Functional connectivity for silvogenesis in Aleppo pine (*Pinus halepensis* Miller) plantations as a base towards an effective landscape biodiversity strategy in southern Apulia (Italy).

A. Sacco[1], G. Tellini Florenzano[2], P. Mairota[1]

[1] Department of Plant Production Science, Agricultural Faculty, University of Bari – via Amendola 165/A 70126 Bari, Italy. Email: p.mairota@agr.uniba.it

[2] DREAM Italia – via dei Guazzi 31, I-52013 Poppi (AR), Italy.

Abstract

This study is based on the hypothesis that early silvigenetic processes occurring in Aleppo pine (*Pinus halepensis* Miller) plantations in southern Apulia (Italy) are favoured by the presence of bird species acting as vectors for broadleaved species colonisation. The aim of the work has been to assess the degree of functional connectivity of Aleppo pine plantations with respect to these vectors. A combination of modelling procedures were applied, one derived from the maximum-entropy principle (MaxEnt), the other form graph theory (Conefor Sensinode 2.2). Results suggest that the use of MaxEnt in combination with the Conefor Sensinode 2.2, not only overcomes the need to make subjective expert judgments about habitat suitability, but also improves the conceptual performance of the Conefor Sensinode 2.2 algorithm itself when "least-cost distance" algorithms are not applicable. The rationale of the model adopted by this software is based on a simplistic *patch-corridor-matrix* conceptual model. MaxEnt assumes the more realistic *landscape continuum* one by considering environmental (*i.e.* context relevant) variables in conjunction to each landscape element. The conceptual and operational switch from the ecological network model to the more realistic ecological continuity model might have crucial consequences for maintaining biodiversity at landscape scale, especially the role such perspectives could play in complementing the protected area network strategies.

Keywords: functional connectivity, silvogenesis, landscape continuity.

Introduction

Aleppo pine (*Pinus halepensis* Miller) plantations in southern Italy and in the Apulia region, were established in three distinct periods (1930's, 1960-70's, 1990's) as part of the response to different policies. These were broadly aimed at reclamation of wetlands and sand dunes for agriculture development, unemployment alleviation and, finally agriculture production reduction. Aleppo pine plantations have generally enhanced semi-natural spatial cohesion at the landscape scale, and particularly so in southern Apulia (De Filippis *et al.*, 2008). Nevertheless, in the last thirty years most plantations were abandoned and a combination of forest fires have occurred and/or silvigenetic processes have led to the formation of an understory comprised of fruit-bearing broadleaved woody species and evergreen *Quercus* species. The vegetation community composition and structure can be regarded as a case of the *understory (re)initiation stage, or transition* (Oliver and Larson, 1990), of the forest developing (*silvigenetic*) cycle, in which the previous stages (*stand initiation stage* and *stem exclusion stage or pole stage*) were replaced by the plantation itself. *Facilitation* mechanisms (Connell and Slayter, 1977) and the *relay floristic* model (Egler, 1954) for plant species replacement (leading to plant community assemblage change) seem to dominate the successional process in this case.

Such dynamic processes demonstrate the tendency of the plant communities towards more mature *seral stages* (*sensu* Clements, 1916; Odum 1969) or, from a non-equilibrium and mechanistic approach, *later sequences* (*sensu* Connell and Slayter, 1977). Understanding the mechanisms underlying such processes can provide information for the implementation of more sustainable silvicultural practices and provide conservation management tools that would be effective within an adaptive management framework (Holling, 1978). In a rapidly changing environment this would allow forest biodiversity to be maintained at the larger scale. Moreover, such processes might significantly contribute to carbon sequestration and accumulation in relatively more stable forest ecosystems rather than just plantations.

Among such mechanisms, those relevant to the restoration of natural forest dynamics, through improvements in landscape functional connectivity, are the main focus of this work. Our hypothesis is that silvigenetic processes occurring in Aleppo pine plantations in southern Apulia are favoured by the presence of bird species acting as vectors for broadleaved species colonisation processes. Other studies carried out in Mediterranean environments are consistent with this hypothesis (Herrera, 1986; Debussche and Isenmann, 1989). This part of Apulia, however, has experienced significant patterns of historical deforestation and current woodland cover is only 2.5% of the land area. The remaining woodlands are characterised by a very high degree of fragmentation and isolation from the wider forest ecosystem (figure 1). Thus, bird-mediated seed dispersal processes can only be maintained if potential vectors can persist as metapopulations (*sensu* Hanski, 1991) in such conditions. Therefore, the aim of the work has been to assess the degree of functional connectivity of Aleppo pine plantations at the sub-regional scale, with respect to these vector bird species.

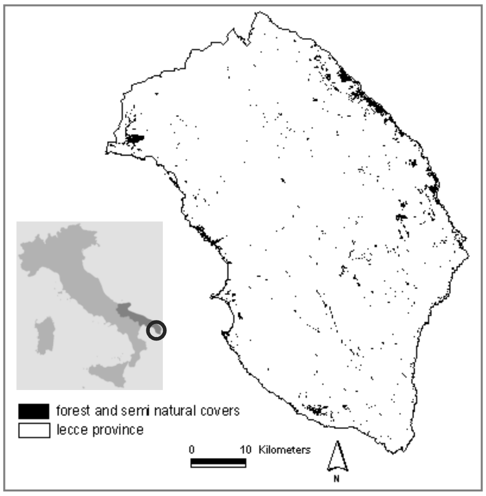

Figure 1. Study area location and forest cover.

Materials and methods

A combination of two different modelling procedures was applied to potential vector species across the southernmost part of the Apulia region (figure 1). The first of these, MaxEnt, is a species geographic distribution model (Philipps *et al.*, 2006; Philips and Dudík, 2008). This was used to generate a prediction of potential vector species distributions as a proxy for habitat suitability. This then provided input for the second model, Conefor Sensinode 2.2 (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal 2007). The MaxEnt model is based on the *maximum-entropy principle* (Jaynes, 1957) and its *niche-based* deterministic algorithms are implemented with both presence-only data and relevant environmental variables. This model, unlike most species distribution models, is considered reliable even with a small number of points and uneven data sets and is capable of estimating the relative importance of the different environmental variables (Elith *et al.*, 2006). The Conefor Sensinode 2.2 is a dispersal model that is based on graph theory. Such an approach was originally proposed as alternative to the percolation-based models in order to overcome computational limitations (Urban and Keith, 2001) as it shows similar threshold behaviour, producing ecologically realistic output. Both structural and functional information (*i.e.* species dispersal distance and habitat suitability) can be used as input parameters. It is capable of producing either binary or probabilistic indices and can produce species specific connectivity measures of a particular habitat mosaic within any given landscape matrix. Moreover, the model provides a measure of the relative importance of individual patches for the maintenance of connectivity across a whole landscape, as well as smaller clusters of more connected patches within that landscape.

A total of eleven bird species were selected for the study with contrasting trophic requirements and phenologies (Cramp, 1980). All of the following species breed in the area and can be considered potential seed vectors: *Parus caeruleus* (blue tit), *Parus major* (great tit), *Sylvia melanocephala* (Sardinian warbler), *Sylvia atricapilla* (blackcap), *Oriolus oriolus* (golden oriole), *Turdus merula* (blackbird), *Streptopelia decaocto* (collared dove), *Streptopelia turtur* (turtle dove), *Luscinia megarhynchos* (nightingale), *Sturnus vulgaris* (common starling), *Pica pica* (magpie) and *Corvus monedula* (jackdaw). Distribution data were derived from the Italian Ornithological Monitoring Program (MITO2000-EBCC). An average of 72 sample points were available for the selected species, with a minimum of 4 (*O. oriolus*) and a maximum of 315 (*P. pica*). For species for which there were more than 15 positive survey points (all but *O. oriolus, S. turtur, L. megarhynchos, S. vulgaris*) the MaxEnt program randomly set aside 25% of the sample records for testing. Twenty environmental variables were also fed into the model which are relevant to morphology (altitude, altitudinal range, inclination, aspect), climate (annual mean, maximum and minimum temperatures, rainfall, potential evapotranspiration), landcover (urban, arable crops, olive groves, vineyards, grasslands, schlerophyllous woodlands and maquis, pine plantations) and landscape configuration and heterogeneity (edge density, mosaic, Shannon's diversity index).

From the MaxEnt output grid files for each species a shape file was obtained where the relevant probability distribution was assigned to the centroids of each pine plantation polygon. The centroid value was then extended to the entire polygon (habitat patch) of the focal habitat type and species-specific probability of occurrence maps for the pine plantation habitat type were then generated. For the next stage of the analysis (Conefor Sensinode 2.2) it was necessary to reduce the computational burden and as a result only pine plantations above 2 ha were considered (32% of patches and 87% of total forest area). The individual pine plantation patch area was then weighted by the sum of individual species probability distributions. This was subsequently used as the "node" attribute file. The average species dispersal distance of 2 km was chosen to locate the selected species within their home ranges. The connection information provided was the Euclidean distance between patch edges, with a distance probability value of 0.5. Although this is generally accepted as a poor indicator of connectivity, insufficient empirical information was available for the species in the study area to implement alternatives, *e.g.* least-cost distance measurements.

Results

A statistical analysis (threshold binary predictions) of the model performance provided as part of the standard MaxEnt model output, indicated good model performance even for species for which only a few data points were available. The omission on training and/or test samples (where performed) generally showed a good match to the predicted omission rate. The area under the receiver operating curve (AUC) on average was higher (0.871±0.0959) than the AUC for a random prediction (0.5). An example is given in figure 2.

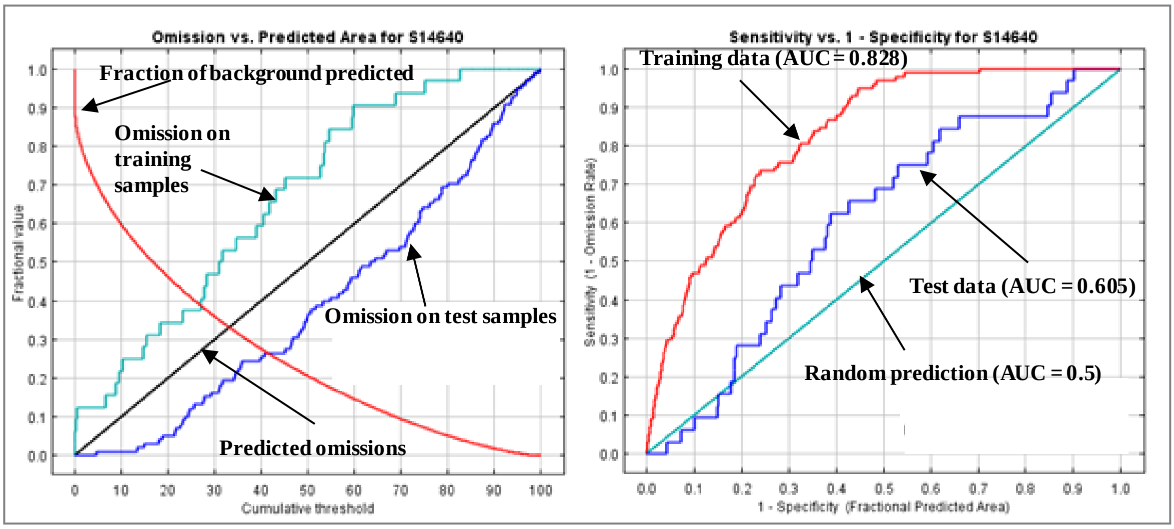

Figure 2. Testing and training omission against predicted area for *Parus major* (130 sample points) (left). Receiver operating curve for training and test data for the same species (right).

As expected, for each species MaxEnt, assigned different probabilities of distributions (proxy for habitat suitability) to different plantation patches even though they belonged to the same broad habitat type. This highlighted subtle differences in suitability for different potential vector bird species. Such differences are also evident when species-specific probability of distribution are summed (figure 3). This is because the model relates each focal habitat (either patch or corridor) to its surrounding context (the matrix) as defined by the niche variables (environmental data) that were fed into the model. Therefore when the probability of distribution ("habitat suitability") is provided as a functional input to the second model, it allows for the incorporation of matrix relevant information which would otherwise be ignored using Euclidean distances rather than effective (least cost) distances.

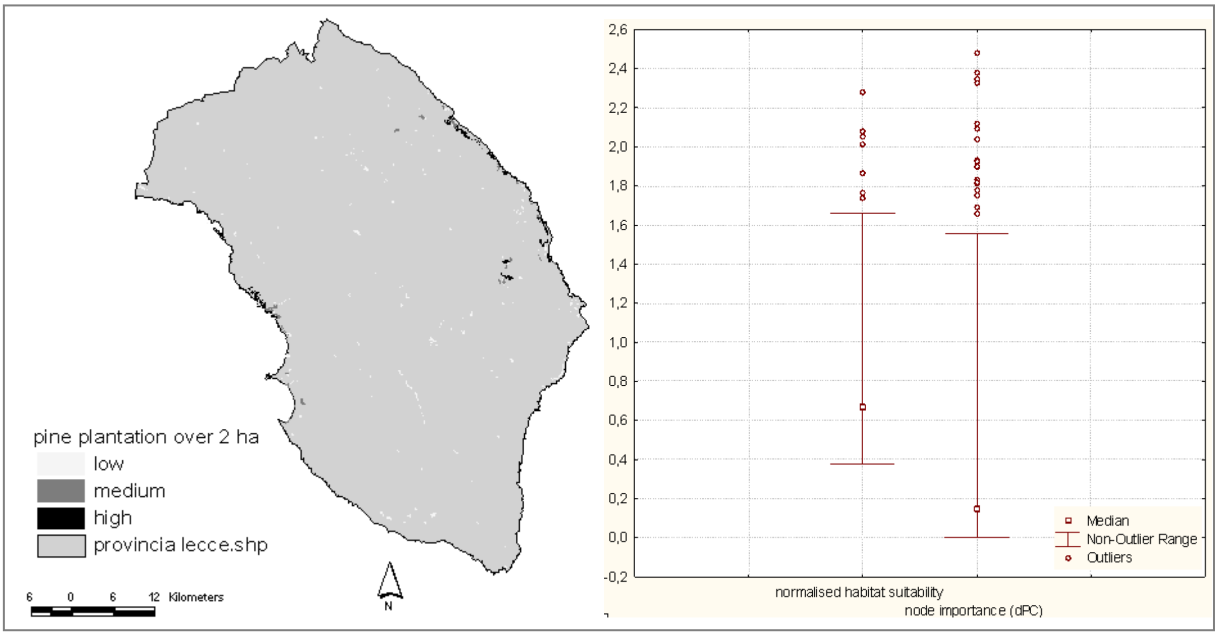

Figure 3. Probability of distribution map for Aleppo pine plantations (left) and variability of both probability of distribution and patch relative importance for connectivity (right).

The probability of connectivity for the whole landscape (range 0-1) yielded by the application of the second model was very low (0.0105451), indicating a very high degree of isolation of these pine plantation fragments even when highly mobile, seed dispersal vectors are considered. The relative importance of individual patches or 'nodes' in maintaining connectivity at smaller scales shows a greater variability than the "habitat suitability" measurement (figure 3). A total of 66 clusters of more connected patches were identified however, 48 of which were comprised of less than 5 patches. Theses accounted for ~17% of the pine plantation area (figure 4, table 1). The two largest clusters (id=16 and id=55) were located on the opposite sides of the peninsula, respectively accounting for ~26% and ~22% of the total pine plantation area.

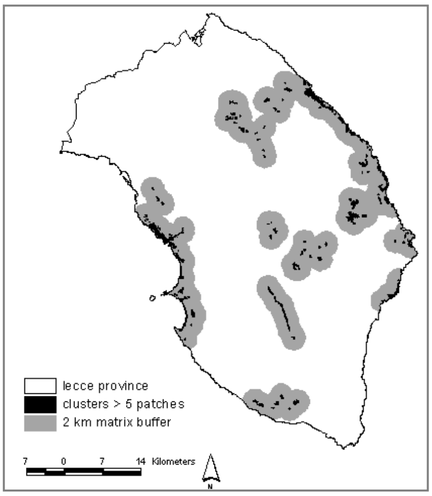

Figure 4. Clusters of relatively more connected patches (> 5 patches) within a 2 km buffer.

Table 1. Main features of the clusters of relatively more connected patches (> 5 patches).

Cluster id	Patch no.	dPC mean	Total area (ha & %)		Mean area (ha)
3	9	0.163	84.57	3.04	9.40
6	14	0.159	111.80	4.02	7.99
14	12	0.153	129.16	4.64	10.76
16	46	3.078	740.20	26.59	16.09
21	10	0.127	51.00	1.83	5.10
26	14	2.025	230.06	8.27	16.43
28	13	0.128	87.79	3.15	6.75
29	6	0.046	32.55	1.17	5.42
32	21	0.094	105.43	3.79	5.02
44	6	1.074	81.74	2.94	13.62
55	37	1.211	615.09	22.10	16.62
66	5	0.081	23.80	0.86	4.76
Total	193	8.340	2.293.19	82.38	11.88
Mean	16.08	0.695	191.10		
St dev	12.81	0.978	234.91		
<5 patch	83	0.080	508.08	18.14	6.12

Discussion

The degree to which species persist in fragmented landscapes and the biological consequences of isolation have been central to the development of thinking in both conservation biology and landscape ecology since the 1960’s (McArthur and Wilson, 1967; Levin, 1970; Baudry and Merriam, 1984; Fahrig and Merriam, 1985, 1994; Wiens and Milne, 1987; Wiens, 1997; Fahrig, 2003; Henle *et al.*, 2004). This body of theoretical and applied knowledge has provided the basis for the design of spatially explicit wildlife conservation strategies (*e.g.* Ingham and Samways, 1996), population viability analysis (*e.g.* Lindenmayer *et al.*, 1995) and a raft of analytical tools that able to quantify structural and, increasingly, functional landscape patterns such as connectivity (Keith *et al.*, 1997; McGarigal *et al.*, 2002; Urban and Keith, 2001; Pascual-Hortal and Saura, 2006). These measures of functional connectivity are important to differentiate from the measures of structural connectivity where it is assumed that direct physical linkage of similar biotopes is necessary for species dispersal.

Habitat availability, dispersal ability and species habitat requirements (habitat type, quality, complementarity), as well as dispersal route quality (Fahrig and Merriam, 1994) are all central to the conceptualisation and measurement of functional connectivity. However, traditionally, the quantification of connectivity has been based on measures of structural connectance associated with the *patch-corridor-matrix* conceptual model (Forman and Godron, 1986; Forman 1995). This has led to the design and implementation of ecological networks where ecological dynamics are confined to the *patch-corridor* sub-system and the *matrix* is treated as a featureless and inert background. Such an approach has consistently been regarded as inadequate because it fails to take into account the complexity of the interactions occurring among patches that might exist in heterogeneous, functional land mosaics (Wiens, 1997; Manning *et al.*, 2004). As Fisher *et al.* (2008) point out, (citing Haila, 2002; Whittaker *et al.*, 2005 and Watson *et al.*, 2005), this is due to the implicit binary classification of land that is often applied (ecologically suitable vs. unsuitable conditions) which can be overly simplistic as it does not allow for any influence of the matrix condition upon the distribution of different taxa.

Even though no empirical validation was performed as yet for the present case, the MaxEnt model, besides providing an objective assessment of "habitat suitability", appears a suitable tool able to incorporate matrix conditions into the computation of any connectivity index. Among such indices, the PC index (Probability of Connectivity, Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007) seems to be able to provide a more realistic and sophisticated representation of potential patch-matrix interactions through the use of a probabilistic approach rather than the binary approaches inherent in most other indices.

This work offers a realistic and ecologically sound approach for the systematic consideration of landscape connectivity that goes beyond simple structural measures even in such cases when not enough empirical data are available to define the resistance values needed to implement an improved connectivity analysis by means of least cost algorithms either using the appropriate option in the Conefor Sensinode 2.2 software or GIS spatial analyst tools (Adriaensen *et al.*, 2003). It is essentially a *landscape continuum* model that is based on the notion of gradient and the organismal concept of *Umwelt* (Manning *et al.*, 2004). The conceptual switch from polarising, binary landscape perspectives to ones that embody ecological continuity might have crucial consequences for maintaining biodiversity at landscape scale. Not only might this be significant to the way in which ecological networks are designed and implemented but also the long term viability of protected areas. Significant evidence has already accumulated that demonstrates that the matrix really does matter (Fisher *et al.*, 2008; Ricketts, 2001) and it is vitally important that spatial models and land use planning start to reflect this fact.

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