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Geographical assemblages of European raptors and owls

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ABSTRACT

In this work we look for geographical structure patterns in European raptors (Order: Falconiformes) and owls (Order: Strigiformes). For this purpose we have conducted our research using freely available tools such as statistical software and databases. To perform the study, presence–absence data for the European raptors and owl species (Class Aves) were downloaded from the BirdLife International website. Using the freely available "pvclust" R-package, we applied similarity Jaccard index and cluster analysis in order to delineate biogeographical relationships for European countries. According to the cluster of similarity, we found that Europe is structured into two main geographical assemblages. The larger length branch separated two main groups: one containing Iceland, Greenland and the countries of central, northern and northwestern Europe, and the other group including the countries of eastern, southern and southwestern Europe. Both groups are divided into two main subgroups. According to our results, the European raptors and owls could be considered structured into four meta-communities well delimited by suture zones defined by Remington (1968) [Remington, C.L., 1968. Suture-zones of hybrid interaction between recently joined biotas. Evol. Biol. 2, 321-428]. Climatic oscillations during the Quaternary Ice Ages could explain at least in part the modern geographical distribution of the group.

1. Introduction

The study of the distribution and assembly of organisms has been one of the major topics in ecology since the middle of the last century (e.g. Diamond, 1975; Connor and Simberloff, 1979). At the end of the last century, many biogeographical studies compared intraspecific phylogeographical patterns of several taxa in order to evaluate the influence of historical factors explaining the geographic distribution of species (Avise, 1992). With this methodology, the current distribution of the European fauna has been explained by considering them as few numbers of non-interacting species (Taberlet et al., 1998; Hofreiter et al., 2004). However, as these studies were based on a set of local populations of single species, their conclusions were restricted to the meta-population level and they do not clearly define the limits of the transition area between regions (Remington 1968; Proches 2005). Consequently, it would be interesting to examine more species and to increase the spatial scale in order to obtain a general pattern (Hewitt, 2000). According to Leibold et al. (2004), the next ecological

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level above the meta-population level would be the community, defined as a group of individuals of all species that potentially interact within a single patch or local area of habitat. Additionally, when local communities are linked by dispersal of multiple interacting species they form a meta-community (Wilson, 1992). An example of the above mentioned meta-community deals with the European species of the Orders Falconiformes and Strigiformes (Class Aves). Falconiformes and Strigiformes species, commonly called raptors and owls, respectively, are large vertebrates which are the focus of many scientific studies and conservation programmes (Watson and Whitfield, 2002; Ferrer and Negro, 2004; Ontiveros et al., 2004; Sergio et al., 2005), and therefore their distribution is usually known in detail, minimizing potential misinterpretations. Studies on their biogeography have classically dealt with few species (Godoy et al., 2004; Bustamante and Seoane, 2004) or with limited geographic areas (Donázar et al., 2005). According to Roselaar (2005), the raptors form a group taxonomically included in the Order Falconiformes, divided into two main suborders, Accipitri and Falconi, the first including the families Accipitridae and Pandionidae, and the latter including the Family Falconidae. Also, the owls are included in the Order Strigiformes, divided into two main suborders, Camprimulgi and Strigi, the first including the Family Camprimulgidae (nightjars), the second including the families Strigidae and Tytonidae (owls). Regardless of taxonomic discussion, globally the group is comprised of 509 species, with 56 species being present in Europe. Many species carry out long flights and migrations which lead to interactions between different breeding populations. Given the enormous capability of flight and the fact that they interact through competition and/or intra-guild predation (Sergio et al., 2003, 2007), the European raptors could be considered as a proper example of meta-communities. Hence, we propose the use of countries as a proper spatial scale, and Europe as an adequate framework for our analysis, given that data are freely available at this scale, thus making our analysis comparable and repeatable.

Here, we look for a biogeographical structuring pattern from the current distribution of species in order to extend it to the higher ecological level (the meta-community) and to clearly define the limits of the transition area between regions. We further discuss how meta-communities could be affected by historical factors that could determine the observed pattern.

2. Methods

2.1. Downloaded data

We downloaded data on raptors and owls from the BirdLife International website (available at http://www.birdlife.org). This is a freely available database of presence–absence data of worldwide fauna on the geographical basis of countries. For our analysis we only used countries included in the European continent (including Turkey, Moldava and the western part of Russia). Small countries or countries with no data were excluded from the analysis (i.e. Andorra, Liechtenstein, Luxembourg, Monaco, San Marino and Vatican City). Thus, we used data for 41 and 15 raptor and owl species respectively within 40 European mainland countries and islands, and a matrix of presence–absence data was constructed. For a complete description of countries and regional limits visit the BirdLife International website.

2.2. Clustering the data

In order to determine if the community of raptors and owls species could be delimited in geographic assemblages Europe-wide, we used cluster analysis based on presence–absence data. This methodology is robust for delineating large-scale biogeographical regions, it is easy to apply and follows the aim of classical biogeography (Proches, 2005).

Hierarchical conglomeration statistics were employed to perform a cluster analysis of countries (Podani, 2000). We downloaded "pvclust", a free statistical software package written in R language, available at http://www.is.titech.ac.jp/~shimo/prog/pvclust/) (Suzuki and Shimodaira, 2005). Although there are several freely available packages to perform hierarchical conglomerations, "pvclust" automatically computes *p*-values for all clusters contained in the clustering of original data. Unlike common bootstrap analysis, where the sample size remains constant and equal to the data matrix size, we used the Multiscale Bootstrap Resampling option where the sample size of the bootstrap sample ranged from smaller to larger sizes than the original matrix (Shimodaira, 2004). In this case, the *p*-value is estimated fitting to a theoretical curve obtained from the range of sizes. This *p*-value, called the approximately unbiased *p*-value (AU) for the pvclust program, is more accurate because it corrects the bias of the bootstrap probability value caused by a constant sample size (Shimodaira, 2004). We used ward clusterisation methodology with the binary index of similarity. The binary index proposed by pvclust corresponds to the well-known Jaccard index (Podani, 2000).

3. Results

When clustered together, the hierarchical cluster ordination revealed that the European raptors and owls are structured into four main assemblages. Each assemblage could be considered as a meta-community and corresponds to well-defined geographical areas (Fig. 1a). The larger length branch separated two main groups: one containing Iceland, Greenland and the countries of central, northern and northwestern Europe, and the other group including the countries of eastern, southern and southwestern Europe. Both groups are divided into four main subgroups each (Fig. 1a). *p*-values ranged between 70 and 89%.

When clustered as isolated, the raptors maintain the same structure as the whole dataset. There are also two main groups, one containing countries of eastern, southern, southeastern and southwestern Europe, and the other including the countries of northern, northwestern, central Europe and Greenland and Iceland, separately. The first group is divided into three main subgroups and the second is divided into four main subgroups (Fig. 1b). For raptors alone, *p*-values ranged between 66 and 92%.

Finally, the cluster of owls showed that this group could be divided into two main groups, one containing the countries of

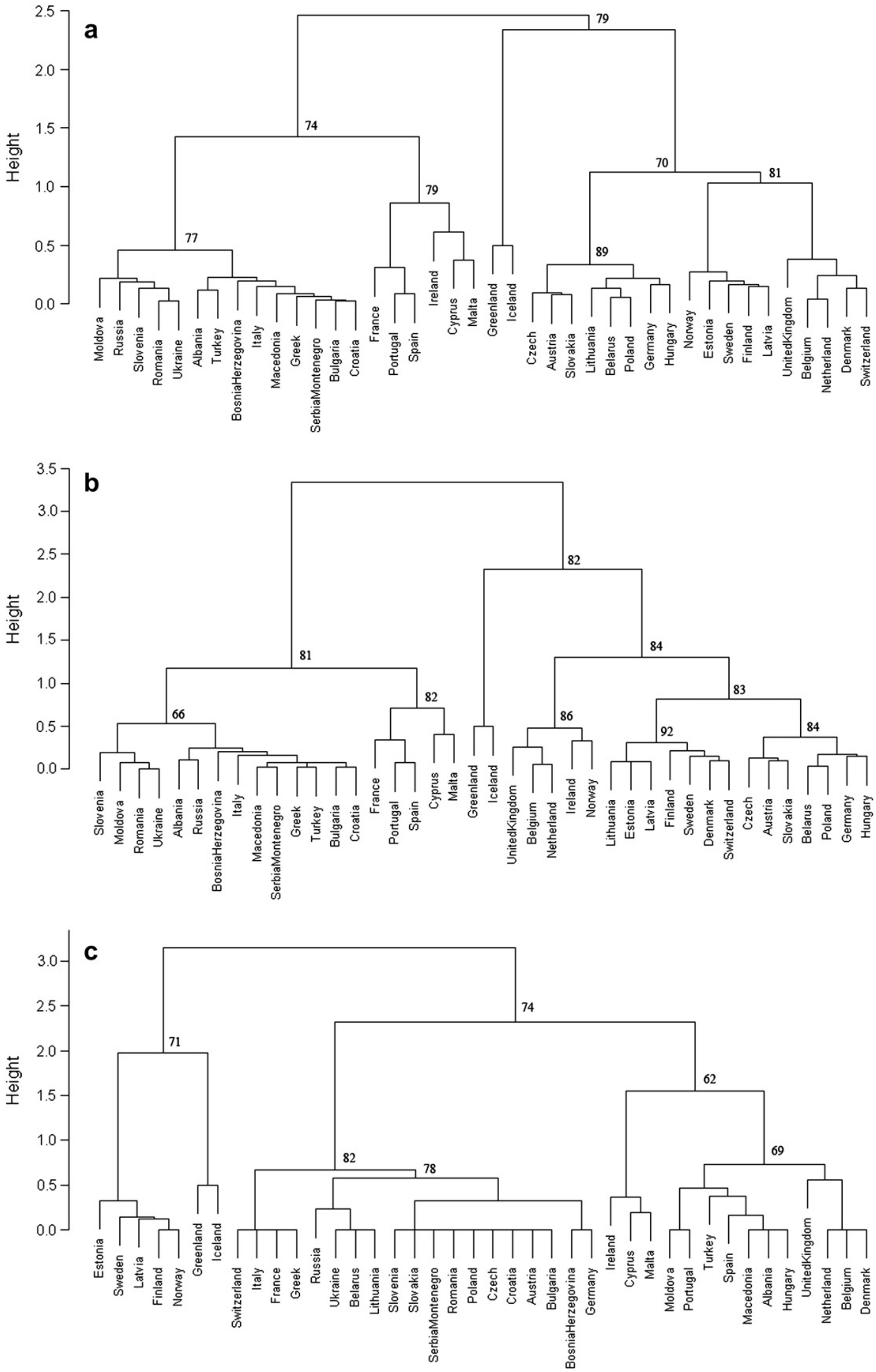

Fig. 1 – Similarities in the composition of (a) raptors and owls, (b) raptors and (c) owls among 40 European mainland and island countries. Topology obtained after Ward distance reconstruction based on Jaccard's similarity index. Values near the edges are *p*-values after 10,000 replicates.

northern Europe and Artic lands (Greenland and Iceland) and the other including the remaining European countries. The first group could be divided into these two main subgroups, and the other branch could be divided into two subgroups, both containing three main subgroups each (Fig. 1c). For owls, *p*-values ranged between 62 and 82%.

4. Discussion

4.1. *Meta-communities structured by the last glaciations?*

Recently Leibold et al. (2004) revised the meta-community concept and explained how its dynamics is shaped by colonisation–extinction ratios between local patches. Colonisation could be caused by speciation or by the immigration of foreign species; and extinction could be the consequence of emigration, competition and depredation. However, evolutionary and geographical processes on larger scales could be the structuring mechanisms of the meta-communities and hence, historical factors (climatic and geographical) could be invoked to explain the observed geographical pattern, modifying considerably the colonization–extinction ratio of both local and regional patches (Hewitt, 1996; Dynesius and Jansson, 2000). In fact, Quaternary cold periods have been argued to explain the current distribution of the European fauna (Hewitt, 1996, Hofreiter et al., 2004). It has been demonstrated that the European fauna concentrated in refugia during glacial periods and expanded northwards in each interglacial period (Bennett et al., 1991; Hewitt, 1996). We consider that this permanent North ice and South refugia could help to explain our results.

A larger length branch of the geographical cluster separated two main groups that match up with the maximum limit of the ice sheets both in the southern and the northern limit (Fig. 1). Additionally, three refugia turned up in southern Europe that can be localised in separated groups of the geographical cluster (Fig. 1): the Iberian refugium (southwestern European group), the Balkanic refugium and the Italian refugium (southern and southeastern European groups) (Taberlet et al., 1998; Hofreiter, 2004).

In addition, our results show a broad pattern of raptor and owl species distribution where the delineation of countries by the four main geographical assemblages (Fig. 1) correspond to well-known suture zones defined by Remington (1968) as bands of geographical overlap between major biotic assemblages (Fig. 2). The northern and northwestern European subgroup (including Greenland and Iceland) could be delineated by the suture zone S1 separating biota from central, southern and eastern Europe. Moreover, the analysis separated communities between the western and the eastern portion of the southern group, a fact that could be explained by the Pyrenean suture zone S2 and the Balkanic suture zone S3 that correlate with the extent of the permafrost limit (Figs. 1 and 2). The southeastern subgroup could include Italian, Greek, Balkanic and Turkey refugia, while the southwestern subgroup could include the Iberian refugium. This assemblage is delineated by the Alpine barrier and extends to the east with the Carpates chain following the permafrost limit S3. Taking into account the difficulty of identifying transition zones with cluster methodology (Proches, 2005), our results show how, under the meta-community concept, suture zones delineated the main geographical assemblages of European raptor and owl species.

According to Leibold et al. (2004) we consider that the meta-community approach can lead to understanding how local and regional processes interact. A synthetic perspective on meta-communities would be a great improvement in understanding how communities are structured by the joint action of processes operating at both local and regional scales

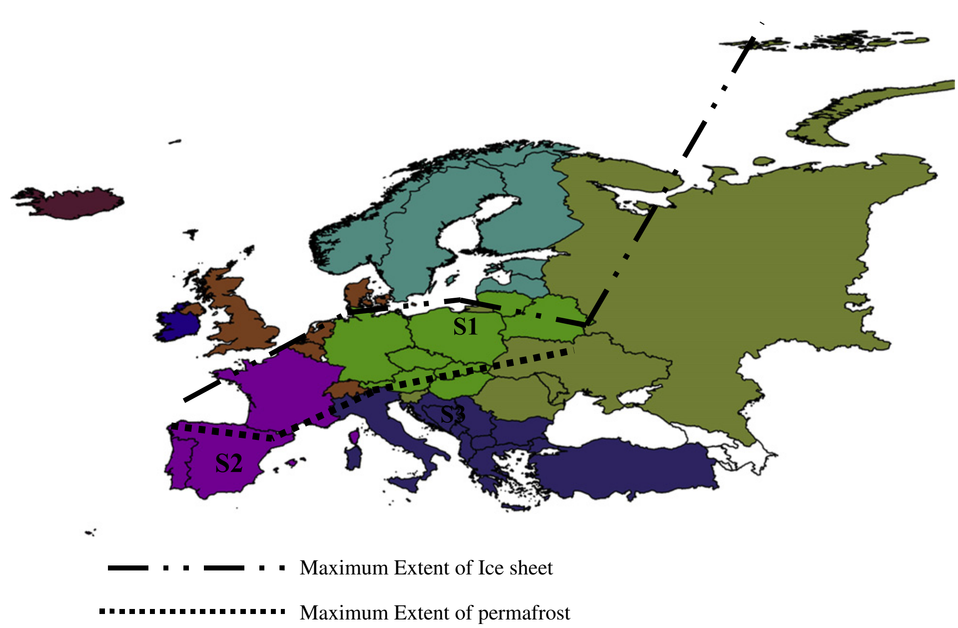

Fig. 2 – Map of the present-day distribution of European communities of raptor and owl species as defined by a country-level cluster analysis. The lines depict the maximum extent limits of ice and permafrost at the end of the last Ice Age 20,000 years BP (modified from Williams et al., 2003).

(Amarasekare, 2003; Kneitel and Chase, 2004). In the case of raptors and owls, adopting a meta-community approach could lead to the understanding of how communities are structured, and consequently to explain the coexistence of species in the same community. As an applied result, we suggest that conservation efforts should consider not only single species requirements, but also ecological relationships between members of each structured community, like intraguild predation (Sergio et al., 2003, 2007) or competition (Carrete et al., 2002; López-López et al., 2004, in press). For example, reintroduction efforts should consider the community in which the focal species interact.

Overall, our results show that European raptor and owl species are structured in meta-communities well delimited by suture zones. Climatic oscillations during the Quaternary Ice Ages could explain at least in part the modern geographical distribution of the group. Our explanation is robust and corroborated by results on genetic structure reported for other study areas (Lovette, 2005) and for other vertebrate species (Avise et al., 1998). It will be interesting to see if the observed pattern can be extended to overall European biota as suggested earlier by other authors. Finally, according to Cassman (2005) we recommend the use of freely available tools such as the statistical software and databases employed in this paper; this allows comparison with other studies that otherwise become difficult to compare.

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