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Frédéric Archaux, Hilaire Martin

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HYBRID POPLAR PLANTATIONS IN A FLOODPLAIN HAVE BALANCED IMPACTS
ON FARMLAND AND WOODLAND BIRDS

Frédéric ARCHAUX

Hilaire MARTIN

Cemagref, Domaine des Barres

F-45290 Nogent sur Vernisson

France

E-mail: frederic.archaux@cemagref.fr

Tel : 00332-38-95-66-79

Fax : 00332-38-95-03-44

Abstract

Hybrid poplar plantations are increasing worldwide and are often accused of impoverishing bird communities in surrounding farmland and woodland areas. We conducted 124 bird point counts in a landscape where plantations, semi-natural forests and farmland occupied similar surface areas. As expected, birds occurred at higher densities in forests than in plantations, mostly due to the scarcity of late-successional forest birds in plantations. Contrary to expectations, bird communities were the poorest in farmland dominated areas and the most specialised in areas dominated by young plantations. Indeed, many grassland species, including some of conservation concern in Europe, frequently or almost exclusively used young plantations. However, plantations have probably depleted grassland bird communities by fragmenting open areas, while playing a limited positive role on forest species. Total length of unpaved roads had a positive effect on community specialisation index, while total length of paved roads and mean forest/plantation patch size played no role. Bird density increased with the development of the understory vegetation in mature poplar plantations. We conclude that poplar plantations should be avoided in areas of high conservation value; in other areas, they may increase the overall diversity of bird communities. At the plantation scale, we advocate stopping understory removal as soon as possible and maintaining old trees and hedgerows alongside or within plantations to provide suitable breeding habitats for bird species that may be foraging in the plantations.

Keywords: Bird; Hybrid poplar; Landscape; Plantation; Management

1. Introduction

Many fertile floodplains in Europe were occupied by large riparian forests dominated by hardwood tree species (oaks, ash) before the Middle Ages (Petts et al., 1989). Human population growth caused a progressive conversion of a large part of these forests into farmland, while most of the remnants were managed as coppices or coppices with standards for fuel wood production (Steiger et al., 2005). The farming on these lands varied greatly over time and space, and the landscape included pastures, hayfields, various ploughed fields, and more recently maize fields and set-asides. From the XVIIIth century onwards, poplars were often planted at the expense of arable lands and the few forest remnants (Petts et al., 1989). Many factors jointly caused an acceleration of this phenomenon after the 1950s: the embankment of large rivers limited the occurrence and magnitude of floods that poplar plantations are sensitive to, the overproduction of dairy and meat production in Europe caused a strong decrease in cattle numbers, the need for wood fibre increased, poplar plantations (from two-year stems) readily took , and fast-growing, fungus-resistant cultivars became available through hybridization among European, Asian and American *Populus* species (Schnitzler, 1994). In France, hybrid poplar plantations now represent 1.6% of the forested area (ca 260,000 ha) and this area is still increasing (+0.8% between 1988 and 2002, SCEES/Terruti data 2003).

Since 1980, hybrid poplar plantations have been accused of contributing to the decrease in bird populations in floodplains in Western Europe (Zollinger and Genoud, 1979; Schmitz, 1986; Pont, 1987; Mourgaud, 1996; Godreau et al., 1999). However, this seems to be an over-simplification. Indeed, several studies have shown that some uncommon/rare birds may use poplar plantations; for example, the Golden oriole *Oriolus oriolus* is restricted to mature poplar plantations in Great-Britain (Dagley, 1994). Furthermore, the ecological impact of plantations depends on the habitats they are compared with: Hanowski et al. (1997) in

North America showed that the number of breeding birds was higher in poplar plantations than in the row crops the plantations were replacing but less than in surrounding forest/shrub habitat. Finally, extensively-managed plantations may be less unfavourable to breeding birds than intensively-managed ones (Pont, 1987; Godreau, 1998).

We believe further studies are needed to confirm some of these results and better understand the impact of hybrid poplar plantations on bird communities. In particular, the previous studies rarely used a landscape perspective (but see Hanowski et al., 1997; Godreau, 1998) and yet, many birds need a mosaic of adjacent habitats to breed and forage (e.g. Virkkala et al., 2004). Furthermore, the poplar plantations studied so far have usually been isolated within a farmland matrix and have always represented a minor proportion of the landscape (e.g. at most 12% in area, Godreau, 1998) and yet isolation of forest fragments is well-known for causing deleterious effects on bird communities, irrespective of tree species (Blake and Karr, 1987; Hinsley et al., 1995). More connected poplar plantations may host more woodland species, as suggested by Godreau (1998).

In this study, we focused on a floodplain area in northern France where semi-natural forests, poplar plantations and farmland represented equivalent proportions in the landscape. Within this landscape, we assessed how bird communities responded to habitat composition at three different spatial scales (100, 250 and 500m-radius circles). More specifically, our main working hypotheses were:

- bird densities decrease with an increasing proportion of poplar plantations in the surroundings,
- the greater the area planted with hybrid poplar, the less specialised the bird communities,
- the presence of forest birds depends mainly on semi-natural forest areas but also, to a smaller extent, on mature poplar plantations,

- bird densities vary with the fragmentation of habitats,
- bird densities in plantations increase with understory vegetation cover due to larger areas suitable for breeding/foraging and/or to a higher number of potential niches.

2. Methods

2.1. Study area

The 6950-ha study area is located between Romilly-sur-Seine and Méry-sur-Seine (France, Aube department, ca 100-120m asl), along 20 km of the Seine River on deep, chalky soils corresponding to modern alluvial deposits. The climate is Atlantic with continental influences (mean annual temperature ca 10°C with 630-700mm annual rainfall). Poplar plantations represent 27% of the area due to the unusual width (2-3km) of the floodplain (nearby confluence of the Seine with the Aube River). Other land uses found in the floodplain were farmland and open areas (36%), forests (22% including abandoned poplar plantations), urban areas (11%) and aquatic areas (4%). The poplar plantations did not differ from that of forests in terms of median size (Wilcoxon rank-sum test, $W = 151758$, $P = 0.52$) but other areas (farmland, other open, urban and aquatic areas) were significantly larger than poplar plantations ($W = 226243$, $P = 0.001$) and forests ($W = 155897$, $P = 0.02$) (Table 1). The study area extended slightly beyond the floodplain bottom onto the intensive row crop fields of the plateau, so as to allow us to calculate habitat areas surrounding bird sampling points up to 500m. Crop fields are also found within the plain (including maize fields), along with set-asides and, to a far lesser extent, hay pastures. The nearest large forest (the “Traconne”) state forest that may be a source of forest birds is about 10km from the study area. As hedgerows are also scarce on the plateau, bird exchanges between forested areas in the valley and the

plateau are probably limited. At a larger scale (Aube and Seine floodplains *sensu* the French National Inventory: 34,025 ha), hardwood forests decreased by 53% between 1974 and 1994, representing only 5.5% of the total area in 1994 (ca 1,660ha) *versus* 3,740ha for poplar plantations (French Forest Inventory data, 1994).

The study area was first mapped from colour aerial photographs taken in 2001 and 2004 (NGI data). We separated unpaved and paved roads and identified nine major habitats: (1) very young VYP, (2) young YP and (3) mature MP poplar plantations; (4) young YF and (5) old OF hardwood forests; (6) farmland Farm (cropland and grassland combined); (7) urban areas; (8) aquatic areas (rivers, ponds, lakes) and (9) other open habitats. We attributed one of these habitat classes to the 1,592 polygons that were individualised from aerial photos; then, in the field, we checked the correctness of this attribution. In the field, poplar stands were attributed to the very young class when the mean diameter at breast height (dbh) was less than 20cm, to the young class when the dbh was between 20 and 30cm, and to the mature class when above 30cm (i.e. when the canopy closes). In the area, poplars are cut when about 20 years old. Mean distance between poplars in plantations is almost invariably 7m in the area (occasionally 6 or 8m). Plantations are ploughed, and sometimes fertilised, at plantation; the clones most often used are *Populus x interamericana* “Beaupré” and *P. x canadensis* “I214”. The understory vegetation is mechanically and/or chemically removed during the first years after planting. This control may be either continued more or less regularly (intensive management) or ceased (extensive). In the case of intensive management, the vegetation understory is limited to sedges and grasses (including Nettle *Urtica dioica*). In extensively managed plantations, a shrubby layer develops with Blackthorn *Prunus spinosa*, Common Elder *Sambucus nigra*, Willow *Salix sp*, and Blue Bramble *Rubus caesius*. All the young forest stands (YF) actually originated from former poplar plantations cleared in December 1999 after the Lothar windstorm (ca 30% of the plantations in the study area were cleared)

and never replanted: these stands could be considered either as very extensive young poplar plantations (due to the presence of naturally resprouting poplars) or young semi-natural forests (due to the rapid recolonisation by ash and other shrubs). Old forest stands (OF) included a variety of forest types, from most to least common: (1) coppiced Hazel *Corylus avellana* with standards of Pedunculate Oak *Quercus robur* and Ash *Fraxinus excelsior*, (2) abandoned over-mature poplar plantations overgrown by Ash, (3) spontaneous riparian forests (including the previously mentioned species, as well as Alder *Alnus glutinosa*, Sycamore Maple *Acer pseudoplatanus*, Smooth-leaved Elm *Ulmus minor* and various willow species *Salix* sp. along river beds) and (4) old Ash/Hazel coppices.

2.2. Bird point counts

124 bird point counts were located throughout the study area, based on a quasi-systematic grid design (ca 400m between points). We located the majority of the points along paths for efficiency and discretion (a few were carried out along roads with limited traffic at the time of the counts). Each point was visited twice (two 5-min counts), first between April 16 and 27 (between 6:30 and 9:43 am), and second between the May 30 and June 8, 2007 (between 5:42 and 9:32 am). All counts were carried out under good weather conditions (no wind, no rain).

During the count, the observer (FA) used aerial photographs centred on the points to localise all singing (the great majority) or moving/flying (a minority) birds. The fact that the landscape was very fragmented helped to locate the birds. As for the territory mapping method, the observer estimated whether the birds recorded during the second visit had already been detected during the first visit (according to the spatial proximity among the contacts). A total of 2,482 individual birds (62 species) were recorded and incorporated in the GIS. Total

cover for the 1-4m and 4-8m vegetation layers was visually estimated (and classified in 5% increments above a minimum 5% total cover). The mean poplar dbh was measured in poplar plantations immediately surrounding the points (but not in more distant plantations).

2.3. Data analyses

To test our working hypotheses, for each point we estimated the bird density, the mean specialisation and preference for mature forests of the bird community. Only birds recorded within 100m of the observer were kept (N=1138, 47 species). To adjust raw count data for imperfect detection, we treated the two visits as two replicate counts and calculated the total number of individuals A (observed abundance) and the number of individuals recorded at only one visit (n_1). We calculated the Jackknife 1 estimator ($Jack1 = A + n_1/2$) and its standard deviation ($SD = \frac{1}{2}\sqrt{(3n_1)}$) for each point as an estimate of the total number of birds (all species) present within 100m. This estimator assumes heterogeneity of detection among species (Burnham and Overton, 1979), a classical phenomenon in bird communities (Boulinier et al., 1998). Density (number of pairs.ha⁻¹) was then estimated as $Jack1/\pi$ (the area 100m around the point, in ha). In models, we used the inverse of the variance of the density estimate to weight observations: observations for which density was known with lesser precision were logically given smaller weight.

We calculated the community specialisation index (CSI), a measure of the mean specialisation of the bird community (Julliard et al., 2003), using data from the specialisation index of 105 common birds by Devictor et al. (2007). The CSI index is known to correlate well with the level of landscape fragmentation and disturbance (Devictor et al., 2007). The higher the CSI, the more specialised the bird community. We followed the same rationale to define the community preference for mature forests (CPMF). Muller (1985) provided the

mean age of the forest stands for 40 common European bird species where these species were observed in French oak regular high forest stands; stand age varied from 10 years for the early-successional Willow Warbler *Phylloscopus trochilus* to 147 years for the late-successional Short-toed Treecreeper *Certhia brachydactyla*. CPMF was calculated as the mean stand age over all species recorded within 100m. The greater the CPMF, the more typical the bird community to mature forests. In analyses, we kept only points for which CSI and CPMF indices could be calculated from at least five species and we weighted the observations in models using the inverse of the variance of the index estimate (as for species richness).

Using the GIS, we extracted the area covered by the nine pre-defined habitats within 100, 250 and 500m of the point. We also recorded the cumulated length of (1) unpaved roads and (2) paved roads within the same radii. Finally, we calculated the mean patch size 100, 250 or 500m around the point (MPS) for plantations and forest patches. We modelled the impact of these explanatory variables on the different community indices defined above using spatially-explicit GAM models. A generalized additive model (GAM) is a generalized linear model (GLM) in which spatial autocorrelation is modelled using a non-parametric, smooth function of the geographical coordinates of the study points (using the gam function from R library mgcv). To limit spurious effects of non-focal habitats (aquatic, gardens, urban, open habitats other than farmland), we excluded from our analyses 20 points where these habitats represented more than 5% of the area within 100m around the point. The final data set contained 104 points for species richness, 85 for the CSI and 79 for the CPMF. To identify the spatial scale that could explain the largest part of the total variance in the community indices, we built models including all nine selected variables (farmed area, very young plantation area, young plantation area, mature plantation area, young forest area, old forest area, mean patch size of plantations and forests, cumulative length of paths, cumulative length

of roads) calculated either on 100, 250 or 500m around the point. Then, we compared the relative merits of the three models with AIC (the lower the AIC value, the better). To further investigate how the community indices varied among the six habitat area variables, we used the model with the lowest AIC value in the preceding step of the analysis and we progressively aggregated habitat area variables whose model coefficients were roughly similar until the AIC of the resulting simpler model did not decrease any further: this step of grouping habitat variables revealed which (groups of) habitats had similar and distinct impacts on the bird communities. The significance of the MPS and length of paths and roads variables was directly tested from an ANOVA (using the ANOVA function in R).

It was difficult to reliably assess the impact of the understory vegetation in plantations on birds. Indeed, many plantations were small, leading to potentially confounding edge effects. Furthermore, the observer rarely stood within the plantations during the counts, so that only part of the larger plantations may have been effectively “sampled” (a positive aspect of this sampling design is nonetheless that singing birds were less disturbed). We addressed this issue by restricting our analyses to birds recorded within 100m of the observer, in mature plantations (mean dbh over 30cm) covering at least 1ha within a 100m radius of the point (ca >30% of the circle area). We further excluded all narrow plantations to limit edge effects, finally retaining a list of 28 patches of mature plantations. We then estimated a density per patch by dividing the number of birds recorded in a given patch (all species confounded, corrected for imperfect detection using the Jackknife 1) by patch size. We built simple linear models on unadjusted bird density with the 1-4m and 4-8m cover indices as explanatory variables. Unadjusted bird density is given in Table 3 for the 20 most common bird species in the six main habitats considered in this study.

3. Results

Mean bird density (Jackknife1) over the 104 point counts was estimated at ca 3.8 ± 1.5 pairs.ha⁻¹ (assuming a singing male corresponds to a breeding pair). Little spatial autocorrelation was found as the effect of the spatial smoother was never significant. Bird density was correlated to neither CSI nor CPMF, but the latter two variables were highly negatively correlated (Pearson's $r = -0.55$, $t = -5.7$, $df = 77$, $P < 0.001$). For the three indices, the model including explanatory variables defined locally (i.e. 100m around the point) had a significantly lower AIC value than models including variables defined at larger scales (250 or 500m) (Table 2). Models explained a reasonable part of the variance for CPMF but a more limited part for CSI and bird density, reflecting either measurement error or less determinism in these variables (Table 2).

Bird density primarily decreased with farmland area and was highest in forests (Table 2). Interestingly, several habitats contributed to the CSI and CPMF but at different levels: CSI increased primarily with the area of very young and young poplar plantations and secondarily with the area of farmland. Similarly, CPMF was mostly related to the area of old forests but the negative impact of the main other habitats gradually decreased with the structural similarity of the habitat to old forest (this similarity increasing from (1) very young plantations, (2) farmland and young plantations, (2) young forest to (3) mature plantations).

None of the three indices was significantly related either to the mean patch size of plantations and woodlands, or to the cumulative length of roads. Only the mean level of specialisation of the species increased with the length of footpaths.

Variation in bird density between plantations increased with the increase in the understory cover. Nonetheless, log-transformed bird density (to limit heteroscedasticity) increased more or less linearly with the understory cover up to 30% (Pearson's $r = 0.62$,

t=3.88, df= 24, P<0.001) and then seemed to stabilise (Fig. 1). On the contrary, bird density was unrelated to the overstory cover (Pearson's $r = -0.22$, $t=-1.1$, $df= 26$, $P=0.17$, Fig. 2).

4. Discussion

Our results show that the impacts of poplar plantations on bird communities are more complex than it is usually claimed: birds in poplar plantations did occur in lower densities than in semi-natural forest stands (whatever stand age) but in higher densities than in farmed areas. Similarly, mature plantations effectively lacked many of the forest birds typically found in old forest stands; yet a truncated succession in bird communities occurred along the poplar rotation, the composition of bird communities in mature plantations being somewhat intermediate between young and old forest stands. Finally, contrary to what is generally thought, the most specialised bird communities were found in the very young and young poplar plantations, whereas mature plantations and forests hosted the least-specialised bird communities.

4.1. Plantations versus farmland

Bird communities were also found to be poorer in intensively-managed farmland than in short-rotation hybrid poplar plantations in North America (Hanowski et al., 1997). Bird populations in our study valley are probably also suffering from the intensive management of the farmland. Obviously, the set-asides and the too few and too artificial grasslands play a reduced protective role for grassland birds in the area. In addition, plantations may have exacerbated the decline in grassland species by fragmenting the grassland areas. Indeed, Godreau et al. (1999) showed that many grassland species were very sensitive to the

fragmentation of open habitats along the Saône River, a few hundred km south of our study site. The relatively large areas planted with poplars in our site probably explain why many of the specialist grassland species that could normally breed in our floodplain were either never recorded (Quail *Coturnix coturnix*, Black-tailed Godwit *Limosa limosa*, Curlew *Numenius torquata*, Meadow Pipit *Anthus pratensis*, Whinchat *Saxicola rubetra* and Yellow Wagtail *Motacilla flava*) or very rarely recorded (Lapwing *Vanellus vanellus*, Skylark *Alauda arvensis*, Corn bunting *Miliaria calandra*, Pied wagtail *Motacilla alba* and finches *Carduelis* sp). Yet, some of these species were regularly observed in the immediate neighbourhood of the study area (the Skylark, Corn Bunting and Yellow Wagtail on the purely agricultural plateau, finches in urban areas), supporting the hypothesis that the valley is repulsive to many grassland birds. Finally, plantations probably favoured the Carrion Crow *Corvus corone* which appreciates the mosaic of interconnected farmland and woodland patches; this species is known to heavily predate on the eggs of grassland ground nesters (Andren, 1992).

Although poplar plantations at the landscape scale may contribute to the near absence of many grassland species, several ground- and shrub-nesters usually found in farmland along hedgerows were commonly recorded in very young and young plantations. The same pattern was found along the nearby Saône River (Godreau et al., 1999). Interestingly, Yellowhammer *Emberiza citrinella* was recorded as frequently in very young poplar plantations as in farmland. Other species found in very young and young plantations included Melodious Warbler *Hippolais polyglotta*, Whitethroat *Sylvia communis*, Grasshopper Warbler *Locustella naevia* and, more marginally, Red-backed Shrike *Lanius collurio*. These species are considered to be habitat specialists (Devictor et al., 2007), a fact that probably explains why the most specialised bird communities were found in areas dominated by very young and young plantations.

4.2. Plantations versus woodland

The lower bird density in plantations compared to semi-natural forests has repeatedly been found in Western Europe and North America (Schmitz, 1986; Hanowski et al., 1997; Godreau, 1998; Twedt et al., 1999). This pattern is mostly due to the scarcity in plantations, even mature, of forest species that prefer old trees with a dense foliage to forage or breed such as the Woodpigeon *Columba palumbus*, Blue Tit *Cyanistes caeruleus*, Nuthatch *Sitta europaea*, Short-toed Treecreeper and Chaffinch *Fringilla coelebs* (Table 3). Although cavity-nesters were logically more frequent in forests than in plantations, mature poplar plantations in our study were regularly used by the Great-spotted Woodpecker *Dendrocopos major*, the Great Tit *Parus major* (breeding in abandoned cavities of the Great-spotted Woodpecker) and the Willow Tit *Poecile montanus*. Dead poplars may be suitable to this species that needs decaying softwood trees to dig its own cavities.

The young stages of poplar plantations hosted bird communities globally distinct from that of the young forests: species like Stock Dove *Streptopelia turtur*, Winter Wren *Troglodytes troglodytes*, Nightingale *Luscinia megarhynchos*, Melodious Warbler, Blackcap *Sylvia atricapilla*, Garden Warbler *Sylvia borin* and Starling *Sturnus vulgaris* preferred young forests to young plantations, probably in response to the higher structural and compositional diversity of the shrub layer (the starling was probably also favoured by the presence of old poplar snags in many young forest patches). Conversely, the Tree Pipit *Anthus trivialis* and Grasshopper Warbler were more frequently found in young plantations: they respectively forage on or close to the ground, in dense herbaceous vegetation; these two species rapidly colonise plantations after planting and desert them a few years later, as the canopy closes.

More surprisingly, the level of specialised bird communities was lowest in the areas dominated by forests (at a level similar to that of mature poplar plantations). Actually, as for

farmland, among the forest specialist species potentially present in floodplain forests (Godreau et al., 1999), some were never recorded (Middle-spotted Woodpecker *Dendrocopos medius*, Wood Warbler *Phylloscopus sibilatrix*) or very rarely (Lesser-spotter Woodpecker *Dendrocopos minor*, Spotted Flycatcher *Muscicapa striata*, Hawfinch *Coccothraustes coccothraustes*). In our study, the semi-natural forest fragments are probably too small and isolated to allow these area-sensitive birds to maintain viable populations.

Several authors argued that the development of understory in extensively-managed poplar plantations is favourable to small birds (Schmitz, 1986; Godreau, 1998). We did in fact observe that bird density increased with the vegetation cover between 1 and 4m (though possibly not linearly), but this was not the case above 4m. Our sample size was too small to statistically assess whether the higher bird density in extensively-managed plantations was primarily caused by a greater number of species or simply by a higher abundance of the same set of species. In the study by Godreau (1998), the number of species more frequently recorded in intensively-managed plantations did not differ statistically from the number of species more frequently found in extensively-managed plantations (16 *versus* 19, binomial test, $P=0.74$). Thus, extensive management of the plantations probably improves the overall quality of the mature plantations more than it provides new niches benefiting new species; as a result, it probably mainly favours the species already able to cope with the initial intensive management of poplar plantations. This hypothesis may also hold in North America since Christian et al. (1996) also conclude that (aspen) stand thinning has a weakly positive and transitory effect on species abundances but none on the number of breeding species.

4.3. Impact of habitat fragmentation

Godreau (1998) noted that the number and abundance of forest birds in poplar plantations increased with the size of the plantation. We found little convincing evidence of any effect of habitat fragmentation, except for a positive impact on the length of unpaved roads on the mean community specialisation. The vegetation along unpaved roads is likely to provide food resources that are otherwise limited in fields for several specialist birds, especially seed-eaters such as yellowhammer and stock dove. The fact that the mean size of forest and plantation patches (MPS) moderately varied among points (MPS within 100-m radius disks exceeded 2ha for only eight of the 104 points) probably explains why we failed to find an effect on bird communities. Similarly, paved roads were present within 100m of the points in only 14 points (by comparison, 87 points included paths within 100m).

4.4. Implications for bird conservation in floodplains

This study gives a balanced view of the impact of poplar plantations on common birds in floodplains. On one hand, plantations do not provide refuge habitats for the most specialised grassland and woodland birds. On the other hand, several woodland birds use mature plantations (although often at lower densities than in semi-natural forests). Thus, the conversion of intensive crop fields by plantations may be beneficial to some open-land and woodland birds (at different ages of the plantations). On one hand, in areas of high conservation value, they probably contribute to the loss of the most area-sensitive birds in floodplains by causing the loss and fragmentation of grassland and woodland. On the other hand, in already fragmented and intensively-managed farming areas such as our study area, many grassland birds, including some that are currently declining all over Europe, use young plantations to breed (although it remains to be demonstrated that young plantations are not also demographic sinks).

At the scale of the plantation, extensive management has a positive impact on bird density. This means that the removal of understory should stop as soon as the understory no longer threatens the growth of poplars. In addition, plantations seem to lack breeding places for many species, although plantations may represent valuable foraging habitats. For instance, the presence of the great tit in mature plantations probably indicates that other cavity-nesters would breed in plantations if sufficient cavities would be available: thus, the retention of large old/decaying poplars, ashes or oaks within or along the plantation would probably favour cavity-nesters. Those trees with a dense crown would also represent breeding sites safer than poplars for species nesting in tree crown. Alternatively, nest-boxes may be installed in plantations as suggested by Twedt and Henne-Kerr (2001). Similarly, hedgerows may be installed between plantations or within large plantations to the benefit of shrub bird species. The supplementary cost related to the retention of old trees and hedgerows may be partly compensated by a better regulation of poplar defoliating insect populations since these measures would be mostly beneficial to insectivorous birds.

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Table 1

Impact of landscape variables on bird assemblages (BD bird density, CPMF community preference for mature forests, CSI community specialisation index)¹. a) AIC values of the three alternative models based on the same set of variables but defined at three different spatial scale (100, 250 and 500m around the point)); in bold the model with the lower AIC before aggregating habitat area variables (Farm to OF variables); the % deviance of this model is provided in b); in superscript AIC of the best model after aggregating the habitat area variables. c) Fitted coefficients and standard errors of the explanatory variables corresponding to the model in bold in a) (removing the intercept) and in superscript (a-d) variables whose aggregation improves model AIC (the AIC of the corresponding model is the value in superscript in a)). For MPS, Paths, Roads and the smoother: *P<0.05, italics P<0.1.

	Variables	BD	CPMF	CSI
a)	AIC (100/250/500)	617 ⁶¹² /619/632	587 ⁵⁸⁴ /599/610	-108 ⁻¹¹³ /-85/-82
b)	%Dev	36.8	67.9	39.1
c)	Farm	1.2±0.6 ^a	10.5±2.5 ^a	-0.27±0.02 ^a
	VYP	3±0.7 ^b	6.5±1.2 ^b	-0.20±0.03 ^b
	YP	3.1±0.7 ^b	11.2±2.1 ^a	-0.24±0.03 ^b
	MP	3.6±0.5 ^b	15.2±1.3 ^c	-0.33±0.02 ^c
	YF	4.5±1 ^c	12.4±1.9 ^a	-0.34±0.03 ^c
	OF	5.1±0.7 ^c	22.1±1.8 ^d	-0.34±0.02 ^c
	MPS	-1.0±0.8	<i>-4.5±2.3</i>	0.03±0.02
	Paths	0.3±0.5	-1.5±1.2	0.03±0.01*
	Roads	0.6±0.4	<i>1.7±0.9</i>	0.0±0.01
	Smooth df	<i>10.8</i>	5.8	3.2

482 ¹Farm farmland, VYP/YP/MP very young/young/mature poplar plantations, YF/OF young/old forests, MPS
483 mean patch size of plantations and forests (all in ha), Paths/Roads cumulated length of paths or roads (km);.
484 Smooth df: estimated degree of freedom of the spatial smoother.

485 Table 2

486 Bird density (number of singers/10ha) of the 20 most common species calculated from the
 487 124 point counts of the study depending on the habitat where the individual was recorded
 488 (#Ind: total number of individuals recorded within 100m around the points, see also Table 2
 489 legend).

Species	#Ind	Farm	VYP	YP	MP	YF	OF
<i>Columba palumbus</i>	39	0	0	0.3	1.1	0.9	2.4
<i>Streptopelia turtur</i>	22	0.2	0	0	0.6	1.8	0.9
<i>Dendrocopos major</i>	14	0	0	0.6	0.8	0	0.3
<i>Anthus trivialis</i>	27	0.4	2.2	0.9	0.2	1.2	0.5
<i>Troglodytes troglodytes</i>	73	0	0.6	0.9	2.7	1.5	3.4
<i>Erithacus rubecula</i>	132	0	0.6	1.1	4.8	3.1	6.5
<i>Luscinia megarhynchos</i>	42	0	0.4	2.0	1.2	2.5	1.2
<i>Turdus merula</i>	50	0	0.4	1.4	1.5	1.8	2.2
<i>Turdus philomelos</i>	18	0	0.2	0	0.6	0	1.1
<i>Locustella naevia</i>	31	0.4	2.8	1.4	0.4	1.5	0
<i>Hippolais polyglotta</i>	17	0.2	0.8	0.3	0.4	1.5	0.2
<i>Sylvia communis</i>	46	0.4	3.2	1.4	1.0	2.8	0.3
<i>Sylvia borin</i>	27	0	0.2	0.9	1.0	1.5	0.8
<i>Sylvia atricapilla</i>	190	0.4	1.4	5.7	7.1	7.1	6.2
<i>Phylloscopus collybita</i>	117	0	2.0	4.0	5.1	2.8	2.8
<i>Cyanistes caeruleus</i>	44	0	0	0.9	1.1	1.5	2.6
<i>Parus major</i>	49	0	0	0.6	2.1	0.3	2.3
<i>Certhia brachydactyla</i>	19	0	0	0	0.4	0.6	1.3
<i>Sturnus vulgaris</i>	16	0.4	0	0.3	0.4	0.9	0.5

<i>Chaffinch</i>	77	0	0.2	1.1	1.9	1.5	4.9
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