in which that closest edge was located). From this information we estimated in each province the average cost of moving a certain Euclidean distance through the landscape matrix. Since we were only interested in the relative changes in the connectivity between the two dates (as measured by  $dECA_{matrix}$ ), we estimated the  $p_{ij}$ 's from a negative exponential function of the effective distance between patches in which  $p_{ij} = 0.5$  for the average cost in the year 1990 estimated for each of the four types of species with different dispersal abilities (moving a Euclidean distance of  $d = 1, 5, 10$  and 25 km). In this way, if in 2000 the matrix became more resistant than in 1990, the  $p_{ij}$  values were reduced and a decrease in connectivity due to the changes in the landscape matrix was reported by  $dECA_{matrix}$  (in addition to what resulted from the changes in the forest habitat pattern itself).

For building the resistance surface we assumed that forest species (particularly specialist species) will be more reluctant to move through land cover types as their characteristics increasingly depart from those of the forested areas where they dwell,



**Fig. 2.** Changes in the connectivity of the European forests at the province level in the period 1990–2000 as measured by dECA (without considering variations in the permeability of the landscape matrix). Results are shown for four different median dispersal distances ( $d$ ) of 1, 5, 10 and 25 km.

unless these cover types are relatively close to forest patches that can act as refuges and facilitators of their dispersal. Therefore we assigned to each CLC class higher friction values as the degree of naturalness and forest canopy cover decreased, ranging from a minimum of 1 for the forested areas up to a maximum of 1000 for the artificial/anthropogenic classes (urban areas and roads). These friction values were smoothed for each CLC patch (except the artificial classes) when they were surrounded by forests within a distance up to 500 m, according to a sigmoidal decreasing function of distance.

All the ECA calculations were performed with a modified version of the Conefor Sensinode software package (Saura and Torné, 2009) (<http://www.conefor.org/>, accessed May 2010) that allowed for batch and optimized processing of the large amount of province files and sets of nodes.

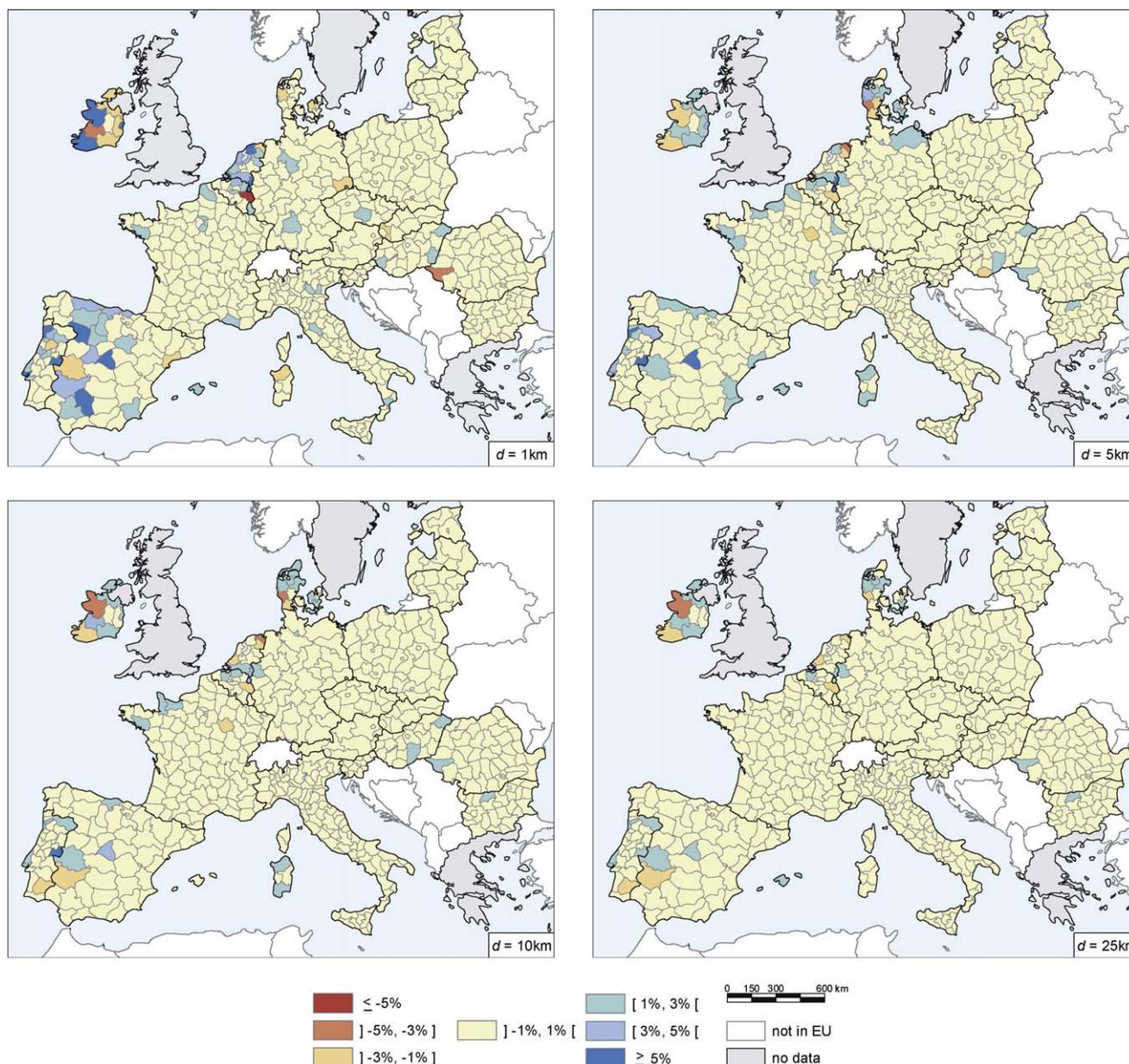
Finally we computed the non-parametric Kendall's rank correlation coefficient ( $\tau_b$ ) between the variables described above (dECA with and without matrix for different  $d$ , A and dA) in order to eval-

uate the degree to which they indicated similar patterns of change in the study area and the relationships of these changes with the amount of forest habitat.

### 3. Results

#### 3.1. Trends in the connectivity of European forests (1990–2000) due to changes in the forest pattern

The degree of connectivity was rather stable over most of the study area in 1990–2000, with dECA values ranging between  $-1\%$  and  $1\%$  in about half of the provinces (Fig. 2). However, there were considerable differences between European countries and regions (Fig. 2). The largest individual changes in connectivity were in general found for  $d = 1$  km, and dECA values tended to be slightly lower as the dispersal capabilities increased (Fig. 2). There was a very slight overall increase in forest connectivity in Europe rang-



**Fig. 3.** Difference between  $dECA_{matrix}$  and  $dECA$  in each of the provinces, indicating where the matrix changes had themselves a more prominent and distinctive effect in the final forest connectivity trends. Results are shown for median dispersal distances ( $d$ ) of 1, 5, 10 and 25 km.

ing from 0.02% for  $d = 1$  km up to 0.24% for  $d = 25$  km (average of  $dECA$  values for all the provinces), which was higher than the analogous increment for  $dA$  (0.22%) only for  $d = 25$  km. Only 10% of the provinces had remarkably high changes in connectivity in the analyzed period, with the absolute value of  $dECA$  higher than 10% for  $d = 1$  km (Fig. 2). The same provinces tended to be those with the largest changes for all dispersal distances (Fig. 2). Kendall's  $\tau_{ub}$  correlation coefficient between the  $dECA$  values for the different distances ranged from 0.793 ( $\tau_{ub}$  between  $dECA$  for  $d = 1$  km and  $d = 25$  km) up to 0.960 ( $\tau_{ub}$  between  $dECA$  for  $d = 10$  km and  $d = 25$  km).

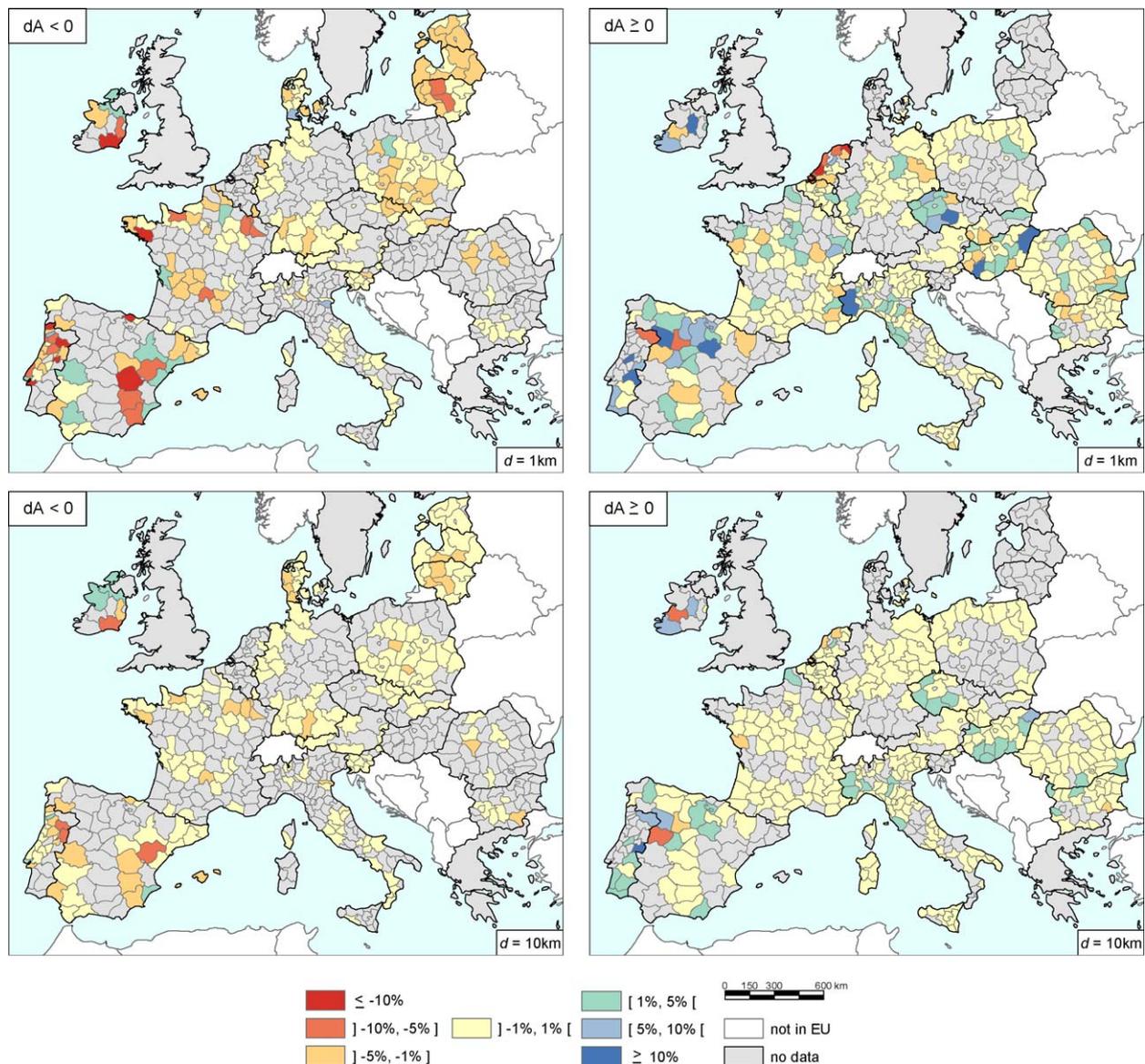
### 3.2. Trends in the connectivity of European forests (1990–2000) considering the changes in the landscape matrix

When the effect of the changes in the matrix was considered, the variations in connectivity were slightly but significantly larger than in the previous case ( $dECA$ ), with the average of the  $dECA_{matrix}$

values for all the provinces ranging from 0.43% for  $d = 1$  km to 0.31% for  $d = 25$  km. For 75% of the provinces  $dECA_{matrix}$  was higher than  $dECA$ , and these differences increased for lower  $d$  (Fig. 3). The sign of the connectivity change was reversed when considering the matrix in about 11% of the provinces for  $d = 1$  and only in 4% of them for  $d = 25$  km. Most of these corresponded to cases in which  $dECA < 0$  but  $dECA_{matrix} > 0$ . However, these differences between the  $dECA_{matrix}$  and  $dECA$  values did not change much the general pattern of connectivity trends in the study area (Fig. 3). The correlations between  $dECA_{matrix}$  and  $dECA$  for all the provinces were high and increased with species mobility ( $\tau_{ub} = 0.855$  for  $d = 1$  km,  $\tau_{ub} = 0.927$  for  $d = 25$  km).

### 3.3. Changes in the ECA index versus changes in forest area

There was a high correlation increasing with dispersal distance between connectivity change ( $dECA$ ) and net forest cover change ( $dA$ ), ranging from  $\tau_{ub} = 0.76$  for  $d = 1$  km up to  $\tau_{ub} = 0.95$



**Fig. 4.** Difference between dECA and dA in each of the provinces. This indicates the degree to which the forest pattern changes had a larger or smaller impact on connectivity than the one that would be expected from the variations in forest area alone. Results are displayed separately for provinces with net forest area gain ( $dA \geq 0$ ) and with net forest area loss ( $dA < 0$ ). Results are only shown for median dispersal distances ( $d$ ) of 1 and 10 km.

for  $d = 25$  km. This correlation decreased slightly when the landscape matrix heterogeneity was taken into account ( $dECA_{\text{matrix}}$ ), with  $\tau_{ub} = 0.72$  for  $d = 1$  km and  $\tau_{ub} = 0.90$  for  $d = 25$  km. In most of the provinces the variation in forest connectivity was rather similar to that for forest area ( $dECA - dA$  below 1% in absolute value), as shown in Fig. 4. In 47% of the provinces dECA was higher than dA (Fig. 4). Considerable connectivity losses ( $dECA \leq -1\%$ ) occurred even with net area gains ( $dA \geq 0$ ) for ten provinces at  $d = 1$  km, and for two provinces for  $d = 10$  km. The opposite ( $dA < 0$ ,  $dECA > 1\%$ ) occurred for only four provinces in the study area.

The percentage of forest cover in the provinces ranged up to 69%, but most of those with large connectivity changes (absolute dECA values above 10% for  $d = 1$  km) had a forest cover below 20%, and 90% of them had a forest cover below 37%. When considering all provinces together, the absolute dECA or  $dECA_{\text{matrix}}$  values presented significantly negative but low correlations ( $\tau_{ub} = -0.09$ ) with the percentage of forest cover.

## 4. Discussion

### 4.1. Changes in connectivity and forest area

The change assessment indicated an overall slight improvement in the connectivity of European forests in the period 1990–2000, which is mostly explained by the correlated increase in forest cover and, to a lesser degree, by a mild increase in the permeability of the landscape matrix. Both types of change may be the result of the combined effects of agricultural land abandonment, afforestation, vegetation naturalization, and conservation policies that are taking place in different areas of Europe (e.g. Haines-Young and Weber, 2006; Feranec et al., 2010).

In about half of the provinces the forest area gains resulted in comparatively larger increases in connectivity ( $dECA > dA$ ). This suggests that, intentionally or as a result of natural processes, the location of these new forest areas allows them to function as stepping stones and connecting elements with particularly beneficial

effects in a wider landscape context. In this way they play a more prominent role for overall habitat availability (reachability) than the one that may be expected just from the area they provide. However, the opposite was true in the rest of the cases, indicating that the dominating processes were either those in which the new forest area was located adjacent to already existing forest patches that were therefore enlarged (e.g. natural regeneration resulting from seed dispersal from nearby stands), or those in which new forest patches were distributed more or less isolated from other forest areas in the landscape.

An adequate landscape and territorial planning that integrates spatial patterns with the perception of the landscape and the dispersal capabilities of forest-dwelling species could improve the effectiveness of conservation, afforestation and land use allocation decisions in terms of the maintenance and enhancement of overall habitat connectivity and availability (e.g. Pascual-Hortal and Saura, 2008; Vasas et al., 2009).

In real-world change assessments a combination of habitat losses and gains of different types (see those illustrated in Fig. 1) will probably coexist distributed across different locations in the landscape. Depending on the dominance and relative importance of each of them in a given situation the resultant aggregated dECA will indicate more or less different trends than dA. Moreover, it is possible that in some cases dECA and dA indicate opposite directions of change within the same assessment, as was reported in a few provinces in the European forests case study. For instance, this would occur if the new habitat areas compensate the losses yielding a net positive dA but they appear as isolated habitat pieces (case 1 in Fig. 1) while the losses affect those patches that had the highest connector value (case 2 in Fig. 1), yielding  $dECA < 0 < dA$ .

#### 4.2. Separating the effects of interpatch connectivity and habitat amount or putting them together in an enriched indicator?

Within the key ecological research objective of quantifying the habitat characteristics that better explain species persistence, many efforts have been dedicated to try to identify the distinctive contribution of habitat spatial configuration that is not already captured by the amount of habitat in the landscape, the latter being recognized as the major and primary biodiversity driver (Fahrig, 2003; Hodgson et al., 2009). Given the failure to find an appropriate configuration metric that is consistently uncorrelated with habitat abundance and that can be generally recommended as such for monitoring purposes, the available alternative consists in calculating a set of covarying landscape indices and then apply certain statistical techniques in order to extract the relative contribution of each of these two major components of landscape structure. However, the results of such approach are controversial and highly dependent on the statistical technique chosen (Koper et al., 2007; Smith et al., 2009) as well as on the particular set of indices used as an input for the analyses. We here argue that instead of pursuing such an independent metric or statistical effect, which if found would be of little value by being unrelated to the more important changes in habitat amount, monitoring applications should be based on indicators that are explicitly sensitive to the amount of habitat but that go beyond a spatially-blind assessment by incorporating the effects and importance of the degree of connectivity within and between habitat patches. In this way, the role of habitat amount is not set aside but integrated in a single currency and enriched indicator (Saura and Rubio, 2010). This is the solution adopted by the indices measuring habitat availability at the landscape scale, such as ECA. If in a given situation the spatial patterning of the habitat is irrelevant to determine the amount of available (reachable) habitat for a species, then ECA will report the same trends as those captured by dA (there is no risk of overweighting the importance of interpatch connectivity in the assessment). If on

the contrary, the connectivity patterns are limiting or enhancing species viability beyond what is expectable only from the amount of habitat in the landscape, then ECA will differ to some extent from dA (but not discard or set it apart in the reported trends). For example, in the case study here described we found that forest area variations had a more prominent effect in connectivity (ECA) when the forest was relatively scarce, agreeing with the reported threshold of 10–30% of forest habitat amount below which the negative impacts of fragmentation and isolation become more critical for species abundance and persistence (Andr en, 1994; Radford et al., 2005; Betts et al., 2006). Indeed, provinces with low forest area and a more fragmented forest pattern (like in Ireland or Denmark) will have a higher probability of suffering large relative decreases in connectivity (and more distinct from dA) than provinces with large, compact patches and an almost continuous forest cover. At the same time, they are likely to respond more positively than the latter to additions of a given amount of forest habitat when this is conveniently distributed in the landscape.

#### 4.3. Responses to landscape pattern changes for different species traits: where to focus?

One of the main difficulties that arise when performing functional connectivity analyses over large areas is the potentially very large number of species that may be involved, each of them making use of the habitat and moving through the landscape in a different way. Although some endangered or flagship species may concentrate considerable research efforts that deliver reliable information usable for these purposes, the biological traits and dispersal capabilities of many others may remain largely unknown. Managers may therefore face considerable uncertainties when trying to deal with their particularities in an analysis of this kind. This lack of information can render the connectivity models hard to parameterize and reduce their reliability and value for operational indicator delivery compared to the more classical (and less data-demanding) focus on habitat amount (Hodgson et al., 2009). However, not all the groups of species are affected in the same way by the spatial changes related to connectivity. Our results show that in many cases the actual impacts of the connectivity-related changes might not differ substantially from those that are simply indicated by the variations in the amount of habitat. Therefore, we suggest that only a small fraction of the total species pool in a given community will need to be considered as the focus of such connectivity analysis. The scale of movements at which the effects of connectivity per se are really important in a given habitat arrangement (and therefore add to habitat loss something significantly distinct) can in fact be detected analytically beforehand (Saura and Rubio, 2010). By directly targeting those species that might really benefit to a larger extent from the available stepping stones and connecting elements in the landscape, the amount of ecological information required as an input can be largely reduced.

For instance, our results for the case study suggest which types of species and ecological flows are those likely to be more distinctively affected by the ongoing forest spatial configuration changes in Europe. This would be the case of processes like the dispersal of reptiles, amphibians, small rodents, passerine birds and plant seeds by wind, which rarely goes well beyond  $d = 1$  km (Sutherland et al., 2000; Tackenberg et al., 2003; Smith and Green, 2005; Vittoz and Engler, 2007). On the contrary, more vagile species (e.g. those with dispersal abilities of  $d = 10$ – $25$  km and beyond) were here found to be less sensitive to the variations in the forest spatial patterns. Animal species with large body masses and home ranges, such as those of Canidae, martens and other big carnivore mammals, male red deers, and most of bird prey species (Accipitriformes, Strigi-

formes) will typically fall into this group (Sutherland et al., 2000; Bowman et al., 2002; Loe et al., 2009).

#### 4.4. Incorporating landscape matrix in the assessment of forest connectivity trends

The comparison of dECA and dECA<sub>matrix</sub> allowed estimating to what extent the matrix changes had a distinctive impact on overall landscape connectivity that was not due to changes in the forest habitat spatial pattern itself. In general quite similar trends were indicated by dECA and dECA<sub>matrix</sub> in the analyzed period, with the exception of some individual countries or provinces (Fig. 3). Species with relatively limited mobility are those potentially more sensitive to the changes and permeability losses in the landscape matrix, especially those that occur within their limited dispersal range. In this sense, the results here reported (higher positive difference between dECA<sub>matrix</sub> and dECA for lower *d*) suggest that the matrix permeabilization in the study area has occurred preferentially in the areas relatively close to forest edges. This is probably the result of contagious process like forest spread or the consequence of the abandonment of agricultural lands of marginal productivity that are usually located in the limits of their altitudinal range and next to previously forested areas.

Although usually the connectivity analyses that explicitly take into account the permeability of the landscape matrix are regarded as more realistic, whether an indicator such as dECA<sub>matrix</sub> should be considered as more relevant than dECA for regional reporting depends on the focal ecological processes and on the degree of detail and empirical support for the information used to parameterize the resistance surface. In practice there is very little quantitative and solid information on the species movement patterns and preferences that can be used to assign the friction values to every pixel throughout the landscape. This process typically relies in some sort of expert knowledge, and further research efforts in this respect are certainly needed. We recognize that this may be a flaw of the particular method here adopted to evaluate dECA<sub>matrix</sub>, but that also applies to other more recent and complete matrix-related approaches that rely in the same type of input information (Theobald, 2006; Drielsma et al., 2007; McRae et al., 2008).

#### 4.5. Limitations and conclusions

The relatively mild changes in connectivity of European forests from 1990 to 2000 were expected due to the relatively short period considered and the assessment of overall changes at the province level. At more local scales, the impacts on connectivity may be more prominent than those reported here. Landscape pattern changes and their impacts on ecological processes show up at different spatial and temporal scales, and a multiscale assessment may be needed to provide a more comprehensive picture in this respect. Although this is out of the scope of our demonstrative application, we recognize that our results on connectivity trends are dependent on the spatial scale and on the forest definition in CLC. For instance, our assessment does not reflect any landscape feature or spatial change below the 25 ha of minimum mapping unit set in this cartography. This does not allow fully capturing fine-scale patterns such as scattered trees, hedgerows, or woodland islets that can be effective conducting the ecological flows of forest species across landscapes dominated by agriculture or other land use types (Rey Benayas et al., 2008; Manning et al., 2009; Wehling and Diekmann, 2009). Finally, as every other map, CLC is not free from classification errors. Although we assume that the impact of these classification errors would be low for the broad-scale changes reported here, this remains untested and the application of error propagation techniques (e.g. Zhang et al., 2009) would be of interest in this respect. This assessment of the connectivity trends in European forests

should be viewed as a reference and demonstrative example of the potential and interest of the described network approach, and not as a conclusive analysis of the connectivity-related changes in the region.

The same approach could be applied in other ecosystem types, in more local assessments where finer spatial and biological details are available (e.g. differentiating the habitat quality or suitability of the source patches), in applications oriented to a single or few endangered or umbrella species, or in assessments over longer temporal horizons as new versions of CLC or other landscape databases become available. In addition, other more comprehensive and recent approaches to account for the permeability of the landscape matrix that were not applied here (Theobald, 2006; Drielsma et al., 2007; McRae et al., 2008) could also be used and integrated with the ECA metric.

There are indeed many possibilities for further refinement and a large number of potential applications of the methodology and ECA index here presented, which presents the following advantages: (1) it is based on a solid habitat availability and graph-based background, as developed in previous studies, where the different roles of habitat patches in the landscape network (sources of dispersal fluxes, stepping stones, etc.) are integrated in a single indicator, (2) it is transparent and easy to understand and to communicate to policy makers and the society in general, (3) it is flexible and adaptable to different degrees of detail in the characterization of the habitat patches and the links between them, being also operational with sparse data as required in practice for wide scale reporting, (4) it allows interpreting the dynamics in functional connectivity in relation with the different types of habitat area changes, and to evaluate to what extent the area gains are being really beneficial to uphold and promote ecological flows throughout the landscape, (5) despite of its solid analytical background, it is computationally feasible even when dealing with large datasets as those here considered, and (6) the software tools required for its quantification (Conefor Sensinode software package and related GIS extensions) are freely available either by directly downloading them from <http://www.conefor.org> (accessed May 2010) or by contacting the authors if their modified versions for batch processing of multiple files are needed.

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