Ecological network design from occurrence data by simulating species perception of the landscape

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Abstract

Context Ecological networks are often designed based on the degree of suitability and permeability of land-covers, as obtained by estimating the statistical relationships between occurrence data and land-covers coverage using Habitat suitability models (HSMs). Considering

- only the coverage of land-covers, but not their spatial arrangement, frequently prevents HSMs
 from correctly identifying nodes and connectivity elements for the target species.
 Objectives We propose a new approach in the design of ecological networks starting from the
 relationship between occurrence data and both land-covers coverage and spatial arrangement, as
 calculated for different simulated species perceptions of the landscape (SSPLs, corresponding to
- 10 different combinations of land-covers alternatively assuming the role of nodes, connectivity elements, or matrix).

Methods The approach consists of comparing the ability of the amount of nodes coverage and the connectivity degree provided by both nodes and connectivity elements, calculated for each SSPL, to explain the observed species occurrence. The SSPL that performs better than the others will

15 provide information about the land-covers that should be used to design an ecological network for the target species, and their role.

Results When applied to the Hazel Dormouse in an agricultural landscape in northern Italy, the method proved effective and allowed us to identify woodlands and hedgerows as nodes, and poplar cultivations, biomasses and reforestations as connectivity elements.

20 *Conclusions* The proposed method can be adopted to identify nodes and connectivity elements for virtually every species sensitive to fragmentation, and has important practical implications when integrated in landscape management plans developed to guarantee ecological connectivity.

Key-words

25 Arboreal plantations, connectivity, forests, fragmentation, Hazel Dormouse, hedgerows.

Introduction

In order to counteract the negative effects of habitat fragmentation, wildlife conservation strategies should be implemented at the landscape level, linking residual habitats to guarantee their ecological connectivity (Noss et al. 1997; Soulè and Terborgh 1999). In this context, the

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appropriate landscape management tool is the ecological network (Bennett 2003; Andersons and Jenkins 2006), an integrated landscape system composed of nodes linked by corridors (Forman 1995). Nodes are fragments of suitable habitat, while corridors are composed of connectivity elements, characterized by permeable habitat, which allow dispersal between nodes. Nodes and connectivity elements are surrounded by matrix, represented by land-covers virtually

impermeable to the animals' passage.

Ecological networks are sometimes designed using an expert-based approach, where nodes and connectivity elements are identified among land-covers regarded as suitable or permeable based on experts' opinions. Since experts' opinions do not always reflect landscape effects on animal dispersal in an accurate manner (Shirk et al. 2010; Zeller et al. 2012; Mateo-Sánchez et al. 2015), some authors proposed the use of Habitat Suitability Models (HSMs; Douglas 1994; Bani et al. 2002; O' Brien et al. 2006; Beier et al. 2008) to identify suitable and permeable habitats (i.e. nodes and connectivity elements, respectively). These models estimate the relationship between the observed species distribution and the amount of land-covers at or around the locations where species occurrence was detected (Mateo- Sánchez et al. 2015), whereby species suitability maps

45 for the whole landscape can be drawn. Suitability maps are often used to identify nodes (i.e. patches belonging to land-covers with the highest suitability degrees) and to set up landscape resistance surfaces, which reflect the local cost of movement experienced by individuals, by associating a value inversely related to suitability to each pixel of the map (Bani et al. 2015;

Mateo-Sánchez et al. 2015). Starting from nodes and resistance maps, routes of low resistance

- between nodes are identified as permeable corridors along which individuals preferentially disperse in the landscape (McRae et al. 2008; Cushman et al. 2013; Mateo-Sánchez et al. 2014). However, habitat suitability and landscape permeability are not necessarily synonymous (e.g. Spear et al. 2010; Zeller et al. 2012) and several studies found that habitat suitability was a poor predictor of permeable corridors (e.g. Horskins et al. 2006; Wasserman et al. 2010; Reding et al.
- 2013; Peterman et al. 2014). More rigorous methods to parameterize resistance surfaces in order to identify corridors are based on movement (Cushman and Lewis 2010; Richard and Armstrong 2010; Zeller et al. 2012) and genetic (Cushman et al. 2006; Storfer et al. 2007; Balkenhol et al. 2009; Shirk et al. 2010; Wasserman et al. 2010; Bani et al. 2015; Mateo-Sánchez et al. 2015) data. Nevertheless, occurrence data are often the only ones available, since they are the most
 easily collectable empirical data (Zeller et al. 2012). It is thus crucial to develop effective methods allowing a correct identification of nodes and connectivity elements starting from occurrence data.

In a landscape fragmented for a sufficiently long time, the occurrence of a species sensitive to fragmentation is the result of how the species perceives the different land-covers (i.e. as nodes, connectivity elements or impermeable matrix) and how the amount and spatial arrangement of land-covers have affected the species over time. Starting from this consideration, the main issues concerning the use of occurrence data to develop HSMs in connectivity studies arise from the assumption that occurrence is affected by the amount of land-covers only, without considering the degree of connectivity between patches belonging to the different land-covers. First, HSMs which not consider the spatial arrangement of land-covers may not identify some land-covers as suitable, i.e. as nodes, for the target species. For instance, if the patches belonging to a potentially suitable land-cover are mostly isolated in the landscape, a HSM could return that the considered

land-cover is not selected or even avoided by the target species. However, the limited species occurrence within this land-cover does not depend on its intrinsic characteristics, but on its own

- 75 spatial arrangement and on the spatial arrangement of other suitable or permeable land-covers within the landscape. The suitability of such a land-cover for the target species can be detected only by taking into account the spatial arrangement of all the non-matrix land-covers within the HSM. The second problem with HSMs is the difficulty of these models to identify which landcovers are perceived as permeable, but not suitable, by the target species, which prevents a
- 80 correct identification of connectivity elements composing corridors. Indeed, connectivity elements are mostly used by dispersing juveniles, and adults and juveniles select habitats and connectivity elements, respectively, in a very different way. Adults select habitats where they can establish home-ranges and breed, while the juveniles' dispersal is mainly driven by permeable habitats that are often unlikely to be suitable habitats for foraging, sheltering, resting or breeding
- 85 (Mateo-Sánchez et al. 2015). The largest part of occurrence data, which are mainly represented by individuals belonging to stable local populations, is thus found within nodes, while connectivity elements are often found not to be occupied by the species. For this reason, HSMs that only estimate the relationship between species occurrence and the coverage of land-covers rarely detect the importance of connectivity elements for the target species (Mateo-Sánchez et al.
- 90 2015). The role of connectivity elements in increasing occurrence probabilities within well connected nodes can be detected, again, only by considering the spatial arrangement of both nodes and connectivity elements within HSMs.

To overcome all these issues, species occurrence should be regressed on the amount of nodes coverage and on the degree of connectivity provided by both nodes (i.e. spaces where

95 connectivity exists; habitat availability concept, Saura and Rubio 2010) and connectivity elements. Disregarding the coverage of connectivity elements within HSMs is not a secondary

issue, because it does not necessarily relate to species occurrence. First, because we do not find occurrence data within connectivity elements, and secondly because connectivity elements are not required to occupy a large part of the landscape to sustain dispersal between nodes.

- 100 Nevertheless, there are some practical constraints in the calculation of the coverage of the land-covers that play the role of nodes and the connectivity degree provided by the land-covers that act as nodes or connectivity elements. Indeed, even if HSMs could theoretically consider all land-covers and their amount and connectivity degree (e.g. Bani et al. 2006), it is not correct to insert them as separate main effects in the model because, if different land-covers are perceived
- 105 by a species in a similar way (as nodes or connectivity elements), they should be merged in a unique land-cover characterized by its own amount and connectivity degree. For instance, if two patches (patch *a* and patch *b*) belonging to two different permeable land-covers connect two nodes, and we calculate three different connectivity indices (one considering the spatial arrangement of the land-cover of nodes, a second one considering the spatial arrangement of the
- land-cover of patch *a*, and the last one considering the spatial arrangement of the land-cover of patch *b*), they all will reveal a low degree of connectivity within the landscape considered.
 Instead, if the connectivity index is calculated merging the land-covers of the two nodes (which, by definition, also act as connectivity elements) and the land-covers of both the patch *a* and the patch *b* in a unique hypothetical land-cover, it will indicate a high degree of landscape
- 115 connectivity. This happens because, in this example, connectivity is guaranteed by the presence of both nodes and permeable patches, which jointly play the role of stepping-stones between the two nodes. Thus, before calculating the coverage and the connectivity degree of land-covers, we need to know which land-covers are perceived by the target species in a similar way (i.e. as nodes or connectivity elements). However, to obtain this information we would need to develop models

120 that already take into account both land-covers coverage (i.e. habitat amount) and connectivity degree.

To overcome this vicious circle, we proposed a new method to define how a given species perceives the different land-covers. We started from the hypothesis that occurrence data are affected by nodes coverage and by the connectivity degree provided by both nodes and connectivity elements in order to set up different simulated landscapes. We then defined the simulated landscape that better fitted the observed occurrence data as the actual species perception of the landscape. We tested the proposed method on the occurrence data of the Hazel Dormouse (*Muscardinus avellanarius*), a protected small-size arboreal rodent (Annex IV of the Habitats Directive; Council Directive 92/43/EEC), in a fragmented agricultural landscape in northern Italy.

Methods

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Theoretical framework

In this paper, we propose a method to identify the elements of an ecological network (i.e. nodes and connectivity elements) for a target species by inferencing the species' perception of the different land-covers starting from its current occurrence within the landscape.

This method can be adopted to identify the species' perception of every land-cover. However, according to the ecology of the target species or to specific research hypotheses, it is reasonable to previously select a subset of land-covers that could play an effective role in an ecological network for the target species. In this case, all the other land-covers would be considered *a priori* as impermeable matrix (Fig. 1a).

The first step of the method consists of building up all the possible simulated species perceptions of the landscape (SSPLs) corresponding to all the combinations of the land-covers considered, alternatively assigning them the role of nodes, connectivity elements or impermeable matrix (Fig. 1b). The assignment of a role affects the way in which landscape metrics will be calculated within each SSPL. Habitat amount will be calculated as the total surface of the patches belonging to all the land-covers that assume the role of nodes, while landscape connectivity will be measured from all the land-covers considered as nodes or connectivity elements, merged together in a single land-cover. For instance, if we consider four land cover types (*a*, *b*, *c*, *d*), in order to build up the SSPL in which land-covers *a* and *b* play the role of nodes, land-cover *c*

plays the role of a connectivity element and land-cover *d* plays the role of matrix, we will calculate the amount of habitat of a new artificially created land-cover composed of the land-covers *a* and *b* merged together, and the landscape connectivity of a new land-cover composed of land covers *a*, *b* and *c* merged together. Land-cover *d* is not included in any calculation.
Considering *n* land-covers, alternatively assuming the three possible roles, we would obtain 3ⁿ

155 SSPLs (Fig. 1c).

The second step of the method consists of identifying the actual species perception of the landscape by comparing the ability of the different SSPLs to explain the variability of the occurrence data of the target species collected within the landscape. This can be achieved by performing, for each SSPL, a statistical regression model where the dependent variable is species

160 occurrence and the independent variables are habitat amount and landscape connectivity, calculated as described above (Fig. 1d). We assume that the model performing better than the others in fitting the observed occurrence data will correspond to the SSPL representing the landscape effectively perceived by the target species (Fig. 1e). The SSPL associated to the best

model will then provide information about the land-covers that should be used as nodes andconnectivity elements in order to design an effective ecological network for the target species.

#Figure 1 approximately here#

A case study: an ecological network for the Hazel Dormouse in a fragmented agricultural landscape in northern Italy

We tested the proposed method on occurrence data of the Hazel Dormouse, a species particularly sensitive to habitat loss and fragmentation (Mortelliti et al. 2010; Keckel et al. 2012), because of its very low dispersal capability (Juškaitis 2008; Bani et al. 2017). For this reason, we can assume that the variability of the species' occurrence at a large scale, where the effect of micro-habitat characteristics is less important, is mainly influenced by the coverage of suitable habitats (i.e. nodes) and by the connectivity provided by suitable and permeable habitats (i.e. connectivity

- 175 elements). We adopted the proposed method to assess the role that hedgerows and arboreal cultivations (poplar cultivations, plantation for biomass production, henceforth defined as biomasses, and reforestations) could play in an effective ecological network for the Hazel Dormouse in a lowland area of northern Italy. We hypothesize that hedgerows and reforestations could play the role of nodes, because they are generally characterized by well-developed shrub
- 180 layers that are particularly suitable for the small rodent (Juškaitis 2008; Dondina et al. 2016). Conversely, we do not have any hypothesis on how poplar cultivations and biomasses are perceived by the Hazel Dormouse, as their effect on this species have never been tested.

Study area

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The study was carried out in the western part of Lombardy (northern Italy, 45°21' N 8°80' E, Fig. 2), in an area of about 1,300 km² bordered by three main rivers, the Sesia, Po and Ticino. This

area shows the typical characteristics of a European lowland agro-ecosystem, with a prevalence of intensive cultivated crops, which represent 77% of the total surface and mainly consist of rice paddies. The remaining area includes built-up areas (9%), poplar cultivations, biomasses and reforestations (7%) and original forest remnants (7%, 99% of which are smaller than 1 km²).

190 Even though the study area shows a high degree of forest fragmentation, its eastern part falls within the boundaries of the Ticino Natural Park, a 220 km² wide protected area with residual continuous forests, which represents the main source area for several forest-dwelling species.

#Figure 2 approximately here#

Sampling design and data collection

Data collection followed a stratified cluster sampling design. Strata corresponded to 10 homogeneous Landscape Units (LUs) composed of 2-km cells grouped through a k-means cluster analysis on five environmental variables: percentage of forest cover, distance from the source area (Ticino Natural Park), density of hedgerows, density of main roads and degree of habitat fragmentation calculated by means of a Modified Proximity Index (MPI; Bani et al. 2006) setting

the proximity radius to 1 km.

Among the 325 2-km cells of the study area, we randomly selected 30 cells (covering about 10% of the study area), allocated in each LU in proportion to its size, as primary sampling units (Fig. 2). Within each primary sampling unit, we randomly selected six 250-m cells, which represent the secondary sampling units. In order to detect the presence of the Hazel Dormouse,

205 we placed nest-tubes baited with hazelnuts in each secondary sampling unit hosting land-covers that were potentially suitable for the species (woodlands, arboreal plantations and hedgerows). In order to maintain a constant sampling effort, we placed a number of nest-tubes proportional to the extension of the potentially suitable land-covers within each secondary sampling unit, setting a maximum of eight nest-tubes per cell. The nest-tubes were located at a distance of 50 m one from

each other (Juškaitis 1997; Mortelliti et al. 2011). We placed 722 nest-tubes in 118 secondary sampling units (see Table S1), which were inspected once each spring during two consecutive years (March-July 2014 and 2015). Overall, we detected the presence of the Hazel Dormouse in 63 secondary sampling units (Table S1). A nest-tube was considered to be occupied if we observed any individuals in it during at least one visit, or if we found any nests or feeding signs
on the hazelnuts that we left to attract the animals.

Simulated Species Perceptions of the Landscape (SSPLs) setup

In order to set up the SSPLs for the Hazel Dormouse, we considered the most recent digital landuse cartographies available for the study area (Forest Management Plan of the Province of Pavia, Provincia di Pavia 2012; DUSAF 4, ERSAF 2014; Agricultural Information System of

220 Lombardy, ERSAF 2013). Among the 18 land-covers characterizing our study area, we considered *a priori* woodlands as suitable habitats for the Hazel Dormouse (Bright and Morris 1990; Juškaitis 2008; Mortelliti et al. 2014), and poplar cultivations, biomasses, reforestations and hedgerows as potentially suitable.

Starting from the spatial configuration of the land-covers considered in the original landscape, we implemented 81 SSPLs. In every SSPL, we always assigned the role of nodes to woodlands, while we alternatively assigned the role of a) nodes, b) connectivity elements, or c) matrix to poplar cultivations, biomasses, reforestations and hedgerows. For each SSPL, we then calculated the *Class Abundance* (*CA*) as a measure of habitat amount and the *Connectance Index* (*CONNECT*) as a measure of landscape connectivity using the software Fragstats 4.0 (McGarigal the patches belonging to a land-cover obtained by merging together all the land-covers playing the role of nodes, divided by 10,000 (for conversion to hectares).

$$CA = \sum_{j=1}^{n} a_{ij} \left(\frac{1}{10000}\right)$$

Where a_{ij} is the area (m²) of the patch *j* belonging to class *i*.

235 *CONNECT* was calculated by dividing the number of the existing connections between all the patches belonging to a land-cover obtained by merging together all the land-covers acting as nodes or connectivity elements (placing a threshold distance beyond which two patches were no longer considered as connected to each other) and the maximum possible number of connections between all patches. The result was then multiplied by 100 to obtain the percentage value.

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$$CONNECT = \left[\frac{\sum_{j \neq k}^{n} c_{ijk}}{\frac{n_i(n_i - 1)}{2}}\right] (100)$$

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Where c_{ijk} is the existing connection between patches *j* and *k*, belonging to class *i*; and n_i is the total number of patches belonging to class *i* within the investigated area. The value of this index ranges between 0, when there is a single patch or there are patches that are not connected to each other, and 100, when each patch is connected to the others. The threshold distance beyond which two patches are considered as not connected to each other should be set to the maximum dispersal ability of the target species in unsuitable habitats. If this information is unknown or doubtful, different threshold distances should be tested, repeating the SSPLs setup for every hypothesized threshold. For this study, we set the *CONNECT* threshold distance to 200 m. We obtained this value by averaging different documented values of Hazel Dormouse dispersal

ability in unsuitable habitats (100 m, Bright 1998; 250 m, Büchner 2008; 100-300 m, Mortelliti et al. 2013).

We chose *CONNECT* as a landscape connectivity index since Wang et al. (2014) highlighted that a good connectivity index should be independent of habitat abundance in order to disentangle the effects of habitat amount and landscape connectivity and, at the same time, it should be able to differentiate landscapes with different spatial aggregations. The authors demonstrated that among the connectivity indexes calculated by Fragstats 4, *CONNECT* shows a very low dependency on habitat abundance, especially in landscapes where the habitat type is rare. Moreover, among all the indexes independent of habitat abundance, *CONNECT* is the only one that can distinguish between landscapes with a different spatial aggregation.

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- 260 The two metrics were calculated using a Moving Window, a buffer area which moves from pixel to pixel of the whole landscape, circumscribing a portion of the landscape where the values of *CA* and *CONNECT* are calculated. The Moving Window should circumscribe an area corresponding to the scale of the target species' perception of the fragmentation phenomenon. In this study, we used a circular Moving Window with a radius of 250 m. This measure
- 265 circumscribes an area that could potentially host a minimum viable population of Hazel Dormouse and that is comparable to the average dispersal distance covered by the species in suitable habitats (Juškaitis 1997), and to the maximum distance covered in unsuitable habitats, as suggested by Mortelliti et al. (2010).

For each SSPL, we thus obtained two raster files, one for *CA* and one for *CONNECT*, in which each pixel takes the value corresponding to the metrics calculated within the Moving Window centred on it.

Layers arrangement was performed using the software ArcGIS 10.0 (ESRI 2011).

Statistical Analyses

We considered the secondary sampling units as Statistical Units (SU). We assigned a value of

- 275 presence to each SU, if the presence of the Hazel Dormouse was detected in at least one nest-tube of the SU, or absence, if none of the nest-tubes were occupied by the species. We excluded the presence of spatial autocorrelation in the Hazel Dormouse distribution data at different distance classes by means of the Moran's I test with 999 permutations (Cliff and Ord 1981) using the *spdep* package in R (Bivand et al. 2005). Subsequently, for every SSPL, we assigned to each SU
- 280 the CA and CONNECT averages of the pixels where nest-tubes were placed within the correspondent SU. In order to assess the influence of habitat amount and landscape connectivity on the presence of the Hazel Dormouse within each SSPL, we performed Generalized Linear Mixed Models (GLMMs) with a Binomial distribution. We used the presence/absence of the Hazel Dormouse as the response variable, the primary sampling units (2-km cells) as a random
- 285 factor and *CA* and *CONNECT* as fixed factors. In order to account for the possible effect of the habitat within which we placed the nest-tubes, we included in each model an independent categorical variable with five levels: woodland, poplar cultivation, biomass, reforestation and hedgerow.
- Recently, different studies have highlighted the need to account for imperfect detection when
 dealing with occurrence data (MacKenzie et al. 2003; Royle 2006; Royle and Dorazio 2006; Kéry and Schaub 2012). In our case, we should have performed mixed (with primary sampling units as a grouping random effect) multi-season models with spatial replicates (nest-tubes) as an alternative to temporal within-season replicates (Kéry and Schaub 2012). However, the inclusion of random effects in occupancy models can be achieved only by a Bayesian approach whereby
 model comparison is a challenge, because the standard Bayesian AIC-analog, DIC, is still

considered unreliable (Kéry and Schaub 2012). As the model comparison is the centrepiece of our approach, we had to adopt a frequentist approach. We decided to disregard the imperfect detection bias and to maintain the random effect, since its influence is inherent in the sampling design. On the other hand, as the use of nest-tubes has been proved to be particularly effective in

300 Hazel Dormouse surveys (Vogel and Duplain 2012), it is very unlikely that, if the species occurs in a secondary sampling unit, it will not colonize at least one of all the nest-tubes placed within the secondary sampling unit in two consecutive years.

Overall, we built up 81 models, one for each SSPL, and evaluated the goodness of fit of each model by the conditional R-squared. The model that performed better corresponded to the landscape actually perceived by the Hazel Dormouse.

All statistical analyses were performed using R v. 3.1 (R Core Team 2014).

Results

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The conditional R-squared values of the models performed for all the 81 SSPLs are shown in Table 1. We created a five-letter code for each SSPL. We adopted 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 for each land-cover. Each code always started with W (in capital letter) because woodlands were only considered as nodes. The rows in Table 1 show the 27 combinations of poplar cultivations, biomasses and reforestations as nodes, connectivity elements or matrix, whereas the columns discern hedgerows as nodes, connectivity elements or
matrix.

The 81 models performed showed conditional R-squared values ranging between 0.256 and 0.530. The 10 best performing models were found to be associated to conditional R-squared values ranging between 0.457 and 0.530. Overall, the model that performed better than all the

others was associated to the SSPL WpbrH (R²=0.530), where hedgerows, other than woodlands,
play the role of nodes, while poplar cultivations, biomasses and reforestations are considered as connectivity elements. Within this model both *CA* and *CONNECT* had a positive effect on species occurrence probability. Other two models only showed an R² higher than the 0.5 threshold; they were associated to the SSPL Wpb0H (R²=0.517) and Wp0rH (R²=0.518) which differ from the best SSPL only for reforestations and biomasses, respectively, in the role of matrix rather than of connectivity elements.

#Table 1 approximately here#

Discussion

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The results obtained by applying the proposed method to distribution data of the Hazel Dormouse in a fragmented area in northern Italy, proved the effectiveness of this new approach. Indeed, the method allowed us to objectively order all the performed models and to identify the model associated to the SSPL that most likely corresponded to the actual species perception of the

landscape. The reliability of the method can be assumed based on the fact that the SSPLs associated with the 10 best performing models were very similar to the SSPL associated with the best model in terms of the role assigned to the different land-covers (Table 1).

- 335 Starting from the SSPL associated with the best model, we were able to define how an ecological network for the conservation of the Hazel Dormouse should be designed in a highly fragmented agro-ecosystem, by clarifying the perception of the different land-covers by the species. In particular, hedgerows, other than woodlands should be considered as nodes, while poplar cultivations, biomasses and reforestations should be treated as connectivity elements.
- 340 These results have important practical consequences. The use of hedgerows as conservation tools

to mitigate the effect of habitat fragmentation has been widely debated over the past two decades (Davies and Pullin 2007). On the one hand, it has been asserted that there is insufficient evidence to define if hedgerows act as connectivity elements or are ineffective in promoting species dispersal. On the other hand, some authors proposed the possibility that hedgerows represent not 345 only effective connectivity elements, but also suitable habitats for small mammals (Henein et al. 1998; Laurence and Laurance 1999; Tattersall et al. 2002; Wolton 2009). The application of our approach confirmed the hypothesis that hedgerows should be used as nodes in an ecological network designed for the Hazel Dormouse and, thus, that they represent suitable habitats for the species in our study area. This result is supported by the discovery of nests occupied by females with litter within hedgerows during our surveys. An adequate spatial configuration of hedgerows 350 and a correct management of their internal characteristics (Dondina et al. 2016) are thus crucial to guarantee the conservation of the Hazel Dormouse in agricultural landscapes. Moreover, this approach allowed us to clarify the role of reforestations in an ecological network for a small mammal particularly sensitive to habitat fragmentation. Differently from what we expected, our analyses revealed that reforestations could play the role of connectivity elements, but not of 355 nodes. This is unlikely to depend on structural and floristic characteristics of reforestations, which, being an intermediate successional vegetation stage, represent the most suitable habitat for the Hazel Dormouse (Capizzi et al. 2002; Juškaitis 2008). Rather, it probably depends on the intrinsic short-time permanence (generally 20 years) of this land-cover in agro-ecosystems, which 360 hinders the establishment of stable populations. Even if reforestations cannot be used as nodes in an ecological network, they remain important as connectivity elements, as also suggested by one of the "Pan-European Guidelines for Afforestation and Reforestation with a special focus on the provisions of the United Nations Framework Convention on Climate Change" (Forest Europe 2008), which recommends promoting reforestation activities in order to improve the ecological

- 365 connectivity of the landscape (García-Feced et al. 2011). However, our approach showed that two other arboreal cultures, not specifically designed to increase connectivity, could play the role of connectivity elements in an ecological network designed for the Hazel Dormouse, as reforestations do. These are poplar cultivations and biomasses, which probably have an internal structure sufficiently adequate to perform the role of connectivity elements for our target species.
- 370 To our knowledge, this is the first study highlighting the importance and the role of these two arboreal cultures in an ecological network, which offers a great opportunity to integrate conservation measures and economic interests.

Conclusion

In this paper, we presented an innovative procedure to identify the elements that should be used to design an effective ecological network for a target species starting from occurrence data. The main contribution of this new method relies on the possibility to identify nodes and connectivity elements for the target species overcoming the main limitations of standard HSMs, which prevent a correct identification of both nodes and connectivity elements due to the fact that they only consider the coverage of land-covers. By adopting the procedure we propose, it is possible to identify which land-covers should be used as nodes and connectivity elements within a network for a target species, by comparing the goodness-of-fit of different SSPLs to observed occurrence data. Species perception of the landscape is simulated by calculating the amount of nodes coverage, for all the land-covers considered as nodes in the SSPL, merged together, and the degree of connectivity, provided by all the land-covers considered as nodes or connectivity

385 elements in the SSPL, merged together. Thus, the hypothesis of this method is that nodes affect species occurrence through both their total coverage and their contribution to connectivity, while connectivity elements affect species occurrence only through their contribution to connectivity. The validity of this hypothesis has been proved by the results of the case study presented. Indeed, the best SSPL, in which poplar cultivations, biomasses and reforestations where considered only

in the computation of *CONNECT* (SSPL: WpbrH), was associated to a much higher R² (0.530) than those associated to the SSPL in which poplar cultivations, biomasses and reforestations were considered in the computation of both *CA* and *CONNECT*, for the same role played by hedgerows (SSPL: WPBRH; R2=0.259). This result confirms that including within HSMs the amount of the coverage of the land-covers perceived as connectivity elements, but not as nodes,

- 395 by the target species, can be highly confusing and can lead to misleading conclusions. In addition, merging together all the land-covers that play the role of nodes in the same SSPL allowed us to overcome the difficulty of HSMs in detecting the suitability of land-covers scarcely represented within the landscape (in our case hedgerows), which is another well-known limit of this kind of models.
- 400 The method we propose still shows some practical constraints. Indeed, the procedure to identify the real landscape perception by the target species, starting from SSPLs setup and ending with the selection of the best model, is still quite complex and involves the use of different software types. Moreover, the procedure can become even more complex if the ecology of the target species is scarcely known and it is necessary to hypothesize different threshold distances405 beyond which two patches are considered as not connected to each other in the calculation of connectivity indices and to perform sensitivity analyses on different Moving Window sizes. On the other hand, even if computationally demanding, the latter point would make the proposed method very useful to indirectly estimate the maximum dispersal distance in unsuitable habitats and the response scale to fragmentation for target species for which this information is unknown.
- 410 The proposed method has other great advantages. First, it overcomes the main limitations of HSMs in identifying nodes and connectivity elements starting from occurrence data. Moreover, it

is an objective procedure aimed at designing an effective ecological network for virtually every species sensitive to fragmentation of potentially every kind of habitat. Achieving this result with a standardized method would have important practical implications. As a matter of fact, it would

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allow obtaining objective information that could be formally integrated in landscape management plans for wildlife conservation.

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Table 1

Table 1. Conditional R-squared values of the models performed for all the 81 SSPLs. The 10 best performing models are indicated in bold.

SSPLs ^a	Hedgerows as Nodes (H)	Hedgerows as Connective elements (h)	Hedgerows as Matrix (0)
	$R^2 c$	$R^2 c$	$R^2 c$
W000	0.457	0.449	0.451
WP00	0.349	0.315	0.321
Wp00	0.493	0.449	0.452
W0B0	0.337	0.331	0.335
W0b0	0.383	0.445	0.451
W00R	0.336	0.337	0.323
W00r	0.477	0.452	0.449
WPB0	0.325	0.286	0.289
WP0R	0.284	0.289	0.281
W0BR	0.294	0.295	0.279
WPbr	0.357	0.324	0.312
WPb0	0.353	0.318	0.327
WP0r	0.360	0.326	0.316
WpBr	0.342	0.340	0.332
WpB0	0.338	0.335	0.335
W0Br	0.349	0.343	0.333
WpbR	0.329	0.332	0.324
Wp0R	0.326	0.331	0.323
W0bR	0.335	0.335	0.325
WPBr	0.329	0.290	0.280
WPbR	0.284	0.289	0.280
WpBR	0.281	0.283	0.277
Wpb0	0.517	0.460	0.450
Wp0r	0.518	0.467	0.450
W0br	0.478	0.451	0.450
WPBR	0.259	0.263	0.256
Wpbr	0.530	0.473	0.448

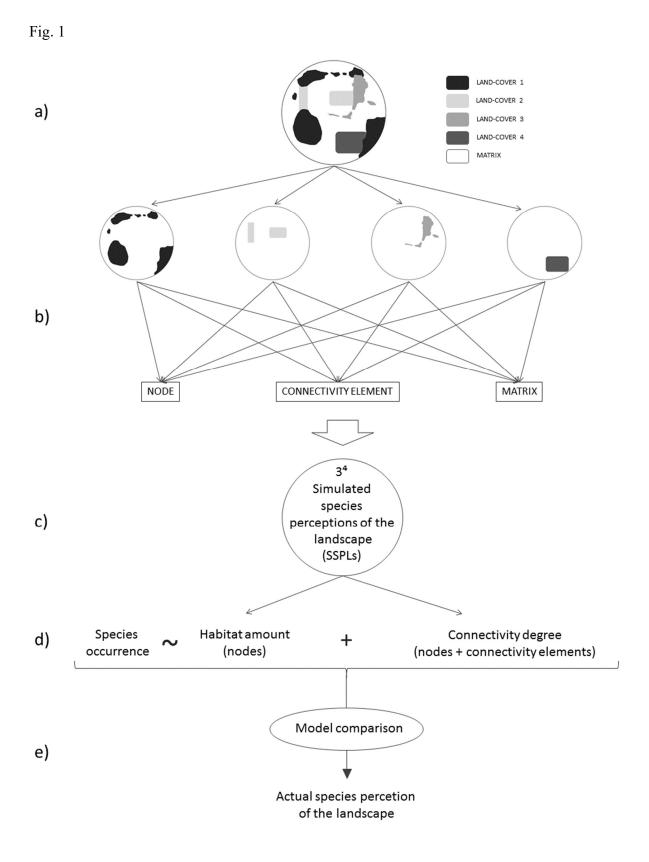
^{*a*} The five letters codes (four letters in row and the last one in column) of the SSPLs are created by assigning to each land-cover (poplar cultivations, biomasses, reforestations and hedgerows) a capital letter to indicate the role of nodes (P, B, R, H), a lowercase letter to indicate the role of connectivity elements

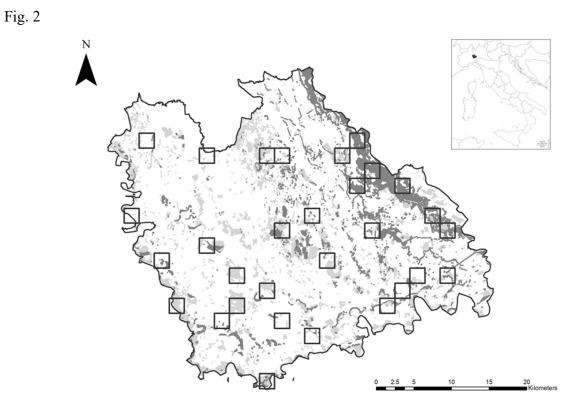
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(p, b, r, h) and 0 to indicate the role of a matrix. Each code always starts with W because woodlands were considered as nodes only. In rows: the 27 combinations of poplar cultivations, biomasses and reforestations as nodes, connectivity elements or matrix. In columns: hedgerows as nodes, connectivity elements or matrix.

- Fig. 1. Rationale of the method. Starting from the actual landscape, four land-covers are considered, while all the others are treated as matrix (a). Subsequently, each land-cover considered is alternatively given the role of node, connectivity element or matrix (b). Each combination results in a SSPL, making a total of 3⁴ SSPLs (c). For each SSPL the habitat amount of nodes and the degree of connectivity provided by both nodes and connectivity elements, are
- 440 regressed on species occurrence data (d). Finally, model goodness-of-fits are compared and the SSPL associated with the best model is considered as the actual species perception of the landscape (e).

Fig. 2. Study area in northern Italy (45°21' N 8°80' E) with forests in dark grey and poplar
cultivations, biomasses and reforestations in light grey. The black squares are the 2-km primary sampling units.





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