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Species specialization limits movement ability and shapes ecological networks: the case study of 2 forest mammals

Olivia DONDINA^{a,*}, Valerio ORIOLI^a, Gianpasquale CHIATANTE^b,
Alberto MERIGGI^b, and Luciano BANI^a

^aDepartment of Earth and Environmental Sciences, University of Milano-Bicocca, Piazza della Scienza 1, Milano 20126, Italy and ^bDepartment of Earth and Environmental Sciences, University of Pavia, Via Ferrata 1, Pavia 27100, Italy

*Address correspondence to Olivia Dondina. E-mail: olivia.dondina@unimib.it.

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Abstract

To counteract the negative effects of forest fragmentation on wildlife, it is crucial to maintain functional ecological networks. We identified the ecological networks for 2 mammals with very different degrees of forest specialization, the European badger *Meles meles* and the Roe deer *Capreolus capreolus*, by differentiating 4 agroforestry elements as either nodes or connectivity elements, and by defining the distance that provides the functional connectivity between fragments. Species occurrence data were collected in a wide agroecosystem in northern Italy. To test the role of hedgerows, traditional poplar cultivations, short rotation coppices, and reforestations as ecological network elements for the 2 species we applied the method of simulated species perceptions of the landscape (SSPL), comparing the ability of different SSPLs to explain the observed species distribution. All analyses were repeated considering different scenarios of species movement ability through the matrix. Model outputs seem to show that the specialist and highly mobile Roe deer has the same movement ability throughout the matrix (2 km) as the European badger, a smaller, but generalist species. The ecological network identified for the European badger was widespread throughout the area and was composed of woodlands, poplar cultivations and hedgerows as nodes and short rotation coppices as connectivity elements. Conversely, the ecological network of the Roe deer was mostly limited to the main forest areas and was composed of woodlands, poplar cultivations and reforestations as nodes and short rotation coppices and hedgerows as connectivity elements. The degree of forest specialization strongly affects both species perception of habitat and movement ability throughout the matrix, regardless of species size. This has important implications for species conservation.

Key words: *Capreolus capreolus*, connectivity elements, forest fragmentation, *Meles meles*, nodes, wildlife conservation

The continuous spread of human settlements and cultivated areas has dramatically decreased the extent of the original forests in many parts of the world, reducing them to fragments scattered in human-dominated landscapes (Fischer and Lindenmayer 2007).

As highlighted by Bennett (2003), forest fragmentation is not a random process, but “it is biased toward those areas that have the most fertile soils or are most accessible, such as plains and fertile river valleys.” Specifically, fragmentation is one of the main drivers of

biodiversity loss in European plains and wide valleys, where the original forests have been widely clear-cut to provide space for increasingly intensive agricultural practices (Darby 1956; Williams 2002).

Habitat fragmentation is the result of 2 distinct processes: the loss of original habitat and the reduction of habitat contiguity into spatially separated fragments (Mortelliti et al. 2010, 2011). Moreover, the often co-occurring overexploitation of natural resources can hasten the effects of the natural habitat degradation of remnants, converting residual fragments into unsuitable areas for many forest species (Fischer and Lindenmayer 2007; Dondina et al. 2015; Zimbres et al. 2017). In these contexts, species sensitive to fragmentation perceive the landscape as a set of small habitat patches surrounded by a hostile matrix, which prevents individual movements between forest fragments (Lindenmayer and Fischer 2013; Tucker et al. 2018). The difficulty to cross the unsuitable matrices decreases the ability to sustain declining populations in other fragments, to recolonize fragments where local extinctions have occurred, or to colonize new habitat patches expanding the species range (Taylor et al. 1993; Bennett 2003).

To counteract the negative effects of fragmentation on forest-dwelling species, it is crucial to ensure the maintenance of the ecological connectivity between forest fragments (Noss et al. 1997; Soulé and Terborgh 1999; Lindenmayer and Fischer 2013). Ecological connectivity in human-modified landscapes not only depends on the availability and spatial pattern of habitat patches (hereafter nodes, according to ecological network terminology), but also on low-quality habitats (hereafter connectivity elements, referring to both continuous corridors and stepping stones), which support movements through the inhospitable matrix (Bennett 2003; Eycott et al. 2012; Vasudev et al. 2015). Connectivity elements for forest-dwelling species in agricultural landscapes are typically represented by semi-natural elements with a physical organization similar to that of the forest habitat (Eycott et al. 2012), such as hedgerows (Hilty and Merenlender 2004; Gelling et al. 2007; Dondina et al. 2016), that is, linear strips of shrubs and trees along field boundaries, as well as arboriculture patches (Dondina et al. 2018). The maintenance and increase of these semi-natural elements in agricultural landscapes are needed to guarantee the functionality of ecological networks for forest-dwelling species, and, thus, to ensure their long-term persistence (Lechner et al. 2015). The use of habitat patches and the degree of connectivity between forest remnants provided by connectivity elements is strongly species-specific (Tischendorf and Fahrig 2000; Trainor et al. 2013; Dondina et al. 2017). First of all, a vegetation patch perceived as a high quality habitat by one species could be perceived as a low quality habitat or non-habitat by another, according to their ecological requirements. Generalist species can use several habitats, whereas specialist species are strongly linked to one or few habitats (Andren 1994). Moreover, the degree of landscape connectivity provided by the spatial arrangement of nodes and connectivity elements is affected by species-specific movement ability through the hostile matrix (Bowman et al. 2002; Cushman et al. 2013). This depends on the combined effect of a species' intrinsic movement ability throughout a habitat where its movement is not hindered by any factor (Ball and Goldingay 2008; Vasudev et al. 2015). This, in turn depends on multiple biological factors such as animal size (Jetz et al. 2004), and the degree of resistance opposed by the matrix. Landscape resistance depends on the species' degree of forest specialization (Beier et al. 2008; Cushman and Landguth 2012), with generalist species able to permeate disturbed and highly fragmented landscapes, due to their ability to use small patches of habitat and their surroundings, and specialists

generally limited to few well preserved, large patches of habitat (Devictor et al. 2008; Bueno et al. 2018). Therefore, when the final goal is the conservation of a whole forest species community, management actions aimed at increasing landscape connectivity should not focus on a single species, but on multiple species with different ecological needs in terms of habitat requirements, degree of forest specialization and movement ability (Cushman et al. 2013; Trainor et al. 2013).

In this study, we focused on a typical European fragmented landscape located in northern Italy and on 2 mammal species sensitive to forest fragmentation (Virgós 2001a, 2001b, 2002; Bani et al. 2002; Coulon et al. 2004), but characterized by a different size (and movement ability in continuous habitats) and degree of forest specialization: the European badger *Meles meles* and the Roe deer *Capreolus capreolus*. The European badger is a generalist forest species with maximum movement ability in continuous habitat of about 20 km (Byrne et al. 2014). Conversely, the Roe deer is a more specialist forest species with very high movement ability in continuous habitat (ranging from 40 to 120 km), and longer distances observed in populations that are colonizing new areas (Gaudin 1993; Wahlström and Liberg 1995). This is the case of the Roe deer population in our study area, where the species is recolonizing lowland areas from the continuous forests of the Ticino Natural Park and the Apennines (see "materials and methods" section for more details).

Our objectives were 1) to investigate whether hedgerows, poplar cultivations, short rotation coppices for biomass production (henceforth defined as biomass crops), and reforestations are perceived as connectivity elements or as nodes by the European badger and the Roe deer; 2) to identify the most likely maximum movement ability of the European badger and the Roe deer through the hostile matrix, defined as the distance at which nodes and connectivity elements are perceived as connected by the 2 species; and 3) to map and compare the current ecological networks for the 2 species in the whole study area.

Materials and Methods

Study area

This study was carried out in an area of about 2900 km² located in the western part of the Lombardy region in northern Italy (45°11' N 9°05' E). The lowland area of northern Italy (i.e., the plain of the Po river) is a typical example of a highly fragmented agricultural landscape, with small forest fragments scattered in an intensive cultivated and urbanized matrix (Canedoli et al. 2017). Specifically, it is characterized by intensively cultivated crops, in particular paddies (39.4%) and other annual crops (wheat, maize, and alfalfa; 29.1%), which cover most of the total surface. The remaining area includes built-up areas (10.3%), traditional poplar cultivations, biomass crops and reforestations (6.8%), and other categories (i.e., orchards, vineyards, meadows, and shrublands) which represent 7.5% of the area. Original forests cover only 4.9% of the total surface (DUSAF 4, ERSAP 2014). Continuous forests are located along the Ticino River, which crosses the study area from North to South, and in the hills of the Apennines, located in the southern part of the study area. The rest of the area shows a high degree of forest fragmentation (99% of forest remnants in agricultural areas are smaller than 1 km²) (Figure 1). The favorable conservation status of the original forests within the study area allows a rich animal community to survive, but at the time of data collection no natural predator or competitor of the European badger and Roe deer was present.

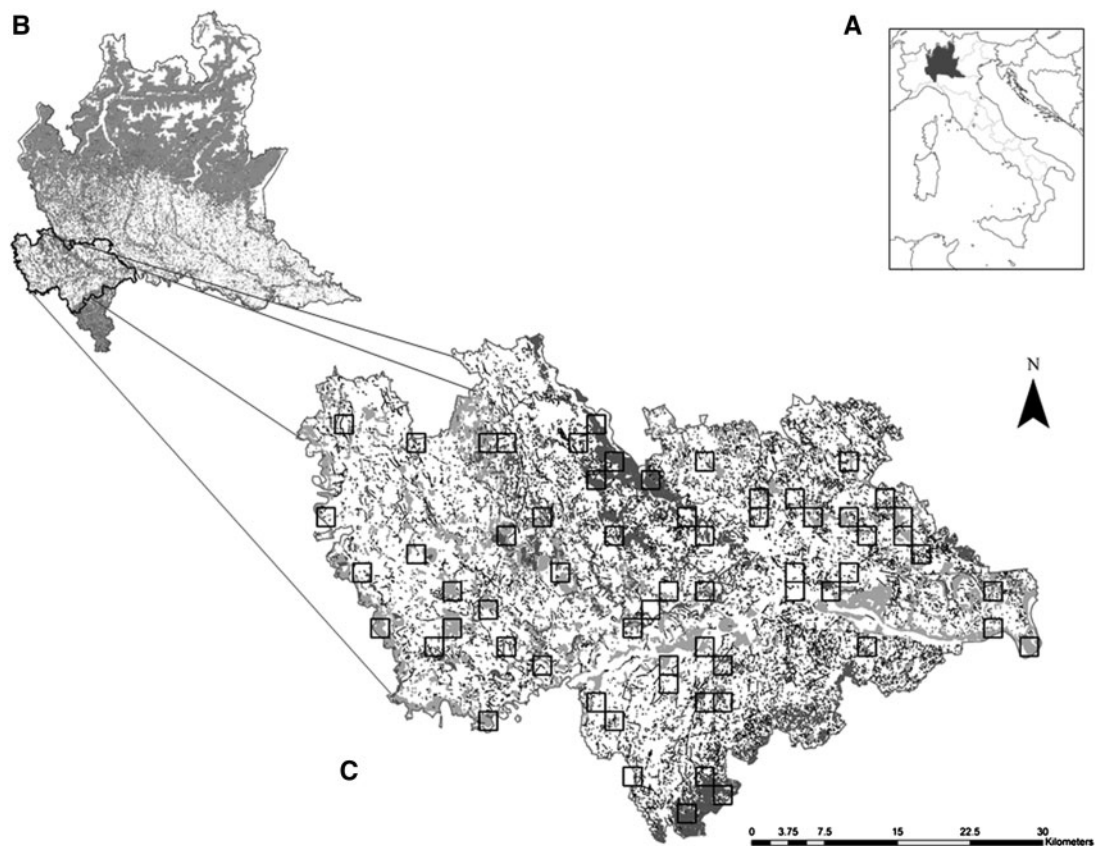


Figure 1. Lombardy region in northern Italy (A); forest cover in Lombardy in grey (B); study area with forests in dark grey, traditional poplar cultivations, short rotation coppices for biomass production and reforestations in light grey, and hedgerows in black (C). The black squares are the 62 2-km sampling cells.

Sampling design and data collection

Data collection followed a stratified cluster sampling design (Krebs 1999; Barabesi and Fattorini 2013). Strata corresponded to 10 homogeneous landscape units (LUs) composed of 2-km cells grouped through a k-means cluster analysis of 5 environmental variables: percentage of forest cover, distance from the nearest source area (continuous forests of the Ticino Natural Park or the Apennine chain), density of hedgerows, density of main roads, and degree of habitat fragmentation calculated using a modified proximity index (Bani et al. 2006) setting the proximity radius to 1 km (see Chiatante et al. 2017 for more details on the analyses performed for the sampling design definition). A 2-km grid was adopted to obtain cells including more than one individual home-range for both the European badger and the Roe deer (European badger: 3.83 km² for a family group, Remonti et al. 2006a; Roe deer: 1 km² for single individuals or small groups in fragmented landscape, San José and Lovari 1998; Cargnelutti et al. 2002; Melis et al. 2004; Lovari et al. 2008). The 10 LUs were defined as follows: LU 1, arable lands far from source areas (28.1%); LU 2, arable lands with high hedgerows density (15.7%); LU 3, moderate fragmented areas near source areas (11.5%); LU 4, source areas (8.5%); LU 5, moderately fragmented areas far from source areas (8.5%); LU 6, highly fragmented areas near source areas (5.7%); LU 7, arable land near source areas (22.3%); LU 8, human infrastructures (1.3%); LU 9, suburban areas (3.1%); LU 10, urban areas (0.7%).

Among the 620 2-km cells of the whole study area, we randomly selected 62 cells (covering 10% of the study area) allocated in the first 7 LUs (excluding human infrastructures, suburban areas and

urban areas) according to their cover percentage (Krebs 1999) (Figure 1). To assess the European badger and Roe deer occurrence within the selected cells we adopted a multi-level sampling design (Sutherland 2006) by superimposing a 250-m grid to each 2-km cell and randomly selecting 6 250-m cells (10% of the 2-km cell). Within each 250-m sampling cell, two 250-m linear transects, opportunistically located along footpaths, were identified. Between April and September 2014, we collected European badger and Roe deer data along 675 linear transects by spotting presence signs (latrines, setts, and footprints for the European badger, and frays, resting places, and footprints for the Roe deer).

Simulated species perceptions of the landscape setup

In order to investigate how the European badger and the Roe deer perceive hedgerows, poplar cultivations, biomass crops, and reforestations in our study area, we applied the simulated species perceptions of the landscape (SSPLs) comparison method proposed by Dondina et al. (2018). This method allows the identification of the role that a land cover type plays for a given species, that is, whether the species perceives the land cover type as a node, as a connectivity element or as hostile matrix. The method assumes that the largest part of the species occurrence data, which are associated to animals belonging to stable local populations, is found within nodes, whereas connectivity elements, even if crucial for the occupancy of nodes, are used only as crossing areas by relatively few individuals and are often found not to be occupied by the species (Dondina et al. 2018).

In this study, we identified the SSPLs corresponding to all possible combinations of hedgerows, poplar cultivations, biomass crops

Table 1. Roles alternatively assumed by woodlands, poplar cultivations, biomass crops, reforestations, and hedgerows in the SSPL setup for the European badger and the Roe deer

	Land cover type	Role		
		Node	Connectivity element	Matrix
European badger	Woodlands	W	–	–
	Poplar cultivations	P	p	0
	Biomass crops	B	b	0
	Reforestations	R	r	0
	Hedgerows	H	h	0
Roe deer	Woodlands	W	–	–
	Poplar cultivations	P	p	0
	Biomass crops	B	b	0
	Reforestations	R	r	0
	Hedgerows	–	h	0

Abbreviations were used to compose a 5-letter code describing each SSPL.

and reforestations, in the role of nodes, connectivity elements, or matrix. The assignment of a role affected the way in which landscape metrics (i.e., habitat amount and landscape connectivity) were calculated within each SSPL. Habitat amount was measured as the total surface of the patches belonging to all the land cover types that played the role of nodes, whereas landscape connectivity was calculated for all patches belonging to all the land cover types defined as either nodes or connectivity elements, merged together into a single land cover type. The simulated landscape model that better fitted the observed occurrence data of each species was considered as the actual species perception of the landscape (for more details see Dondina et al. 2018).

To set up the SSPLs for the European badger and the Roe deer, we merged 3 digital cartographies available for the study area (DUSAF 4, ERSAP 2014; Forest Management Plan of the Province of Pavia, Provincia di Pavia 2012; Agricultural Information System of Lombardy, SIARL-2013, ERSAP 2013) by using ArcGIS 10.0 (ESRI 2011). Among the land cover types of our study area, we considered *a priori* woodlands as nodes for both the European badger (Virgós 2001b; Balestrieri et al. 2009a; Piza Roca et al. 2014) and the Roe deer (Barančková 2004). We alternatively defined hedgerows, poplar cultivations, biomass crops, and reforestations as a node, a connectivity element, or a matrix for the European badger, whereas for the Roe deer we identified poplar cultivations, biomass crops, and reforestations as either a node, a connectivity element, or a matrix, and hedgerows as either a connectivity element or a matrix (Table 1). We tested hedgerows as a node for the European badger because the importance of this semi-natural element as a habitat for different mustelids has been highlighted in several studies (Hilty and Merenlender 2004; Šálek et al. 2009; Červinka et al. 2013). Conversely, we did not test hedgerows as a habitat for the Roe deer, as hedgerows can hardly represent nodes for a species of such size. We obtained 81 and 54 SSPLs for the European badger and the Roe deer, respectively.

For each SSPL, we calculated *Class Abundance (CA)* as a measure of habitat amount and the *Connectance Index (CONNECT)* as a measure of landscape connectivity by means of the software Fragstats 4.0 (McGarigal et al. 2002), for both species. CA was calculated as the sum of the areas (m²) of all the patches of a given land cover type obtained by merging together all the land cover types that played the role of nodes. CONNECT was calculated by

dividing the number of the existing connections between all the patches of a given land cover type obtained by merging together all the land cover types acting as nodes or connectivity elements (a threshold distance was defined beyond which 2 patches were no longer considered as connected to each other) and the maximum possible number of connections between all patches.

Both CA and CONNECT were calculated using a circular moving window, that is, a buffer area which moves from pixel to pixel of the whole landscape. Since the moving window should circumscribe an area corresponding to the spatial scale of the target species perception of the fragmentation phenomenon, we used a moving window with a radius of 2 km to calculate CA for both species. Conversely, we used moving windows with a different radius corresponding to different likely maximum movement abilities to calculate CONNECT for both the European badger and the Roe deer (see next paragraphs), under the assumption that species-specific landscape connectivity is mainly determined by species movement ability through the matrix.

Selection of the most likely movement ability of species through the matrix

To our knowledge, no empirical study has been carried out to evaluate the maximum movement ability through a hostile matrix, either for the European badger or for the Roe deer. The simple assumption of a single likely maximum movement distance from literature is hazardous, as movement ability plays a dominant role in affecting the degree of connectivity for a species in a fragmented landscape (Cushman and Landguth 2012). To correctly calculate CONNECT, we thus tested 3 different hypothetical maximum movement abilities for both species.

For the European badger, we tested 1 km, 2 km, and 4 km as likely maximum movement abilities through the matrix. We chose these distances because we excluded that a European badger would be able to cross the hostile matrix for more than 4 km, as the average of the mean daily movements in mosaics of habitat and non-habitat, calculated for 8 European badger populations in Europe, was 3.8 ± 0.7 km (Kowalczyk et al. 2006). Moreover, Loureiro et al. (2007) stated that the distance more frequently walked by the European badger in half an hour is 200 m, which, considering a mean summer night span equal to approximately 10 h, corresponds to 4 km travelled during a night. As individuals of this species only move during the night (during the day they rest in woodland areas), we assumed that the European badger cannot wait outside its habitat, or outside another semi-natural vegetation patch, not even for 1 day and, thus, that the distance between 2 nodes or connectivity elements should not be longer than the distance it can cross during a night, that is, 4 km. On the other hand, we set the minimum likely movement ability to 1 km because, considering the movement ability of the European badger, it is quite hard to imagine a minimum movement ability shorter than this distance.

For the Roe deer, we tested 3 different distances as likely maximum movement abilities through the matrix: 2 km, 4 km and 8 km. We chose these distances because in most of the Roe deer populations that have been studied in fragmented landscapes, where the species is typically closely tied to forest remnants (Hewison et al. 2001; Cargnelutti et al. 2002; Cimino and Lovari 2003), movement distances have been found to be rather short, that is, in the order of a few kilometers (San José and Lovari 1998; Coulon et al. 2004; Melis et al. 2004; Lovari et al. 2008). Coulon et al. (2004) reported that preliminary results showed a Roe deer movement ability of about 3 km in a highly fragmented area in southwestern France.

We thus set the minimum hypothetical movement ability of this species to 2 km and tested 2 higher hypothetical movement distances.

By combining the number of the land cover types alternatively considered as nodes, connectivity elements or matrix, and the 3 tested hypothetical movement abilities, we obtained a total of 243 SSPLs for the European badger and 162 SSPLs for the Roe deer.

Statistical analyses

For both the European badger and the Roe deer, we assigned a value of presence or absence to each 2-km cell, if the presence of the species was detected in at least one of the six 250-m sampling cell within the 2-km cell, or if none of the 250-m cells were occupied by the species, respectively. We assumed the absence of false negatives within our samples, as it is very unlikely that if both species occurred in a 2-km cell they would not be detected in at least one of the six 250-m cells (i.e., along 12 transects) (Tyre et al. 2003). We checked for spatial autocorrelation of the distribution data of both species at different distance classes (results not shown) by means of a Moran's I test with 999 permutations (Cliff and Ord 1981) using the *spdep* package (Bivand and Piras 2015).

For each SSPL set up, for both the European badger and the Roe deer, we assigned each 2-km cell the average of the *CA* and *CONNECT* values calculated for all the pixels falling within the cell. To assess the influence of habitat amount and landscape connectivity on the occurrence of the 2 species, we performed a binomial logistic regression model for each SSPL with the presence/absence of the species within each 2-km cell as the response variable and *CA* and *CONNECT* as independent variables. We considered the effect of the landscape context (i.e., the LUs used for the stratified sampling design) by including in each model an independent categorical variable with 7 levels, corresponding to all LUs except human infrastructures, suburban areas, and urban areas, where we did not locate 2-km sampling cells. For the European badger, we also considered the distance of the 2-km cell centroids to streams and rivers as a control covariate, as it has been demonstrated that this species does not build dens close to rivers in areas with a high risk of flooding (Hipólito et al. 2016), as is the case of our study area.

Considering the low number of presences (38 for the European badger and 23 for the Roe deer) compared with the number of independent variables (3 continuous and one categorical variable with 7 levels for the European badger; and 2 continuous and one categorical variable with 7 levels for the Roe deer) we performed the logistic models by applying a ridge regression penalty using the *rms* package (Harrell 2016) in R. By means of the *pentrace* command we solved for the optimum penalty factor for each model and, subsequently, we fitted the models using penalized maximum likelihood estimations.

Overall, we built up 243 models for the European badger and 162 for the Roe deer and evaluated the goodness of fit of each model by the bias-corrected R^2 , obtained by performing a resampling validation of each model by using the *validate* command with 500 repetitions. All statistical analyses were performed using R v. 3.1 (R Development Core Team 2014).

In order to present the results, we used a 5-letter code associated to each SSPL, where poplar cultivations, biomass crops, reforestations, and hedgerows were abbreviated in capital letters to indicate the role of nodes (P, B, R, H) and in lowercase letters to indicate the role of connectivity element (p, b, r, h), whereas 0 was used to indicate the role of matrix. Each code always starts with W because woodlands were only considered as nodes for both the European badger and Roe deer (see Table 1).

Results

European badger

Among the models performed for all 243 SSPLs built up for the European badger, those that generally better fitted the observed data belonged to the set of models based on a maximum species movement ability through the matrix of 2 km (Appendix, Table A1). Overall, R^2 values for the models pertaining to the 2-km movement scenario ranged between 0.085 and 0.189 (Figure 2). The best performing model was the one associated with the SSPL WPb0H ($R^2 = 0.189$), where poplar cultivations and hedgerows, other than woodlands, play the role of nodes, biomass crops play the role of connectivity elements, and reforestations are considered an unsuitable matrix. Starting from the best model we then predicted the species presence probability for the whole study area in order to create a map showing the most suitable and well-connected areas, that is, the current ecological network for the European badger. The priority areas for the European badger cover a large part of the territory (76% of the study area has a species presence probability higher than 50%) and, apart from a slight concentration along the Ticino River, they are quite uniformly scattered throughout the study area (Figure 4).

Roe deer

Among the models performed for the 162 SSPLs of the roe deer, those that generally better fitted the observed data belonged to the set of models with maximum species movement ability through the matrix of 2 km (Appendix, Table A2). Overall, R^2 values of the models pertaining to the 2-km movement scenario ranged between 0.242 and 0.360 (Figure 3). The best performing model was the one associated to the SSPL WPbRh ($R^2 = 0.360$), where poplar cultivations and reforestations, other than woodlands, play the role of nodes, whereas biomass crops and hedgerows play the role of connectivity elements. Starting from this model, we predicted the suitability for the species and created a map showing the current ecological network for the Roe deer in the study area. The priority areas for the Roe deer cover a small part of the territory (14% of the study area has a species presence probability higher than 50%) and they were found to be limited to the forest areas of the Ticino Natural Park (in the central part of the study area) and of the Apennines (in the southern part of the study area) and, secondly, to the most extensive poplar cultivations and reforestations (Figure 4).

Discussion

The comparison method of the SSPLs revealed a different perception of the landscape by the European badger and the Roe deer in our study area. Although our results are consistent with the literature and the ecological knowledge of the species in the study area, method assumptions, and limitations should be carefully accounted for.

If the method assumption of differential species occupancy between nodes and connectivity elements is not met, it may result that some land cover types are perceived as nodes although they actually only serve as connectivity elements for the studied species (see Dondina et al. 2018 for more details). In our study, we are quite confident that the analyzed data matched the method assumption, since the ecology of both the target species in the study area guarantees that their presence signs can generally only be found within nodes. Conversely, it is very unlikely to detect presence signs of the few dispersing individuals moving through

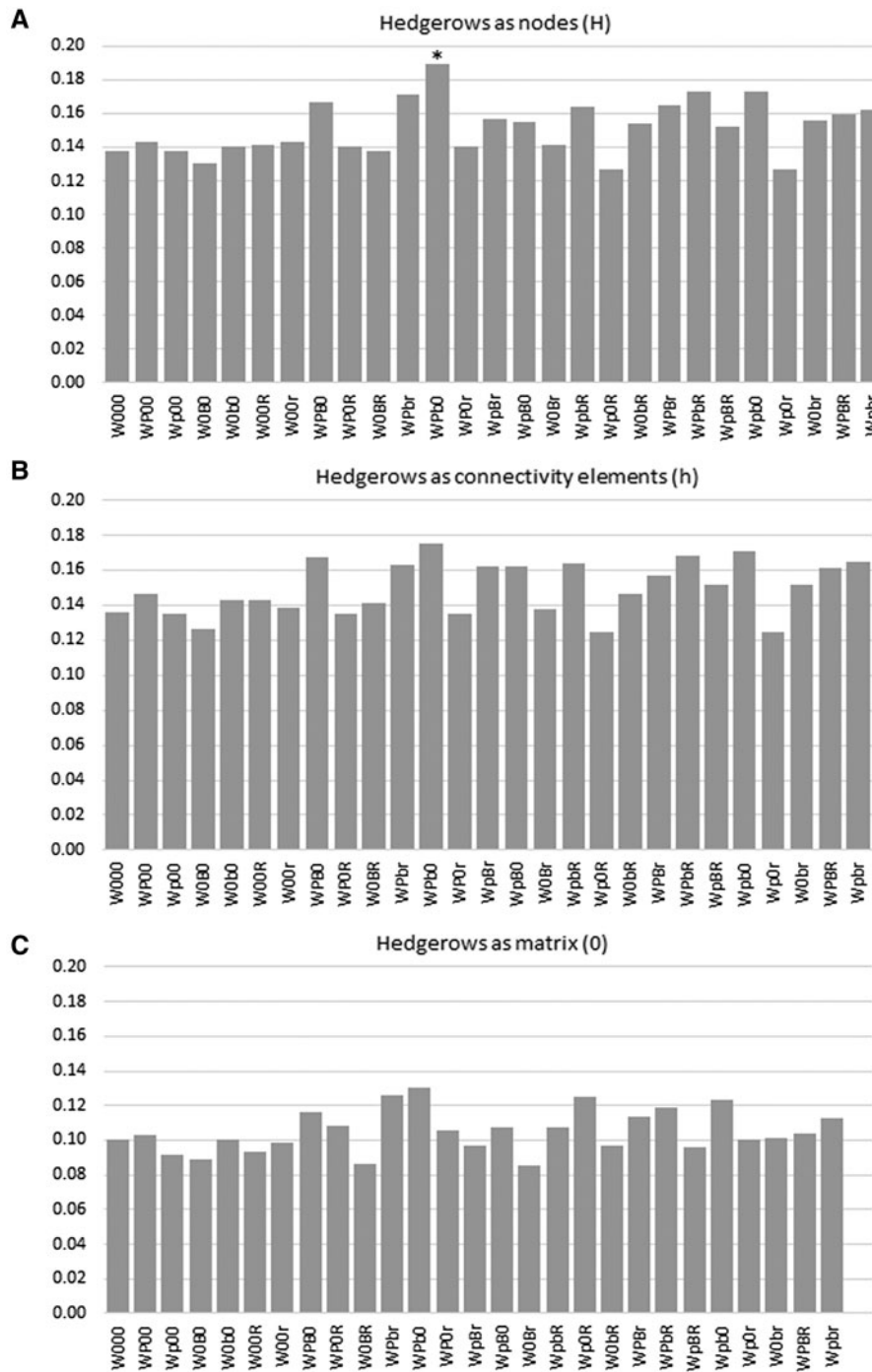


Figure 2. R² values of the European badger models belonging to the 2-km movement ability scenario. On the x-axis the 27 SSPLs combinations of poplar cultivations, biomass crops and reforestations as nodes (capital letters), connectivity elements (lowercase letters) or matrix (0) when hedgerows were considered as nodes (A), connectivity elements (B) or matrix (C), respectively. *The best performing model.

connectivity elements. The great difference of individual density between nodes and permeable areas is guaranteed for the European badger by its tendency to live in family groups in areas closely related to their dens complex that are located in nodes (Cresswell and Harris 1988; Carpenter et al. 2005; Remonti et al. 2006b; Balestrieri et al. 2009a). Similarly, Roe deer individuals were strongly linked to their home range within nodes during the study period, since in the first part of the period males were

territorial and females were engaged in giving birth, whereas in the second part both sexes were involved in reproduction (Hewison et al. 1998).

On the other side, a relevant limitation of the applied method is the lack of a statistical test to select the best model, particularly when differences between model goodness-of-fits are very small. This was the case of the European badger models, which were thus carefully discussed.

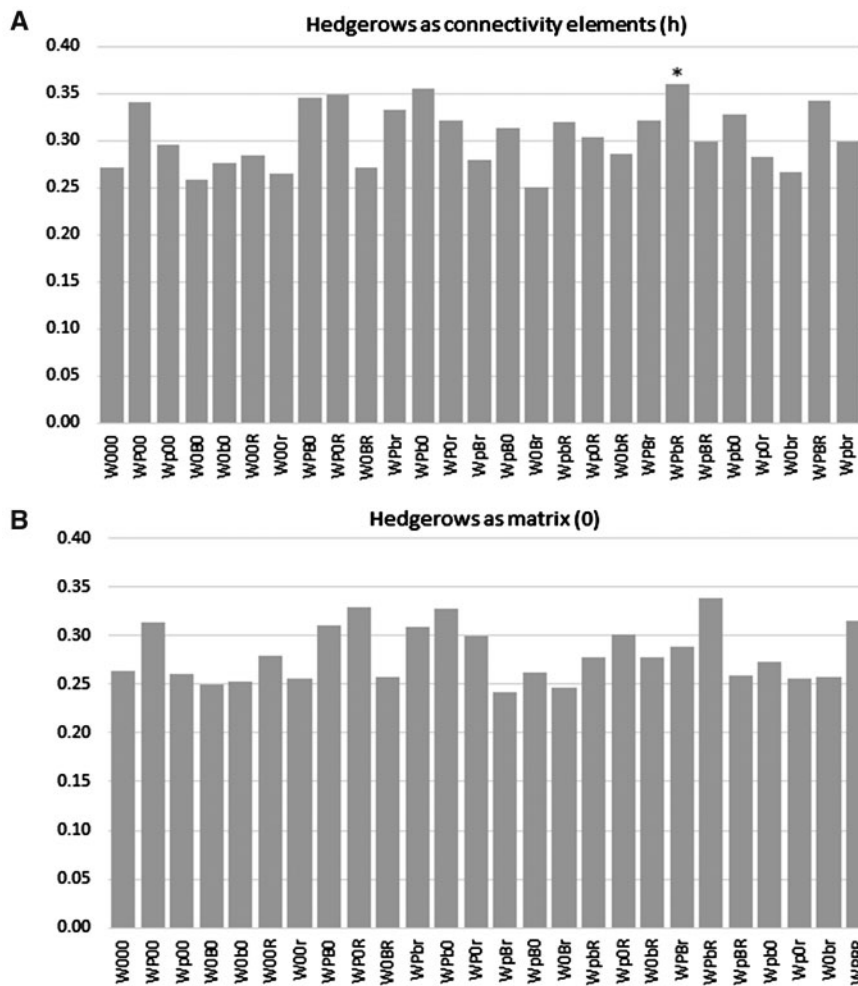


Figure 3. R² values of the Roe deer models belonging to the 2-km movement ability scenario. On the x-axis, the 27 SSPLs combinations of poplar cultivations, biomass crops, and reforestations as nodes (capital letters), connectivity elements (lowercase letters) or matrix (0) when hedgerows were considered as connectivity elements (A), or matrix (B). *The best performing model.

The SSPLs analysis showed that individuals of European badger use poplar cultivations and hedgerows as nodes and complementary resources of woodlands (Dunning et al. 1992), whereas biomass crops are only used as connectivity elements. As the European badger mostly feeds on earthworms living in the soil (Kruuk 1978; Balestrieri et al. 2004, 2009b; Cleary et al. 2009), the use of poplar cultivations as nodes could be due to the suitability of these arboreal plantations in providing foraging resources, whose abundance can improve badger occupancy in not extremely isolated patches (Mortelliti and Boitan 2008). Indeed, the scarcity of shrubs in typical poplar cultivations, as well as their ground layer management (i.e., plowing, mechanical weeding, etc.), increases the probability of finding food because of the easiness of digging in short grass layers (Piza Roca et al. 2014). On the other hand, in agricultural areas, hedgerows may offer coverage and suitable sett locations for the European badger (Dondina et al. 2016; Chiatante et al. 2017), as confirmed by the finding of setts during our surveys. Also O'Brien et al. (2016) remarked the importance of hedgerows for the European badger in areas with a very limited forest cover, suggesting that this species probably selects hedgerows because they provide shelters and abundant and diversified food resources (Thomas and Marshall 1999; Gelling et al. 2007; Facey et al. 2014).

In agricultural landscapes with few forests and meadows, which generally act as optimal foraging sites, poplar cultivations and hedgerows seem to be able to sustain European badger populations by ensuring suitable sites for foraging and den building. Conversely, biomass crops are probably used only as connectivity elements because of the low cut-frequency, which allows the growth of a well-developed shrub layer. In fact, the European badger tends to avoid areas with an excessive dense shrub layer (Virgós 2001b) as this prevents both the possibility of digging dens and that of searching for food in short grass.

The Roe deer models showed that this species tends to use woodlands, poplar cultivations and reforestations as nodes and biomass crops and hedgerows as connectivity elements. Early stage reforestations characterized by a well-developed and diversified shrub layer are, in fact, optimal habitats for this ungulate (Gill et al. 1996), both because they supply important food resources, such as fresh buds, and because they provide a complex vegetation structure offering suitable shelter (Gaillard et al. 1993). Reforestations are probably particularly important for this species during the vegetation period in late spring and early summer, which coincides with the period of births, when females choose places rich in understory to give birth and hide fawns (Hewison et al. 1998). Like the European badger,

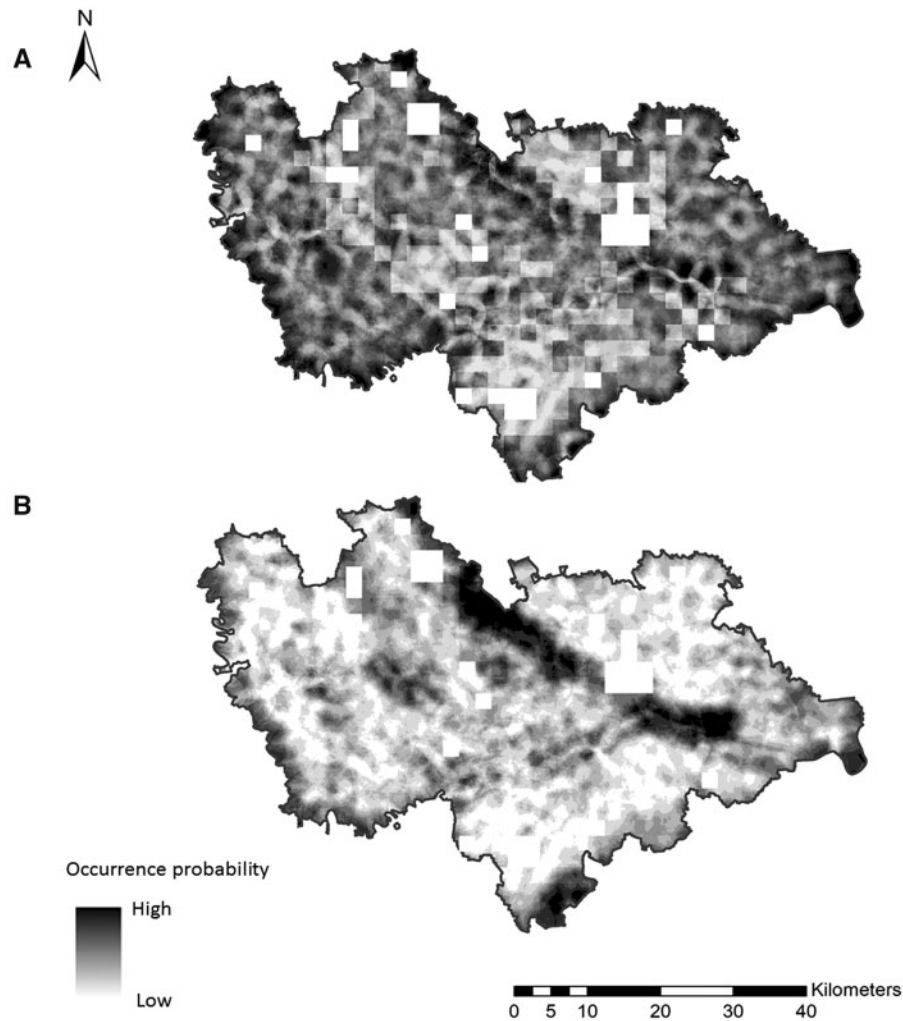


Figure 4. Ecological network for the European badger (A) and the Roe deer (B) in a highly fragmented area in northern Italy. The degree of suitability (i.e., occurrence probability) was predicted for both species based on habitat amount (CA) of all the land cover types that play the role of nodes and the connectivity degree (CONNECT) provided by all the land cover types that play the role of either nodes or connectivity elements. The predicted values also included the effect of distance to streams and rivers and LUs for the European badger, and of LUs for the Roe deer. White 2-km cells pertain to the LUs classified as human infrastructures, suburban areas, and urban areas for which no models were performed.

the Roe deer probably uses poplar cultivations as foraging sites, complementing and supplementing (*sensu* Dunning et al. 1992) the natural resources it can find in woodlands. Indeed, the Roe deer tends to move to open areas close to woodlands for searching of additional food resources within its home range (Cimino and Lovari 2003), and poplar cultivations are optimal grazing sites in agricultural landscapes because of the scarcity of shrubs and because poplars offer a good degree of canopy cover during the vegetation season. Conversely, biomass crops are only used by this species as connectivity element as they can provide shelters, but not adequate food resources. Being characterized by a well-developed mono-specific shrub layer, biomass crops are not suitable either for grazing activities or for finding diversified fresh buds.

The different perception of the considered land cover types and their different degree of suitability for the 2 species, together with the varying effect of landscape connectivity, led to large discrepancies in the predicted spatial distribution of the 2 species, with a widespread distribution of the generalist European badger as opposed to a clustered distribution for the specialist Roe deer. This pattern

follows simulated predictions, which estimated that specialist species occupy a smaller proportion of sites respect to generalists when the amount of unsuitable habitat increases and the colonization rate (inversely correlated to habitat fragmentation) decreases (Marvier et al. 2004).

The second main result of our study was the identification of the most likely maximum movement ability for both the European badger and the Roe deer through a matrix mainly composed of intensive crops. The analyses showed that it is plausible to hypothesize that both species can hardly cross the hostile matrix for more than 2 km in the absence of a landscape element that can act as a connectivity element. The average movement distance covered by the European badger in a mosaic of habitat and non-habitat patches along a convoluted night paths is 4 km (Loureiro et al. 2007) and, since this species only moves during the night (Kowalczyk et al. 2003; Goszczyński et al. 2005; Do Linh San et al. 2007) and we considered straight movements between nodes or connectivity elements, it is reasonable to assume that the maximum movement ability throughout the matrix is approximately half. This result is

consistent with a recent study carried out in southwest Britain in a landscape mainly characterized by pasture areas (Woodroffe et al. 2017), which reported about 2 km as the maximum distance travelled by GPS-collared individuals during a night. Conversely, 2 km is a very low maximum movement ability for a larger species, such as the Roe deer, but it is in agreement with the few known studies on movement ability in fragmented landscapes (Coulon et al. 2004; Lovari et al. 2008). Thus, in a human-modified landscape a species with a very high movement ability in continuous habitats, such as the Roe deer, can have the same maximum movement ability as a species characterized by much shorter movement ability through continuous habitat, but with a lower degree of forest specialization. These findings improve our understanding of the mechanisms that reduce the spatial displacement of mammals in anthropogenic landscapes and suggest that the degree of species forest-specialization can be a driver of the differential responses of animals to habitat fragmentation and modulates the general individual-behavioral or species-level mechanisms of matrix avoidance (Tucker et al. 2018).

Model spatial predictions allowed us to define a pattern and find differences in the extension and distribution of suitable and well-connected areas for the 2 species, that is, the functional ecological networks currently existing within the investigated landscape (Figure 4). The most suitable and well-connected areas for the Roe deer essentially follow the distribution of woodlands and, secondly, of reforestations and poplar cultivations (Figure 4b). This result highlights the strong tie that the Roe deer retains with woodlands or woodland surrogates in fragmented landscapes (Hewison et al. 2001) and the way in which this ecological requirement shapes the ecological network of the species. Lovari and San José (1997) suggested that the Roe deer does not stray from the woodland habitat to ensure a rapid escape to cover, whereas other authors reported that the strong link with wooded habitats during summer is probably mainly due to specific life stages, such as the birth and postnatal period (Gaillard et al. 1993), and social factors, such as the expression of male territoriality (Hewison et al. 1998). Conversely, a larger part of the study area was found to be quite suitable and well connected for the European badger (Figure 4a), for which the suitability of the area seems to be mainly affected by landscape context (corresponding to the LUs represented by the 2-km squares). These results highlight how the low degree of specialization of the European badger makes the species able to also exploit small patches of natural or semi-natural habitats, thus maintaining viable populations even in highly fragmented areas (Devictor et al. 2008; Chiantante et al. 2017). Nevertheless, we caution that this result arises from the comparison between low performing models (low R^2 values), which could confound the low degree of forest specialization of the European badger with the lack of other environmental variables that were not considered in our models and that may affect the species distribution.

The different spatial patterns of the ecological network identified for the European badger and the Roe deer suggest that, when implementing an environmental planning process for the conservation of the whole community, it should be carefully considered that the combined effect of the degree of suitability of different land cover types and the movement ability through the matrix of each species (Vasudev et al. 2015) leads to the identification of very different networks for specialists and generalists. If management actions for improving landscape connectivity were planned according to specialist species' network, conservation measures would probably be excessively extensive and economically inefficient. Conversely, ecological networks designed for generalist species would cover a high

percentage of the area, and management actions based on these networks would probably be excessively scarce and unable to significantly improve landscape suitability and connectivity for a large number of more demanding forest species. An effective intermediate approach would be the performance of multi-species studies by prioritizing the areas identified for habitat restoration from the ecological networks designed for specialist species according to 2 selective criteria. Indeed, both the connectivity gain that each area could guarantee for the specialist species if restored (see e.g., Clauzel et al. 2015) and the overlap of these areas with those identified as important areas for restoration from ecological networks designed for a generalist species should be considered.

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Author contributions

L.B., A.M., and O.D. conceived and designed the study; O.D. and G.C. collected data; O.D. and V.O. performed the analyses and wrote the paper.

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Appendix

Table A1. R² values of the binary logistic models performed for the 3 sets of 81 SSPL assuming a maximum movement ability of the European badger in the unsuitable matrix equal to 1 km, 2 km, and 4 km

SSPL ^a	Movement ability: 1 km			Movement ability: 2 km			Movement ability: 4 km		
	H	h	0	H	h	0	H	h	0
W000	0.116	0.116	0.138	0.138	0.136	0.100	0.130	0.136	0.096
WP00	0.131	0.130	0.116	0.143	0.146	0.103	0.138	0.148	0.111
Wp00	0.125	0.124	0.098	0.138	0.135	0.092	0.126	0.130	0.100
W0B0	0.120	0.123	0.135	0.130	0.126	0.089	0.137	0.134	0.122
W0b0	0.134	0.131	0.150	0.140	0.143	0.100	0.147	0.147	0.136
W00R	0.126	0.124	0.140	0.141	0.143	0.093	0.154	0.152	0.092
W00r	0.126	0.125	0.148	0.143	0.139	0.099	0.151	0.151	0.106
WPB0	0.140	0.140	0.092	0.167	0.167	0.116	0.164	0.158	0.095
WP0R	0.134	0.142	0.114	0.140	0.135	0.108	0.155	0.144	0.105
W0BR	0.135	0.130	0.112	0.138	0.141	0.086	0.156	0.162	0.085
WPbr	0.165	0.167	0.100	0.171	0.163	0.126	0.179	0.177	0.109
WPb0	0.146	0.142	0.103	0.189	0.175	0.130	0.173	0.174	0.099
WP0r	0.140	0.140	0.113	0.140	0.135	0.106	0.150	0.150	0.113
WpBr	0.161	0.160	0.085	0.157	0.162	0.097	0.154	0.152	0.083
WpB0	0.147	0.140	0.085	0.155	0.162	0.107	0.145	0.139	0.087
W0Br	0.136	0.128	0.115	0.141	0.138	0.085	0.156	0.160	0.082
WpbR	0.168	0.164	0.087	0.164	0.164	0.107	0.165	0.166	0.090
Wp0R	0.135	0.137	0.103	0.127	0.125	0.125	0.132	0.134	0.102
W0bR	0.136	0.132	0.118	0.154	0.146	0.097	0.168	0.167	0.090
WPBr	0.159	0.158	0.094	0.165	0.157	0.114	0.171	0.166	0.090
WPbR	0.162	0.167	0.107	0.173	0.168	0.119	0.179	0.182	0.099
WpBR	0.154	0.157	0.086	0.152	0.152	0.096	0.153	0.159	0.080
Wpb0	0.145	0.146	0.146	0.173	0.171	0.123	0.155	0.158	0.090
Wp0r	0.139	0.140	0.100	0.127	0.125	0.100	0.136	0.135	0.103
W0br	0.144	0.138	0.130	0.156	0.152	0.101	0.166	0.164	0.093
WPBR	0.162	0.160	0.092	0.159	0.161	0.104	0.175	0.164	0.091
Wpbr	0.169	0.165	0.100	0.162	0.165	0.113	0.164	0.162	0.096

Bold value denotes the best performing model.

^aThe 5 letters codes (4 letters in row and the last 1 in column) of the SSPLs is created assigning to each land-cover type (poplar cultivations, short rotation forestry for biomass production, reforestations, and hedgerows) the capital letter to indicate the role of node (P, B, R, H), the lowercase letter to indicate the role of connectivity element (p, b, r, h) and 0 to indicate the role of matrix. In row, the 27 combinations of poplar cultivations, short rotation coppices for biomass production, and reforestations in the role of nodes, connectivity elements or matrix. In column, the hedgerows in the role of nodes, connectivity elements or matrix, at 3 different maximum movement distances.

Table A2. R² values of the binary logistic models performed for the 3 sets of 54 SSLPs assuming a maximum movement ability of the Roe deer in the unsuitable matrix equal to 2 km, 4 km, 8 km

SSPL ^a	Movement ability: 2 km		Movement ability: 4 km		Movement ability: 8 km	
	h	0	h	0	h	0
W000	0.271	0.263	0.262	0.279	0.265	0.273
WP00	0.341	0.314	0.308	0.283	0.297	0.310
Wp00	0.296	0.260	0.254	0.253	0.268	0.263
W0B0	0.259	0.250	0.242	0.248	0.245	0.244
W0b0	0.276	0.253	0.260	0.264	0.264	0.277
W00R	0.284	0.279	0.280	0.275	0.286	0.274
W00r	0.265	0.256	0.254	0.259	0.258	0.270
WPB0	0.346	0.311	0.300	0.289	0.291	0.293
WP0R	0.348	0.329	0.324	0.329	0.331	0.326
W0BR	0.271	0.257	0.260	0.257	0.258	0.257
WPbr	0.333	0.309	0.300	0.300	0.303	0.300
WPb0	0.355	0.328	0.311	0.302	0.300	0.294
WP0r	0.322	0.300	0.301	0.302	0.304	0.306
WpBr	0.279	0.242	0.236	0.243	0.243	0.240
WpB0	0.313	0.262	0.245	0.239	0.247	0.237
W0Br	0.250	0.247	0.245	0.244	0.242	0.240
WpbR	0.320	0.278	0.281	0.285	0.282	0.286
Wp0R	0.303	0.301	0.271	0.274	0.286	0.288
W0bR	0.286	0.278	0.282	0.269	0.286	0.277
WPBr	0.322	0.288	0.287	0.293	0.287	0.332
WPbR	0.360	0.339	0.324	0.341	0.328	0.320
WpBR	0.298	0.259	0.258	0.260	0.263	0.262
Wpb0	0.328	0.273	0.258	0.253	0.264	0.259
Wp0r	0.282	0.256	0.252	0.251	0.267	0.266
W0br	0.267	0.258	0.264	0.264	0.262	0.257
WPBR	0.342	0.315	0.327	0.324	0.315	0.308
Wpbr	0.299	0.259	0.257	0.262	0.266	0.266

Bold value represent the best performing model.

^aThe 5 letters codes (4 letters in row and the last 1 in column) of the SSLPs is created assigning to each land-cover type (poplar cultivations, short rotation forestry for biomass production, reforestations and hedgerows) the capital letter to indicate the role of node (P, B, R), the lowercase letter to indicate the role of connectivity element (p, b, r, h) and 0 to indicate the role of matrix. In row, the 27 combinations of poplar cultivations, short rotation coppices for biomass production and reforestations in the role of nodes, connectivity elements or matrix. In column, the hedgerows in the role of connectivity elements or matrix, at 3 different maximum movement distances.