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Bird biodiversity in relation to forest composition in Sweden

Annabelle Finck

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Department of
Physical Geography and Ecosystem Science
Lund University
Sölvegatan 12
S-223 62 Lund
Sweden

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Male Lesser Spotted Woodpecker © Garth Peacock

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Supervisors: Paul Caplat, Centre for Environmental and Climate, Veiko Lehsten, Department of Physical Geography and Ecosystem Science
Lund University

Exam committee: Oskar Löfgren, Department of Physical Geography and Ecosystem Science

Laurent Marquer, Department of Physical Geography and Ecosystem Science

Abstract

The large development of timber activities, and the changes in forest composition that it has implied, threatens the survival of certain bird species in Sweden. Today, bird biodiversity restoration plans try to re-establish, in harvested forests, the structural straits that will foster high bird diversity. The aims of this study were: 1) to identify in the literature which forest composition traits are essential for forest birds in Sweden; 2) to find the environmental variables that explain the occurrence and abundance of forest bird species in Sweden, using regression analyses conducted on data from a national monitoring program.

Past studies have identified several main drivers of bird diversity, notably the presence of old standing trees, of decaying timber and the amount of deciduous trees. Lack of information on such variables limited the power of our analysis. However, regression models revealed the importance of forest edges, which can compensate the lack of deciduous trees in harvested forests. Thus in a biodiversity perspective the scope of concern should be broadened to the areas close to forests. The lack of clear links between the distribution of forest indicator species and forest composition traits in the data analysed also questions the practical relevance of indicator species as they are currently defined.

Keywords: Forest composition – bird occurrence – indicator species – bird biodiversity – timber production

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Contents

1. Introduction: forest management and biodiversity

Commercial forestry has been largely developed in Sweden and represents today an important source of income for the Swedish economy. As a result, natural forests are nowadays difficult to find in Sweden, and remnant areas of old forest are particularly fragmented and reduced (Nihlgård & Sallnäs, 2005).

Intensive methods have been put in place in order to benefit more from exploitations. Thus trees are cut before a certain age - between 80 and 120 years - (Nilsson et al., 2005). This can be explained by the decreases of productivity past these ages. Actually past these ages many of them get infected by fungi and can die afterward (Spitznagel, 1990). Harvesting results in a diminished representation of older trees in managed forest compared to virgin forest, where a large gradient of tree ages can be found. In virgin forests trees represent all age, whereas in managed forest most of the trees have the same age (Sverdrup & Stjernquist, 2002).

In virgin forest, the tree cover is not continuous; gaps resulting of natural fires and grazing are found. Actually, in certain forests such as boreal forests, fire is a natural phenomenon that occurs at an interval of 20-50 years. After a fire, most of the young trees disappear. The tree density is reduced, allowing the survival of old large trees (Wirth et al., 1999). According to Hultkranz and Wibe (1989) less than 10 % of the wood is consumed during a fire, while 95-98 % of the wood is removed after clear-cutting in Sweden. In virgin forests, animals such as deers, bisons, and before they extinctions, aurochs, wild horses and fores elephants, participated by grazing to maintain gaps in forest (Bengtsson et al., 2000; Nilsson and Ericsson, 1997; Owen-Smith, 1987; Vera, 2000).

Today managed forests are denser. Dead trees are removed to use the largest part of the area. As a consequence, in managed forests, dead trees, which have a diameter at breast height (DBH) higher than 40 cm, represent less than 1 % of their original densities (Harmon et al., 1986; Nilsson et al., 2005; Warren and Key, 1991). Besides, with the control of natural disturbances such as fires, there are less open areas in managed forests.

In addition of clear-cutting, logging residues – called FWD, fine woody debris - that host numerous types of beetles, are more and more extracted with the development of the bio energy field (Dahlberg et al., 2011).

In managed forest certain tree species have also been removed because they are considered to be less productive or because they host fungus. It is the case of aspen trees, which have been selectively removed, by fear of the *Melanpsora pinitorqua* that they can host. The *Melanpsora pinitorqua* is a fungi which negatively affects the growth of Scot pine (Angelstam, 1990). Thus a shift from deciduous forests to conifer forests has been observed, particularly in Southern Sweden (Nihlgård & Sallnäs, 2005).

In addition, if the taiga and the boreal forest are regarded as being naturally fragmented in relation to the fire regime, forestry practices, with the multiplication of roads, infrastructures but also the urbanization seem to have strengthened this fragmentation (Angelstam, 1990).

These changes in forest composition and structure clearly threaten bird species according to experts (Angelstam and Mikusinski, 1993). This is why public and private forest managers are trying to adapt forestry practices (note that private individuals own the greatest part of forest lands in Sweden) (Swedish Forest Industries Federation, 2011). In 1993, with the Swedish Forestry Act, the government highlighted two goals for the Swedish forestry: productivity but also environment protection (Niklasson et all., 2005). Today managers try to reproduce this in harvested forests, retrieving forest composition and structure that offer good habitats for birds, and allow maintaining or restoring biodiversity (Swedish Forest Industries Federation, 2011) .

The first question thus appears clearly: which factors influence the presence of birds in the forest? Which of them seem to be more important in term of bird biodiversity? And what is the most important factor between forest composition and forest structure?

At first in this review, I have tried, by searching in previous studies, to find elements of landscape composition and structures that seem essential to consider in a biodiversity perspective. Secondly, I have studied, with statistical tools, the occurrence and the abundance of the Swedish bird species that indicate forests of good quality (our “indicator species” in this study). The aim was to identify on which factors depend their presence and then to compare such factors with those found in the literature.

Working hypotheses

According to the literature study, forest age should be positively correlated with the abundance, and specific richness of indicator species. Second this correlation is expected to be particularly clear for the deciduous trees. We anticipate a high number of the indicator species in areas where a lot of old deciduous trees are found.

On the contrary, a negative influence of agricultural areas on both abundance and species richness is expected. For water areas, a hypothesis is more problematic to express, since contradictory conclusions about riparian edges have been presented. Nevertheless several studies underline their positive effect, in relation with the higher density of mosquitoes, dead and deciduous trees that would de found within them (Brazaitis, 2011; Aulen, 1988; Enokson et al., 1995).

2. Background: factors influencing bird occurrence in the forest

2.1. Forest composition

In this part, I have focused on the elements of forest composition: the type and specificities of the vegetation and species present.

2.1.1. Proportion of old trees, dying trees, snags.

The decrease in old-tree cover is particularly problematic for bird communities since old trees constitute an important substrate to nest and in certain cases to forage. Trees seem to be suitable for nesting uniquely after a certain age. In oaks, for instance, hollows mainly develop in trees older than 150 years old. Actually most cavities in trees are the result of the decay process, which occurs with a fungi development at a rather late tree life stage (Bunnell, 2013). This long decay process which softens the wood inside also permits the excavation by birds. At a certain stage, the wood is soft inside and hard outside, making possible excavation, but also preventing predators from tearing open the nest. This configuration is favoured by the heart rot, a disease caused by the presence of fungi called conks on the bark of the tree (Walters et al, 2002).

In addition, to welcome the birds and their offspring the branches should also be large enough. Consequently birds clearly favour large diameter trees (Bunnell, 2013).

Moreover some species show a preference for snags and old trees to forage. It is the case of the three-toed woodpecker, which mainly forages on snags (Steeger and Dalissse, 1997). This preference is explained by the important presence of bark beetles – which are saproxylic species, depending on recently decayed dead wood, at least at certain stages of their life - in weak, dying and recently dead trees (Grove, 2001). These insects constitute a great part of some species' diet (Imbeau et al., 2014). Nevertheless ensuring the satisfaction of this diet requirement is quite complex since after a couple of years, the decay in the tree is too advanced and the tree gets unsuitable for the insects (Coulson and Witter, 1984). That is why the three-toed woodpecker prefers recently dead or dying trees. As a consequence, there is a need to ensure a continual recruitment of recently dead snags as foraging substrates (Imbeau et al., 2014). Black-backed woodpeckers (it is an American species but relatively close to the European three-toed woodpecker) feed on dead wood debris and snags, and still preferentially when they have large diameters (Nappi et al. 2003; Tremblay et al. 2010). In fact, the wood-boring insect density is higher when the bark thickness is important, a thickness which directly depends on the tree diameter (St Germain et al. 2004b). The study of Tremblay et al. also underlines that if snags are scarce, black-backed woodpecker tends to forage on live trees. One can think that they would prefer old trees, which have a thick bark, and consequently a higher insect density. Tremblay et all. conclude that this species has a clear preference for post-mature coniferous stands. All in all the diet and nesting requirements of several bird species such as cavity nesting birds highlight the necessity of letting trees reach a certain age and die, and of ensuring mixed tree ages stand with a continuity of dying trees. Such natural structures are more and more scarce in managed forest because of large and regular clear cuttings.

2.1.2. Importance of deciduous trees

The decline of certain populations of birds has been linked with the disappearance of a lot of deciduous trees in forests. Pine forest is considered as being species poor. This constitutes a problem today since pines have been the main species used for regeneration after clear cutting (in northern Swedish boreal forests) (Kempe et al., 1992). Some species are associated with deciduous trees, which represent a necessary nesting and foraging substrate. For instance excavators prefer broadleaved trees because their wood, soft on the inside (in relation to the decay process) makes the excavation easier, and the hard shell around prevent “predators from tearing open the nest” (Bunnell, 2013). Some birds need deciduous trees to forage since they feed on aphids found in the canopy of those types of trees (Angelstam et al., 1993), as it is the case of the great spotted woodpecker (Angelstam et al., 1993). Nevertheless, it is important to mention, that some species prefer coniferous trees. The three-toed woodpecker prefers old spruce forests to excavate for example (Koskomies, 1989).

Some experts consider mixed forest, and for instance mixed boreal forest as a distinct type of forest, which is_characterised by its floral diversity and its structural heterogeneity (Hobson and

Bayne 2000). It can also be defined according to its tree composition in a way that no single species should compose more than 80 % of the area (Young et al. 2005). More and more species are now characterised as being “mixed forest specialists” (Enoksson et al. 1995) but Young et al. (2005) underline that there is a lack of knowledge concerning the use of both conifer and deciduous trees in the same area. The study of Young et al. (2005) in the New Brunswick highlights that Blackburnian warblers are present in deciduous and conifer trees, which have a DBH higher than 30 cm. The preference of those birds for mixed forest may be explained by the important foraging opportunities that can be found in deciduous trees. On top of that, in mixed forests which contain multiple tall trees, large crown volumes are associated with high average food availability. To conclude tree species diversity and especially the presence of deciduous tree enhances foraging and nesting opportunities (Whelan 2001; Young et al. 2005).

2.1.3. Humid areas

Some studies as the one of LaRue et al (1995) show that forests close to water or bog, which can be called « riparian edges », have a positive influence on the presence of birds. LaRue et al. underline that in Canadian boreal forest the bird abundance, richness and diversity were much higher in the riparian stands than in non-riparian areas, while the only difference between these two areas was the presence of water. Some explain the richness of riparian edges by the high density of certain insects such as mosquitoes, which reproduce close to water. Mosquitoes also represent the main source of food for several species, like flycatchers (Brazaitis, 2011). Ripanian edges would constitute a foraging area.

Riparian edges are often composed by shrubs. Sunlight is available for all vegetation layers and so the vertical foliage profile of this area is almost continuous. That forms a high lateral visual obstruction - « edge wall » -, protecting birds against predators (Gates and Giffen, 1991).

Aulen (1988) and Koskimiens (1989) advocate the importance of the “water-edge forest”. Actually forest adjacent to water may be characterised by floodings which weaken trees, and thereby favour the formation of dead wood. Wood-living beetles would be also more abundant since these zones are particularly exposed to sunlight. Besides, the soil fertility would also favor the presence of deciduous trees. According to Enoksson et al. (1995), a great number of deciduous trees in managed forests are associated with streams and lakes.

Nevertheless, in the literature, contradictory conclusions about riparian zones are found. Some think for instance that instead of constituting a shelter zone against predation, they could be an ecological trap for predators (Gates and Giffen, 1991). Actually predator activity is often concentrated at the interface between adjacent habitats. Besides streams can concentrate predator activity and are used as travel corridors by mammals as raccoons (Gates and Giffen, 1991).

2.2. Forest structure

In this part, I have focused on the layout of forest composition elements described before. The notion of layout refers to the size of the highly suitable patches, and to their spatial repartition.

2.2.1. The "area effect": the effect of decreased patch size on the occurrence of species

As we have seen earlier the intensive forestry practices have decreased the size of patches suitable for birds in forests. According to the "island biogeography theory" (Mac Arthur and Wilson, 1967), the density of individuals is function of the size of the suitable habitat. Larger the habitat is, the lesser the risk of extinction exists (Lindenmayer et al. 2002). So in the long-term, biodiversity is dependent on the size of habitat patches. This is particularly true for resident species since, staying the whole year in an area, they need more resources in this area than the migrant species. Thus they need a larger area to forage. Besides resident species have a bigger average body than migrant species: they require larger home ranges (Schmiegelow and Monkkonen 2009).

Nevertheless the effect of habitat size is complex. Medium-size remnants can be linked to the highest level of biodiversity, because they contain enough food sources and shelters but at an insufficient level for potential predators or competitors. In small remnant habitats, there would be a lack of suitable habitats, and in larger ones, some birds would be excluded by predators or competitors (Lindenmayer et al. 2002).

2.2.2. Fragmentation

Different conclusions have been found concerning the effects of fragmentation on bird biodiversity, there are still differences between theories and results of field works (Harrison and Bruna, 1999). Fragmentation does not only lead to a habitat loss but also combines an increase of edge amount and an increase of isolation between habitat patches (Bender et al., 1998). This fragmention is induced by human activities, which can create large separations between forest patches (in case of forest cutting for timber activities, but also to build infrastructure or to develop agricultural activities) or more minor ones (in case of roads crossing the inner forest for example).

* Edge effect

Forest harvesting results in physical edges, which have an effect on remnant forest (Angelstam, 1992). In edges, microclimatic conditions are changed: the exposition to sunlight can get more important, the wind is generally increased. This threatens certain species of lichens, causing the decrease of insect density, and thereby affecting birds populations (Essen 1994).

In addition, in temperate forest many studies have shown an increase of predation on bird nests at forest edges (Schmiegelow & Monkkonen, 2009). Nevertheless, this effect would be more dependent on the type of landscape found in the surrounding of the edge area (Schmiegelow & Monkkonen, 2009). There would be an increased predation when the edge is beside an agricultural land, but in other cases (for example if the edge cut is still inside a forest land) this aftermath is not evident (Mönkkösen et al. 2000). This highlights the difference of effects between an edge created by forest harvesting and an edge as a result of forest clearing for agriculture. Corvids, which can be predators for certain bird species, are more numerous in agricultural lands (Andren, 1992). This is one of the elements that could explain why predation would be strengthened at edges close to agricultural areas. Hahn and Hatfiels (1995) also underline that parasitism is higher in a large portion of the forest, if this one is situated close to agricultural infrastructures such as fields, cattle, farms.

However studies have shown opposite results. For some, the density of insects could be higher at edges, thereby increasing the presence of birds. For others also, there would have no important effect on predation (Schmiegelow & Monkkonen, 2009).

Roads crossing the inner forest also induced negative edge effects. Roads increase the level of stress for birds (caused by noise). Northern spotted owls (*Strix occidentalis caurina)* (a nothern-American species) living close to forest roads were found to have higher levels of stress hormones than owls nesting in areas without roads (Wasser et al. 2003). Stress has a negative effect on survival, reproduction and resistance to disease for a great number of species (Wasser et al., 2003; Wingfield and Farner, 1993).

Construction of roads also creates opened areas which will favour predators (Robinson et al., 2010). Exotic or generalist plant species can start competing with interior forest plants and thus degrade and fragment interior forest (Robinson et al., 2010). Specialists requiring interior forest conditions are particularly sensitive to the creation of roads, which decreases foraging sources and shelter possibilities (Robinson et al., 2010).

* Isolation

According to some experts, fragmentation would have no considerable effects until the suitable habitats for bird communities constitute only 10 to 30 % of the area. That is the case today for old-tree habitats in Sweden (Mikusiński & Edenius, 2006).

Isolation of habitats by fragmentation can threaten certain species by a decrease of the amount of suitable habitats, but it is really function of every species mobility capacities. In the study of Mikusiński & Edenius (2006), species with mobility of 200 m and 400 m could live in the whole old forest, which was highly functional for them. However for species with mobility of 50 m and 100 m, the spatial functionality declined.

2.2.3. The matrix composition, as factor of fragmentation mitigation

The composition of the matrix – area between habitat patches – can mitigate the effect of fragmentation, according to the ability of each species to use the matrix area, for example to forage (Lindenmayer et al., 2002; Saab, 1999). Actually the surrounding of habitat patches is not always inhospitable (Norton et al., 2000). This is particularly true for harvested forests where new successional habitats have been introduced and where logging caused a perforated, rather than a truly fragmented landscape. Pileated woodpecker (an American species) can use patches beside their original habitats (Bonar, 2001) .

This underlines the phenomenon of "habitat compensation". Some species can "compensate for a loss or fragmentation of their preferred habitats by shifting to less preferred habitat types" (Norton et al. 2000). It calls into question the main conclusion of the island biogeography theory, which links the level of biodiversity of an area to the size of the suitable patch. The notion of habitat compensation prompts us to change this patch-centred analysis. Loss of absolute amount of forest habitat would be more dangerous than reduced area of forest patches or patch isolation (Norton, 2000).

2.3. Relative importance of drivers

The factors that influence the most the bird repartition are also different according to the species. Within one bird community forest-interior specialists, interior-edge specialists, interior-edge generalists, edge and field edge species can be distinguished (Brazaitis, 2011). Thus certain species seem to be more sensitive to the changes in forest composition and structure that have occurred. Interior species are particularly sensitive since birds of this group cannot shift and live at the edges of the forest.

Impacts are also different between resident and migrant species. Resident species are more sensitive to the size decrease of suitable habitats since, staying in the same area during the whole year, they need a larger area to forage (Lindenmayer et al., 2002). In Fennoscandia, the populations of resident species that depends on old successional forest stages has declined whereas the populations of migrant species, that prefers clearcuts or young forests has shown a corresponding increase (Järvinen et al., 1977). The most important causes for the decline of resident species would be the loss of old boreal stands on one hand, and on the other hand the decrease of the total amount of deciduous trees (mainly aspens and birches) (Angelstam and Mikunski, 1993).

For some authors (Harrison and Bruna 1999) habitat degradation is a more crucial issue than isolation and fragmentation. Actually ecological losses are a function of the total amount of habitat and not of its configuration (Harrison and Bruna 1999). Besides according to Harrison and Bruna (1999) isolation and fragmentation are not spatial problems but more a matter of habitat degradation, in relation with edge effects. That's why we will focus on habitat degradation in this study.

To conclude, the changes of forest composition which threaten bird biodiversity in Swedish forests. These changes - the reduction of the amount of deciduous, dead trees, the decrease of the average tree age, the reduction of the number of snags - are directly linked to the timber activities.

3. Analyses - Methodology

3.1. Swedish forests

The study focuses on Sweden, where forests represent an important issue, since forest land (defined by the Swedish Forest Agency as “contiguous area where trees have a height of more than 5 meters, in which the canopy cover is more than ten per cent, or an area inside which trees have the potential to reach this height, and the canopy this cover, without measures to increase production”) covers 70 % of the country, with 28 million of hectares (Swedish Forest Agency, 2013). Moreover, the timber production has an important weight in Swedish economy; it represents 12 % of the Swedish export income, and 100.000 employees depend on it (Swedish Forest Agency, 2014).

In Swedish forests, the main tree species are spruce (*Picea abies*) which represents 45 % of the forest, pine (*Pinus sylvestris*) which covers 39 % of the forest and birch (*Betula*) which covers 10 % of the forest land, and represents two-thirds of the deciduous trees (Swedish Forest Agency, 2014). The harvesting rotation period is estimated between 65-110 years, but is dependent on the geographic situation (Swedish Forest Industries Federation, 2012).

Different forest types can be distinguished in Sweden according to the climatic conditions. In the North, forests are defined as boreal: they are dominated by conifers. More to the South, hemiboreal forests are composed of coniferous and deciduous trees. To the South of the hemiboreal belt, in the nemoral part, oak and beech are considered as typical species (Swedish Forest Industries Federation, 2012).

3.2. Study species

The population of certain bird species has decreased for the last 30 years in Sweden (Miljömål, 2014). This would be related to the human-induced transformations which occurred in Swedish forests. The population of some birds, such as the marsh tit and the willow tit have been divided by two (Red List report, 2010). For example the lesser spotted woodpecker has declined with an annual rate of 7 % since the middle of the 1970's (Nilsson et al. 1992). The white-backed woodpecker has disappeared from most boreal forests (Aulen 1988). Vaisanen et al (1986) sum up the situation in this way: the population of several birds which depend on old successional stages, mainly resident species, has declined, but the population of some birds preferring open-ground and young forest, mainly migrating species, has increased.

Today, in order to maintain and restore the bird biodiversity, forest managers identify areas where it is necessary to regulate forestry. This type of maps are created using bird requirement studies, showing which types of habitats, how much of them are needed, and in which configuration.

Nevertheless, studying in details spatial requirements for each species would be, on the one hand, too much time-consuming, and on the other hand, there is still a lack of knowledge for certain species requirements. That is why protection plans are often uniquely based on the requirements of indicator species. The notion of indicator is quite difficult to grasp, since a species can be the indicator of different elements. It can indicate a high level of bird diversity in a forest, meaning that if this species is found in a given forest, a lot of other bird species will be found. With statistical analyses, experts determine which species indicates the best the presence of the others for a given area (de Jong and Lonnstad, 2002). In an indirect way, the presence of such species highlights that these areas have a high level of habitat suitability for the whole bird community. But an indicator species can also directly reveal the quality of these forest habitats. In this case, the indicator species are associated with certain forest compositions: presence of deciduous trees, of old forest remnants for example. It is this latter type of indicator species which has been used is this study.

I used the forest indicator species identified within the “sustainable forest” objective of the Swedish National Environmental Objectives (miljomal.se). The forest species are the capercaillie (*Tetrao urogallus),* the hazel grouse (*Tetrastes bonasia),* the lesser spotted woodpecker (*Picoides minor),* the three-toed woodpecker (*Picoides tridactylus),* the wood pigeon (*Columba palumbus),* the long-tailed tit (*Aegithalos caudatus),* the coal tit (*Periparus ater),* the crested tit (*Lophophanes cristatus*), the marsh tit (*Poecile palustris),* the willow tit (*Poecile montanus),* the Siberian tit (*Poecile cinctus),* the treecreeper (*Certhia familiaris),* the Siberian jay (*Perisoreus* *infaustus)*, the nutcraker (*Nucifraga***)**, the bullfinch (*Pyrrhula pyrrhula*) and the green woodpecker (*Picus viridis)*. These species have been divided in three groups. Each indicates a certain trait of forest composition (see table 1). First there are the dead wood specialists: the green woodpecker, the lesser spotted woodpecker, the three-toed-woodpecker, the marsh tit, the willow tit; second, the deciduous forest specialists which include the green woodpecker, the lesser spotted woodpecker, the three-toed woodpecker, the wood pigeon, the long-tailed tit, the marsh tit, ans the treecreeper. And finally there is the old-growth forest specialists group, which is composed of the capercaillie, the three-toed woodpecker, the coal tit, the crested tit, the willow tit, the Siberian tit, the treecreeper, the Siberian jay, and the bullfinch (Miljömål, 2014).

	Dead wood specialists	Deciduous forest specialists	Old-growth forest specialists
Capercaillie			x
Hazel grouse			
Lesser spotted woodpecker	x	x	
Three-toed woodpecker	x	x	
Wood pigeon		x	
Long-tailed tit		x	
Coal tit			x
Crested tit			x
Marsh tit	x	x	
Willow tit	x		x
Siberian tit			x
Treecreeper		x	x
Siberian jay			x
Nutcracker			
Bullfinch			x
Green woodpecker	x	x	

Table 1: Bird indicator species and their affiliations to the indicative groups.

3.3. Aim of the statistical analyses

The Swedish plans of biodiversity aim to recreate, insofar as possible, and without excluding all timber activities, the original forest compositions and structures, which were linked to a high level of bird biodiversity. These favourable forest compositions and structures are defined by studying the occurrence and the repartition of the indicator species. This study precisely tries to identify the elements of composition, which explain the occurrence of the forest indicator species.

3.4. Bird and Forest data

I analysed bird data from the fixed route scheme of the Swedish Breeding Bird Survey (SBBS, Lindström and Green 2013), an annual monitoring scheme that was initiated in 1996. The scheme consists of 716 plots systematically located throughout Sweden in a 25 km grid. At the centre of each grid cell the survey takes place over an eight kilometre square transect. The surveys are conducted once a year during the breeding season for most birds, approximately between 15 May - 10 June (in the south) to between 15 June - 5 July (in the north). The survey starts at 4 am, timed to coincide with the greatest singing activity. The observer walks at 30–40 min per km and records all birds seen and heard. If obstructions prevent the surveyor from following the line, deviations of up to 200 m are allowed. The surveys are carried out by a combination of experienced volunteers and professional surveyors. The number of annually surveyed routes increased during the first period of the project, reaching 200 in year 2000, and 400 in year 2003. In 2003–2012, between 400 and 584 routes were surveyed each year.

To describe forest composition I used several datasets. Indeed, high quality forest description exists only in limited points, and not necessarily matching the bird data. I thus used forest variables from i) “on the ground” sampling in the context of the Swedish Forest Inventory (Riksskogstaxeringen), limited to a small number of points, and ii) vegetation maps derived from remote sensing and ground-data, allowing to use most of the SBBS points but with lower accuracy in the description of forest composition than the forest inventory.

3.5. Data preparation

*** Forest inventory***

The Swedish Forest Inventory (riksskogstaxeringen) relies on a campaign of forest sampling on a grid of points across Sweden (Figure 1). The sampling points provide a complete description of the forest composition within a 7 to 10 meter radius (see variables below; Figure 2). However, the bird survey and the forest inventory were not realised at the same spatial or temporal scale: the forest inventory points do not completely overlap the SBBS routes, and I had only access to forest inventory points sampled between 1992 and 2001, whereas the SBSS data was sampled between 2000 and 2012. I had to combine information from different sources to infer the forest composition that would be relevant for the analysis. I used i) the CORINE Land-Cover (CLC) map from 2000 and 2006, which describes forests in four categories (broadleaf, coniferous, mixed forest, woodland-shrubland transitional forest), as polygon data, at 100m resolution; ii) raster data showing the loss of forest between 2001 and 2012, at 20m resolution (Hansen et al. 2013).

First I identified which of the Forest Inventory points could be used. I used ArcGIS to select only the points that overlapped the SBBS routes (see figure 1 and figure 2).

Then I checked that each point was part of a polygon identified as forest by the CLC 2000 map. I assumed for each point that the results of the vegetation measurements were also valid for the whole polygon (as forest management is usually implemented at larger scale than the sampling points). I documented how much of the selected forest polygon overlapped the SBBS route. If it was less than 80%, the point was not taken into account.

I then estimated maximal ages reached by forests in the years of the bird sampling using the following analysis: for each point, I started from the year for which the forest inventory dataset gave me a “for age stock”, and I checked with the CORINE Land-cover 2000 if the forest was still present or not in 2000. The same was done with CORINE Land-cover 2006 (figure 2), and at the end I checked if the forest had been cut between 2001 and 2012 (figure 3). For each point, I noted if the forest had been cut before 2012, and if it had been, I indicated the year of the cut, and if the cut had been partial or not. I also mentioned whether the forest was close to a stream or a lake since such locations influence necessarily the presence of certain bird species. Age from the forestry and year cut were combined to produce a “stand age” variable for every year between 2000 and 2012.

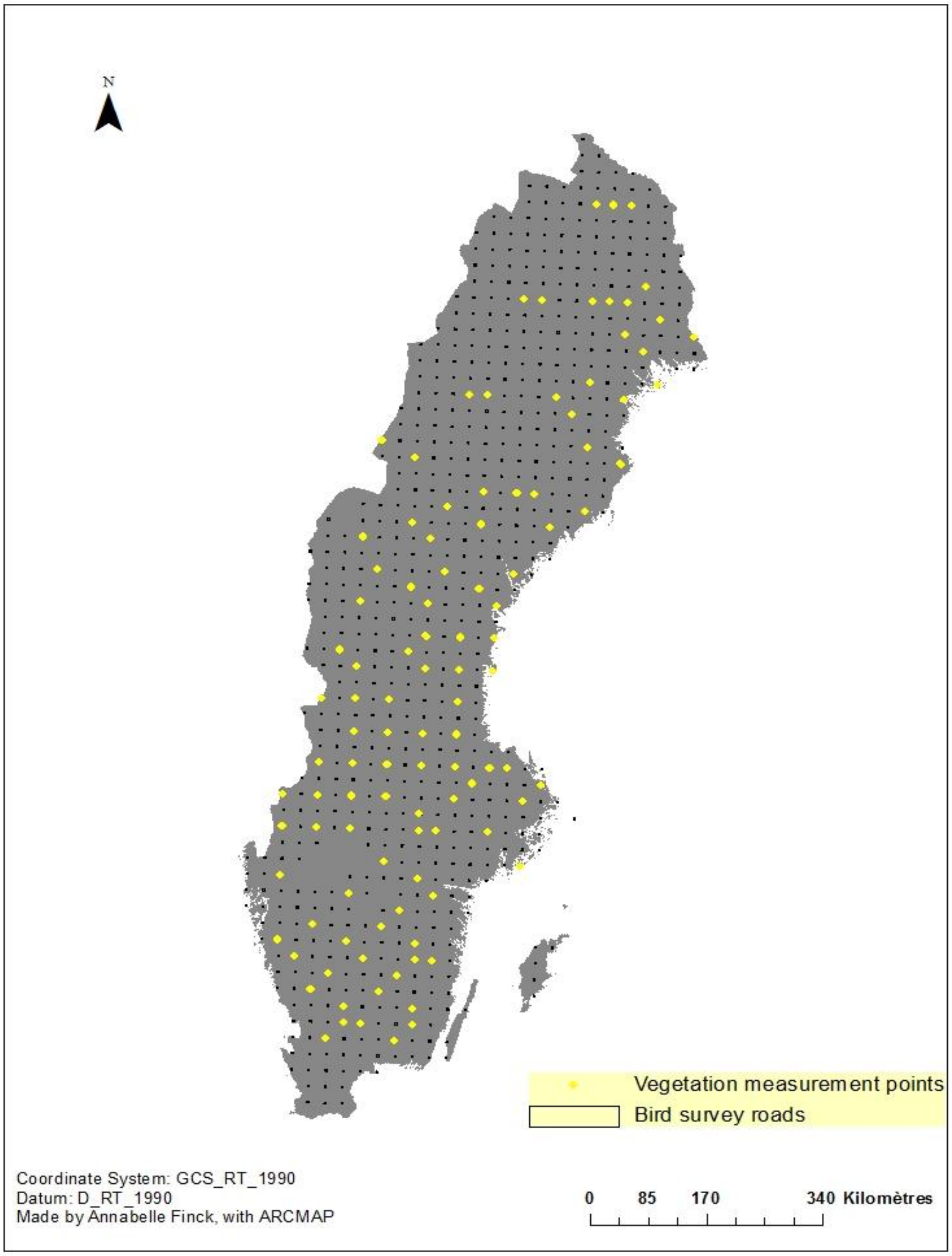


Figure 1: Location of the sampling points of the Swedish Forest Inventory, showing in yellow the 185 points used for the first set of analyses.

Illustration of the sequence:

Here is an example of the method for a vegetation point located in the center of Sweden. The riksskog data indicate that the forest was 125 years old in 1996. The first step consisted in determining if the forest has been cut between 1996 and 2000 using the raster layer Corine Land cover 2000. In this case, it has not been cut.

Second the land cover in 2006 was examined.

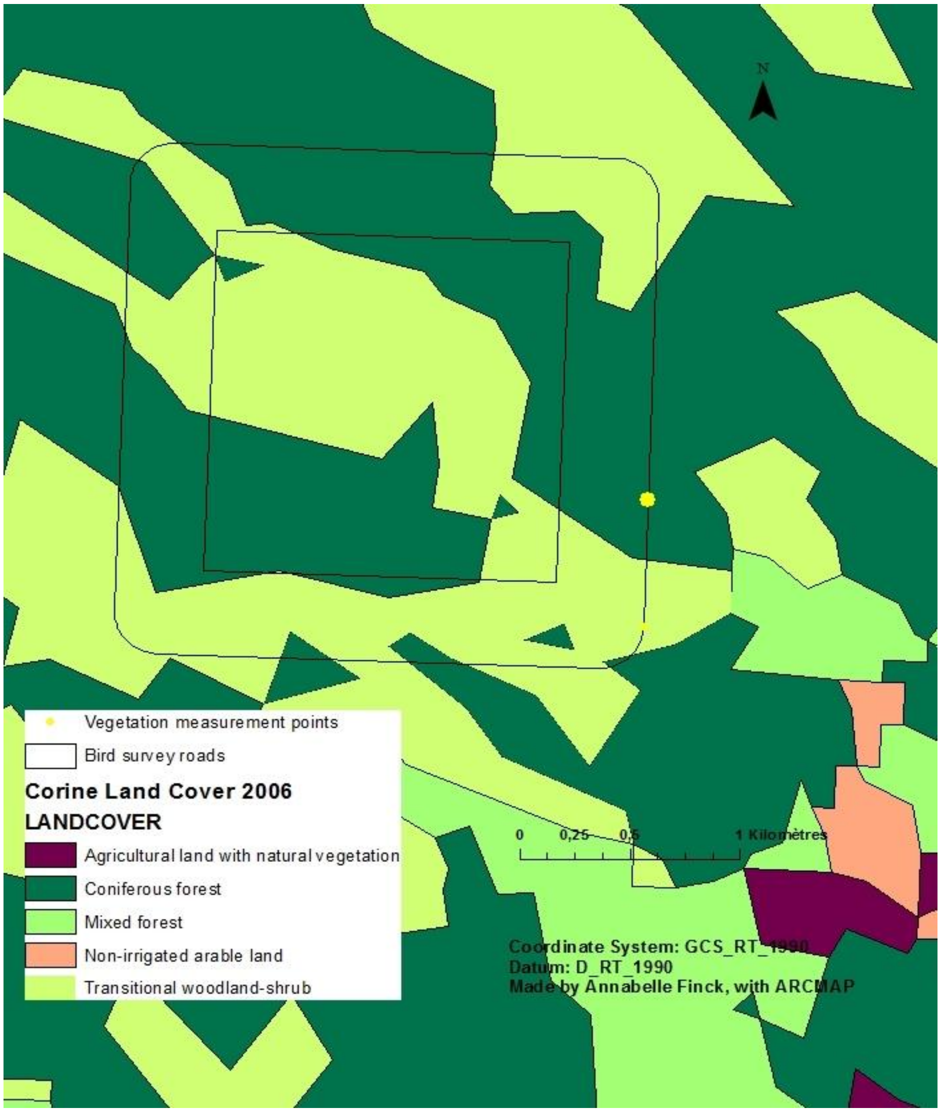


Figure 2: Land cover map in 2006 (from the Corine Land cover 2006 vector layer).

Around the point, a coniferous forest is still found: the forest was not cut between 2000 and 2006 either.

Finally, with the GCF loss data, I confirmed if the forest had been cut or not between 2001 and 2006, and I checked if it had been cut between 2006 and 2012.

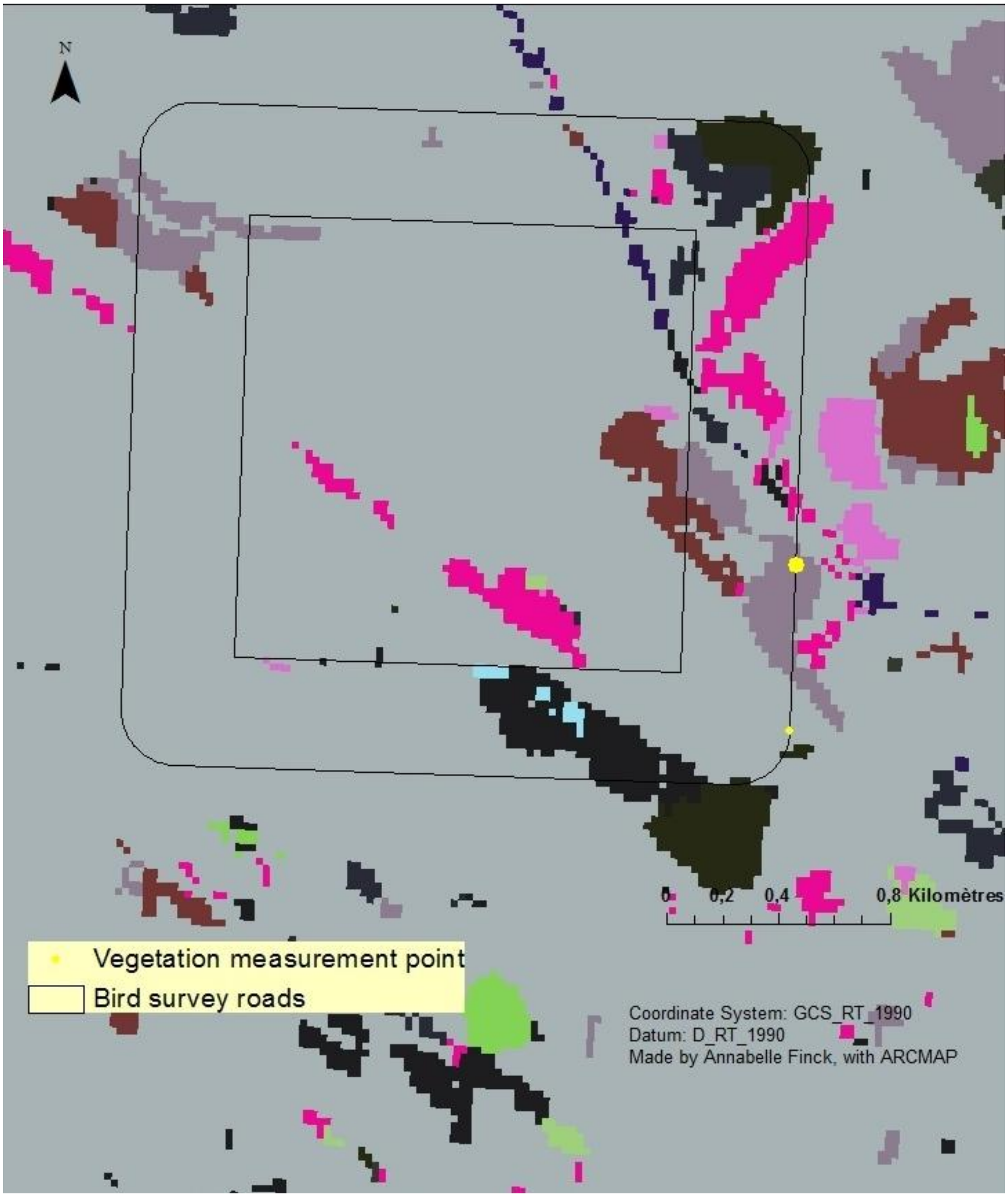


Figure 3: Map of the loss of forest between 2001 and 2012 (from the GCF raster layer).The pale grey indicates that the forest has not been cut, on the contrary all the other colours indicate that it has been cut, and each of these colours is associated with a year cut.

For the point which has been taken in example, the forest was cut in 2010, and thus has reached a maximal age of 139 years.

Forest maps

To be able to use more points of the SBBS, I used a map describing Swedish forest composition at 20m resolution (Skogskarta; Reese et al. 2002). Skogskarta is actually derived from the Swedish Inventory points we used, but interpolated and combined with remote-sensing data. The description of forest composition is coarser, but it covers all productive forest of Sweden.

I used a pre-existing dataset consisting of variables from Skogskarta, along with elevation data and land-cover data from CORINE, extracted in 300m buffers around the bird survey routes.

3.6. Regression analyses

I used the R software (R development core team 2011) for multivariate regressions analyses. Errors were modelled using a Poisson distribution. I did not use a method for variable selection since shortcomings of variable selection have been demonstrated (Whittingham et al. 2006). Instead delta-AIC was used (Schmuki et al. 2006). Variables with a correlation higher than 0.7 with a simple Pearson test were not included together in the models. This only affected stand age and stand height.

The regression models aimed at fitting the occurrence and number of individuals belonging to different groups of indicator species, against environmental and forest variables.

I used 2 sets of predictor variables:

- forest inventory data (riksskogstaxeringen): age of forest, number, volume and age of each tree species (pine, spruce, birch, other deciduous trees).

- Forest map and environmental data: longitude, latitude, elevation, forest density, volume of each tree species, maximal and average age of forest, tree height, presence of agricultural or humid areas.

I built regression models to link these variables with a) the species richness, and b) the abundance (total number of individuals) for the following species or groups of species:

- All forest indicator species

- Dead wood specialists
- Deciduous forest specialists
- Old forest specialists
- Woodpeckers
- Tits
- the models were finally built for each of those species: capercaillie, hazel grouse, green woodpecker, woodpigeon, long-tailed tit, coal tit, crested tit, marsh tit, willow tit, treecreeper, jay and bullfinch.

With the second set of vegetation data, I realized a comparison of models. I tested models including different variables (see appendix for a description of each model tested) in order to isolate the more relevant explanatory factors of birds occurrence. I selected only the best model for each group or species, using the Akaike information criterion (AIC) which measures the relative quality of a model for a given set of data. The AIC rewards the model, which fits with the data in the best way. The preferred model was the one with the minimum AIC value.

Finally, I used Conditional Inference Trees (Hothorn et al. 2006) to better visualise the role of predictors for bird diversity. Like traditional regression trees, CIT recursively perform, splits of a response variable (here, “occurrence of group X”) based on values of covariates (Hothorn et al. 2006). CIT are great to communicate results to managers because they present the role of each variable in an intuitive way (Caplat et al. 2014).

3.7. Accuracy assessment

For each model:

1. I calculated the regression coefficient to evaluate to what extent the curves from the regression equations fitted with the point distribution, in other words, to what extent the factors included in the models explain the bird occurrence.
2. I assess the accuracy of the models by choosing indicators often used in medicine, which are the proportion of true presences well-predicted (also called sensitivity), the proportion of true absences well-predicted (specificity) and the AUC (Area under the

ROC curve) (Pearson, 2014). Here is presented the calculation:

Table 2: Accuracy measurement, table from Pearson (2014)

	Recorded present	Recorded absent
Predicted present	a (true positive)	b (false positive)
Predicted absent	c (false negative)	d (true negative)

Sensitivity = a / (a + c) and specificity = d / (b + d)

(The calculation was done with the software R.)

If one model has a sensibility of 70 %, its means that 70 birds out of 100 recorded present will be detected by the model. If one model has a specificity of 70 %, 70 birds out of 100 recorded absent will be indicated as absent by the model.

3. The Receiver Operating Characteristic (ROC) curve is drawn thanks to different threshold-values. For our models, the thresholds were calculated within the function in such way as to maximise the sensitivity and the specificity. Closer to 1 the AUC is, more accurate the statistical model is. An AUC of 0.5 (its corresponds to the area under the dotted line, figure 4) indicates that the model is not significant (Pearson, 2014).

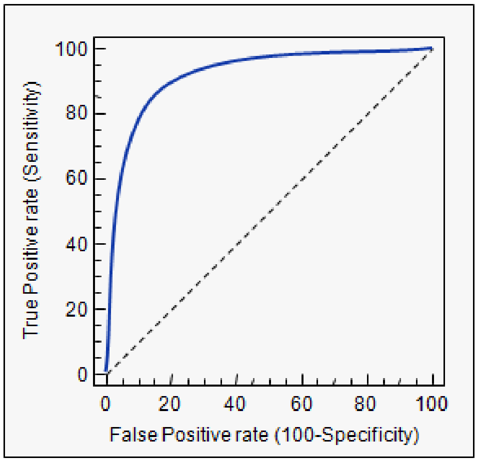


Figure 4: Example of graph, from which is calculated the area under the ROC curve (AUC). The ROC curve is represented in blue.

4. Results

In this section, we will first take a stock of the age of the forests studied. Then a general presentation of the results from the regression analyses will be presented, followed by a more precise description of them. Finally, the Conditional Inference Trees that we got will be presented.

4.1. Calculation of maximal ages

In a first time, the maximal age reached by 180 forests was determined (see data preparation). It confirms what has been underlined in the literature study: old-growth forests are pretty rare in Sweden, most of forests are cut before they grow old (according to the Swedish Forest Agency, an old growth-forest is “a forest over 140 years in Northern Sweden and over 120 years in the rest of the country”). The average maximal age is about 79 years for our 180 forests. About 41 % of those forests have been cut before they reach more than 60 years. This is quite early for cutting, it may be more thinning. Actually thinning are often planned when forest reaches around 40 years. Nevertheless in both cases, the forest is negatively affected. Only 18 % of these forests have reached an age superior to 120 years. As old-growth forests represent a keystone structure for bird biodiversity, such figures are quite alarming and highlight the effect of timber activities on the forest age structure. Thus this study totally confirms the assessment of Nilsson et al. (2005), according to which, with the implementation of intensive methods, most of the harvested forests are now cut before 80 to 120 years.

Table 3: Forest maximal ages for the forests studied in the first analysis (Swedish Forest Inventory data). 5 forests were not considered since contradictions between the Forest Inventory data and data from Corine Land Cover were found. Percentages have been rounded up to the unity.

Maximal ages reached by forests	**Number of forests having reached these ages**	**Percentage**
Between 0 and 30 years	18	10
Between 30 and 60 years	55	31
Between 60 and 90 years	41	23
Between 90 and 120 years	33	18
Between 120 years and 150 years	21	12
Above 150 years	12	6
Total	180	100.00%

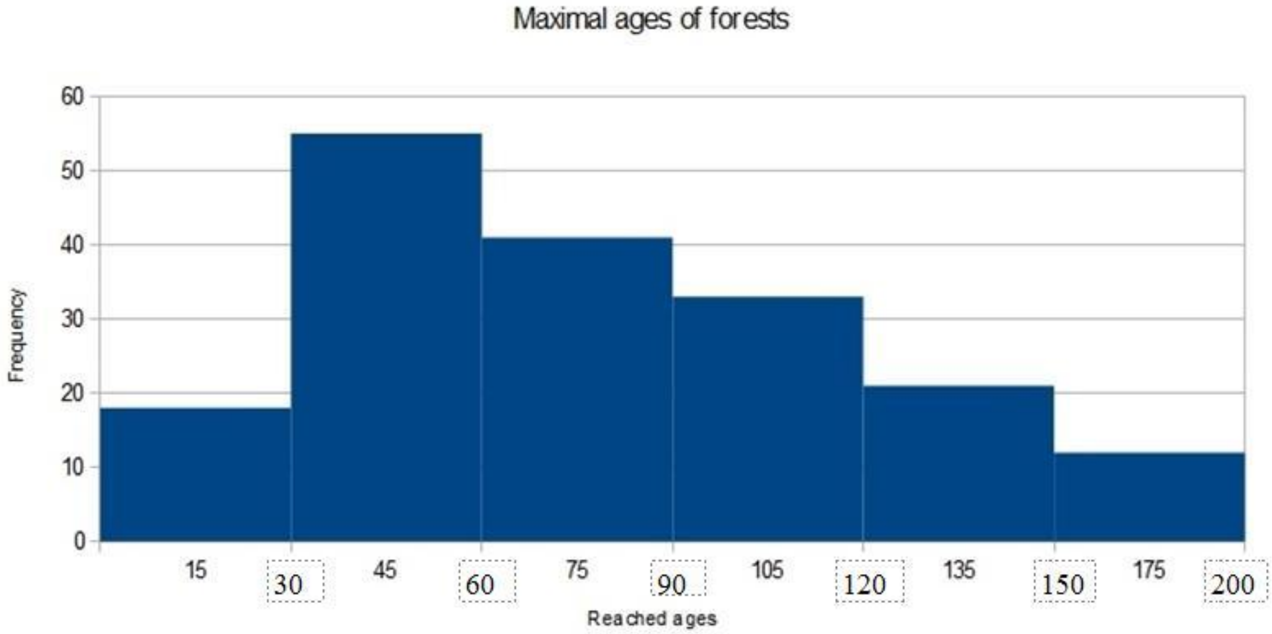


Figure 5: Diagram representing the frequency of maximal ages (for the forests studied in the first analysis).

4.2. Assessment of the regression analyses

- *Regressions analyses with the forest inventory data (Riksskogstaxeringen data)*

No relevant results have been found when we used the Riksskogstaxeringen data (high precision data in term of environment description but limited to a small number of points). Some significant correlations were established, but after having investigated the abundance levels, these correlations have appeared to have no sense anymore.

For example, with a regression model using a GLM function, a correlation between the number of birch having reached a certain age and the abundance of all the indicator species was found. But this result is not relevant since the abundance of the indicator species is too low. Within the bird survey lines which have been studied, the average abundance for this group is about 2 birds, and the maximal abundance is 13 (see figure 7). The total absence of indicator species is often recorded (see figure 6).

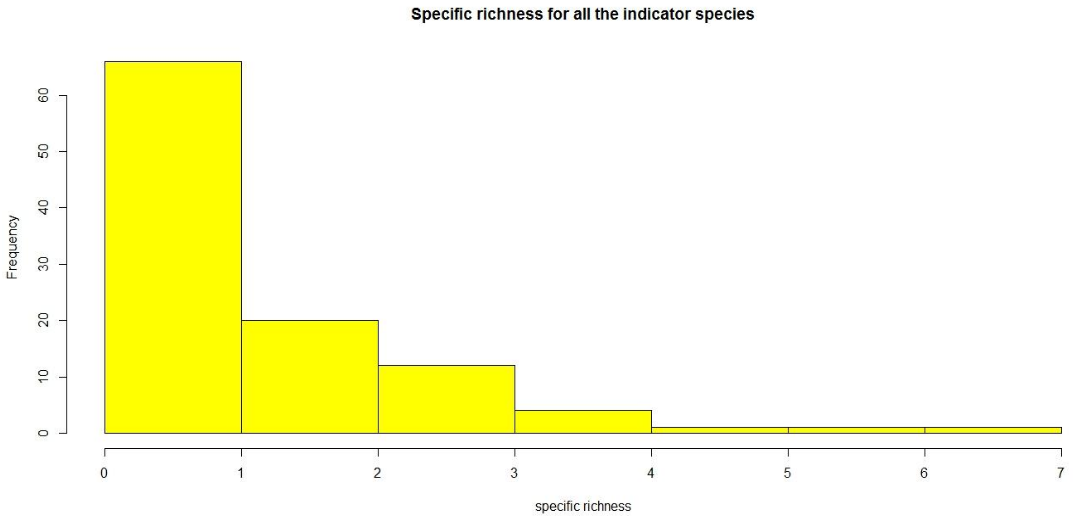


Figure 6: Diagram representing the frequency of the indicator species occurrence in the forests studied in the first set of analyses (with Riksskogstaxeringen data)

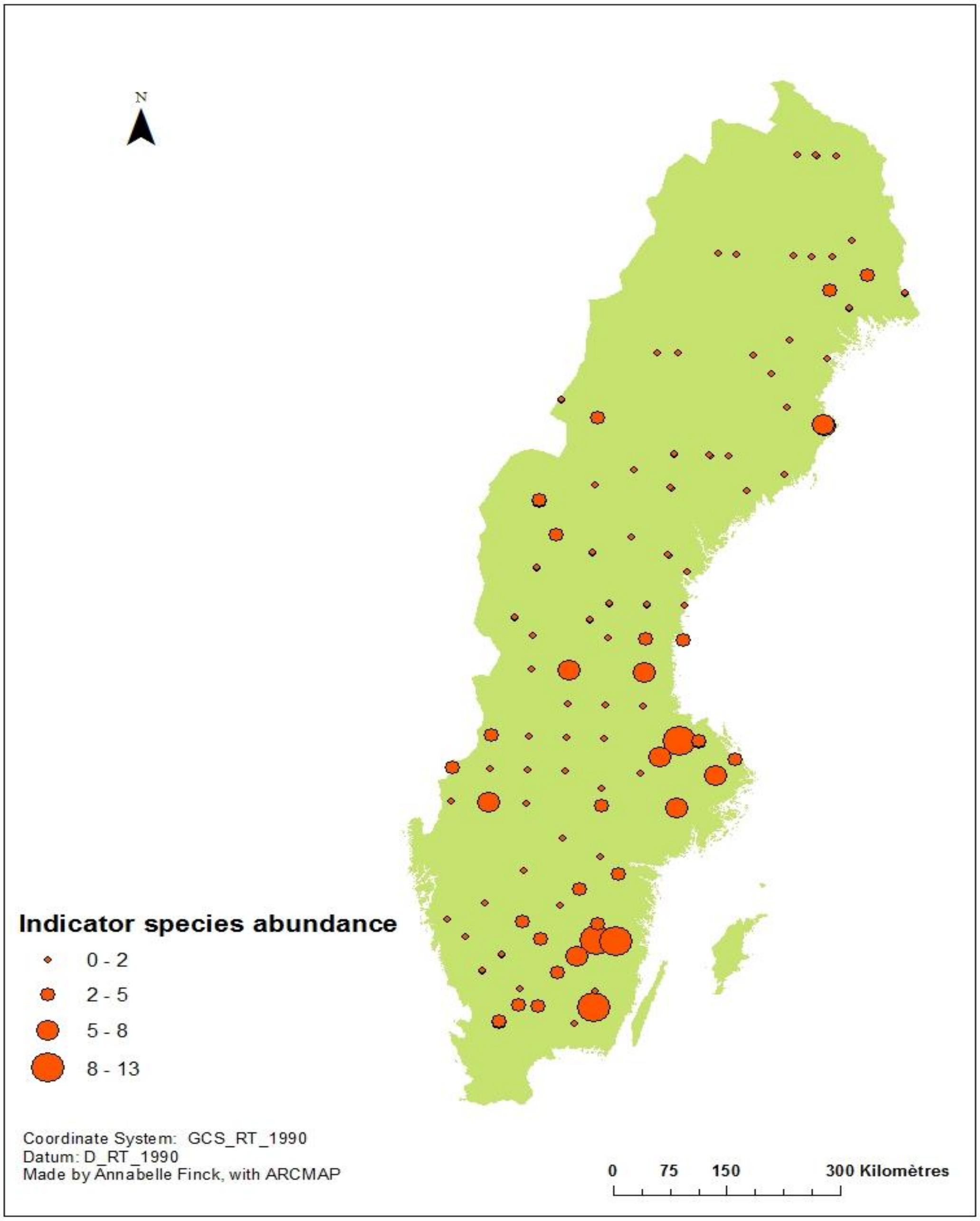


Figure 7: Abundance of the indicator species for the forests studied in the first analysis (based on the Riksskogstaxeringen data).

- *Regressions analyses with the forest map and environmental data*

Interesting results have been found when we took into account more SBBS points in our analyses with the forest map and environmental data (data with lower accuracy in the description of forest composition than the one of the first dataset), since it permitted to have points with higher abundance levels (figure 8). This dataset has allowed us to make a comparison of models (see appendix) in order to identify which factors influence the most bird biodiversity.

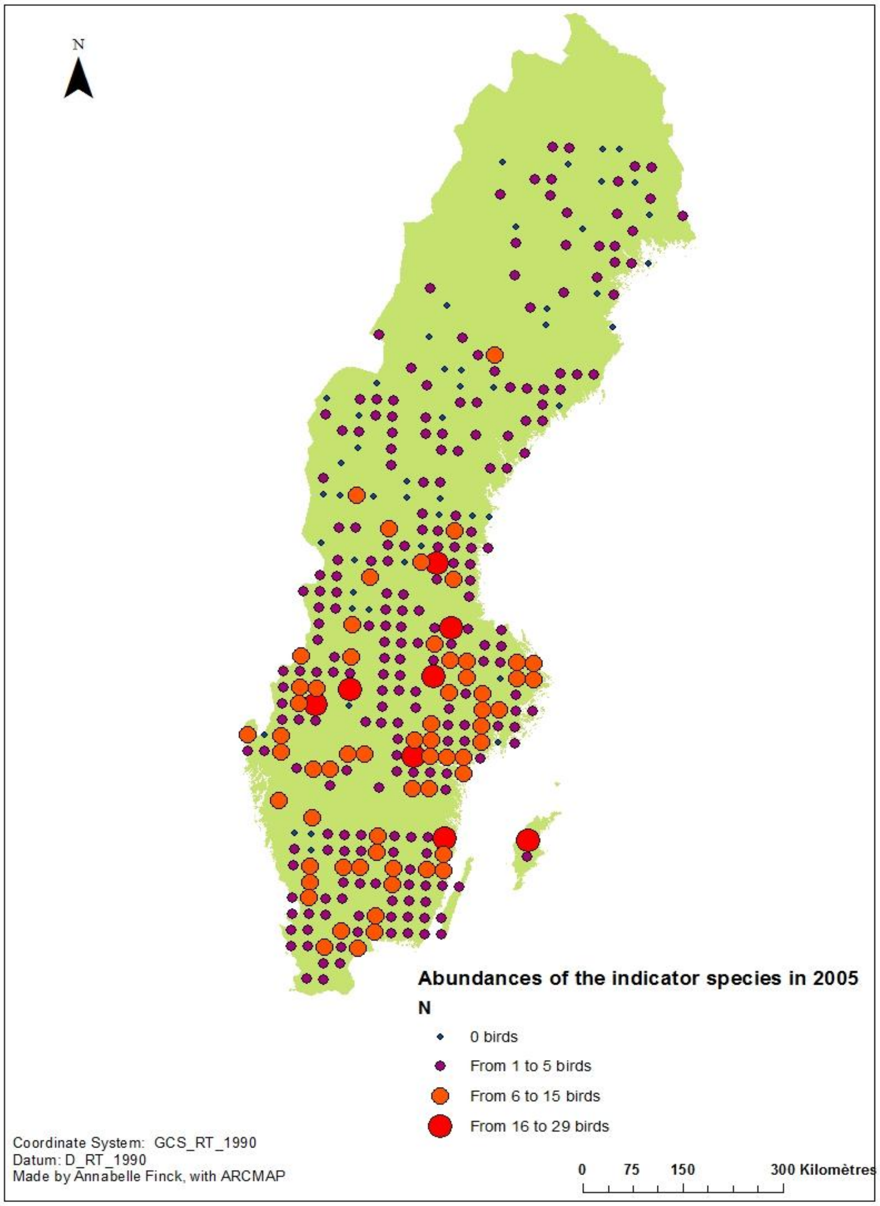


Figure 8: Abundances of the indicator species in 352 bird survey plots in 2005 (plots used in the second series of analyses).

4.3. Analysis per groups

Table 4: Results of the best models, from the correlation analyses for each group of indicator species

Variables	All indicator species	Dead wood specialists	Deciduous forest specialists	Old forest specialists	Woodpeckers	Tits
X	- (NS)	+ (NS)	- (NS)	+ (.)	- (NS)	+ (*)
Y	- (***)	- (*)	- (***)	- (**)	+ (*)	- (**)
Elevation	- (***)	- (NS)	- (***)	- (NS)	- (.)	+ (NS)
GFC	+ (***)	+ (NS)	+ (*)	+ (***)		+ (***)
Spruce		- (**)	- (**)			
Pine		- (NS)	- (NS)			
Birch		+ (*)	+ (*)			
Deciduous		- (NS)	- (*)			
Average age						
Maximal age		+ (*)	+ (NS)			
Height		- (NS)	+ (NS)			
Agricultural areas	+ (***)	+ (NS)	+ (***)	+ (NS)	+ (.)	- (NS)
Humid areas	- (*)	- (.)	- (*)	- (*)	- (NS)	- (*)
Regression coefficient	0.09	0.03	0.08	0.04	0.02	0.04
Sensitivity	0.7	0.65	0.72	0.66	0.76	0.79
Specificity	0.61	0.55	0.6	0.53	0.46	0.44
AUC	0.66	0.6	0.66	0.6	0.61	0.61
Threshold	0.36	0.08	0.32	0.14	0.06	0.08

How to read the table

For each bird group column, the + or – indicates if the variables influence positively or negatively the occurrence of such birds. When no sign is found for a variable, it means that this variable was not taken on as an explanatory variable by the model. The second signs are the significance codes for the model results. They correspond to p-values, meaning the estimated probability of rejecting the null hypothesis of a study when this hypothesis is true (Statsdirect, 2014). This table refers to the p-value with an asterik rating system:

$P< 0.001$: *** , $P< 0.01$: ** , $P< 0.05$: * , $P<0.1$: '.', $P< 1$: 'NS'

They indicate to what extent the correlation established is reliable. Sensitivity, specificity and AUC are accuracy indicators (*see p. 21*). The last line indicates the threshold-values with which sensitivity and specificity have been calculated. I have assessed the accuracy of models in combining these different indicators. The values of the regression coefficient and other accuracy indicators were rounded up to two decimal places.

Presentation of the results

For each bird group the regression coefficient of the best model was in general very low (under 0.1), which means that a lot of factors lack to explain what happens. Concerning the accuracy, the best models predict quite well the true presence (on average the sensitivity is around 0.70). But the specificity is low (between 0.4 and 0.6, on average about 0.53). The AUC is also really low, on average equivalent to 0,6 , meaning that our variables have only 60 % of probabilities to truly influence the bird occurrence. This underlines once again that our models definitely lack of precision, and that more factors should be included to improve them. Also it is difficult to obtain really significant results, since the species studied have turned out being particularly rare species. Their abundances are very low (figure 8), that makes complicated any statistical study focusing on them.

Factors which seem to explain in the most relevant way the bird occurrence are first and quite logically the latitude, longitude, elevation and forest density, but also the presence of humid or agricultural areas. The forest density seems to be a really essential factor for the presence of indicator species: it is linked with a good significance level (if we look at the significance code) to the abundance of all the indicator species, and also to the old forest specialists and the tits abundance. A significant relation between agricultural lands and the abundance of the indicator species, and of the deciduous trees specialists is highlighted.

The factors linked to the age, which were expected to be one the most important elements of the bird occurrence explanation, are only present in the best models of the dead wood and deciduous specialists. But this correlation is for those groups too few significant to be taken into account.

4.4. Analysis per species

Table 5a: The best models for capercaillie, hazel grouse, green woodpecker, wood pigeon, long-tailed tit, coal tit.

Variables	Capercaillie	Hazel grouse	Green woodpecker	Wood pigeon	Long-tailed tit	Coal tit
X	- (NS)	- (NS)	+ (NS)	- (NS)	- (NS)	+ (**)
Y	+ (NS)	+ (NS)	+ (NS)	- (**)	- (NS)	- (*)
Elevation	- (NS)	- (NS)	- (**)	- (***)	- (NS)	- (NS)
GFC		+ (.)		+ (NS)		
Spruce						+ (**)
Birch						+ (NS)
Pine						+ (NS)
Deciduous						- (NS)
Average age						
Maximal age						
Height						
Agricultural areas				+ (***)		
Humid areas				- (*)		
Regression coefficient	0.01	0.23	0.03	0.05	0.02	0.08
Sensitivity	0.36	0.75	0.85	0.63	0.7	0.56
Specificity	0.75	0.9	0.45	0.63	0.55	0.83
AUC	0.55	0.82	0.65	0.63	0.63	0.69
Threshold	0.02	0.07	0.06	0.32	0.04	0.08

Table 5b: The best models for crested tit, marsh tit, willow tit, treecreeper, jay, bullfinch.

Variables	Crested tit	Marsh tit	Willow tit	Treecreeper	Siberian jay	Bullfinch
X	- (NS)	+ (NS)	+ (NS)	+ (NS)	+ (NS)	+ (NS)
Y	- (NS)	- (.)	- (NS)	- (**)	+ (NS)	- (NS)
Elevation	+ (NS)	- (NS)	+ (*)	- (NS)	+ (NS)	+ (NS)
GFC	+ (*)		+ (***)	+ (***)	+ (*)	+ (*)
Spruce		- (*)				
Birch		+ (*)				
Pine		+ (.)				
Deciduous		- (NS)				
Average age						
Maximal age						
Height						
Agricultural areas						
Humid areas						
Regression coefficient	0.01	0.09	0.03	0.05	0.08	0.03
Sensitivity	0.71	0.48	0.81	0.81	0.83	0.51
Specificity	0.49	0.84	0.32	0.43	0.58	0.76
AUC	0.6	0.66	0.61	0.62	0.71	0.64
Threshold	0.05	0.06	0.06	0.05	0.04	0.05

For the Siberian tit, the crested tit, the nutcracker, the three-toed woodpecker and the lesser spotted woodpecker, the GLM function did not work because of their too low abundances, so they have been excluded from the results table.

The level of relevance and accuracy is quite similar than for the analysis per group. The regression coefficient is on average quite low for the best models. The sensitivity is about 69 % (on average) and the specificity about 63 %. The AUC is as low as for the analysis per groups, except for the Siberian jay and for the hazel grouse.

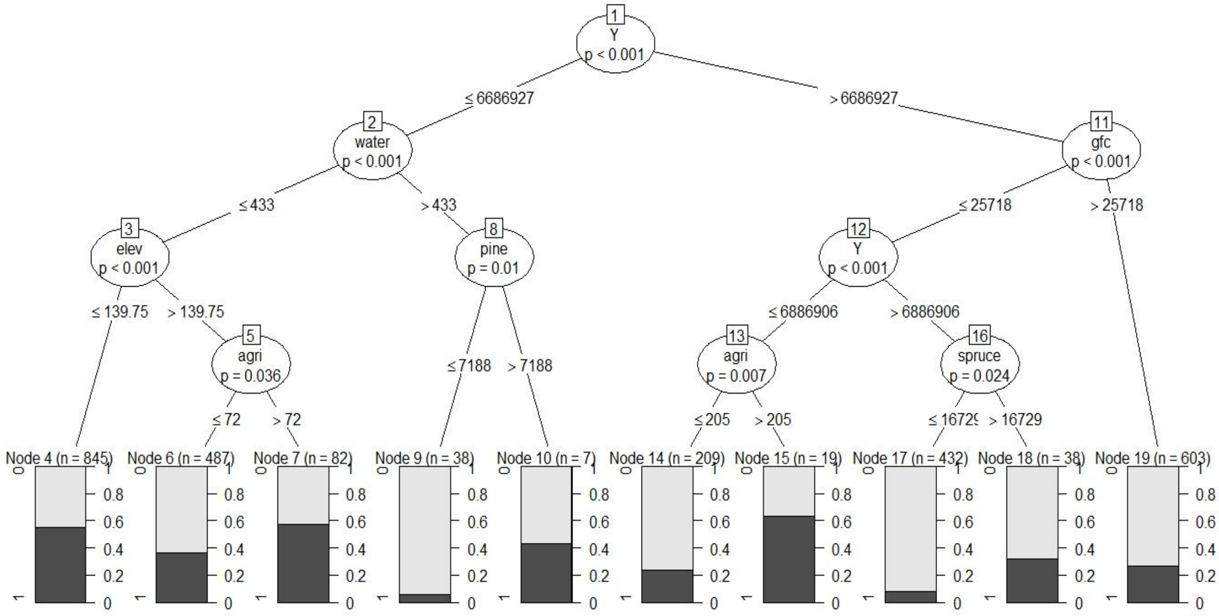
The best models for the analysis per species are in most of the cases the simplest ones, which include the latitude, the longitude, the elevation and the forest density. The analyse per species has given less interesting results – in term of investigation of the most suitable forest compositions for birds - than the analyse per group. Only the models for the wood pigeons, the coal tits and the marsh tits isolate interesting traits of the forest composition. As for two groups in the first analysis, the agricultural areas favour the wood pigeon occurrence. Otherwise the birch volume influences positively the marsh tit occurrence, as the spruce volume for the coal tits.

Such multiple testing can cause statistical bias. Actually when the number of variables is multiplied in a model, the probability to reject just by chance the null hypothesis increases. Thus for this type of analyses a higher significance threshold must be used (Napierala, 2012). The significance threshold can be re-evaluated using the Bonferroni correction for example. That is why in this study, some correlations with a significance code of only 0.01 (*) may not be relevant.

That could apply to the surprisingly negative correlation between the deciduous trees and the occurrence of deciduous forest specialists (table 3). Such result has been for this reason excluded from those which will be interpreted.

4.5. Conditional Inference Trees

The conditional inference trees highlight the factors which have the highest probabilities to influence birds abundance. Such probabilities are calculated with the second set of vegetation data. At each node, the p-value is indicated and gives an idea of the significance of such probabilities.



- All indicator species

Figure 9: Conditional Inference Tree of the group "all indicator species".

According to the conditional inference tree of the all the indicator species, the first factor on which depends the occurrence of all these birds is the latitude. Second factors are the limited presence of humid areas and the forest cover. But in any way, agricultural areas have an influence when the humid areas are limited, and when the elevation is higher than 139 meters, the same for areas where the forest cover is more reduced and the latitude lower. The probalities of birds presence when agricultural areas are not limited is about 0,6, it the highest probality of the tree. The influence of agricultural areas is quite significant since the p-values are between 0,01 and 0,05.

- Deciduous forest specialists

The first factors which seem to explain the occurrence of deciduous forest specialists are the elevation and the latitude (quite logically since the presence of deciduous trees is strongly dependent on these two elements). The other factors are the longitude, the presence of humid areas (a factor which has a great influence) and as for all the indicator species there is positive effect of the agricultural areas. When the elevation does not exceed 141 m and the area is located relatively more to the South, areas with a more significant presence of agriculural lands have a higher probabilities to host deciduous specialists (0,5 against 0,3). This influence is significant since the p-value is inferior to 0,01.

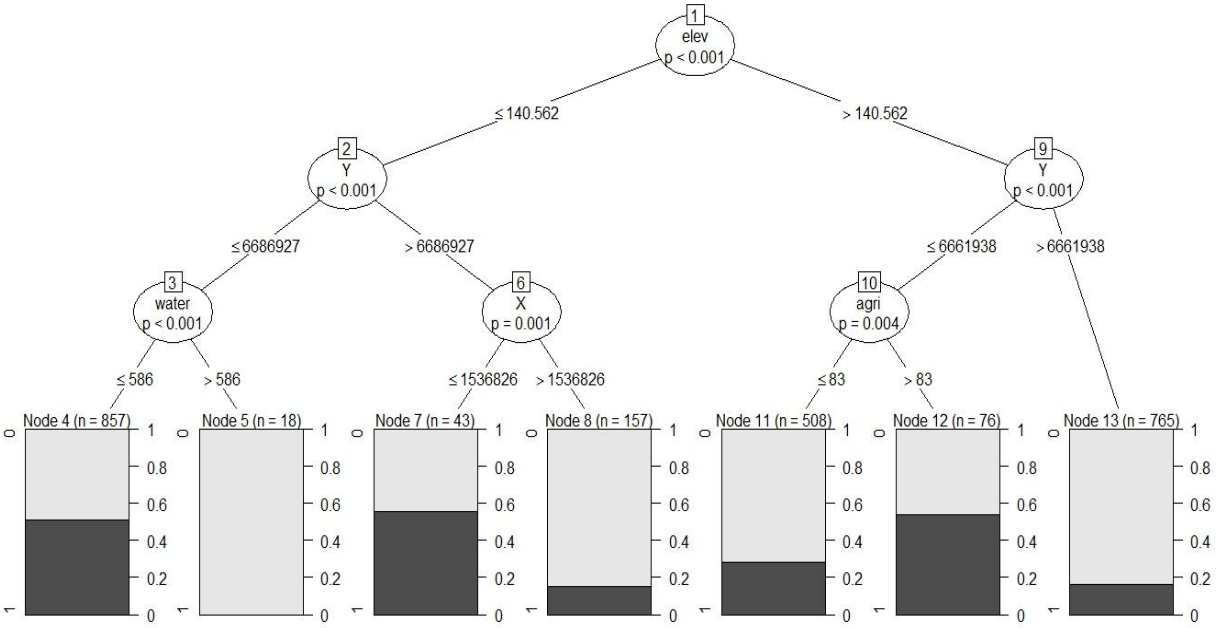


Figure 10: Conditional Inference Tree of the deciduous forest specialists.

- Old forest specialists

The first explanatory factor for such birds presence is the density of the forest cover (the significance of this influence is good, the p-value is inferior to 0,001). Secondary factors are the latitude and the longitude.

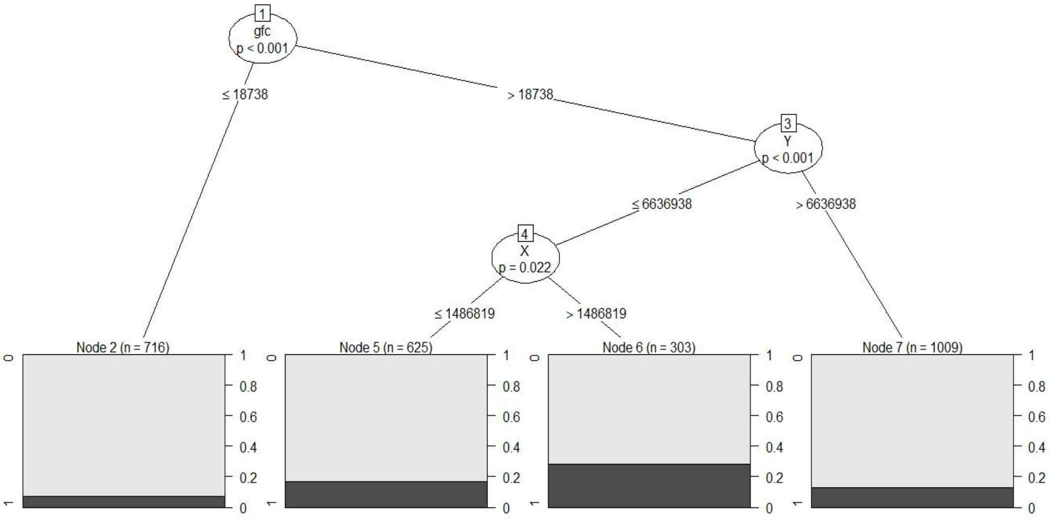


Figure 11: Conditional Inference Trees of the old forest specialists.

- Woodpeckers

The volume of spruce seems to impact negatively the occurrence of such birds. But this influence is limited, the probabilites in relation with both spruce volume levels are quite close.

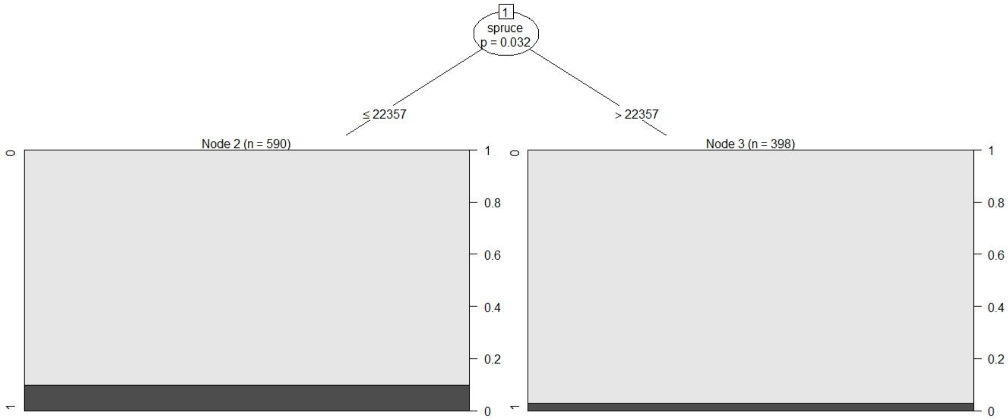


Figure 12: Conditional Inference Tree of the woodpeckers.

- Tits

The essential factor for tits is the forest cover. The significance of this influence is really significant since the p-value does not exceed 0,001 in this case. When the forest cover is less dense, birch trees favour their occurrence, but this influence is quite weak.

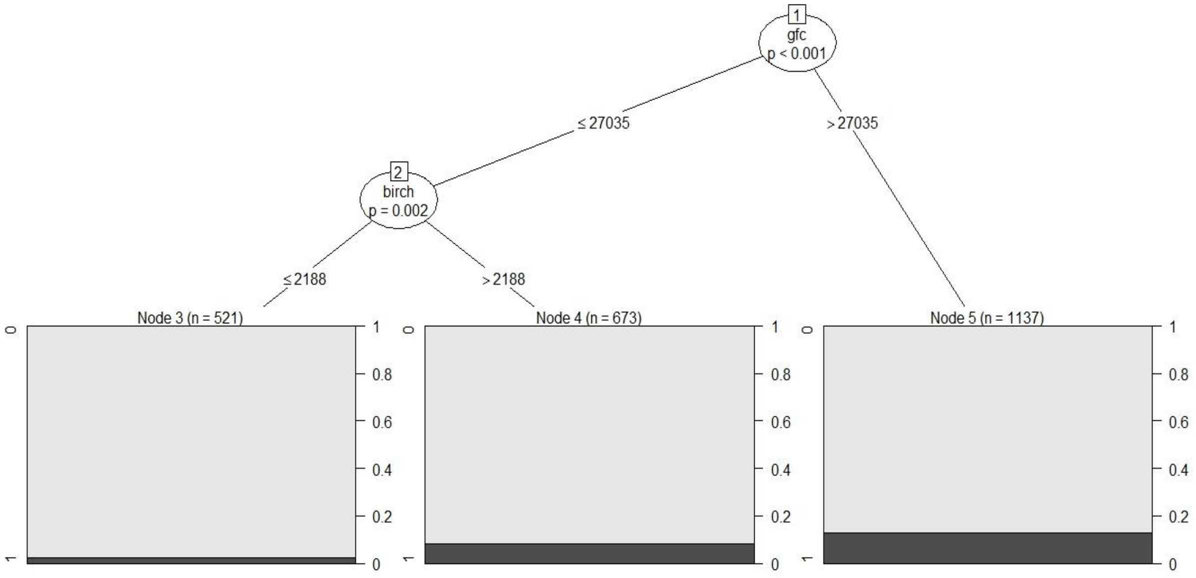


Figure 13: Conditional Inference Tree of the tit group.

The tree of the dead wood specialists is not present here, since it does not distinguish any factor of explanation.

5. Discussion

5.1. Results vs. hypotheses

The few significant models did not produce the results we expected. Age, for instance, was significant in only one model, in which it was positively correlated with the occurrence of deadwood specialists. This result is surprising, but might reflect three different causes: i) the age estimated from the Forest Inventory points is bound to include errors, as the points did not overlap the bird sampling routes, and were not sampled in the same decade, requiring a quite complex methodology (see Data preparation); ii) the age variable provided by Skogskarta results from interpolation of few data points, and as such is probably not very reliable; iii) harvested forests almost never get old enough to really benefit the species that require old stands. In addition, forest age is only a proxy variable for structural elements that matter for birds, such as old stumps and decaying wood. Including variables about thinning would have also been interesting. We could not find any variable documenting those, and using a stand age variable might not be enough to capture the variability in forest composition and structure that is important for birds.

The amount of deciduous trees has an influence in only few models: in the best model for deciduous forest specialists there is a negative correlation between the amount of deciduous trees (except birch) and the occurrence of such birds (but the significance level is quite low, table 4, so this surprising result may not be relevant). Positive correlations between bird occurrence and the presence of birch have been found: in the best models for dead wood specialists, deciduous specialists (table 4) and for marsh tit, the conditional inference tree for tits also highlights this influence (figure 13). Nevertheless there is maybe an effect of correlation between deciduous trees and the latitude. The influence of deciduous trees may be highlighted by the influence of the latitude since broad-leaf deciduous forests are mainly found in Southern Sweden. Thus if the correlaton is negative (table 4) between the amount of deciduous trees and the occurrence of deciduous specialists, the correlation is highly significant with the latitude and may indirectly underline the positive effect of deciduous trees. This effect of correlation does affect the birch variable since birches occur in the whole Sweden. The birch variable gives information not including in the latitude.

Interestingly, total forest cover was included in quite a lot of models (in 9 best models and in 3 conditional inference trees). Of course it makes sense that the amount of trees matter for forest bird species, but one would expect more detailed variables to have more importance.

A negative influence of the humid areas is highlighted both in the best models and in the tree probability diagrams whereas a positive riparian edges effect could have been expected.

A specially unexpected result is the positive influence of agricultural lands observed in the best models and in the tree probability diagrams of all the indicator species and of the deciduous forest specialists (figure 8 and 9).

Such results lead us to develop three main points. First, the absence of forest composition factors considered as essential by the ecologists in many best models, second the unexpected positive correlation between bird occurrence and presence of agricultural areas, and finally the usefulness of birch in bird habitats.

5.2. The concept of indicator species: relevant or not?

For most of the indicator species studied here, relevant conclusions are difficult to find. Links between a certain forest composition and the presence of such birds are impossible to highlight since their abundances are particularly low, particularly when using the Forest Inventory points (figure 6 and 7).

When using vegetation maps, for 4 species (the Siberian tit, the crested tit, the three-toed woodpecker and the lesser spotted woodpecker) the regression function did not work. Actually, the lesser spotted woodpecker, the three-toed woodpecker, the Siberian tit, the bullfinch, and the Siberian jay are found in the IUCN Red list of threatened species, and classified as "near threatened species" (which means they nearly fill the criteria of the threatened groups, or that they will fill them in a near future) (Red List report, 2010).

Such low abundances prompt us to think about the notion of indicator species. Their presence should indicate a good "quality" of the forest, but few forests could be considered as forest of quality, if the presence of such species would be the only criterion taken into account. If we look at the level of abundance in 2005 for 352 bird survey plots (figure 8), we clearly see that for most of the forests it is really low (below 5 birds present). In only 70 forests, there are more than 5 indicator birds.

It may be a completely normal and logic result, since few "natural" forests still exist in Sweden, and since timber production has radically changed forest composition of harvested forests. As Richard D. Gregory and Arco van Strien (2010) underline it, if a species declines, its habitat preference may also be narrowed since it cannot live in marginal habitats anymore.

Nevertheless, the statistical analyses, especially the comparison of models with the AIC, have underlined the difficulty to associate their presence with the composition elements, which, according to previous and micro ecological studies favour bird biodiversity. Thus, for 11 indicator species out of 13, the most valid models are the simplest models (which included only the longitude, latitude, elevation and forest density), and as for the analyses per group, for 4 groups out of 6, the best models are also the simplest ones. Such models do not take into account the composition elements, of which the modification by the timber production could lead to a loss of biodiversity. This could lead us to conclude that those indicator species may not be adapted to elaborate bird biodiversity restoration plans in forests, where timber production has been developed without environmental control, and that less rare species should be used in this perspective. Nevertheless if less rare species would be preferred, the risk would be that our indicative groups would not indicate anything anymore. Actually the quality of an indicator species depends on its degree of specialisation (Gregory & van Strien 2010). Of course generalists species are important for the good functioning of ecosystems, but they can only help to detect habitat degradation, and not more precise changes.

Another problem of indicator groups is the heterogeneity of habitat requirements between birds whithin a same group (even if they have been gathered for their common points in term of habitats demand). For example, in a same group some species can benefit from anthropogenic changes when others do not (Gregory & van Strien, 2010). Thus as it will explained later (see 5.3. *Influence of farmland edges*) woodpigeons can take advantage of the intensification of agriculture but it is not the case of all the birds from the deciduous specialists group.

Analysing abundance and specific richness is also complicated since many factors can be taken into account, and some are not directly related to the ecological integrity of a local ecosystem (Steele & al 1984). The phenomenon of habitat compensation, for instance (see 5.3.) can come into play and makes more complicate the assessment of quality for a given habitat.

These conclusions highlight the limits and the complexity of the notion of indicator species. They do not call into question the use of birds as indicator species, but call for a cautious use of them and a cautious interpretation of the repartition of such indicator birds (Carignan & Villard 2001).

5.3. The influence of farmland edges

The analyses underline that agricultural areas have a positive effect on the occurrence of birds from the indicator species and the deciduous forest specialists groups (table 4). Yet at first view, the development of agricultural areas can be expected to threaten birds considered as indicators of the good quality of forests.

The fact that the correlation is particularly significant for the deciduous forest specialists (table 3) could let us think that birds compensate the lack of deciduous trees in the inner forest (a lack linked to the fact that timber production favours coniferous trees regarded as more productive) by occupying the farmland edges, where they can still find deciduous trees, on which they can nest or forage. So these results may highlight the phenomenon of “habitat compensation”, defined by Norton et al. (2000) as the ability for birds to compensate the lacks of their original habitat (here the forest).

Such an interpretation prompts us to stress as Roberge, Andersson and Stigha (2011) the necessity to examine edge habitats, when studying forest species occurrence. To deal with bird biodiversity in the forest the scope of interest must be broadened to non-forest areas, which surround forests. This questions again the indicator species definition, as witnesses of the forest good quality, since their occurrence would be linked to the quality of the edges. The question is, if the presence of the indicator species is linked either to the quality of the forest or to the quality of its edges, in what extent these birds can still allow us to detect forests of good quality?

Another explanation of this correlation could be the openness that offers agricultural areas. For Mikusinski (1997), the decline of green woodpeckers is connected to forestry but also to the disappearance of pastures and other grasslands in favour of reforestation. This species needs habitats in semi-open cultural landscapes, where birds can find ants (ants occupy in large number forest openings) and forage on the ground. Thus the agricultural areas in the surrounding of forests can represent an essential forage substrate for some forest species, since the agricultural activities ensure a certain degree of openness.

In addition of the quality of the edges, birds occurrence could be linked to positive edge effects like the sun exposure. In virgin forests, clearings are found but nowadays with forestry practices, which favour an equal age of the forest stand, the clearings are more rare. A greater sun exposure can benefit birds since it favours the growth of fruit-bearing shrubs and thickets. Such types of habitat offer a diversity of foraging opportunities and nesting sites.

However the effect of farmland edges must be qualified. Actually this effect would be strongly influenced by wood pigeons. Such birds have particularly high levels of abundance in comparison with the majority of the other birds, and belong to the deciduous trees group (and as mentioned before, a positive correlation was found between this group and agricultural edges). In addition, even though they are considered as forest species, they can forage in open-fields, searching there seeds and roots.

5.4. The richness of mixed forests

No significant positive correlations between deciduous trees and bird occurrence have been found whereas according to ecologists deciduous trees make the richness of a lot of habitats, but it may be the positive influence of birch that could confirms such a statement.

The occurrence of deciduous forest specialists is positively correlated to the presence of birch (table 3). That tree species seems to be important since it favours also the occurrence of dead wood specialists. First of all, birch has an important influence since it is the most common deciduous species and it is found even in the northern part of the country, where other deciduous trees cannot survive. Then, birch is often associated with spruce and pine, in what it is called “mixed forests”. 70 % of the young birch populations are found within conifer dominated forests (Götmark et al., 2005). Some studies have shown a positive correlation between mixed forest and bird community, and recommend replacing monoculture of coniferous trees by polyculture containing a mix of pine/spruce and birch. These types of forest would have a higher level of bird biodiversity: on the one hand, since they would be able to welcome both coniferous and deciduous trees specialists, on the other hand, since this mix increases nesting and foraging opportunities. Actually sometimes, coniferous are more suitable to nest on, and birds can find more food resources on deciduous trees (Young et al, 2005). To conclude, one can say that this positive influence of birch trees could reveal the high quality of mixed forest habitats. However our forest data may not be good enough to give information about the usefulness of scattered deciduous trees.

5.5. Management implications

Most of the conservation plans grant importance to mixed forests and highlight the necessity to increase the proportion of deciduous trees in Swedish forests. Today, different types of measure are taken to achieve this goal. First, areas of mature deciduous forest are set aside, and protected by the legislation of natural reserves for instance (Swedish Forest Industries Federation, 2012).

In harvested forests, conservation agreements with landowners can be established. In this case, a strategy of adapted forestry management (AF) is put in place, with active measures such as the conversion of conifer-dominated stands to deciduous-dominated stands, in removing directly coniferous trees (Jong and Lonnstad, 2002).

My study also underlines the necessity to change the scale of the protection plans, to include in the scope of regulation forest edges. In reading biodiversity protection plans, one can notice that measures mainly focus on inner forests and on forestry activities. This study lets us think that nearby areas and the activities practiced within them, such as agricultural activities, should be more taken into account in the future. Pastures should be maintained: their reforestation should be avoided. The farming of lands close to forest stands should be regulated. For instance scattered deciduous trees between fields represent a precious habitat for birds and must be protected against the development of open-field structures.

Nevertheless this issue starts appearing in conservation plans. In the report of the restoration plan “White-backed woodpecker landscapes and new nature reserves” the problem of the grassland abandonment is underlined (Jong and Lonnstad, 2002). The strategy could be to favour the return of farmers to these areas, thanks to subventions for extensive breeding for example, as it made in some countrysides of medium-altitude mountain in France (Ministère de l'agriculture, de l'agroalimentaire et de la forêt 2012).

6. Conclusion

According to the literature, the factors which favour the most bird biodiversity are factors of composition: presence of old, dead and deciduous trees mainly.

The statistical analyses done in this thesis seem to show the good quality of mixed forest habitats in which deciduous trees and above all birch are found. They also highlight the importance of edges. It is not only the composition elements of the forest which must be taken into account but those of nearby areas too. Even birds that are considered forest specialists may complement their resources by foraging outside forests. This study confirms the importance of landscape effects on animal distribution, and suggests a possible role of agricultural lands situated close to forest. Pastures, grasslands or agricultural fields with a traditional structure can favour bird biodiversity since they often contain some deciduous trees. These areas constitute a rich foraging substrate as well; they are rather open, whereas such open-areas are less and less numerous in forests with timber production (that often implies fire control and dead tree removing).

Including forest edges in bird biodiversity plans and thus taking into account the phenomenon of habitat compensation could be a good way to find a compromise between biodiversity protection and the maintain of timber activities.

Our results also call for a cautious use of indicator species. Because of landscape effects, the repartition and demographic trends of such indicator birds must not only be linked to changes in habitats they are supposed to indicate. A careful consideration of species to use as indicators must then be carried on depending on the context of any new ecological analysis.

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8. Appendices

Appendix A

Models used for the second serie of analyses (models comparison with forest map and environmental data)

Model 1: Occ~X (longitude)+ Y (latitude) + elev (elevation)
Model 2: Occ~X + Y + elev + gfc' (forest cover)
Model 3: Occ~X + Y + elev + spruce + birch + pine + decid'
Model 4: Occ~X + Y + elev + spruce + birch + pine + decid + medAge'
Model 5: Occ~X + Y + elev + spruce + birch + pine + decid + maxAge + medAge'
Model 6: Occ~X + Y + elev + spruce + birch + pine + decid + maxAge + height'
Model 7: Occ~X + Y + elev + gfc + spruce + birch + pine + decid'
Model 8: Occ~X + Y + elev + gfc + spruce + birch + pine + decid + medAge'
Model 9: Occ~X + Y + elev + gfc + spruce + birch + pine + decid + maxAge + medAge'
Model 10: Occ~X + Y + elev + gfc + spruce + birch + pine + decid + maxAge + height'
Model 11:Occ~X + Y + elev + agri + water'
Model 12:Occ~X + Y + elev + agri + water + gfc'
Model 13: Occ~X + Y + elev + spruce + birch + pine + decid + maxAge + height+
agri + water'
Modem 14: Occ~X + Y + elev + gfc + spruce + birch + pine + decid + maxAge + height+
agri + water'

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