

Focus

Consequences for avifauna of landscape encroachment by woody vegetation in northern Catalonia

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In the past century, there was a notable exodus of rural inhabitants from the inland hills surrounding the plains of northern Catalonia, which led to an inexorable increase in woody vegetation and frequent large wildfires. The contrast between gradual landscape closure (due to vegetation encroachment) and sudden opening (due to fire) seriously affects the region's birdlife. The progressive encroachment of woody vegetation following land abandonment or wildfires has resulted in a succession from open-habitat avifauna towards forest avifauna. From a conservation point of view, this is threatening bird species of the highest great conservation concern in Europe (Species of European Conservation Concern: SPEC) that live in the early ecological succession stages of habitats colonized by pioneer plants. From a biogeographical point of view, the species adapted to these pioneer stages typically have more southerly ranges and are often close to the northern limit of their distributions in Catalonia. As a result, globally, vegetation encroachment is favouring northern species at the expense of southern species. In the Albera Massif, for example, despite frequent fires, the landscape has become increasingly dominated by forest and scrub over the last 50 years. The frequency of fires has not been sufficient to prevent the encroachment of vegetation. As a result, despite climate warming and recurrent wildfires, southern open-habitat species such as the Black Wheatear *Oenanthe leucura* – a species classified as Vulnerable on the European Red List – have disappeared from this area and are retreating southwards. Vegetation encroachment, wildfires and global warming have either synergistic or antagonistic effects on birds in Catalonia. The impact of landscape closure on the composition of the avifauna is counteracting the effects of climate warming. Contrary to climate-based predictions and despite recurrent wildfires, there is good reason to predict that in the mid-term – with the exception of cultivated areas – the effects of landscape closure on birds will prevail.

Key words: succession, rural exodus, wildfire, vegetation structure, shrubland, forest, conservation, biogeography, *Oenanthe leucura*.

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Landscape changes in northern Catalonia

Since Neolithic times, human impact on Mediterranean landscapes has inexorably – albeit irregularly – increased, with regressive phases occurring during wars, crises and epidemics.

Pressure from farmers, herders, charcoal producers and loggers peaked at the end of the nineteenth century and at the beginning of the twentieth century, when rural population densities were at their highest. However, since then, in the rugged mountain landscape of northern Catalonia (both on the Spanish and French

sides of the eastern Pyrenees), there has been a notable rural exodus and human pressure on the cultivated plains has intensified. This large-scale trend has multiple causes that have provoked a number of synergistic effects: the abandonment of traditional farming, the near disappearance of extensive livestock grazing in rugged upland areas, the replacement of wood and charcoal by fossil fuels, and the concentration of intensive agriculture, industry and urban growth on the fertile soils of the plains, which have gone hand-in-hand with crises in the wine-producing sector, World Wars I and II, and the population shift to the coast in the context of the tourism boom. These multiple processes (see Bielsa *et al.* 2005, Poyatos *et al.* 2003, Otero *et al.* 2015 in Catalonia, and Rey Benayas *et al.* 2007 for a general review of causes and consequences) have resulted in a decrease in human pressure in hilly or mountainous 'back country' areas (hinterlands: *arrière-pays* in French; *rempais* in Catalan) that were previously grazed, mowed, cultivated, or exploited for charcoal (see Becat 1973 on the Albera Massif). In these areas, the unchecked growth of woody vegetation has led to the gradual closing up of the landscape, first by shrubs of various heights and density, and then by coppices or young woodland. The resulting accumulation of fuel and the decrease in landscape patchiness create ideal conditions for the propagation of large wildfires.

It remains unclear whether or not wildfires counterbalance this trend towards landscape closure and the situation varies from one area to another. At a given location, the type of woody cover – low scrub, tall shrubland or woodland – depends on the average fire frequency in recent decades. Vegetation encroachment after a fire is faster on previously forested land than on abandoned grassland, since in the former the stumps or seeds of woody plants are present in the soil. It is also faster on an acidic substrate than on limestone (Herrando *et al.* 2002). On the northern side of the Albera Massif (excluding the foothills) (42°24'-42°31'N; 2°50'-3°10'E), the overall trend since the mid-twentieth century has been a decrease in open habitats and an increase in forest cover, despite the recurrence of wildfires (Figure 1) (a similar trend has been recorded in the nearby valley of Conflent; Roura-Pascual *et al.* 2005). In Catalonia as a whole, the mean interval between fires has been estimated to be either over

50 years (Terradas *et al.* 1998) or 23–42 years (Diaz-Delgado *et al.* 2004), a frequency that is low enough to allow the regeneration of woodland cover between fires. In the case of holm oak forests, the forest avifauna has been estimated to return within 35–45 years after an intense wildfire (Jacquet & Prodon 2009). This growth potential allows holm oak forests to tolerate a period of 30–50 years between fires (compared to one of 25–30 years between felling under traditional coppiced woodland management; Espelta *et al.* 1999). As a result, this resilient forest type may act as an 'absorbing state' in landscape dynamics, with the capacity to dominate increasingly large areas of uncultivated land.

Vegetation encroachment and changes in avifauna

The contrast between progressive landscape closure (due to vegetation growth) and its

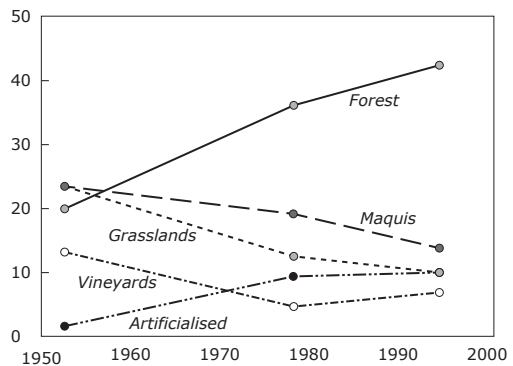


Figure 1. Land-cover change on the northern side of the Albera Massif in 1953–1995. Seven landscape classes, of which five are shown (artificial, forest, maquis or Mediterranean scrub, grasslands and vineyards), were distinguished and measured using aerial photographs at 100 random points in an area bordered by Argelès, Saint-André, Saint-Genis to Le Perthus (also including the upper southern side of the massif). Heterogeneous or ill-defined land cover was not taken into account (from Tomas 2000).

Canvi de cobertes del sòl al vessant nord del massís de l'Albera, de 1953 a 1995. Es distingeixen i es mesuren a partir de fotografies aèries set classes de paisatge, de les quals se'n mostren cinc (artificial, boscos, matollars mediterranis, prats i vinyes, en 100 punts aleatoris, d'una zona delimitada per Argelers, Sant Andreu de Sureda, Sant Genís de Fontanes i El Pertús, inclosa també la part superior del vessant sud del massís). No es van tenir en compte cobertes del sòl heterogènies o mal definides (a partir de Tomas 2000).

sudden opening (due to fire) has a serious effect on birdlife. The gradual encroachment of woody vegetation after land abandonment or after a wildfire leads to the replacement of open-habitat species (e.g. larks, wheatears, pipits and buntings) by shrubland species (e.g. Mediterranean warblers), followed eventually by forest species (e.g. chaffinches, robins, tits, treecreepers and firecrests). During this successional process, some 50 bird species may occur, although none is able to breed throughout the whole succession; only certain Fringillidae such as the goldfinch, for example, are found – breeding or otherwise – in any vegetation stage. This sequence of bird species is the natural result of the succession of dominant plant species of ever-increasing height and cover. On the siliceous substrate of the Albera Massif, for example, on abandoned land below ~700 m, the plant succession runs from grasses and leguminous plants (e.g. Poaceae, Fabaceae) to chamaephytes (e.g. *Thymus*, *Lavandula*), low-growing shrubs (e.g. *Cistus* spp., *Ulex parviflorus*), heathers (e.g. *Erica arborea*, *E. scoparia*) and small trees (e.g. *Arbutus unedo*, *Phillyrea* sp.), and, ultimately, to sclerophyllous woodland (e.g. oaks *Quercus ilex* and *Q. suber*). However, more than the turnover of plant species, it is the turnover in bird species in relation to the increasing height and structural complexity of the plant cover profile that has the greatest effect, as shown by calculations based on a set of point counts. A parameter as simple as the degree of vegetation cover measured at different heights above the ground is sufficient to allow – through ordination and/or regression techniques – a fairly accurate prediction of the breeding avifauna in a given successional stage (Prodon & Lebreton 1981).

Post-fire succession

Like successions following land abandonment, post-fire successions also give rise to the replacement of closed-habitat bird species with open-habitat species. However, these two processes do not result in equivalent bird successions. In burnt woodlands, the early successional stages are clearly differentiated from post-abandonment successions as they harbour not only species of open habitats but also certain species belonging to woody, forest or pre-forest stages

(Jacquet & Prodon 2009). This persistence of certain forest species is due above all to a tendency for phylopatric behaviour, which is made possible by the persistence of part of the forest structure after the fire (Llimona *et al.* 1993).

Ordination and regression techniques based on bird records and vegetation measurements can be used to measure the return times of pre-fire avifauna in burned areas. In the studied area of Catalonia (42°22'–42°33'N; 2°41'–3°10'E), these have been found to be about 4–6 years in low Mediterranean scrub, 10–12 years in heathlands, 35–45 years in young holm oak stands, and about 30 years in mature cork oak woods (Pons & Prodon 1996, Jacquet & Prodon 2009, and *in prep.*). In these *Quercus*-dominated landscapes, return times are generally fairly short on the siliceous substrates and under the rather rainy climate that dominates in this part of northern Catalonia. Any recurrence of fire at intervals shorter than these return times leads to a regression in plant succession. Nevertheless, except in certain areas where the frequency of fire is very high, fires alone cannot counteract the trend towards landscape closure in the mid- and long terms.

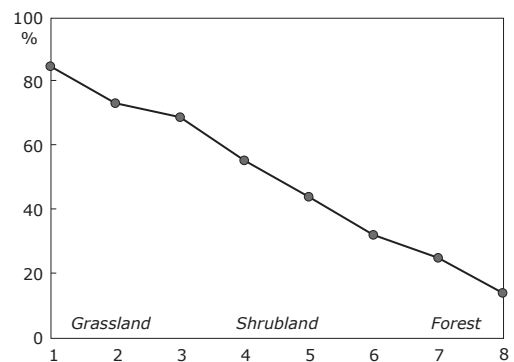


Figure 2. Variation in the relative number of birds belonging to the 'Species of European Conservation Concern' categories SPEC2 and SPEC3 across eight stages of a grassland-to-forest gradient (from 180 20-min-long point counts with unlimited detection distances; see Prodon and Lebreton 1981 for methodological details) performed in the western Albera Massif). *Variació en el nombre relatiu d'ocells que pertanyen a les categories "Species of European Conservation Concern" SPEC2 i SPEC3 a vuit etapes d'un gradient que abasta des de pastures fins a boscos (a partir de 180 punts d'escolta de durada de 20mn i de distància de cens il·limitada; vegeu Prodon i Lebreton 1981 per a detalls metodològics), realitzat a l'occident del massís de l'Albera).*

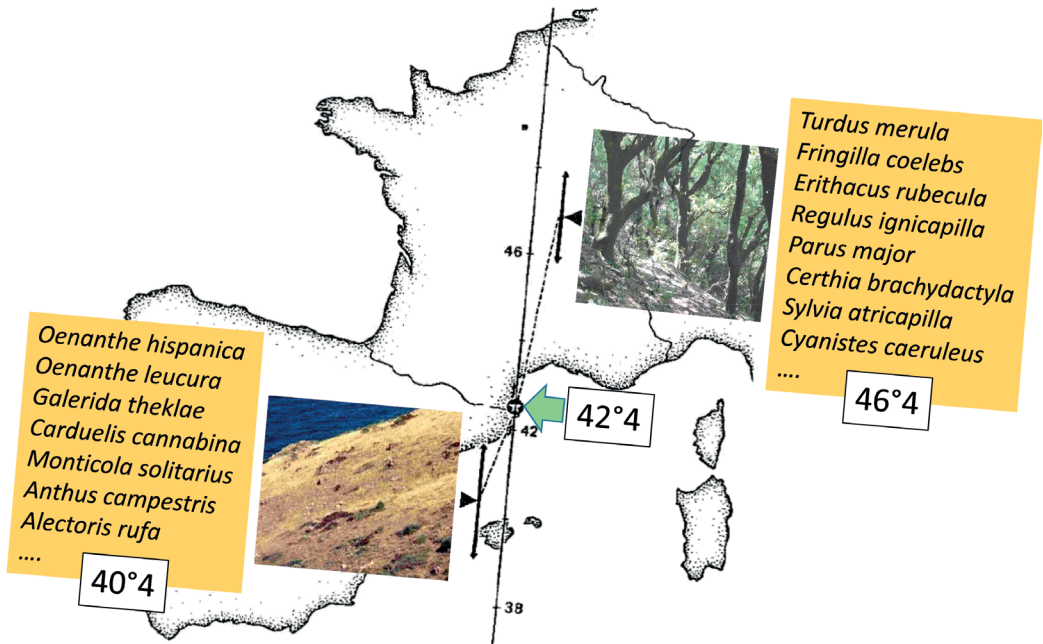


Figure 3. Mean latitudes of the avifauna in two contrasting land cover types – dry grassland vs. holm oak forest – in the western Albera Massif, compared to the latitude of the study area (rounded to 42°4). The mean latitude of the avifauna in each land cover was calculated by averaging the mean latitudes of the ranges of the bird species present in 10 samples (20-min-long point counts with unlimited detection distances) in each land cover type (modified from Prodon 1993).

Latitud mitjana de l'avifauna en dos tipus de cobertes del sòl contrastades –prats secs versus bosc d'alzines- de l'occident del massís de l'Albera, en comparació amb la latitud de la zona d'estudi (arrodonida a 42°4). La latitud mitjana de l'avifauna a cada coberta del sòl es va calcular mitjançant la mitjana de les latituds dels rangs de les espècies d'ocells presents en 10 mostres (punts d'escolta de durada de 20mn i de distància de cens il·limitada) en cada tipus de coberta del sòl (modificat a partir de Prodon 1993).

Conservation issues

Only about 14% of European terrestrial bird species can be considered strictly Mediterranean if their geographical distributions are analyzed. Of these, about 50% are considered endangered, vulnerable, rare or in decline (Prodon 2000). Almost all are species of open habitats, rocky areas, or habitats with low-growing scrub vegetation, and many are absent from intensively farmed environments. Nationally, this phenomenon gives rise to geographical rarity. For example, the rarest species of birds in France are concentrated in the early stages of succession in northern Catalonia (Prodon 2000). In a European context, this is also true if both distribution and status (more or less favourable) of species' populations are taken into account using the SPEC criteria (BirdLife International 2017). From a conservation point of view, landscape closure results in the improve-

ment of avifauna, as the most threatened bird species in Europe (SPECs) live in pioneer successional stages. This is especially true in Catalonia (Figure 2), which explains why the impact of fire is not detrimental to the rarest or most threatened species (Prodon 1987, Clavero *et al.* 2011), even if the colonizers of burned areas are mostly species with a broad habitat tolerance (Pons & Bas 2005).

This result in a paradox for conservationists: European old-growth forests are today rare due to the long history of human pressure on the landscape; therefore these habitats deserve careful protection. And yet they shelter bird species that are widely distributed in Europe. Conversely, dry grasslands, low scrublands and rocky areas – often considered degraded wastelands to be rehabilitated (e.g. by replanting or cultivation) – host some of the least common of all European bird species. Yet these open habitats are disappearing almost everywhere due to the natural encroachment

of woody vegetation. Preserving them requires active conservation practices such as mechanical clearing, prescribed burning, extensive grazing or any combination of these techniques in a context of sustainable agricultural practices. Moreover, open spaces such as these help in the fight against large and catastrophic wildfires, whose frequency is likely to increase with global warming and associated droughts.

Biogeographical perspective

The biogeographical status of a bird species, sometimes simplified by its classification in a discrete category (or biogeographical type) (e.g. Voous 1960), can be quantitatively summarized by measuring the extent of its distribution. The latitudinal extent of a species' range – and its corresponding mean or latitudinal centroid – is particularly useful due to its close relationship to latitudinal climate zones (Prodon 1993). Bird species adapted to the pioneer stages of succession tend to have southerly distributions. In Catalonia, these species are often relatively close to the

northern limits of their ranges (hence their rarity in this region). Conversely, most bird species adapted to forests have more central-European or even northern distributions. Hence, from a biogeographical point of view, vegetation encroachment in an area results in an overall northward shift of the latitudinal average of its avifauna, i.e. an apparent 'cooling' of the latter. This can be illustrated by comparing the average latitudes of the distributions of breeding bird species in two extreme successional stages (relatively rocky dry grasslands vs. dense holm oak forests) in the eastern hills of the Albera Massif (Figure 3). A consequence of the afforestation of the landscape is thus the replacement of Mediterranean avifauna by non-Mediterranean avifauna: as paradoxical as it may seem, mature Mediterranean vegetation ends up hosting non-Mediterranean birdlife.

A flagship species: the Black Wheatear

The Black Wheatear *Oenanthe leucura* belongs to a genus of species found in Old World deserts

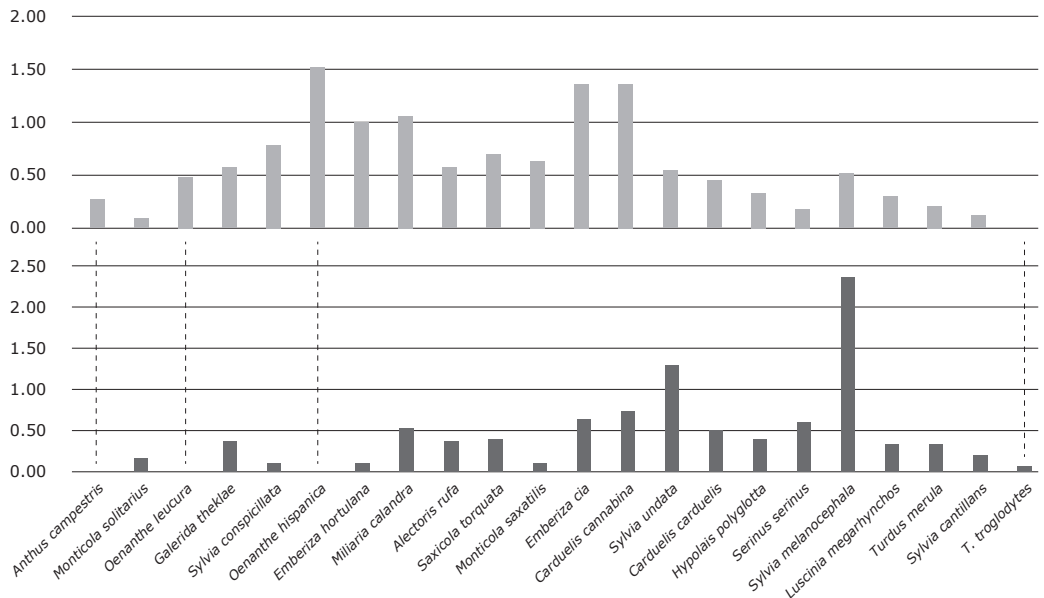


Figure 4. Mean number of bird species recorded by point counts at four sites in Madeloc (western Albera Massif) in 1975-1985 (a) and 2006-2014 (b). The dotted lines highlight the extinction or appearance of certain species. *Mitjana del nombre d'espècies d'ocells registrades per punt d'escolta a quatre indrets de Madeloc (oest del massís de l'Albera) durant el període 1975-1985 (a) i el període 2006-2014 (b). Les línies puntejades posen de manifest l'extinció o l'aparició d'algunes espècies.*

and arid zones. This particular wheatear, whose behaviour is so unusual among European passerines, is one of the rarest birds in Catalonia. Present in French Catalonia until 1996, it is now no longer found at any of its previously known sites in the Albera Massif. It also disappeared from Cap de Creus (42°19N-3°18E) in 2000 and its northerly limit has now retreated to south of Barcelona to the Garraf Massif (Noguera *et al.* 2014). Indeed, the northern boundary of its range has receded continuously since the end of the eighteenth century: from Liguria to Provence, Languedoc, then Catalonia. Of the 51 breeding birds present in the Albera Massif in the 1980s, a statistical analysis of a set of point counts showed that the most intolerant species to woody cover was the Black Wheatear (Lebreton *et al.* 1988). Its current decline in Catalonia is due beyond any doubt to vegetation encroachment. This wheatear is not the only bird species in this situation as field surveys of its historic sites in the Albera Massif – from where it is now absent – repeated after about 30 years show that a general modification of the avifauna has occurred (Figure 4). Open-habitat species have decreased or disappeared and have been increasingly replaced by mid-successional species. In this context, wildfires favour the Black Wheatear as they open up the vegetation; in fact, this bird is able to colonize certain recently burned rocky areas, albeit with constraints imposed by connectivity (e.g. Zozaya *et al.* 2012). One example is its colonization of the Montserrat Massif in central Catalonia after the serious fires in 1986 (Real 2000). However, over the long term this positive effect of fire does not persist due to the great resilience of woody vegetation, with the result that the Black Wheatear cannot colonize permanently these newly opened-up sites.

The opposing forces of landscape closure and global warming

One of the expected consequences of global warming in the northern hemisphere is a northwards shift in distribution ranges. In Western Europe, some data seem to confirm this northern shift in bird species (in France: Devictor *et al.* 2008). In Catalonia, climate envelop models predict a decrease in certain species – especially forest

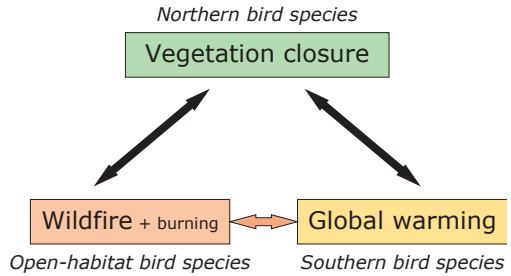


Figure 5. Synergistic or antagonistic relationships between three major trends that are likely to affect the avifauna in Catalonia in coming years: landscape closure, wildfires and global warming. *Relacions sinèrgiques o antagòniques entre tres grans tendències que probablement afectaran l'avifauna a Catalunya en els propers anys: tancament del paisatge, incendis forestals i escalfament global.*

species – whose distributions are forecasted to shift northwards as a result of warming temperatures that may make a large part of the Iberian Peninsula unsuitable (Willis *et al.* 2007). This is the case, for example, of the Coal Tit *Periparus ater*, which is expected to become extinct in Catalonia by the end of the century, and the European Robin *Erithacus rubecula* and Firecrest *Regulus ignicapilla*, whose distributions in Catalonia are projected to become limited to a few restricted areas in the Pyrenees and coastal ranges (e.g. the Montnegre Massif). But the predicted decrease or extinction of these forest species with increasing temperatures is likely to be offset or negated by the general trend towards the afforestation of abandoned land currently occurring, which is likely to continue over coming decades. As we have seen, this afforestation favours more northerly species at the expense of open-environment species, which have a more southerly distribution (see also Seoane & Carrascal 2008).

The example of the Black Wheatear is illustrative: although its range is very southerly (its centroid is around the 35°N) and reaches its northern limit in Catalonia, this bird is not favoured by warming temperatures. Indeed, the encroachment of its habitat by woody vegetation in all its historic sites is pushing it southwards, forcing it to progressively abandon all its northernmost sites in the Albera Massif and the Pyrenees. For this species – and for certain other uncommon open-habitat species (e.g. *Galerida theklae* and *Oenanthe hispanica*) – the effects of

changes in vegetation structure counterbalance and even outweigh those of climate change.

To conclude, landscape closure, wildfires and global warming have either synergistic or antagonistic effects on Catalanian bird species adapted to open habitats (Figure 5). Intensively cultivated or anthropic environments remain open to colonization by exotic open-habitat species, which may be a potential source for colonizing burned areas (Pons & Bas 2005). These burned areas can themselves constitute reservoirs for the maintenance of open-habitat bird populations and the colonization of other burned areas (Zozaya *et al.* 2012). Moreover, the expected decrease in precipitation may interact with and enhance the effects of global warming on the avifauna (Herrando *et al.* 2019) and decrease the resilience of the vegetation after fires (Puis-Girones *et al.* 2017). Nonetheless, in contrast to purely climate-based predictions and despite the probable increase in the recurrence of wildfires, there is good reason to believe that in the coming decades and on uncultivated and abandoned land the effects of woody vegetation encroachment on the avifauna will prevail over the effects of warming.

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Resum

Conseqüències de la invasió del paisatge per la vegetació llenyosa per a l'avifauna del nord de Catalunya

Durant el darrer segle, hi ha hagut un marcat èxode rural a les àrees de muntanya que envolten les planes del nord de Catalunya. Aquest procés ha provocat l'increment inexorable de la vegetació llenyosa, acompanyat de l'aparició freqüent de grans incendis forestals. Aquesta dinàmica contrària de tancament gradual del paisatge (a través de la invasió de la vegetació) versus obertura sobtada (a través del foc), afecta considerablement la comunitat ornítica de la regió. La progressió de la vegetació llenyosa després de l'abandonament de terres o dels incendis forestals, ha derivat en una successió des d'una avifauna d'hàbitats

oberts cap a una avifauna forestal. Des del punt de vista de la conservació, es tracta de la rarefacció de les espècies d'ocells de més gran preocupació per a la conservació a Europa (Species of European Conservation Concern: SPEC), perquè aquestes espècies viuen en les primeres etapes de successió ecològica d'hàbitats colonitzats per plantes pioneres. Des d'un punt de vista biogeogràfic, les espècies d'ocells adaptades a aquestes etapes pioneres solen tenir una distribució més meridional i a Catalunya sovint es troben prop del límit nord de la seva àrea global de distribució. Com a resultat, en general, el tancament de la vegetació afavoreix les espècies septentrionals a costa d'espècies meridionals. Al massís de l'Albera, per exemple, malgrat els incendis freqüents, el paisatge dels darrers 50 anys està dominat cada cop més per boscos i matollars. La freqüència d'incendis no ha estat suficient per evitar el tancament de la vegetació. Com a resultat, malgrat l'escalfament climàtic i els incendis forestals recurrents, les espècies meridionals d'hàbitats oberts, com el còlit negre *Oenanthe leucura*, una espècie considerada com a vulnerable a la Llista Vermella Europea, han desaparegut d'aquesta zona i han retrocedit cap al sud durant el segle passat. La invasió de vegetació, els incendis forestals i l'escalfament global poden tenir efectes sinèrgics o antagònics sobre els ocells a Catalunya. L'impacte del tancament del paisatge sobre la composició de l'avifauna està contrarestant el causat per l'escalfament climàtic. Al contrari de les prediccions basades en el clima i malgrat els incendis forestals recurrents, hi ha una bona raó per creure que a mig termini –excepte a les zones conreades– prevaldran els efectes del tancament del paisatge sobre els ocells.

Resumen

Consecuencias de la invasión del paisaje por la vegetación leñosa en la avifauna del norte de Cataluña

Durante el siglo pasado, ha habido un marcado éxodo de rural en las montañas que rodean las llanuras del norte de Cataluña. Este proceso ha llevado al aumento inexorable de la vegetación leñosa, acompañado por la ocurrencia frecuente de grandes incendios forestales. Esta dinámica opuesta de cierre gradual del paisaje (a través de la invasión de vegetación) versus apertura repentina (a través del fuego), afecta considerablemente la vida de las aves de la región. La invasión progresiva de la vegetación leñosa después del abandono de la tierra o los incendios forestales, han resultado en una sucesión de la avifauna de hábitats abiertos hacia la avifauna forestal. Desde el punto de vista de la conservación, se trata del empobrecimiento de aves de mayor preocupación de conservación en Europa (Species of European Conservation Concern: SPEC),

porque estas especies viven en las primeras etapas de sucesión ecológica de hábitats colonizados por plantas pioneras. Desde un punto de vista biogeográfico, las especies de aves adaptadas a estas etapas pioneras suelen tener una distribución más meridional y en Cataluña a menudo están cerca del límite norte de su área de distribución. Como resultado, en general, la cobertura de la vegetación está favoreciendo a las especies del norte a expensas de las especies del sur. En el macizo de Albera, por ejemplo, a pesar de los incendios frecuentes, el paisaje de los últimos 50 años ha estado cada vez más dominado por bosques y matorrales. La frecuencia de los incendios no ha sido suficiente para evitar la cobertura de la vegetación. Como resultado, a pesar del calentamiento climático y los incendios forestales recurrentes, las especies meridionales de hábitats abiertos, como la collalba negra *Oenanthe leucura*, una especie considerada vulnerable en la Lista Roja Europea, han desaparecido de esta área y se han retirado hacia el sur durante el siglo pasado. La invasión de la vegetación, los incendios forestales y el calentamiento global pueden tener efectos sinérgicos o antagónicos en las aves en Cataluña. El impacto del cierre del paisaje en la composición de la avifauna contrarresta el causado por el calentamiento climático. Contrariamente a las predicciones basadas en el clima y a pesar de los incendios forestales recurrentes, hay buenas razones para creer que a medio plazo, con la excepción de las áreas cultivadas, prevalecerán los efectos del cierre del paisaje en las aves.

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