The long-term evolution of Cantabrian mountain landscapes and its possible role in the capercaillie drama.

Juan M. Rubiales, Francisco J. Ezquerra, Fernando Gómez-Manzaneque, Salvia García Álvarez, Ignacio García Amorena, & Carlos Morla.

Within the Iberian Peninsula, at the south-western boundary of its distribution area, the capercaillie is restricted to the Cantabrian and the Pyrenean Mountains. Cantabrian capercaillie *Tetrao urogallus cantabricus* has undergone a dramatic decline during the last three decades, as reported in the last Iberian Survey (Robles et al. 2006) and in previous issues of Grouse News (Bañuelos et al., 2004, 2008). As a consequence, it is currently the only subspecies of capercaillie critically threatened worldwide.

Although considerable efforts have been made to understand the reasons of this decline, the long-term ecology of this subspecies has received little attention, due probably to the absence of data in the palaeozoological records. Nevertheless, palaeoecological information based on their habitats can provide a useful insight that in the case of the Cantabrian Mountains offers a large body of data that covers the forest history of the last thousands of years.

Cantabrian landscapes over time: the history of pinewoods during the Holocene

It is traditionally assumed that this subspecies is the only one, all over the capercaillie's range, adapted to live during the whole year on non conifer forests, mainly of beech *Fagus sylvatica*, birch *Betula pubescens*, sessile oak *Quercus petraea* and Pyrenean oak *Q pyrenaica.* However, it still persists in the few remaining natural pinewoods and uses regularly recent pine afforestations over the range. Furthermore, accumulating evidence suggests that the role of conifers in the landscape of the Cantabrian range was much more important than today. The compilation of the available palynological data and the analysis of new macrofossil sites support a wider distribution area for pine *Pinus sylvestris* over the Holocene, registering regional and recent extinctions in Cantabrian environments. Today, great difference is shown in precipitation and temperature between the northern and southern slopes of the range, defining the Atlantic-Mediterranean biogeographical boundary in northern Iberia. Oceanic influence is greater in the western areas and in the northern slopes of the cordillera while in the inner slopes submediterranean conditions determine the existence of important differences on vegetation.

Patterns of pine decline were therefore roughly marked by the previous climatic framework. Western and northern deposits reflect changes in vegetation from the onset of the Holocene, when sudden changes occurred and the expansion of hardwoods rapidly affected conifers. However, under drier, subcontinental locations, pines were able to endure until the late Holocene in several areas of the range. During the late Holocene (last 3500 BP) an intense anthropogenic activity (including the extensive use of fire) seems to be the major cause responsible for the regional extinction of pinewoods in different sites of the cordillera. Today, only some stands and scattered pine trees persist over the southern slopes (the best known of them is the Lillo pinewood).

Taking into account the historical information it therefore seems more than plausible that pines and capercaillie were geographically linked at least during part of the Pleistocene and the whole Holocene (last 10000 years) and this fact also fit quite well with the long-isolation model obtained from the genetic analysis of both species that support a coupled history of long term isolation and evolution in the Iberian territories (Chedaddi et al. 2006, Duriez et al. 2007).

Further, beech forests, nowadays the major tree species of the habitat of the capercaillie in the northern slopes of Cantabrian mountains (Quevedo et al. 2006) did not develop in the area until ≈4000 yr BP (Magri et al 2006). It is also surprising that while globally capercaillie prefer (at least during the snow-free season) habitats with open and well-lit spaces and moderate canopy coverage (see e.g. Storch 2007), beech forests offer the shadiest and most dense canopied forests in the cordillera. This could be explained by: i) climatic and physiographic factors and a long-term (millennial scale) anthropogenic disturbance reduce capercaillie's habitat availability to montane environments where beech found the best niche to prosper during the late Holocene; ii) during the last decades, rural depopulation and subsequent abandonment of traditional land use systems are responsible of a severe change in the beech forest structure. The end of an intense anthropogenic activity (including tree-felling, pruning and livestock management) that maintained unusually open beech forests, favoured the densification and disappearance of open areas; iii) in an important part of existing beech forests that are today occupied by capercaillie, forest structure is highly limited by abiotic factors (such as poor soils, high slopes, regular occurrence of snow damages) and permits the existence of open areas with a dense ground cover of bilberry, more typical of a birch forest structure; and iv) in most parts of the beech forests, capercaillie preferentially uses open areas, and when they do not exist, the timberline zone relegating dense forest areas just for

refuge. In summary, the arguments cited above can well explain the reasons why capercaillie was so abundant in beech forests and that this fact may not be linked with the species itself.

Pine-capercaillie interactions: do winter diet and tree sheltering counts as key factors for the survival of marginal populations?

Western capercaillie is closely associated in the major part of its range with conifers (Storch 2007). Some authors have explained this connection by the importance of needles in the winter diet and the use of trees as refuge under extremely adverse meteorological events. Early research on capercaillie in Iberian environments already pointed out that winter was a crucial period affecting the survival of the species over time (Castroviejo 1975). Snow cover considerably limits the availability of ground food and consequently alternative food resources are in trees. Rodríguez & Obeso (2000) analysed the peculiarities in the diet of Cantabrian capercaillie. With the exception of the few individuals living close to the relict pine stands of the southern slopes and other pine plantations, capercaillie are forced to include other evergreen trees (such as holly *Ilex aquifolium*) or buds and other parts of deciduous trees (such as beech) in their diet. An interesting conclusion of the study is that their winter diet varies widely depending on the food availability. Secondly, this irregularity may be a limiting factor as predation risk increases for capercaillie feeding in deciduous forests compared to those feeding on coniferous needles.

Tentatively, we focused on the connections between those two species and we presented briefly this association in Rubiales et al (2008). Even if we strongly agree with the main conservation threats and measures already proposed for the Cantabrian populations, we discuss the idea that the absence of conifers in the enclaves best conserved might aggravate the status of capercaillie in these marginal areas of its distribution range.

The consequences of this fact could be far from being trivial. On the one hand, studies of habitat selection have only been achieved on the northern (Asturian) slopes of the range. Although these studies are extremely useful and interesting *per se*, they remain biased since the southern slopes (notably different from northern slopes and more suitable for well restored pine landscapes) were not included. Researchers should therefore be urgently encouraged to continue investigations in that sense. On the other hand, population re-enforcement targets, management focusing habitat amelioration and priorities for conservation related to the capercaillie could include a more open perspective in which pines can be incorporated as precious elements of these mountain ecosystems. As an example of this lack of conscience, the Cantabrian relics of pine are not included as habitats of European interest in the Habitats Directive (although some of them are fortunately protected with regional laws)

Implications for management

During the decades between 1940 and 1970 one of the forest policies that were extensively developed in Spain was the conifer afforestation, which was primarily defended by the administration by their benefits to protect disturbed soils from erosion. This large-scale afforestation policy was certainly accompanied by conflict over the social and environmental effects of plantations. Some prominent people from both the scientific and conservationist communities expressed concerns over the impacts of pine afforestation that took root in social contexts and ended up questioning the autochthonous nature of pines and their role in the forest dynamics of Iberian environments. Fortunately, palaeoecological and historical data are scientifically contributing to solve this debate, but the inertia of the previous ideas certainly exist and part of a misinformed society still shows contempt for pine forests. It would be a misfortune if these prejudices prevented to include and understand the role of the pines in the ecology of Cantabrian capercaillie, and the opportunity that can represent for their recovery.

Theoretical models and ongoing observations on Cantabrian capercaillie are not hopeful, as the extinction of the whole population is envisaged in the near future. Furthermore, the environmental anthropogenic change is now quickly adjusting selection pressures on biological communities and makes predictive forecast even more pessimistic. However, there are still reasons for hope, since surveys does not reflect constant decreasing trends in all of the discrete Cantabrian populations (Robles et al. 2006) and experiences abroad (such as those from Scotland, Kortland 2004) also show that patterns of recovering of populations are possible. It is evident that the decline in Cantabrian capercaillie is not a simple issue and that species-habitat relationships are often highly complex but necessary to assess conservation planning. In our case, the link between pines and capers should not be considered as an attempt to simplify the problem but, on the contrary, to integrate and seek, above all, any of the available solutions that may contribute to the recovery of these populations. What is clear is that the palaeoecological information available proves that pines were an important part of the ecological system in the cordillera during the last millennia and that until present there is no sign proving that capercaillie did not use pinewoods in the past. Further, the scarce data available indicate that pine was probably widely used and that its disappearance could have been a key factor in the long-term.

From the perspective of the management of the species, it would be a mistake to pose the question in the form of whether or not the capercaillie need pinewoods to survive, even at the large-scale. The important question now is whether pine presence ever actually helps southern capercaillie to recover, at least in some of it populations. The experimental information that is being recovered from several areas in León is highly positive in that sense.

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Juan M. Rubiales jm.rubiales@upm.es, Fernando Gómez-Manzaneque fernando.gmanzaneque@upm.es, Salvia García Álvarez salvia.garcia@upm.es, Ignacio García Amorena ignacio.garciaamorena@upm.es & Carlos Morla, Departamento de Silvopascicultura, Escuela Técnica Superior de Ingenieros de Montes, Universidad Politécnica de Madrid, 28040. Madrid, Spain.
Francisco J. Ezquerra, Servicio de Espacios Naturales. Dirección General del Medio Natural, Junta de Castilla y León, C/ Rigoberto Cortejoso, 14, 47014.Valladolid, Spain. ezqbotfr@jcyl.es