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# Décomposition des effets des changements des paysages et des pratiques d'exploitation sur la biodiversité des milieux agricoles et forestiers

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**THESE DE DOCTORAT DE  
L'UNIVERSITE PIERRE ET MARIE CURIE**

Spécialité Ecologie  
Ecole Doctorale Diversité du Vivant (0392)

Présentée par  
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Pour obtenir le grade de  
**DOCTEUR de l'UNIVERSITÉ PIERRE ET MARIE CURIE**

Sujet de la thèse :

Décomposition des effets des changements des paysages et des pratiques d'exploitation sur la biodiversité des milieux agricoles et forestiers

préparée au sein de l'UMR 7204 MNHN-CNRS-UPMC : Conservation des Espèces, Restauration et Suivi des Populations

soutenue le 22/09/2009, devant le jury composé de :

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## Résumé

La destruction des habitats est considérée comme la première cause d'extinction d'espèces. Cependant, il est maintenant envisagé que la transformation des habitats en elle-même soit moins importante que la manière dont l'habitat transformé est utilisé. La conservation porte donc un intérêt croissant sur les milieux exploités, et les biologistes de la conservation recherchent activement des moyens de concilier production et maintien de la biodiversité. La plupart des efforts de recherche destinés à définir les pratiques d'exploitation optimales pour la conservation, consistent à comparer des modalités d'exploitation. Adopter une modalité d'exploitation implique en fait plusieurs décisions pour le gestionnaire. Dans ce contexte, j'ai cherché à décomposer les effets de ces décisions et particulièrement distinguer les décisions de gestion liées à l'intensité de production en elle-même, de celles liées à l'homogénéisation des paysages induite par l'intensification de la production. Dans cette optique, ce travail de thèse a consisté à analyser les variations spatiales des communautés d'oiseaux et de chauve-souris, dans les milieux agricoles et forestiers français. L'approche adoptée était à la fois (i) de mesurer l'abondance de chaque espèce pour identifier un éventuel appauvrissement de la communauté, et (ii) de comparer les réponses aux facteurs anthropiques des espèces spécialistes et généralistes, pour révéler une éventuelle homogénéisation biotique. Les résultats ont avant tout montré une prévalence des effets de l'intensité de production sur les effets de l'hétérogénéité des paysages. Ce travail de thèse s'est poursuivi par la recherche de stratégies possibles pour concilier production et conservation. Dans ce but, j'ai comparé la performance de scénarios dans lesquels l'intensité de production est soit répartie de manière homogène (« wildlife-friendly exploitation ») soit intensifiée sur une partie pour préserver la partie restante (« land sparing »). Les résultats ont alors plaidé en faveur de stratégies différentes pour les deux systèmes : une intensité de production modérée sur l'ensemble des forêts, et la mise en réserve des milieux agricoles extensifs.

## Mots-clés

Ecologie des communautés, oiseaux, chauve-souris, sylviculture, agriculture, stratégie de conservation, intensité de production, hétérogénéité du paysage, fonctions densité-rendement, spécialisation.

## Summary

Habitat destruction is considered as the most important cause of species extinction worldwide. However, it is now suggested that habitat conversion *per se* may be less important than how that converted habitat is used. There is thus an increasing interest in exploited habitats for conservation, and researchers actively look for ways to conciliate wood and food production with conservation of biodiversity. Most research efforts designed to define optimal exploitation practices for conservation consist in comparing existing options. Adopting one management option implies in fact several decisions for the manager. In this context, I aimed to decompose the effect of these decisions while particularly paying attention to the dichotomy between management decisions linked to production intensity *per se* from those linked to landscape homogenization induced by production intensification. For that purpose, this thesis investigated spatial variations of bird and bat communities in French farmland and forest as a case study. The adopted approach was (i) to measure abundance of each species to reveal potential impoverishment of the community and (ii) to compare species responses of habitat specialists and generalists to anthropogenic factors to reveal potential biotic homogenization. Above all, the results showed a prevalence of production intensity effects on bird and bat communities compared to landscape heterogeneity effects. This thesis further looked at possible strategies conciliating production and conservation. For that purpose, I used the same models to compare scenarios where production intensity is either homogeneously distributed (wildlife-friendly exploitation) or intensified on one part to spare the remaining part from adverse effects of exploitation (land sparing). The results then pleaded for opposing strategies: a widely applied compromise in forest and for a land sparing of extensive farmlands.

## Key-words

Community ecology, birds, bats, forestry, agriculture, conservation strategy, production intensity, landscape heterogeneity, density-yield functions, habitat specialization.

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**Bas, Y.**, Renard, M., Jiguet, F. 2009. Nesting strategy predicts farmland bird response to agricultural intensity. *Agriculture, Ecosystems & the Environment*. doi:10.1016/j.agee.2009.06.006

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**MANUSCRIT 2** **53**

**Bas, Y.**, Jiguet, F. Contrasting the effects of field margin habitats with production intensity on farmland birds. *in prep.*

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**Bas, Y.**, Julien, J.F., Kerbiriou, C., Jiguet, F. Forestry impacts birds and bats communities through different processes. *in prep.*

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**Bas, Y.**, Jiguet, F. Conciliating forestry and woodland bird conservation: should we promote wildlife-friendly forestry or forest reserves? *in prep.*

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**MANUSCRIT 7** **125**

**Bas, Y.**, Devictor, V., Moussus, J.P., Jiguet, F., 2008. Accounting for weather and time-of-day parameters when analysing count data from monitoring programs. *Biodiversity and Conservation*. 17, 3403-3416.

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**MANUSCRIT 8** **140**

**Bas, Y.**, Julien, J.F., Kerbiriou, C., Julliard, R., Jiguet, F. A simple method to assess distance-related biases on counts for animal surveys. *in prep.*

## Avant-propos

Cette thèse a eu pour but d'étudier deux problématiques de conservation portant sur deux systèmes différents dont le socle commun est l'exploitation par l'humain de leur matériel végétal : l'agriculture et la sylviculture. Dans cette perspective, des manuscrits spécifiques examinent des questions similaires de conservation dans ces deux systèmes pour atteindre l'ultime objectif de cette thèse, qui est de discuter des convergences et divergences entre les deux problématiques. Cet avant-propos présente d'abord les soutiens et collaborations dont cette thèse a bénéficié.

Cette thèse a été réalisée dans le cadre du Laboratoire de Conservation des Espèces, Restauration et Suivi des Populations (CERSP) du Muséum National d'Histoire Naturelle (MNHN), et a bénéficié de l'appui scientifique et logistique de ce laboratoire. Le financement provient d'une allocation (AMN) du Ministère de l'enseignement supérieur et de la Recherche.

Le projet de recherche initial de cette thèse s'est appuyé sur le développement de collaborations entre notre laboratoire, l'Inventaire Forestier National (IFN, projet Corylus) et l'Office National des Forêts (ONF). L'objectif de ces projets était d'examiner les effets potentiels des pratiques sylvicoles et des structures de paysages forestiers sur les communautés d'oiseaux en comparant des données sylvicoles et géographiques aux données du Suivi Temporel des Oiseaux Communs (STOC). Cette thèse a aussi développé une autre collaboration avec l'organisation non-gouvernementale SOLAGRO et le Centre Commun de Recherche de la Commission Européenne (JRC, Ispra, Italie). Cette collaboration avait pour but d'évaluer un indicateur de zone agricole à Haute Valeur Naturelle (HVN) à l'aide du STOC. Cela nous a aussi permis d'accéder à des statistiques agricoles détaillées et ainsi d'étudier l'impact des pratiques agricoles sur les oiseaux.

Cette collaboration a permis d'étudier la question de l'impact de l'exploitation des milieux sur la biodiversité, en suivant une démarche similaire pour l'agriculture et la sylviculture.

Cette thèse a aussi bénéficié d'échanges fructueux avec des collègues travaillant sur le programme de Suivi des Chauve-souris Communes, Christian Kerbiriou et Jean-François Julien. Cette collaboration a permis d'étudier en parallèle les effets de l'exploitation forestière sur les oiseaux et les chauve-souris afin d'étudier la généralité des résultats obtenus pour les oiseaux.

Le manuscrit de cette thèse suit la forme recommandée, selon laquelle la totalité du travail de recherche est présentée sous forme d'articles destinés à être soumis à la publication dans des revues scientifiques internationales. Ainsi, la première partie de cette thèse va introduire le contexte scientifique et les idées qui ont guidé cette thèse. La deuxième partie du manuscrit va présenter les problématiques communes de la conservation concernant l'agriculture et la sylviculture, ainsi que les différents objectifs de cette thèse. La troisième partie va

décrire et discuter deux importantes difficultés méthodologiques rencontrées pour atteindre ces objectifs. La quatrième partie confronte et discute les résultats des différents articles produits pendant la réalisation de cette thèse. Enfin, les annexes contiennent les huit articles qui présentent en détail l'ensemble du travail de recherche (deux de ces articles ont déjà été acceptés pour publication).

# **I La recherche en écologie appliquée à la conservation : pourquoi et comment ?**

## **I. 1. La Biologie de la Conservation : une science militante**

Comme la plupart des biologistes de la conservation, nous sommes en premier lieu des écologues, c'est-à-dire essentiellement des chercheurs intéressés par le fonctionnement de la nature. En conséquence, les questions habituellement soulevées par nos recherches peuvent se résumer à : « Comment ça marche ? ». Mais cet objet d'étude exerce aussi une fascination sur nous, rendant la question plus proche de : « Comment cela peut-il être possible ? ». Cette fascination, combinée avec le fait que les objets de notre étude sont menacés par le changement global, nous donne une motivation supplémentaire car nos travaux peuvent aider à la conservation de nos objets d'études (Soulé, 1985). Il est effectivement gratifiant que notre recherche soit non seulement intéressante, mais aussi qu'elle puisse aider une grande cause.

Mais cela nous met aussi sous des pressions contradictoires (i) de rester neutre envers les politiques de conservation, pour éviter le risque de discréditer la science (Lackey, 2007), et (ii) de défendre les mêmes politiques de conservation (Chan, 2008). Cela implique que chaque biologiste de la conservation puisse présenter des arguments efficaces justifiant la conservation de la biodiversité. Beaucoup de justifications se concentrent sur la conservation des espèces, car il est encore plus difficile de s'appuyer sur des échelles plus fines ou plus larges de la biodiversité. Les arguments utilisés couramment pour justifier la conservation des espèces sont : (i) les espèces sont « utiles », id est elles rendent des services écosystémiques qui contribuent à notre confort (Diaz et al., 2006), (ii) les espèces sont « belles », id est nous aimons les voir et les entendre et (iii) les espèces sont « intéressantes », id est nous voulons en savoir plus à leur sujet. Ce dernier argument peut fonctionner pour pratiquement toutes les espèces, mais il concerne plus la satisfaction des scientifiques que celle d'un public plus large. Il peut donc paraître un peu égoïste pour un écologue de mettre en avant cet argument pour le public. Les deux premiers arguments peuvent être plus efficaces, mais malheureusement ils excluent un grand nombre d'espèces. Je suis toutefois convaincu que le public peut souffrir de la perte d'espèces qui ne sont considérées comme ni utiles, ni belles. Prenons l'exemple du Hanneton commun en Europe (Fig. 1), une espèce qui n'est généralement pas considérée comme belle ou utile. Etant un ravageur agricole, il a été éradiqué dans de nombreuses régions européennes. Pourtant, beaucoup de gens semblent trouver inquiétant de ne pas avoir vu d'invasions de hannetons depuis des décennies. Je pense que cela vient du sentiment que si une espèce disparaît c'est la nature dans son ensemble qui en pâtit. Plus

généralement, je pense que l'importance de la conservation pour le bien-être humain est souvent sous-estimée. Par exemple, l'évaluation par le Millenium Ecosystem Assessment des services culturels rendus par la biodiversité est limitée aux simples valeurs spirituelles, esthétiques et de loisirs. (Millennium Ecosystem Assessment, 2005). Les invasions de hannetons ne semblent correspondre à aucun de ces trois critères.

Dans ce travail, nous avons donc considéré que chaque espèce compte, chacune au même niveau d'importance.



Figure 1. Le hanneton commun, généralement considéré comme une espèce déplaisante, même s'il peut paraître assez beau sur une telle vue rapprochée. La plupart des gens ne prennent pas la peine d'observer de près ces animaux et craignent plutôt qu'ils les heurtent de manière répugnante lors de leur vol maladroit et bruyant. (Yves Bas)

## **1.2. Une approche corrélative spatiale.**

La plupart des recherches en biologie de la conservation consistent à identifier les différents moteurs du déclin de la biodiversité. Pour cet objectif, l'approche la plus simple est d'établir une corrélation entre le changement temporel de la biodiversité et le

changement temporel des facteurs anthropiques. Pourtant, les données de suivi à long terme de la biodiversité sur le long terme sont encore rares et limitées à quelques taxons et pays. Cela mène souvent à étudier des corrélations entre des variations spatiales de la biodiversité avec des variations spatiales de facteurs anthropiques. Identifier ce genre de corrélation comme des liens causaux entre le facteur anthropique et le déclin de la biodiversité sous-tend l'hypothèse que les variations spatiales de biodiversité résultent de variations temporelles passées. De ce fait, une telle approche corrélatrice semble avoir une capacité limitée à révéler les mécanismes écologiques, en comparaison des méthodes expérimentales, mais une large échelle et une grande quantité de données permettent de répondre à des problématiques qui sont difficilement abordable par l'expérimentation, sous la condition que les hypothèses testées soient formulées a priori (Yoccoz et al., 2001).

### **I. 3. Le piège de la richesse spécifique**

Suivant cette approche, nous avons besoin de comparer les différents environnements locaux et la biodiversité au niveau local. Survient ici le problème que la mesure de la biodiversité au niveau local doit être utile à la poursuite des objectifs à large échelle de la conservation. Pendant longtemps, les mesures locales de la diversité (diversité alpha) ont été considérées comme des indicateurs fiables de la diversité globale (diversité gamma). Pourtant, il est maintenant bien établi que ces deux niveaux de diversité peuvent être négativement corrélés dans de nombreux cas (Devictor et Robert, 2009; Kerbiriou et al., 2009; Sax & Gaines, 2003), du fait du remplacement des espèces spécialistes par les généralistes (Devictor et al., 2008A, Van Turnhout et al., 2007). Il peut donc être délicat de déduire des recommandations pour la conservation à partir de l'étude de la diversité locale. Il est donc essentiel de distinguer deux types de perte de biodiversité : (i) un appauvrissement où les niveaux de diversités alpha et gamma déclinent de manière concomitante et (ii) une homogénéisation biotique où la présence d'espèces gagnantes (généralistes) rend les niveaux de diversité alpha et gamma divergents. De ce fait, nous avons adopté dans ce travail l'approche qui consiste (i) à mesurer l'abondance de chaque espèce pour identifier un éventuel appauvrissement de la communauté, et (ii) à comparer les réponses aux facteurs anthropiques des espèces spécialistes et généralistes, pour révéler une éventuelle homogénéisation biotique.

### **I.4. Qu'implique la spécialisation pour l'habitat ?**

La spécialisation des espèces pour un habitat a été considérée ici comme une simplification d'un concept plus large de la vulnérabilité des espèces aux changements globaux (Hughes et al. 2000; Munday 2004). Bien que d'autres facteurs écologiques influencent la vulnérabilité des espèces (Owens and Bennett, 2000), une importante littérature a montré que les espèces spécialistes étaient particulièrement sujettes à

l'extinction, indépendamment d'autres caractéristiques (ex : Munday 2004; Norris and Harper 2004; Safi and Kerth 2004). Nous soutenons donc que la distinction des espèces suivant leur degré de spécialisation est un moyen pratique de révéler une homogénéisation biotique des communautés.

Un autre avantage de l'approche « spécialiste versus généraliste » est qu'elle peut répondre aux arguments habituellement avancés à l'encontre de l'utilité de l'écologie des communautés pour la conservation de l'écologie des communautés. Étudier les communautés, implique effectivement l'utilisation de protocoles à large spectre qui ne sont souvent pas en mesure de recueillir suffisamment de données pour de nombreuses espèces, en général les plus rares. Ces espèces rares ont beaucoup plus de probabilité d'être vulnérables aux pressions anthropiques, et sont donc l'objet de beaucoup plus d'intérêt en conservation que les autres espèces. La rareté est cependant bien corrélée à la spécialisation (Brown, 1984). Ainsi, lorsqu'on met en relation les réponses des espèces à un facteur anthropique et leur degré de spécialisation, nous nous attendons à ce que les espèces rares soient situées à l'extrémité du gradient de cette relation (voir Fig. 2). Par conséquent, cette approche donne des indications précieuses pour la conservation des espèces, même pour celles qui ne sont pas directement étudiées.

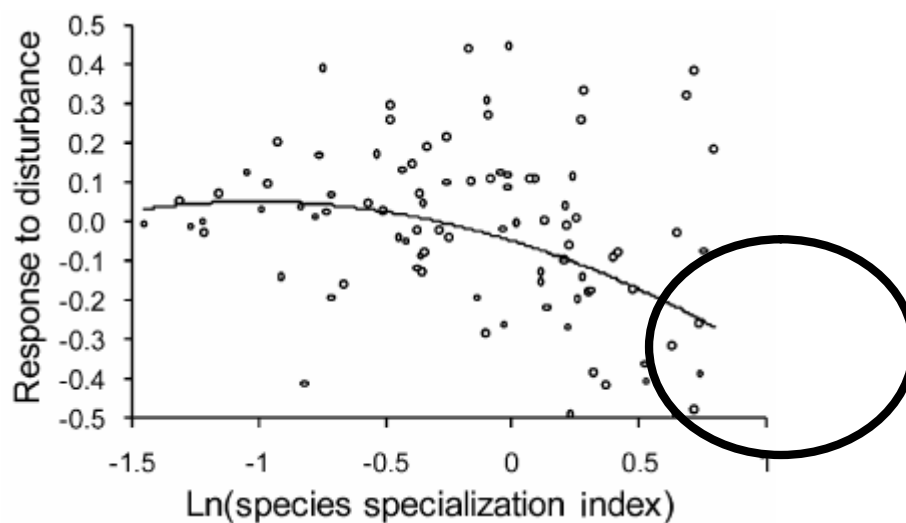


Figure 2. Les réponses des espèces d'oiseaux à la perturbation des habitats, rapportées en fonction de leur degré de spécialisation pour l'habitat, selon Devictor et al. (2008b). Nous ajoutons un cercle pour montrer la zone où les réponses d'espèces rares non étudiées sont censées se situer dans la mesure où la rareté est corrélée positivement à la spécialisation.

La mesure du degré de spécialisation pour l'habitat entraîne généralement de synthétiser le volume d'une niche d'habitat multidimensionnelle en une métrique à une dimension (Tilman 1982; Julliard et al. 2006; Fridley et al. 2007). Dans cette approche, la spécialisation de l'habitat doit rester indépendante du type de milieu auquel chaque

espèce est adaptée. Cependant, le fait de se concentrer sur un unique type d'habitat supprime une telle contrainte, et la spécialisation pour l'habitat serait simplement mesurée par le ratio entre l'abondance des espèces à l'intérieur et celle à l'extérieur de l'habitat considéré. Les espèces échantillonnées sont ainsi distinguées selon qu'elles soient présentes car elles sont spécialistes du milieu ou qu'elles soient présente car elles sont généralistes, puisque les espèces spécialistes d'autres milieux ne pourraient être présentes que de manière marginale. La mesure de la spécialisation pourrait être aussi mise en relation avec la responsabilité du milieu considéré pour la conservation des espèces d'une manière analogue à la définition des priorités de conservation dans les politiques nationales qui sont fonction du ratio entre la population nationale de l'espèce et de sa population globale (Schmeller et al. 2008). Cette priorisation de la conservation pourrait être particulièrement utile si l'habitat étudié est concerné par une politique de conservation spécifique comme les milieux agricoles ou forestiers. Dans cette thèse, nous avons adopté l'approche consistant à mesurer le degré de spécialisation des espèces au milieu agricole ou au milieu forestier selon le système étudié.

Notre mesure de la spécialisation est donc liée à la fois aux prédictions écologiques de la plus grande vulnérabilité des espèces spécialistes et à la priorité de conservation des espèces dans ces habitats exploités. Ce point renforce l'hypothèse selon laquelle une corrélation possible entre la spécialisation des espèces et la réponse des espèces à des facteurs anthropiques révèle des enjeux importants en conservation (Devictor et al., 2007).

## **II. La conservation en milieu exploité**

Cette seconde partie va présenter les questions communes de conservation de l'agriculture et de la sylviculture et introduire les six manuscrits qui concernent directement des questions de conservation. Les deux articles méthodologiques seront donc présentés dans la troisième partie. Les parties agricoles et sylvicoles de la thèse ne sont volontairement pas dissociées pour pouvoir considérer pleinement leurs aspects communs qui sont probablement plus importants que ce qui est habituellement supposé.

### **II. 1. Un besoin de conciliation**

La destruction des habitats est considérée comme la plus importante cause globale d'extinction des espèces (Pimm et Raven, 2000). La surface d'habitats vierges modifiés par l'homme a même été avancée comme permettant de prédire le déclin de la biodiversité (Brooks et al., 1997). Cependant, on suggère aujourd'hui que la transformation des habitats en elle-même peut être une cause de déclin des espèces moins importante que la manière dont l'habitat est utilisé par l'homme (Gibbs et al., 2009). Il y a donc un intérêt croissant pour la conservation des habitats exploités par l'homme



(Scherr and McNeely, 2008), conduisant à un appel à la réconciliation entre l'écologie et l'économie (Rosenzweig, 2003).

Dans cet esprit, il est maintenant bien reconnu que les terres agricoles conservent une biodiversité unique qui ne peut être rencontrée dans aucun milieu vierge, du moins là où il y a une longue histoire de l'agriculture (Stoate et al., 2001). Ainsi, bien que l'intensification de l'exploitation réduise la biodiversité des terres agricoles (Donald et al. 2001), la conservation de cette biodiversité nécessite le maintien de l'exploitation (Krebs et al., 1999). Même dans les zones tropicales, les terres agricoles ont un intérêt plus important qu'initialement supposé pour la conservation (Ranganathan et al., 2008).

D'autre part, les intérêts des biologistes de la conservation et de l'industrie du bois se dirigent de plus en plus vers les forêts secondaires et les plantations forestières, étant donné que ces forêts se répandent sur tous les continents (Imbeau et al., 2001; Nasi et al., 2006; Wright, 2005, Zhang et al., 2000). Il est aussi maintenant bien établi que ces forêts exploitées complètent la valeur en conservation des forêts primaires (Barlow et al., 2007; Brockerhoff et al., 2008). Par conséquent, il y a un effort de recherche croissant pour déterminer quelles pratiques sylvicoles optimisent la conservation de la biodiversité (Donald et al., 1998; YASUE & Ebeling, 2009; Putz et al., 2001).

## **II. 2. Décomposition des paramètres d'exploitation**

Les efforts de recherche destinés à définir des pratiques d'exploitation optimales consistent plutôt à comparer les options existantes (Attwood et al., 2008), par exemple l'agriculture biologique par rapport à l'agriculture conventionnelle (Bengtsson et al., 2005), les coupes forestières sélectives opposées aux coupes claires (Foley et al., 2007), les mesures agro-environnementales (Kleijn & Sutherland, 2003), les systèmes de certification forestière (Gullison, 2003), etc. Toutefois, les résultats diffèrent généralement selon les taxons et /ou le contexte du paysage, restreignant les recommandations générales (Barlow et al., 2007; Bengtsson et al., 2005; Kleijn & Sutherland, 2003). Les modalités d'exploitations proposées diffèrent toujours par plusieurs aspects, par exemple l'agriculture biologique diffère de l'agriculture conventionnelle par son usage des pesticides, des engrais, des rotations culturales, etc. Ainsi, l'adoption d'une modalité de gestion implique en fait plusieurs décisions pour le gestionnaire.

Notre objectif est de décomposer les effets de ces décisions, en nous concentrant sur les variables impliquant différentes décisions de gestion différentes et différents mécanismes écologiques affectant la biodiversité (Poulsen, 2002, voir tableau 1). Discriminer ces effets devrait nous aider à déterminer quel levier utiliser pour atténuer les effets de l'exploitation sur la biodiversité. En outre, examiner les gradients d'exploitation plutôt que les modalités d'exploitation permet de rendre compte de disparités potentiellement grandes entre les différentes exigences écologiques des espèces (Fischer & Lindenmayer, 2006).

Il est important de noter à ce sujet que certaines décisions de gestion (remembrement et régularisation des peuplements forestiers) sont davantage destinées à améliorer la commodité des opérations d'exploitation plutôt qu'à augmenter la production. On pense donc qu'agir sur ces leviers améliore la biodiversité à faible coût (Halpern & Spies, 1995; Kerr, 1999; Tschardt et al., 2005), en permettant le maintien d'une production intensive (Fig. 3). La restauration de l'hétérogénéité du paysage est parfois même considérée comme un eldorado de la conservation (Benton et al., 2003; Lindenmayer et al., 2000).

Néanmoins, les effets positifs de l'hétérogénéité des paysages ont surtout été montrés à partir de mesures de diversité locale ou de richesse spécifique, qui peuvent produire des messages trompeurs pour la conservation (voir 1.3.). L'évaluation de l'effet réel de l'hétérogénéité du paysage sur l'abondance des espèces est donc cruciale pour la conservation.

Tableau 1. Liste de variables d'exploitation dont les impacts ont été mesurés sur la biodiversité dans les manuscrits 1, 2 et 3. Leurs liens supposés avec les décisions des gestionnaires et l'écologie des espèces sont brièvement exposés brièvement

<b>Variable mesurée</b>	<b>Décision de gestion</b>	<b>Conséquences écologiques</b>
<i>Agriculture</i>		
Intensité de production (rendements des cultures ou charge animale des prairies)	Surtout apport d'engrais et de pesticides	Quantité de ressource alimentaire (graines et invertébrés) Perturbations (machine ou bétail)
Densité de bordures de champ	Remembrement	Quantité de milieux non cultivés riche en ressources Disponibilité en refuges
<i>Sylviculture</i>		
Age du peuplement (circonférence maximum)	Durée du cycle sylvicole	Quantité de ressource alimentaire (biomasse) Disponibilité en cavités
Régularité du peuplement (proportion d'arbres non dominants en surface terrière)	Méthode de régénération	Hétérogénéité verticale Densité du sous-bois
Conifères (en proportion de surface terrière)	Introduction de conifères à fort rendement	Habitat ne convenant pas aux espèces spécialistes des boisements feuillus
Ouverture de la canopée	Intensité et fréquence des éclaircies	Modification de la structure du milieu Etablissement d'espèces spécialistes des milieux ouverts.

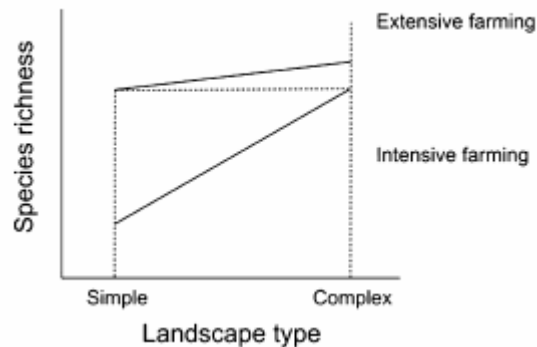


Figure 3. Interactions entre l'intensité des pratiques agricoles, la complexité des paysages et la biodiversité d'après les résultats de Roschewitz et al. (2005) et tire de Tschardt et al. (2005).

Dans ce contexte, le **Manuscrit 1** étudie l'impact de l'intensité de la production agricole sur les oiseaux, en identifiant les traits d'histoire de vie expliquant les réponses différentes entre espèces.

Le **Manuscrit 2** vise plus particulièrement à comparer les effets de l'intensité de production et des densité de bordures de champ sur les oiseaux du milieu agricole, en distinguant les espèces en fonction de leur degré de spécialisation.

Le **Manuscrit 3** vise à comparer les effets de quatre paramètres d'exploitation forestière (Tableau 1) sur les oiseaux et les chauves-souris, en distinguant les espèces en fonction de leur degré de spécialisation.

Le **Manuscrit 4** a examiné une question transversale impliquant l'effet de l'un des aspects de l'exploitation agricole, la densité en haies, sur les oiseaux forestiers, émettant l'hypothèse que les haies constituent des corridors pour les oiseaux forestiers.

## II 3. La courbe densité / rendement

Déterminer l'importance relative des différentes décisions de gestion en fonction de leur impact sur la conservation ne suffit malheureusement pas à concevoir des stratégies de conservation efficaces. Cette thèse s'est donc poursuivie par l'examen des stratégies possibles de conservation face aux contraintes de production de l'agriculture et de l'exploitation forestière.

Green et al. (2005) ont identifié deux stratégies de conservation concurrentes pour concilier la production agricole et la conservation de la biodiversité: (i) une stratégie de mise en réserve (« land sparing »), dans laquelle la production est atteinte par les pratiques les plus intensives, ce qui permet d'épargner un maximum de surface de l'exploitation et (ii) une stratégie de pratiques d'exploitation respectueuse de la biodiversité (« wildlife friendly farming ») où l'on minimise l'intensité de production, mais

qui demande un maximum de surface à exploiter. Les résultats de ces deux stratégies de conservation peuvent être comparés en analysant la forme graphique de la relation entre les rendements agricoles et la densité relative des espèces (Fig. 4).

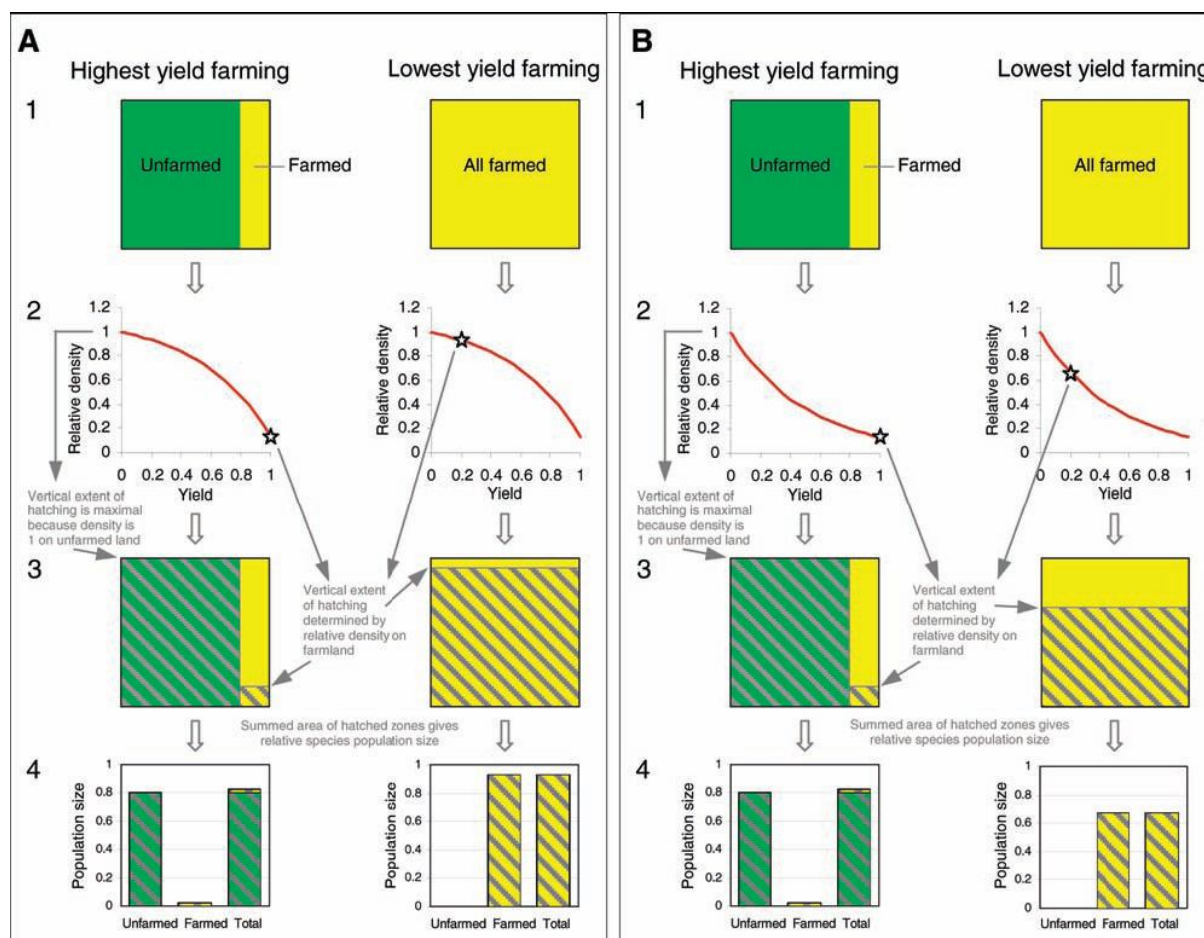


Figure 4. Comparaison de la stratégie de mise en réserve (land sparing) et de la stratégie de pratiques d'exploitation respectueuse de la biodiversité (wildlife friendly farming), par l'étude de leur effet sur la population d'une espèce. Dans le cas A, la courbe densité / production est concave, ce qui implique que la stratégie « wildlife friendly farming » devrait aboutir à un effectif plus important que dans le cas de la stratégie « land sparing ». Dans le cas B, la courbe densité / production est convexe, ce qui implique que la stratégie « land sparing » devrait aboutir à un effectif plus important que dans le cas de la stratégie « wildlife friendly farming ».

Green et al. (2005) ont opposé les terres agricoles aux terres inexploitées et l'application de leur modèle a montré des résultats contrastés (Dorrough et al., 2007; Makowski et al., 2007; Steffan-Dewenter et al., 2007). Néanmoins, ils ont construit un modèle capable de répondre à un large panel de questions sur la stratégie à préconiser pour concilier production et conservation, soit (i) un compromis général sur l'intensité des pratiques d'exploitation, soit (ii) opter pour l'exploitation intensive sur une partie des

terres disponibles, autorisant la mise en oeuvre de pratiques extensives optimales sur la partie restante. En effet, on trouve des signes évidents de la concurrence de ces stratégies dans de nombreux contextes différents. Par exemple, Whittingham (2007) préconise de faire fonctionner des mesures agro-environnementales comme les systèmes traditionnels d'aires protégées, avec des groupes agrégés de fermes gérés à l'aide de méthodes d'exploitation extensive, au lieu de disperser ces mesures agro-environnementales dans l'espace. Il y a également un débat sur l'opportunité de préconiser plutôt une généralisation de la certification forestière ou la création de réserves forestières intégrales (McGeoch et al., 2007).

Nous avons donc utilisé ce modèle pour évaluer différentes stratégies de conservation dans nos deux contextes d'étude. Le **Manuscrit 5** reprend la modélisation de l'abondance des espèces du Manuscrit 2 intégrant les deux variables de gestion (intensité de production et densité de bordures de champ) pour ajuster les réponses concaves ou convexes des espèces. De même, le **Manuscrit 6** reprend la modélisation de l'abondance des oiseaux du Manuscrit 3, intégrant deux variables de gestion que l'on suppose liées linéairement au rendement en bois (âge du peuplement et proportion de résineux) pour ajuster les réponses concaves ou convexes des espèces. Nous n'avons pas appliqué cette modélisation aux cinq espèces de chauve-souris spécialistes forestières, parce que (i) trois des cinq espèces ont montré un ajustement très médiocre au modèle, id est des réponses à la fois extrêmes et non significatives, et (ii) les deux dernières espèces n'ont pas révélé de différence significative entre les scénarios concurrents.

Les Manuscrits 5 et 6 sont des brouillons à un stade très précoce de leur rédaction. Je présente mes excuses à l'avance pour leur qualité et leurs discussions brèves et incomplètes. J'ai néanmoins choisi de les inclure dans le but de les confronter et de discuter leurs résultats.

### **III Points méthodologiques**

Cette partie abordera deux importants points méthodologiques concernant l'ensemble du travail de cette thèse. Des aspects plus spécifiques de la méthodologie sont abordés dans les différents manuscrits.

#### **III. 1. Les modèles statistiques d'utilisation de l'habitat**

L'approche générale de cette thèse se situe dans la continuité de la première des trois approches exposées par Norris (2004) : les modèles statistiques d'utilisation de l'habitat (Fig. 5). Norris (2004) a souligné que ces modèles ont une applicabilité limitée, car ils ne peuvent produire des prédictions quantitatives fiables sur les futurs environnements que lorsque certaines populations de l'espèce étudiée ont déjà expérimentées des environnements comparables, passés ou présents. Il a donc plaidé en

faveur de modèles intégrant le comportement des individus (« behaviour-based models »), qui peuvent prendre en compte les processus évolutifs. Cependant, ces modèles nécessitent une énorme quantité de données diverses (Beissinger et al. 2006). Bien qu'ils ignorent les processus complexes, les modèles statistiques d'utilisation de l'habitat ont besoin d'une quantité minimale de données simples. Leur mérite est qu'ils sont souvent le seul moyen d'obtenir des réponses sur les questions de conservation avec les données disponibles.

Par exemple, les taillis à courte rotation constituent un tout nouvel environnement visant à produire de l'énergie renouvelable, mais les réponses sur son impact sur la biodiversité proviennent de modèles statistiques d'utilisation de l'habitat, tirées des quelques données collectées lors des premières applications de ce nouveau type d'habitat exploité (Berg, 2002; Sage et al., 2005; Schardt et al., 2007).

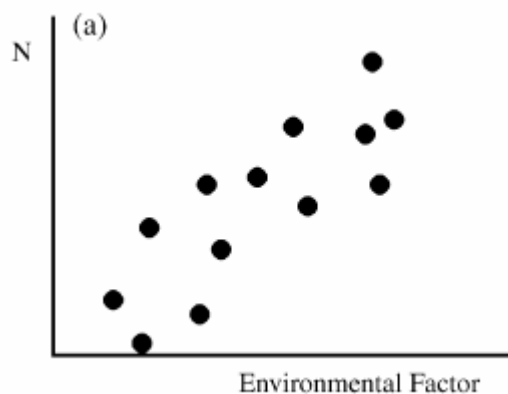


Figure 5. Exemple de modèle statistique de l'utilisation de l'habitat, tiré de Norris (2004). La densité de population (N) est modélisée par rapport à un facteur environnemental en utilisant des données provenant de différents sites (points). Cette approche a été adoptée en dans les Manuscrits 1, 2, 3, 5 et 6, et avec des indices synthétiques de biodiversité dans le Manuscrit 4.

Comme nous l'avons vu, ces modèles statistiques de la gestion de l'habitat ont besoin de données qui incluent les futurs environnements potentiels pour donner des indications utiles sur l'avenir potentiel de la biodiversité. Pour maximiser cette potentialité, l'échantillonnage recherche l'hétérogénéité la plus grande possible dans les environnements échantillonnés. Cette hétérogénéité d'environnement est particulièrement bien réalisée par les pratiques agricoles françaises qui sont parmi les plus diversifiées en Europe, allant des plus intensives au plus traditionnelles. En outre, une grande hétérogénéité dans la mise en oeuvre des remembrements a abouti à un large gradient de densité de bordures de champ.

De même, les forêts échantillonnées en Ille-et-Vilaine pour les Manuscrits 3 et 6 présentent des pratiques forestières très hétérogènes grâce à une forte proportion de propriétés privées. De fait, les propriétaires fonciers ont diverses motivations et contraintes financières, ce qui a des répercussions sur l'exploitation forestière réalisée.

Ces environnements hétérogènes ont aussi permis des corrélations faibles entre les paramètres de gestion étudiés, et ainsi nous ont évité les problèmes de multicollinéarité, qui nous auraient empêché de décomposer leurs effets (James et McCulloch, 1990).

## III. 2. Le fardeau de la détectabilité

Cette thèse, comme de nombreuses recherches en écologie, repose sur des mesures de variations spatiales de l'abondance des espèces, habituellement appelée abondance relative, et résultante de comptages. Un problème récurrent à propos de ces comptages est que l'hétérogénéité de la détectabilité des individus dans l'espace ou le temps peut biaiser les estimations de l'abondance relative, et conduire à des conclusions erronées (Elphick, 2008). Pour contourner ce problème, les méthodes d'estimation de la probabilité de détection ont récemment proliféré, et les écologues subissent une pression croissante pour adapter leur protocole d'échantillonnage afin d'être capable de mettre en œuvre ces méthodes (Allredge et al., 2007b; Kery, 2008; Royle, 2004a).

Cependant, toutes ces méthodes ont été construites pour en déduire des valeurs d'abondance absolues, alors qu'on a souvent besoin uniquement d'estimations d'abondance relative. En pratique, ces méthodes nécessitent soit des réplifications spatiales et temporelles (Kery et al., 2005; Royle, 2004b), soit une réplification temporelle et le marquage des individus (Allredge et al., 2007a; Farnsworth et al., 2002). Ainsi, la recherche d'estimations d'abondance absolue sans biais entraîne un effort excessif d'échantillonnage dans les protocoles récents et contraint les écologues à se concentrer sur quelques espèces et/ou à échantillonner quelques sites (Johnson, 2008). De plus, comme de nombreux facteurs écologiques tel que les caractéristiques de l'habitat, sont mesurés très localement, des études écologiques ont souvent besoin d'une mesure de l'abondance relative sur une échelle très locale (par exemple, pour chaque point de comptage), qui, malheureusement, empêche d'obtenir une réplification spatiale des données de comptage.

Ainsi, dans de nombreux cas, une estimation directe de la détectabilité est encore impossible. Encore plus inquiétant, Efford et Dawson (2009) ont récemment montré que toutes ces méthodes ne sont pas en mesure de corriger des biais répandus qui sont dus à l'hétérogénéité de la détectabilité des individus les plus éloignés de l'observateur.

La détection d'un individu est en fait conditionnée par deux processus avec différents facteurs sous-jacents qui les influencent (Kery & Schmidt, 2008, Fig. 6) : (i) la disponibilité, id est la probabilité pour un individu d'être disponible au comptage (par exemple, pour un oiseau chanteur : la probabilité qu'il chante au cours de la période de comptage) et (ii) la détectabilité sensu stricto, la probabilité de sa détection conditionnellement à sa disponibilité (par exemple, pour le même oiseau : la probabilité que son chant soit détecté par l'observateur).

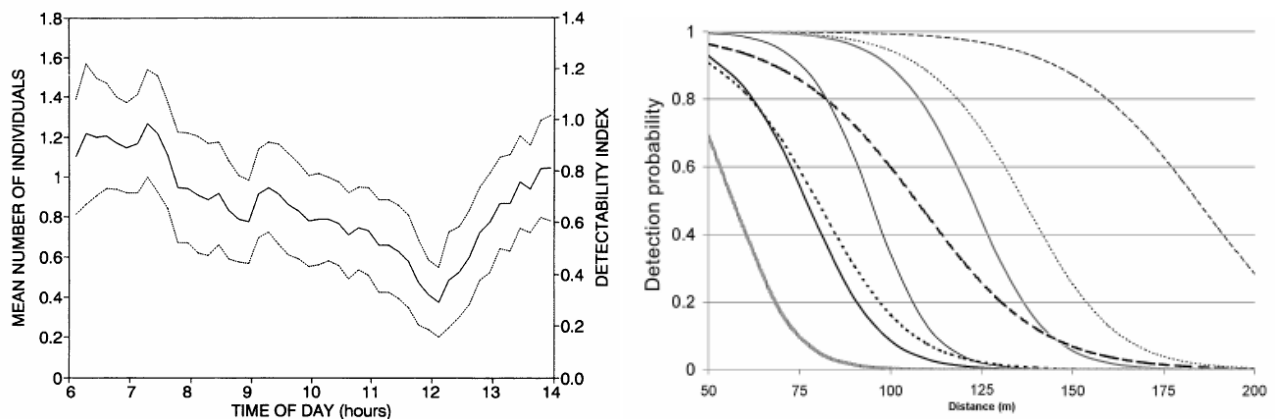


Figure 6. Exemples de variations typiques des deux processus de détectabilité. Le graphique de gauche montre les variations de la disponibilité du grimpeur des jardins chanteurs en fonction de l'heure de la journée (selon Palmeirim & Rabaca, 1994). Le graphique de droite montre les variations de détectabilité sensu stricto des chants émis par la paruline bleue en fonction de la distance à l'observateur (selon Pacifici et al., 2008). Les différentes lignes représentent différents environnements de végétation et de bruit de fond.

Le premier processus, la disponibilité, est souvent supposé être indépendant de l'habitat, et généralement, les protocoles d'échantillonnage évitent toute corrélation entre les facteurs l'influençant (la saison, moment de la journée, conditions météorologiques ...) et les facteurs écologiques étudiés. Néanmoins, cela produit toujours de l'hétérogénéité dans la détectabilité et accroît la variance de l'abondance mesurée, et un biais inattendu peut toujours survenir. Pour cette raison, l'objectif du **Manuscrit 7** était de mesurer le biais potentiel et la diminution de la puissance statistique induite par les effets de la météo et de l'heure du jour sur les comptages d'oiseaux du Suivi Temporel des Oiseaux Communs. Comme prévu, nous avons montré que les conditions météorologiques et l'heure du jour ont entraîné une hétérogénéité importante dans la détectabilité des individus. Toutefois, les résultats ont aussi montré qu'il était inutile de contrôler statistiquement cette hétérogénéité pour une étude écologique typique (dans le cas étudié, les effets de la fragmentation sur l'abondance des oiseaux). Le contrôle de ces variables n'a en effet corrigé aucun biais et n'a pas augmenté la puissance statistique. Cela a confirmé que les grandes bases de données sont relativement robustes vis à vis de l'hétérogénéité de la détectabilité, dans la mesure cette hétérogénéité peut être considérée comme indépendante du facteur écologique étudié.

Le deuxième processus, la détectabilité sensu stricto, est considéré comme étant lié à la distance, c'est-à-dire lié au rayon de détection de l'observateur, qui peut varier dans le temps et l'espace (Buckland et al., 2001). Ce processus peut être beaucoup plus corrélé aux caractéristiques de l'habitat que la disponibilité (par exemple, la structure de la végétation, Pacifici et al., 2008; Schieck, 1997). Malheureusement, les biais liés à la distance sont mal corrigés par des méthodes prétendant traiter l'ensemble du processus de détection (Effort & Dawson, 2009). Seul la méthode du « distance sampling » semble



être en mesure de corriger ces biais, mais les conditions prérequis à son application sont difficiles à réaliser sur le terrain (Buckland et al., 2001; Effort & Dawson, 2009).

Pour contourner ces difficultés, nous avons développé dans le **Manuscrit 8** une méthode simple pour corriger les biais liés à la distance. Son principe est d'analyser si les variations du ratio entre les détections proches et lointaines sont influencées par le facteur écologique étudié. Cette méthode diffère fondamentalement du « distance sampling » en utilisant seulement deux classes de distance et surtout, en faisant beaucoup moins d'hypothèses.

Nous avons également appliqué cette méthode sur des enregistrements de chauves-souris, en utilisant l'intensité des cris enregistrés comme un indicateur de la distribution des individus en fonction de la distance. Ce travail a montré que la densité des strates basses dans les forêts d'Ille-et-Vilaine réduit la détectabilité des chants d'oiseaux, mais pas celle des cris d'écholocation des chauves-souris. Pour la Fauvette des jardins, une espèce connue pour chanter bas dans la végétation, sa détectabilité a diminué de 83% entre les sous-bois de densité faible et ceux de densité élevée. Ceci indique que les nombreuses études qui n'ont pas tenu compte de ce genre de biais ont fortement sous-estimé la valeur pour la conservation des forêts riches en sous-bois (Schieck, 1997 ; Pacifici et al., 2008).

Ensuite, nous avons appliqué cette méthode dans le manuscrit 5 où nos quatre paramètres d'exploitation forestière pouvaient être corrélés à la détectabilité, et ainsi biaisés nos résultats. Seule, l'ouverture de la canopée a été liée de façon significative à la détectabilité, les individus éloignés étant plus détectables en canopée ouverte qu'en canopée fermée. Il peut sembler étrange, en confrontant les résultats des manuscrits 5 et 8, que la régularité des peuplements n'entraîne pas une augmentation de la détectabilité, puisque la gestion en futaie régulière réduit la densité du sous-bois, mais il faut remarquer que ce paramètre est plus corrélé aux strates intermédiaires qu'aux strates basses qui sont responsables de la baisse de la détectabilité (Tableau 2). Néanmoins, le fait que la végétation basse et l'ouverture de la canopée sont corrélés de manière significative à la détectabilité des individus éloignés montre que la relation entre la végétation et la détectabilité est probablement complexe et que davantage de recherches sont nécessaires pour mieux anticiper ces biais.

Densité de végétation des strates	Age du peuplement	Régularité du peuplement	Conifères	Ouverture de la canopée
1-2 m	-0.053	-0.284	-0.195	-0.153
2-4 m	-0.093	-0.459	-0.314	-0.470
4-8 m	-0.107	-0.419	-0.308	-0.707
8-16 m	0.175	-0.145	-0.354	-0.736
>16 m	0.357	0.075	-0.499	-0.665

Tableau 2. Coefficients de corrélation de Pearson entre les quatre paramètres d'exploitation forestière (en colonnes) et la densité de la végétation correspondant à cinq strates horizontales (en lignes).

## IV Discussion générale

Les résultats de cette thèse sont tous analysés spécifiquement dans les huit manuscrits. Cependant, cette discussion générale reprend trois points généraux qui sont abordés dans plusieurs manuscrits. La première partie confronte les résultats des Manuscrits 1, 2, 3 et 4 concernant les effets respectifs de l'intensité de la production sensu stricto et l'homogénéisation des paysages induite par cette intensité de la production. La deuxième partie a pour but d'établir une synthèse des résultats des Manuscrits 5 et 6 testant le modèle de Green et al. (2005). Enfin, la troisième partie commente les apports de la méthode d'inférence adoptée dans cette thèse.

### IV.1. Intensité de production vs. hétérogénéité du paysage

Comme nous l'avons vu, une grande partie des changements dans les pratiques agricoles et forestières ont plus pour objectif d'améliorer la commodité des opérations d'exploitation que de d'augmenter la production proprement dite (ex : remembrement, régularisation des peuplement, etc). Ces changements de « commodité » ont tous eu pour résultat divers types d'homogénéisation du paysage. De ce point de vue, la restauration de l'hétérogénéité du paysage a été présentée comme la solution miracle contre la perte de biodiversité dans les milieux exploités (Benton et al., 2003; Carey, 2003), permettant de plus le maintien de l'exploitation intensive. Toutefois, nous devons reconnaître que nos études ont pris en compte l'hétérogénéité du paysage sur une échelle relativement

petite : l'échelle du peuplement en sylviculture et celle de l'exploitation en agriculture (Benton et al., 2003). Donc, nous avons pu manquer un éventuel effet d'une homogénéisation du paysage à une échelle plus large comme la spécialisation régionale de l'agriculture. Selon notre estimation, les études préconisant l'hétérogénéité du paysage à large échelle souffrent de trois types de points faibles.

Premièrement, de nombreuses études relient l'hétérogénéité des paysages uniquement à une augmentation de la richesse spécifique (e.g. Aauri & de Lucio, 2001; Haslem & Bennett, 2008; Loehle et al., 2005; Pino et al., 2000). Les résultats de ce type d'études n'ont pas mis en évidence d'effet positif de l'hétérogénéité des paysages sur les espèces individuellement et peuvent être dus à un pur effet « mosaïque » (Naihara, 2007). En effet, comme les espèces sont adaptées à un nombre restreint d'habitats, augmenter le nombre d'habitats disponibles va augmenter le nombre d'espèces présentes sans aucun effet positif de la diversité des habitats sur chacune des espèces présentes. Cet effet positif des mosaïques sur la richesse globale en espèces est donc d'un intérêt limité pour la conservation (Bennett et al., 2006) et peut même s'avérer négatif s'il est associé à une perte d'espèces spécialistes (Devictor et al., 2008b). De manière intéressante, l'hétérogénéité du paysage est nommée différemment suivant l'effet supposé : fragmentation de l'habitat lorsqu'elle produit une homogénéisation biotique (Devictor et al., 2008b), et diversité ou complexité du paysage lorsqu'elle est liée à une augmentation de la richesse spécifique (Pino et al., 2000; Roschewitz et al., 2005). De plus, l'hétérogénéité du paysage est mesurée comme la densité en lisière entre habitats (« edge density »). Donc, bien que nommée différemment, il s'agit définitivement de la même chose.

Deuxièmement, de nombreuses autres études démontrent l'effet positif de l'hétérogénéité des paysages sur l'abondance des espèces mais ces effets positifs sont souvent restreints aux espèces généralistes (Gil-Tena et al., 2007; Jonsen & Fahrig, 1997; Weibull & Ostman, 2003). Les modèles de métacommunautés et les résultats empiriques ont suggéré que cette augmentation des espèces généralistes était un effet indirect de l'effet de l'hétérogénéité des paysages du fait du relâchement de la compétition d'espèces spécialistes négativement affectées. En effet, dans un tel cas, l'abondance des espèces spécialistes semble dépendre en premier lieu de la qualité du milieu et être affectée négativement par l'hétérogénéité du paysage (Aavik et al., 2008; Gil-Tena et al., 2007; Schweiger et al., 2007). Encore une fois, l'hétérogénéité du paysage est d'un intérêt limité pour la conservation si cela favorise uniquement des espèces généralistes prospères.

Troisièmement, quelques études révèlent une corrélation positive significative entre l'abondance d'espèces spécialistes et l'hétérogénéité des paysages (Barbaro et al., 2007; Robinson et al., 2001). Il semble pourtant que dans de tels cas, l'hétérogénéité des paysages soit fortement corrélée à la proportion d'un habitat minoritaire particulièrement attractif pour les organismes étudiés, par exemple des boisements de feuillus dans une zone dominée par les conifères (Barbaro et al., 2007) ou des cultures dans des systèmes pastoraux (Robinson et al., 2001). Une telle corrélation peut être à l'origine de déductions fausses dans des analyses statistiques et produire des messages trompeurs (James &

McCulloch, 1990). Dans ce cas, le lien causal était plus probablement le type d'habitat que l'hétérogénéité de l'habitat sensu stricto (Heikkinen et al., 2004).

Pour conclure cette courte revue, le miracle de l'hétérogénéité ne semble pas devoir se produire, du moins pour les oiseaux. Ainsi, la restauration de l'hétérogénéité des paysages associée au maintien d'une intensité de production élevée ne devrait avoir que des effets limités en ce qui concerne la conservation des oiseaux. Comme nous l'avons vu, l'hétérogénéité des paysages pourrait même avoir des effets négatifs en conservation si cela favorise les généralistes aux dépens des spécialistes (Devictor et al., 2008a). De tels mécanismes de compétition entre spécialistes et généralistes peuvent empêcher les écologues d'évaluer correctement les menaces pesant sur la biodiversité si ces mécanismes ne sont pas appréhendés, par exemple en considérant uniquement la richesse spécifique ou l'abondance sans discriminer les espèces. Dans cette thèse, les Manuscrits 1, 2 et 3 révèlent un équilibre entre les réponses positives et négatives des espèces aux paramètres de l'exploitation des milieux, plutôt qu'une réponse globalement positive ou globalement négative. Malheureusement, la plupart des études ont pris pour hypothèse une réponse globalement univoque à ces paramètres d'exploitation puisqu'elles ne considèrent pas l'homogénéisation biotique comme une conséquence possible des changements anthropiques. Dans cette thèse, si les espèces n'étaient pas différenciées en fonction de leur degré de spécialisation, les effets de l'intensité de la production sur les oiseaux auraient été fortement sous-estimés à la fois en agriculture et sylviculture (Manuscrits 1 et 2). Cette approche nous a aussi permis de démontrer l'effet de la régularité des peuplements forestiers et de l'ouverture de la canopée sur les oiseaux alors que ces effets n'étaient pas significatifs globalement.

Plus inquiétant, l'approche "richesse spécifique" peut promouvoir des structures de paysages qui pourraient avoir des effets négatifs sur la conservation des espèces. Premièrement, augmenter l'hétérogénéité des paysages sans tenir compte de l'échelle pourrait réduire la taille des parcelles d'habitat et donc être nuisible aux espèces spécialistes (Devictor et al., 2008a; Shirley, 2006). Deuxièmement, certaines caractéristiques des paysages peuvent avoir à la fois un effet positif sur la richesse en espèces et un effet négatif pour des espèces menacées. Au vu de nos résultats, cela semble être le cas des clairières dans les forêts (Manuscrit 3) et des haies dans les terres agricoles (Manuscrit 2). Et ces deux éléments du paysage ont été préconisés en partant du fait qu'ils engendrent une augmentation de la richesse spécifique ou de l'abondance, mais sans tenir compte de la nature des espèces qui en bénéficient (e.g. Griffiths et al., 2007; Loehle et al., 2005; Merckx et al., 2009). Nos résultats montrent que seulement une proportion limitée d'espèces spécialistes bénéficient des haies dans les milieux agricoles et des clairières dans les forêts (Manuscrits 2 et 3). Ainsi, les haies et les clairières ne devraient pas être préconisés de manière générale mais seulement là où les espèces cibles pour la conservation dépendent de ces éléments.

En outre, le Manuscrit 4 a montré que les haies n'apportaient pas d'avantage d'intérêt pour la conservation en tant que corridors potentiels pour les oiseaux forestiers. Nous devons toutefois admettre que les oiseaux sont parmi les taxons les moins dépendants des corridors car ils montrent une sensibilité réduite aux contraintes de la

dispersion, même les spécialistes forestiers (Bowne & Bowers, 2004; Graham et al., 2006). Mais les Manuscrits 2 et 4 suggèrent que l'importance des haies pour la conservation est probablement exagérée du moins en Europe (Gillings & Fuller, 1998; Grashof-Bokdam & van Langevelde, 2005). Une explication possible vient du fait que la récente destruction des haies en Europe a été précédée par une explosion de leur densité au 19ème siècle (Baudry et al., 2000; Deckers et al., 2005). Dans ce contexte, les espèces européennes auraient été adaptées à une densité historiquement basse des haies dans les paysages et, donc, le déclin récent des haies pourrait être relativement bien supporté par ces espèces.

## **IV. 2. Densité/rendement : une fonction seuil ?**

Nos résultats ont montré une prévalence des effets de l'intensité de production sur la biodiversité à la fois en milieu agricole et forestier (Manuscrit 1, 2 et 3). En outre, la FAO prédit un accroissement drastique de la production de bois et de nourriture dans un proche avenir (Alexandratos et Mernies, 2000 ; FAO, 2009). Ainsi, concilier la production de bois et de nourriture avec la conservation de la biodiversité est effectivement un enjeu majeur. De ce fait, la validité de l'approche de Green et al. (2005) devrait s'en trouver renforcée.

Nous avons utilisé le modèle de Green et al. (2005) concernant la relation entre abondance et rendement en milieu agricole et forestier (Manuscrit 5 et 6). Nos résultats ont montré que la plupart des réponses des oiseaux forestiers aux rendements en bois sont « concaves » alors qu'une majorité d'oiseaux des milieux agricoles ont une réponse « convexe » aux rendements agricoles. Ces résultats ont plaidé pour des stratégies de conservation opposées : une intensité de production modérée sur l'ensemble des forêts, et la mise en réserve des milieux agricoles extensifs. Il n'est pas surprenant, bien sûr, que ces deux systèmes se comportent différemment. Toutefois, on peut penser que l'abondance des espèces et les rendements soient liés par des fonctions plus complexes. Nos résultats forestiers et agricoles peuvent probablement être expliqués par une fonction unique dans laquelle la réponse de l'abondance est premièrement concave pour des rendements faibles et ensuite convexe pour des rendements élevés (Fig. 7). Cette hypothèse suggère alors que l'intensité de production observée en forêt dans le Manuscrit 6 a été relativement faible (donc dans la partie gauche de la Fig. 7) comparée à l'intensité de production observée dans les milieux agricoles français (Manuscrit 5, partie droite de la Fig. 7). De plus, d'autres études confirment cette hypothèse en suggérant que l'appropriation par l'homme de la biomasse était plus basse dans les forêts que dans les milieux agricoles en Europe (Haberl et al., 2001; Haberl et al., 2005). Par conséquent, de tels modèles impliquant un seuil de production devraient être testés même si, en introduisant plus de complexité, ils nécessitent plus de données pour être ajustés, et donc ne peuvent pas être testés sur autant d'espèces que notre simple fonction quadratique.

Si de telles fonctions seuil s'appliquaient véritablement à une majorité d'espèces, la meilleure stratégie de conservation devrait donc dépendre des objectifs de production. Pour cette raison, la forte augmentation de la demande en nourriture et en bois prévue à court terme aurait pour conséquence que des stratégies de mise en réserve de terre gagnent rapidement en intérêt face aux stratégies de compromis sur l'ensemble. Nos résultats en ce qui concerne la forêt indiquent que les productions actuelles soient principalement en dessous du seuil mais il est concevable qu'une baisse drastique de la rotation sylvicole due à une demande beaucoup plus forte en bois-énergie changerait la donne. Une telle intensification de la production forestière serait donc mieux atténuée par une mise en réserve des vieux peuplements forestiers.

Une des limites de notre étude vient du fait qu'elle concerne uniquement les oiseaux, à l'instar des récents autres tests du modèle de Green et al. (2005 ; Balmford et al. 2008). Des éléments suggèrent que d'autres taxons pourraient répondre différemment (Buddle & Shorthouse, 2008). Cela reste à tester largement mais un manque de consensus parmi les taxons serait un petit handicap pour la conservation (Barlow et al., 2007). Cependant, l'utilisation de ce modèle serait tout de même à recommander pour la mise en place de stratégie de conservation, puisque les deux stratégies, de compromis et de mise en réserve, sont toujours appliquées du fait d'a priori non testés (Daily, 2001; Donald, 2004). Ainsi, malgré ses limites, l'utilisation du modèle de Green et al. (2005) devrait accroître l'efficacité de la conservation des espèces.

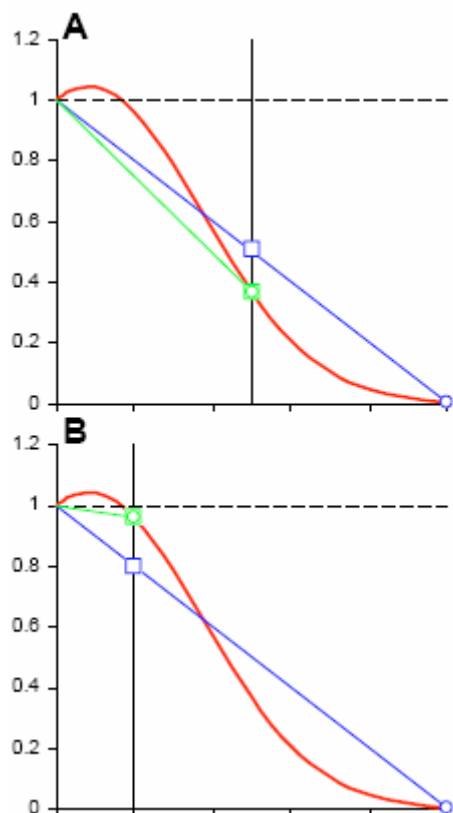


Figure 7. Un exemple de densité décroissante d'une espèce (axe des ordonnées) en fonction du rendement (axe des abscisses) dont la forme n'est ni concave ni convexe, d'après Green et al. (2005). La meilleure stratégie de conservation peut tout de même être identifiée. La solution dépend ici de l'objectif de production. Le graphique A illustre une situation dans laquelle la production est élevée et où la mise en réserve est plus bénéfique pour l'espèce. Le graphique B illustre une situation dans laquelle la production est faible et où le compromis sur l'ensemble est plus bénéfique pour l'espèce.

## IV. 3. Magnitude vs. p-value

Un des points centraux de cette thèse est l'importance de la mesure de la magnitude des effets des différents paramètres, plus que leur simple significativité. Cela a permis de prédire la performance relative de stratégies de conservation (Manuscrits 5 et 6). Cette approche prédictive n'a pas seulement identifié la meilleure stratégie mais a aussi montré dans quelle mesure cette stratégie est meilleure que les autres (Manuscrits 5 et 6).

Deuxièmement, interpréter les effets non significatifs est impossible sans déterminer l'intervalle de confiance de la magnitude de l'effet, bien qu'une majorité d'études d'écologie interprètent encore les effets non significatifs comme une absence d'effets (Fidler et al., 2006). En estimant l'intervalle de confiance de l'effet non significatif de la végétation sur la détectabilité des chauves souris, nous avons pu conclure qu'un effet fortement négatif tel qu'observé pour les oiseaux, était improbable chez les chauve-souris (Manuscrit 8). Ainsi, la mesure de l'intervalle de confiance de la magnitude a montré que les détectabilités des oiseaux et des chauve-souris répondaient différemment à la densité de la végétation. Cette utilisation des intervalles de la confiance est très commune en médecine mais reste rare en écologie en dépit de son potentiel pour invalider des hypothèses (Di Stefano, 2004) Malheureusement, de nombreuses études produisant des résultats non significatifs restent souvent non publiées bien que certaines d'entre elles pourraient prouver, avec suffisamment de données, que certains effets sont moins importants que supposés (Petticrew et al., 2008). L'utilisation des intervalles de confiance permet de plus des comparaisons entre études dans la mesure où les paramètres de gestion sont mesurés de la même manière. En effet, le fait qu'un paramètre d'exploitation a un effet significatif dans un contexte A et non dans un contexte B, ne prouve rien. Mais, les intervalles de confiance peuvent prouver que l'effet du paramètre d'exploitation soit moindre dans le contexte B que dans le contexte A.

Dans ce contexte, le biais de la publication vers les résultats significatifs devrait avoir l'effet pernicieux de favoriser la validation par rapport à l'invalidation des hypothèses. Il s'ensuit que les effets significatifs s'accumulent à grande vitesse alors que les effets majeurs sont lentement distingués des effets mineurs. L'examen par Benton et al. (2003) des menaces sur la biodiversité des milieux agricoles, est symptomatique d'une longue liste de facteurs significatifs, et le fait de tenter de les unifier derrière une définition très large de l'hétérogénéité n'aide pas réellement la conservation. Pour distinguer les facteurs majeurs et mineurs affectant la biodiversité, nous avons besoin de comparer leurs magnitudes respectives (Yoccoz, 1991). Dans cette perspective, les Manuscrits 2, 3, 4 et 7 ont standardisé les variables explicatives en les divisant par leur écart-type. Cette méthode permet de comparer objectivement la magnitude des différents effets. Le Manuscrit 2 a identifié la densité des haies et l'intensité de la production agricole comme des effets négatifs majeurs pour les oiseaux des milieux agricoles, en

comparaison de la densité des autres effets des bordures de champ. Le Manuscrit 3 a montré, entre autres choses, la prévalence de l'effet de la proportion de conifères sur l'abondance globale et la composition de la communauté des chauves-souris forestières. Le Manuscrit 4 a montré la prévalence de l'effet de la surface en habitat forestier sur les effets de la fragmentation, de l'isolation et de la densité des haies dans les variations de la richesse et la composition de la communauté des oiseaux forestiers.

Bien que la standardisation soit fortement influencée par le contexte de l'étude, cette approche de la magnitude devrait offrir des potentialités supplémentaires pour des comparaisons entre études. Il est possible que cela favorise l'émergence de patterns généraux et puisse apporter des réponses plus claires sur les menaces majeures pesant sur la biodiversité.



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# **ANNEXES**





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1

2 Nesting strategy predicts farmland bird response to agricultural intensity

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ABSTRACT

Large-scale studies investigating impacts of agricultural practices on biodiversity showed that farmland bird population sizes are negatively related to national agricultural intensification indices in Europe. Here, it was tested whether the nesting strategy of farmland species predicted their abundance variations along a gradient of agricultural production intensity. Ground-nesters, which are strongly declining all over Europe, were expected to be impacted more directly by production intensity than hedge-nesters which would be instead impacted by hedge loss. To test this prediction, previously unavailable fine-scale agricultural data were used over an entire country representing highly diverse farmlands. We modelled the local abundance of 43 farmland bird species, using data from the French breeding bird survey, along an index of agricultural production intensity based on standardized crop yields and herbivore stocking rates, controlling the analysis for local climate and farmed habitat type. 68% of ground-nesters had lower relative abundance in more productive farmlands, whereas only 17% of hedge-nesters did. Nesting strategy explained an important part of bird species responses to spatial variation in agricultural production intensity. Our results suggest that although hedge loss and production intensification were parts of the strong agricultural intensification in Europe, these two phenomena are impacting different bird species.

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1. Introduction

Agricultural intensification largely impacts biodiversity (Krebs et al., 1999) and threatens diverse ecosystem services (Bjorklund et al., 1999). More particularly, the implementation of Common Agricultural Policy in numerous eastern European countries could amplify wider farmland bird declines over the continent (Habeck, 2004). Such declines have been linked to both spatial and temporal variations in agricultural production intensity (Chamberlain et al., 2000; Donald et al., 2001, 2006; Wretenberg et al., 2007). However, similar patterns of agricultural intensification in various European countries do not necessarily result in similar farmland bird trends (Fox, 2004). In addition, similar trends can result from different patterns in agricultural changes (Wretenberg et al., 2006). Farmland bird declines have been associated with (i) direct effects of production intensification, such as depletion of food supply (Morris et al., 2005), farming operations (Burton et al., 1999) or cattle trampling (Pavel, 2004), or (ii) more indirect effects such as loss of natural microhabitats within farmlands (Gillings and Fuller, 1998) or landscape homogenisation (Benton et al., 2003), these components being often correlated and hence difficult to disentangle.

This study takes advantage of the French context where a strong heterogeneity in land consolidation implementation resulted in a low correlation between hedge density and local production intensity (Baudry and Burel, 1984; Vitikainen, 2004). This allows to investigate the impact of agricultural practices intensification independently from the impact of the decrease in landscape features.

Nesting on the ground has been proposed as a promoting factor of farmland species sensitivity to intensification but poorly explains recent trends (Siriwardena et al., 1998). Besides, the loss of hedgerows in western European landscapes is presumably responsible for the decline of many species nesting in these elements (Gillings and Fuller, 1998). It was hypothesized that ground-nesters would respond more negatively to local production intensity than hedge-nesters, and that hedge-nesters abundance should be positively linked to the presence of bush/tree elements. The robustness of the nesting strategy effect was tested against other potentially correlated traits.

2. Methods

Data on breeding birds was obtained by a national Breeding Bird Survey scheme launched in France in spring 2001 (Jiguet et al., 2007). In this scheme, volunteer ornithologists counted all visible and singing individual birds at permanent points. Surveyed sites are two-by-two km squares randomly selected for each observer

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51 within a 10 km radius around a locality specified by the volunteer.  
 52 Observers carried out 10 point counts of 5 min each per square,  
 53 twice per spring, i.e. once before and once after the 8th May, with  
 54 4-6 weeks between sessions, with points separated by at least  
 55 300 m. Counts were repeated yearly by the same observer at the  
 56 same points, on about the same date, and at the same time of day.  
 57 The 7307 points which were localized adjacent to farmland were  
 58 selected from this dataset.

59 For each species and each point, the yearly count with the  
 60 maximum number of individuals detected among the two sessions  
 61 was retained. Only individuals detected within a 100 m radius  
 62 around the observer were considered so that the birds were  
 63 actually seen in their habitat. Yearly counts were averaged for  
 64 squares that were monitored over several years between 2001 and  
 65 2006.

66 Observers were also asked to classify land use/habitat within  
 67 100 m of each point into 11 types, i.e. maize, other cereals, rape,  
 68 root crop, sunflower, other temporary crop, permanent crop, dry  
 69 grassland, grazed heathland, wet meadow and classical pasture.  
 70 The frequencies of 11 farmland habitat types per point were then  
 71 calculated by averaging yearly frequencies, thus taking into  
 72 account inter-annual crop rotations. Non-farmland habitat fre-  
 73 quency was not used in the statistical modelling because it was a  
 74 simple linear combination of the 11 farmland habitat types  
 75 frequencies (1 sum of them). Thus, species responses to non-  
 76 farmland habitats was accounted for by the mean of the 11  
 77 farmland frequencies. Observers also recorded the presence of  
 78 bush/shrubs and trees. The 50 species that were detected on at  
 79 least 50 different points and were more abundant adjacent to  
 80 farmland than in other habitats were then retained. Among these,  
 81 *Phasianus colchicus*, *Pterodroma perterodroma* and *Alectoris rufa* were excluded  
 82 as their local abundances strongly depended on releases for  
 83 hunting purposes, as well as *Ardea cinerea*, *Merops apiaster*, *Hirundo*  
 84 *rustica* and *Acrocephalus scirpaceus* because of their specific nesting  
 85 strategies. The 43 remaining species were classified as either  
 86 ground- (n = 19), or hedge-nesters (n = 24) as described in Cramp  
 87 and Perrins (1994).

88 **3. Agricultural data**

89 An overall estimate of local agricultural production intensity  
 90 was developed using data from the French Farm Structure Survey  
 91 Census conducted in 2000 (SCEES, 2001). These data contain the  
 92 farmed area of the 36,027 French municipalities, detailed through  
 93 37 crop and five pasture types, and the number of herbivorous  
 94 livestock per municipality, detailed through 21 types. Data from  
 95 the French Annual Agricultural Statistics were also gathered: crop  
 96 yields of 161 crop types for the 94 French departments (SCEES,  
 97 2005b). For each crop, yields were averaged over the 2000-2004  
 98 period.

99 To summarize local production intensity using yields for the  
 100 different crops and livestock density for pastures, these metrics  
 101 had to be standardized to obtain an overall index. This  
 102 standardization was performed in three steps.

103 First of all, livestock density was calculated for each munici-  
 104 pality containing pastures, using a livestock unit table that  
 105 provided equivalences between different types of herbivores  
 106 (SCEES, 2005a) and dividing this herbivores quantity by the total  
 107 area of local pasture systems.

108 Secondly, we looked for reference values for all crop yields and  
 109 livestock density which could all represent an equivalent level of  
 110 production intensity. For this purpose, European agricultural data  
 111 from the FAOSTAT database was used (FAO, 2006) and a European  
 112 mean yield for each crop was calculated, adjusted to the effect of  
 113 country. This calculation allowed us to obtain reference values  
 114 representing an equivalent level of production intensity for each

115 crops and for pastures. To synthesize these measures in one  
 116 production intensity index by municipality (Fig. 1), the production  
 117 intensities of all cropping and pasture systems was standardized,  
 118 averaged and weighted by the corresponding covered areas:

$$PI_m = \frac{1}{ALA_m} \sum_i \left( \frac{Y_{im} - R_i}{R_i} \times A_{im} \right)$$

119 where  $ALA_m$  is the agricultural area of the municipality  $m$ ,  $Y_{im}$  is the  
 120 local yield of the  $i$ th cropping system,  $R_i$  is the reference yield and  
 121  $A_{im}$  is the cropping system area.

122 Lastly, the municipalities delimitation was overlaid to the BBS  
 123 grid to obtain  $PI$  of each surveyed BBS square:

$$PI_s = \frac{\sum_m PI_m \times ALA_{sm}}{\sum_m ALA_{sm}}$$

124 where  $PI_s$  is the production intensity in the square  $s$  and  $ALA_{sm}$  the  
 125 agricultural area intersected by the square  $s$  and the municipality  $m$ .

126 **4. Statistical analysis**

127 The impact of production intensity ( $PI$ ) on farmland birds was  
 128 analysed in two steps (as in Jiguet et al., 2006). First, each species  
 129 responses to  $PI$  and to woody elements were estimated thanks to  
 130 French BBS data. Then, the effect of nesting strategy on the 43  
 131 species estimated responses was assessed.

132 For that purpose, local abundance of each 43 species was  
 133 modelled by a multiple regression with production intensity ( $PI$ ) as  
 134 independent variable associated with variables controlling for  
 135 potential habitat and climate effects. Climatic requirements were  
 136 controlled by using quadratic functions of four basic climatic  
 137 variables from the WorldClim database: BIO5, BIO6, BIO13 and  
 138 BIO14 at a 2.5 arc-minutes precision (Hijmans et al., 2006).

139 Each of the 43 models was formulated as follows:

$$140 \text{Abundance} \sim F_1 + F_2 + \dots + F_{11} + C_1^2 + C_1 + C_2^2 + C_2 + C_3^2 + C_3$$

$$141 + C_4^2 + C_4 + TP + SP + PI$$

142 where  $F_s$  are the 11 farmland habitat frequencies,  $C_s$  are the four  
 143 climatic variables, TP is tree presence/absence, SP is shrub  
 144 presence/absence and  $PI$  the production intensity index.

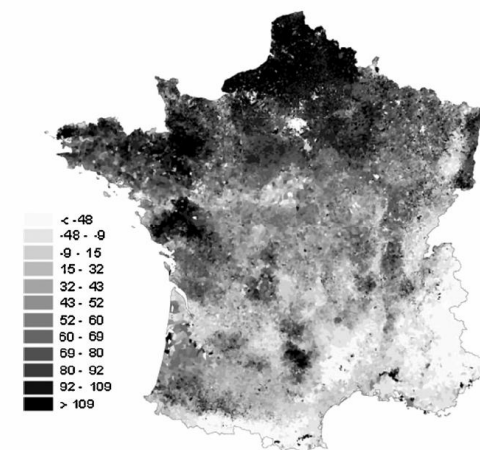


Fig. 1. Graphic output of the agricultural production intensity index ( $PI$ ) as used in this study (see Section 2). The darker the colour, the more intensive the local agricultural production.

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146 To test our predictions, the slope response parameters of each  
147 43 species to *PI*, to tree presence and to shrub presence were  
148 extracted from these models (see S1), as well as the associated  
149 standard errors. The three types of species response were then  
150 analysed with linear models:

Species response slope  $\sim$  Nesting strategy

152 To satisfy normality assumption, species responses to *PI* were  
153 square-root transformed. Additional tests were also performed to  
154 control potential biases in the observed responses due to  
155 heterogeneity in estimation precision and to evolutionary depen-  
156 dency between species. For that purpose, the previous tests were  
157 repeated using a weighted Generalized Least Squares phylogenetic  
158 comparative method (Freckleton et al., 2002) and Grafen's (1989)  
159 covariance structure implemented in the 'ape' package of the R-  
160 software to run the GLS models (Paradis et al., 2004). The  
161 classification published by Sibley and Ahlquist (1990) was used  
162 and adapted from the updates by Jonsson and Fjeldsa (2006) and  
163 by Moller (2006). Heterogeneity in estimation precision was taken  
164 into account by weighting the response estimates by their inverse  
165 squared standard errors.

166 Nesting strategy ability to predict the species responses to *PI*  
167 was further investigated by comparing the explanatory power of  
168 nesting strategy effect with those of several environmental and  
169 climatic niche characteristics as well as major life history traits  
170 that have already been shown elsewhere to strongly influence bird  
171 dynamics:

Species response slope to *PI*  $\sim$  Trait<sub>*i*</sub>

173 As environmental niche measures, we included (1) the species  
174 specialization for farmland habitats (Siriwardena et al., 1998),  
175 using the difference between mean abundance in farmland and  
176 mean abundance in non-farmland divided by mean abundance in  
177 farmland habitats; (2) the overall habitat specialization, estimated  
178 in a similar way but initially including the 18 main habitat types  
179 recorded by observers on BBS points (see Julliard et al., 2006). As  
180 climatic niche measures, we included (see Jiguet et al., 2007 for  
181 further details): (3) the thermal average; (4) and the thermal range.  
182 Some life history traits were also considered: (5) migration  
183 strategy (Wretenberg et al., 2007), with species classified as long-  
184 distance migrant, partial migrant or resident; (6) feeding habit  
185 (Robinson et al., 2001), with species classified as feeding  
186 predominantly on vertebrates, invertebrates or plants during the  
187 breeding season; (7) log-transformed body mass (Owens and  
188 Bennett, 2000); (8) annual brood number and (9) annual fecundity  
189 (Jiguet et al., 2007). Data sources were the French BBS 2001–2006  
190 for (1) and (2), the EBCC Atlas of European Breeding Birds  
191 (Hagemeijer and Blair, 1997) and the WorldClim database (Hij-  
192 mans et al., 2006) for (3) and (4), and Cramp and Perrins (1994) for  
193 (5), (6), (7), (8), and (9). The robustness of the relationship between  
194 nesting strategy and the response to *PI* was also evaluated by  
195 performing nine different models with two predictors:

Species response slope to *PI*  $\sim$  Nesting strategy + Trait<sub>*i*</sub>

196 This control is particularly essential with specialization to farm-  
197 land which is correlated to nesting strategy ( $r = 0.59$ ).

198 All tests were performed using the statistical software R 2.5.1 (R  
199 Development Core Team, 2005).

## 201 5. Results

202 Of the 19 ground-nesters, 13 responded negatively to *PI* (five of  
203 the 24 hedge-nesters), whereas 18 of the hedge-nesters showed a  
204 positive response to trees and 13 to shrub (compared to six and five  
205 ground-nesters). As predicted, responses to *PI* consisted of  
206 significantly more negative slope values for ground-nesters than

**Table 1**

Summary of the three univariate linear models comparing ground-nesters and hedge-nesters response to local agricultural production intensity (*PI*), tree and bush presence. For each variable, the average linear estimated slopes of both species groups are given with their standard errors ( $\pm$ SE), as well as the part of explained variance ( $r^2$ ) by the corresponding univariate model (see Section 2).

Response to	$r^2$	Ground-nesters	Hedge-nesters	<i>t</i>	<i>P</i>
<i>PI</i>	0.19	-0.335 $\pm$ 0.162	0.335 $\pm$ 0.145	3.08	0.004
Tree presence	0.23	-0.236 $\pm$ 0.080	0.140 $\pm$ 0.071	3.51	0.001
Bush presence	0.10	-0.199 $\pm$ 0.090	0.057 $\pm$ 0.079	2.14	0.038

207 for hedge-nesters (Table 1;  $P = 0.004$ ), and this difference remained  
208 significant when accounting for phylogenetic relatedness or  
209 weight ( $t = 2.89$ ;  $df = 41$ ;  $P = 0.006$ ). Moreover, responses were  
210 much better explained by nesting strategy ( $r^2 = 19\%$ ) than by  
211 farmland specialization ( $r^2 = 3.5\%$ ) or any of the other environ-  
212 mental niche measures or life history traits considered (maximum  
213 of variance captured for thermal optimum:  $r^2 = 10.3\%$ ). This effect  
214 remained robustly significant when first adjusting the model to  
215 anyone of the niche measure or life history trait: *P*-values ranging  
216 from 0.0027 when combined to thermal optimum to 0.0118 when  
217 combined to habitat specialization.

218 As expected, hedge-nesting had a significant positive effect on  
219 species response to tree presence and a nearly significant positive  
220 effect on species response to bush presence (Table 1), and these  
221 results were confirmed when accounting for taxonomic related-  
222 ness among species (weighted GLS models; tree presence:  $F = 2.52$ ;  
223  $df = 41$ ;  $P = 0.016$ ; bush presence:  $F = 1.69$ ;  $df = 41$ ;  $P = 0.099$ ).  
224 Nesting strategy had similar explanatory power to explain  
225 differences in species response to tree presence and to production  
226 intensity.

## 227 6. Discussion

228 The nesting strategy explained a large part of farmland birds  
229 responses to spatial variation in agricultural production intensity.  
230 More precisely, the abundance of 68% of ground-nesters responded  
231 negatively to increased local agricultural production intensity (*PI*),  
232 whereas only 17% of hedge-nesters were negatively affected. Our  
233 results argued in favour of a direct link between nesting strategy  
234 and response to *PI*. Firstly, among 11 species-specific traits, nesting  
235 strategy was the best predictor of abundance variations along the  
236 gradient of *PI*. It is particularly important to note that nesting  
237 strategy was by far a better predictor than species specialization to  
238 farmland which was previously identified as the best predictor of  
239 farmland bird trends (Siriwardena et al., 1998). Secondly, the link  
240 between nesting strategy and species response to *PI* proved to be  
241 robust when multiple regression of responses to *PI* were done with  
242 both nesting strategy and other species-specific traits. Thirdly, this  
243 link was not biased by taxonomic relatedness between species and  
244 heterogeneity in estimation precision.

245 Besides, the control analysis showed that unlike ground-  
246 nesters, hedge-nesters benefited from the presence of woody  
247 elements. The recent agricultural changes in Western Europe  
248 embodied increases in production intensity but also landscape  
249 modifications such as rooting up of hedges (Gillings and Fuller,  
250 1998). The simultaneousness of these two phenomena could thus  
251 explain why both ground-nesters and hedge-nesters were con-  
252 comitantly declining: ground-nesters because of production  
253 intensification and hedge-nesters because of the loss of woody  
254 elements. This can also explain why Siriwardena et al. (1998)  
255 found that species specialization to farmland explained species  
256 declines better than nesting strategy.

257 The depressed abundance of ground-nesters due to high  
258 production intensity may also explain the positive response of  
259 83% of the hedge-nesters to *PI* through a possible loosening of

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interference competition for food. Such competition mechanism remains to be investigated, but similar unexpected positive response to production intensity was found by Donald et al. (2006) on eight recently increasing farmland bird species in Europe.

Indeed, our results were consistent with previous observations on farmland bird trends induced by changing agricultural practice (Chamberlain et al., 2000; Wretenberg et al., 2007). Actually, among the 29 species considered by Chamberlain et al. (2000), all the 7 ground-nesters showed similar trend pattern (situated on the same side of the first axis in a principal component analysis on species annual trends) whereas the hedge-nesters did not. In addition, Wretenberg et al. (2007) found a similar dichotomy between species which responded or not to temporal changes in agricultural production intensity. Their dichotomy matched the nesting strategy dichotomy for five out of seven species. Interestingly, the two remaining species were among the five species of our list to have ambiguous nesting behaviour (see S1). Moreover, the results presented here are more contrasting than some previous large-scale studies on farmland birds (Siriwardena et al., 1998; Fox, 2004; Wretenberg et al., 2006), probably because the analysis was restricted to species that were at least slightly more abundant in farmland, thus excluding species which were less likely to respond to agricultural changes.

This study showed that hedge-nesters conservation was likely to depend on preservation of woody elements, whereas ground-nesters conservation was likely to depend on maintenance of low intensity agricultural practices. This suggested that hedge-nesters were more likely to recover from their past decline than ground-nesters since many European agri-environment schemes aim to increase the presence of woody elements in the landscape while maintaining high production intensity (Merckx et al., 2009).

This study highlighted that fine scale agricultural statistics at large spatial scale were highly valuable to assess farmland biodiversity threats, as they can produce accurate and powerful indices of local agricultural practices. In the present context of intense efforts made to monitor landscape and biodiversity at large spatial scales (Balmford et al., 2003), the EU monitoring data of agricultural practices (Eurostat, 2007) should add complementary information to fully discriminate the various proposed threats to farmland biodiversity.

To conclude, our results may be generalized to other taxonomic groups as similar dichotomies between hedge-avoiding and hedge-dependent species seemed to prevail in other biodiversity compartments, such as carabids (Fournier and Loreau, 1999), spiders (Drapela et al., 2008) or plants (Petersen et al., 2006).

#### 306Q1 Uncited reference

307 McCullagh and Nelder (1989).

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## MANUSCRIT 2

# Contrasting the effects of field margin habitats with production intensity on farmland birds

Running title: Field margins vs. production intensity

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## Summary

1. Biodiversity losses in farmlands have been associated with either direct effects of production intensification or landscape homogenization, these components being often correlated and hence difficult to disentangle. Yet, disentangling production intensity effect from landscape homogenization effect is crucial for the design of Agri-Environment Schemes which are able to mitigate the effect of agricultural intensification.
2. This study takes advantage of the French context where a strong heterogeneity in land consolidation implementation has resulted in a low correlation between farmland heterogeneity and local production intensity. Thanks to the French Breeding Bird Survey database, we then asked whether production intensity or field margins density were the best predictor of farmland bird species abundance, contrasting responses of specialist species with generalist ones.
3. Results showed that the intensity of agricultural production had a stronger effect on farmland bird species abundance than their preferred field margin type.
4. Moreover, the effect of production intensity was more negative on specialist species than on generalists, suggesting that production intensification is causing an homogenization of farmland birds community.
5. Another finding of this study is the importance of negative effects of hedgerows on a majority of farmland bird species.
6. Synthesis and Applications. These results argued strongly in favour of the prevalence of agricultural intensification on farmland bird threats compared with landscape homogenization due to the destruction of field margins. Thus, increasing field margin density is unlikely to mitigate farmland birds decline in an intensive farming context. On that account, Agri-Environment Schemes which promote landscape heterogeneity by increasing field margins density should have a poor efficiency for farmland birds, despite their relatively low cost. Our study instead suggests that Agri-Environment Schemes which promote extensive farming practice and which target within-field area will be more beneficial to farmland birds.

## Key-words

Agriculture, biotic homogenization, conservation, extensive farming, grass margins, landscape complexity, line-transect sampling, microhabitats, non-cropped habitats, photointerpretation.

## ***Introduction***

Agricultural intensification currently causes large biodiversity losses (Krebs et al. 1999) and threatens diverse ecosystem services (Björklund et al. 1999). Biodiversity losses in farmlands have been associated with either (i) direct effects of production intensification, such as depletion of food supply (Robinson and Sutherland 2002), farming operations (Kragten et al. 2008) or cattle trampling (Pavel 2004), or (ii) more indirect effects such as loss of natural microhabitats within farmlands (Gillings and Fuller 1998) or landscape homogenization (Benton et al. 2003), these components being often correlated and hence difficult to disentangle. Yet, disentangling production intensity from landscape homogenization effects is crucial for the design of Agri-Environment Schemes which would be able to mitigate the effect of agricultural intensification (Tschardt et al. 2005; Whittingham 2007). This study takes advantage of the French context where a strong heterogeneity in land consolidation implementation has resulted in a low correlation between farmland heterogeneity and local production intensity (Baudry and Burel 1984; Vitikainen 2004). This allows to investigate the impact of the intensification of agricultural practices independently from the impact of the decrease in landscape features. We then asked whether production intensity or field margins density were the best predictor of farmland bird species abundance. Farmland bird species were expected to exhibit different Preferred Field Margin type (PFM): either grassy margins, shrub hedgerows or tree hedgerows (Hinsley and Bellamy 2000). We thus aimed to compare production intensity effect to the effect of the PFM for each species. We also asked whether species responses to each of these factors varied with species degree of habitat specialization, as it is a symptom of biotic homogenization (Devictor et al. 2008a), decreasing diversity at a global scale (Sax and Gaines 2003) and which could be caused by landscape disturbance (Devictor and Robert 2009).

## **Methods**

### ***Bird data***

Data on breeding birds were obtained by a national Breeding Bird Survey scheme launched in France in spring 2001 (Jiguet et al. 2007), using data for the period 2001 to 2006. In this scheme, volunteer ornithologists counted all visible and singing individual birds at permanent points. Surveyed sites are two-by-two km squares randomly selected



for each observer within a 10 km radius around a locality specified by the volunteer. Observers carried out 10 point counts of five min each per square, twice per spring, i.e. once before and once after the 8th May, with four to six weeks between sessions, with points separated by at least 300m. Counts were repeated yearly by the same observer at the same points, on about the same date, and at the same time of day. The 7307 points which were localized adjacent to farmland were selected from this dataset.

For each species and each point, the yearly count with the maximum number of individuals detected among the two sessions was retained. Only individuals detected within a 100m radius around the observer were considered so that the birds were actually seen in the farmed habitat. Yearly counts were averaged for squares that were monitored over several years between 2001 and 2006.

Observers were also asked to classify land use/habitat within 100 m of each point into nine types, i.e. maize, other cereals, rape, root crop, sunflower, other temporary crop, permanent crop, wet meadow and pasture. The frequencies of the nine farmland habitat types per point were then calculated by averaging yearly frequencies. Non-farmland habitat frequency was not used in the statistical modelling because it was a simple linear combination of the nine farmland habitat type frequencies (1 – sum of them). Thus, species responses to non-farmland habitats were accounted for by the mean of the nine farmland frequencies. The 46 species which were detected on at least 50 different points and which were more abundant in farmland than in other habitats were then retained. We further aimed to define each species degree of specialization to farmland habitats (Siriwardena et al. 1998) by using the difference between mean abundance in farmland and mean abundance in non-farmland divided by mean abundance in farmland habitats, according to the French Breeding Bird Survey data (Bas et al. in press).

### *Agricultural data*

An estimate for each BBS site of the local agricultural production intensity (PI) was developed using yields for the different crops and livestock density for pastures. These metrics were standardized thanks to European reference values. Thus, PI measured the local agricultural production intensity as the standardized difference between local yields and European reference yields (see Bas et al. in press for details).

Landscape features delimiting fields and pastures were sampled thanks to interpretation of aerial photographs at a 1/4000e scale. A 7.66 km transect allowed line-intersect sampling of field margins for each BBS square, following de Souza & Batista's (2004)'s design (Fig. 1), and performed by a single trained photo-interpreter (YB). All field margins were then counted along the transect and classified as either "Tree" if it contained at least a tree, "Shrub" if it instead contained shrubs, or "Grass" if it contained neither any tree nor any shrub. Field margins of more than 25 m width were not considered as those are not directly linked to farming management.

This photo-interpretation led to the exclusion of data from BBS sites which contained farmlands which were not divided into plots (128 sites, essentially highland extensive pastures) and BBS sites which contained less than 20% of farmland (23 sites). We calculated the density of each of the three field margin types by dividing their number by the length of farmland area covered by the transect, for the 880 squares with available data.

### *Statistical analysis*

First, the responses of each species abundance to PI and to field margins density were estimated thanks to French BBS data. For that purpose, local abundance of each of the 46 species was modelled by a multiple regression with PI and field margins density as independent variables associated with variables controlling for species habitat and climate requirements. Climatic requirements were controlled by using quadratic functions of four basic climatic variables from the WorldClim database: maximum temperature of the hottest month, minimum temperature of the coldest month, precipitations of the wettest and the driest months (BIO5, BIO6, BIO13 and BIO14 at a 2.5 arc-minutes precision, see Hijmans et al. 2006). Quadratic functions allowed the model to account for optima in species climatic requirements.

Each of the 46 models was formulated as follows:

$$\text{Abundance} \sim F1 + F2 + \dots + F9 + C1^2 + C1 + C2^2 + C2 + C3^2 + C3 + C4^2 + C4 + \text{PI} + \text{Tree} + \text{Shrub} + \text{Grass}$$

where Fs are the nine farmland habitat frequencies, Cs are the four climatic variables, PI the Production Intensity index and Tree, Shrub and Grass the density of the three field margin types. All variables were z-transformed to allow comparisons of their effect magnitude.

To test our predictions, we identified the major predictor for each species among PI and field margins density, i.e. the variable whose effect has the highest magnitude. We also identified the Preferred Field Margin type (PFM) of each species as the field margin type whose effect was the higher among the three types. Each species response to PI were then compared with their response to PFM. We compared PI and PFM effect on the whole community by performing a paired t-test between species responses to PI and to PFM. To satisfy normality assumption, species responses to PI and to PFM were square-root transformed.

Finally, we tested correlations between species degree of habitat specialization and species responses to PI and to PFM.

## Results

Major effect on species abundance was one of the field margin density for 31 of the 46 species, but this effect was negative for 27 of them (Table 1). Most of these negative responses concerned tree or shrub hedgerows (Table 1). Even so, 40 of the 46 species responded positively to at least one of the field margin type (see Appendix S1). Preferred Field Margin (PFM) type was grass for 24 species, shrubs for 15 species and trees for 7 species (see Appendix S1).

Besides, Production Intensity (PI) had a stronger effect on abundance than the species PFM density for 32 of the 46 species (Table 1). In addition, PI effect magnitude was on the whole significantly higher than PFM effect magnitude (paired t-test,  $t = 2.30$ ,  $df = 45$ ,  $p = 0.026$ ). PI effect was also significantly negatively correlated to species degree of habitat specialization, whereas PFM effect was not correlated to species degree of habitat specialization (Fig. 2).

## Discussion

In this study, we found that agricultural production intensity had a stronger effect on farmland bird species abundance than the species preferred field margin type, being either grassy margins or hedgerows depending on species preferred habitat (Green and Griffiths 1994; Whittingham and Evans 2004). Moreover, the effect of the agricultural production intensity index was negatively linked to the species degree of habitat specialization, being more negative for specialist than for generalist species. This suggests that production intensification is causing an homogenization of farmland birds community, favouring generalists at the expense of specialists (Devictor et al. 2008a; Filippi-Codaccioni et al. 2009). These results argue strongly in favour of the prevalence of agricultural intensification on farmland bird threats compared with landscape homogenization due to the destruction of field margins (Haberl et al. 2005).

Another finding of this study is the importance of negative effects of hedgerows on the abundance of a majority of farmland bird species. Whittingham & Evans (2004) reviewed evidence that hedgerows could both reduce foraging efficiency and predation risk for several bird species. They however stated that hedgerows were detrimental to only a small number of species and that an equivalent number of species benefit respectively from large and small hedgerows. In our study, species which were more abundant in non-farmland habitats than in farmland were not considered, as their abundance in farmland should be of poor relevance for conservation. This can explain why our proportions of species response differ from those of Whittingham & Evans (2004). This further suggests that (i) hedgerows mainly benefit to non-farmland species and (ii) the negative effect of hedgerows on farmland birds species is stronger than

previously thought, as it hits a majority of farmland bird species. It is also important to note that grassy field margins can also enhance predation risk and thus, they are not necessarily positive for farmland birds (Bro et al. 2004).

The limited benefit from field margins to farmland birds can also be explained by a reduced accessibility for foraging compared with within-field area, despite invertebrate resources are denser in field margins (Douglas et al. 2009). The positive effect of field margins is indeed well documented for invertebrates and plants (e.g. Roschewitz et al. 2005; Schmidt et al. 2005; Ekroos et al. 2008). Nevertheless, most of these effects have been shown on measures of local diversity or local species richness indicators which can show confusing trends and even provide misleading messages for conservation (Devictor and Robert 2009). High local diversity is indeed not necessarily linked to a conservation improvement but it can instead result from the spread of generalist species which is symptomatic of a biotic homogenization (Van Turnhout et al. 2007; Kerbiriou et al. 2009), and thus leads to a global decrease of diversity (Sax and Gaines 2003).

To conclude, our study showed that increasing the density of field margins in farmland habitats is unlikely to mitigate farmland birds' decline in an intensive farming context, since production intensity seems to prevail over the abundance of most farmland birds (Tscharntke et al. 2005; Merckx et al. 2009). And it is still unclear if field margins can benefit to farmland specialist species of other taxa or if field margins are increasing local species richness by only benefiting to generalist species. On that account, the Agri-Environment Schemes (AES) which promote landscape heterogeneity by increasing field margins density may be of poor efficiency, despite their relatively low cost (Rodriguez et al. 2006). Our study instead suggests that AES which promote extensive farming practices and which target within-field area will be more beneficial to farmland biodiversity (Whittingham 2007). In addition, we argue that the AES which promote field margins density have to carefully address potential negative effects on farmland birds, by, for example, not planting tree hedgerows where farmland birds community is dominated by sensitive open-habitat-specialists.

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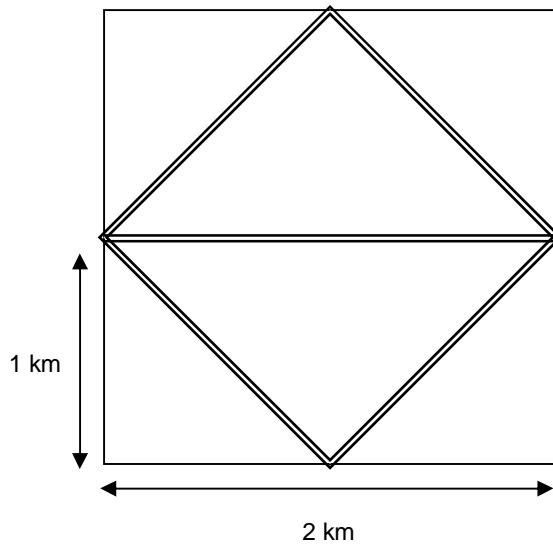
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Table 1. Number of farmland species for which production intensity or one of the three field edge density variables is the major factor impacting their abundance, i.e. the factor which has the higher magnitude. Positive and negative effects are separated in the second and the third column. The fourth column also counts species according to the major factor impacting their abundance, but without considering widespread negative responses to field margins density. It thus amounts to only compare the responses of each species to its Preferred Field Margin and to Production Intensity.

Number of species whose major effect is	Positive	Negative	Considering only PFM
<i>Production Intensity</i>	6	9	32
<i>Field margins density</i>			
Grass	3	2	8
Shrubs	0	8	5
Trees	1	17	1

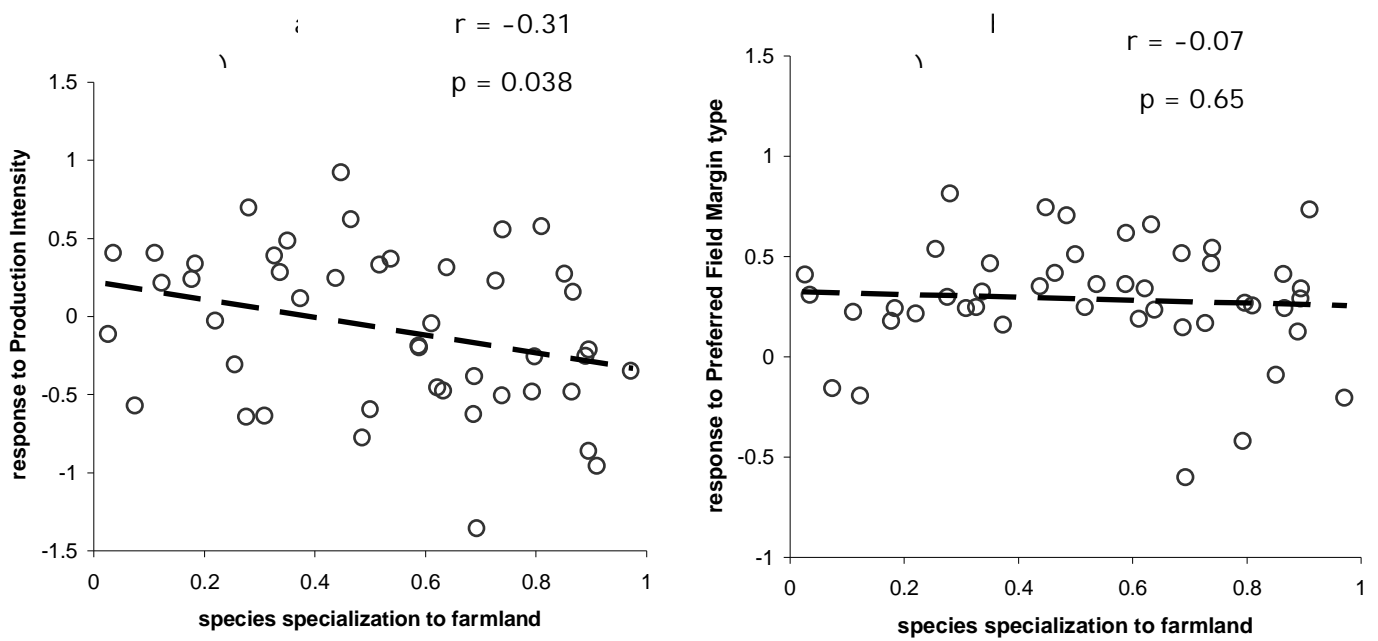


Figure 1.



Scheme of the transect (double line) used to sample intersections with field margins within each Breeding Bird Survey square (delimited by the external simple line)

Figure 2.



Correlation between species degree of specialization to farmland habitat and (a) species response to Production Intensity, (b) species response to Preferred Field Margin type. Pearson correlation coefficient and associated p-value are computed.

## Appendix

List of the 46 farmland bird species studied. Their estimated response to the four factor of interest is detailed, as well as their Preferred Field Margin type and their degree of specialization to farmland

Species	Response to Production Intensity	Response to Grass margins	Response to Shrub margins	Response to Tree margins	Preferred Field Margin type	specialization degree
<i>Acrocephalus palustris</i>	0.696	0.814	-0.478	-0.421	Grass	0.280
<i>Alauda arvensis</i>	-0.254	0.126	-0.343	-0.762	Grass	0.889
<i>Alectoris rufa</i>	-0.384	0.145	-0.251	-0.383	Grass	0.688
<i>Anthus campestris</i>	-1.358	-0.920	-0.600	-1.633	Shrub	0.692
<i>Anthus pratensis</i>	-0.476	0.659	-0.213	-1.244	Grass	0.632
<i>Anthus trivialis</i>	-0.644	-0.348	-0.277	0.299	Tree	0.276
<i>Burhinus oedicephalus</i>	-0.349	-0.204	-0.704	-0.683	Grass	0.971
<i>Buteo buteo</i>	0.331	0.231	-0.310	0.248	Tree	0.517
<i>Carduelis cannabina</i>	-0.188	0.361	-0.246	-0.581	Grass	0.587
<i>Carduelis carduelis</i>	0.216	-0.193	-0.348	-0.217	Grass	0.123
<i>Cettia cetti</i>	0.407	-0.299	0.223	0.211	Shrub	0.111
<i>Circus cyaneus</i>	0.273	-0.366	-0.090	-0.684	Shrub	0.851
<i>Cisticola juncidis</i>	-0.635	0.243	-0.349	-0.605	Grass	0.309
<i>Corvus corone</i>	0.388	-0.262	-0.416	0.246	Tree	0.326
<i>Corvus frugilegus</i>	-0.309	0.537	0.488	-0.867	Grass	0.255
<i>Coturnix coturnix</i>	-0.483	0.413	-0.451	-0.583	Grass	0.864
<i>Emberiza calandra</i>	-0.212	0.317	0.341	-0.794	Shrub	0.895
<i>Emberiza cirius</i>	-0.456	0.296	0.341	0.336	Shrub	0.621
<i>Emberiza citrinella</i>	0.227	0.135	0.168	-0.237	Shrub	0.727
<i>Emberiza hortulana</i>	-0.777	-0.500	0.705	-1.270	Shrub	0.485
<i>Falco tinnunculus</i>	0.315	0.233	-0.431	-0.231	Grass	0.638
<i>Galerida cristata</i>	-0.483	-0.420	-0.628	-1.411	Grass	0.793
<i>Hippolais polyglotta</i>	0.247	-0.362	0.350	-0.360	Shrub	0.437
<i>Jynx torquilla</i>	-0.571	-0.301	-0.156	-0.516	Shrub	0.074
<i>Lanius collurio</i>	0.157	0.243	0.206	-0.171	Grass	0.866
<i>Lanius senator</i>	-0.506	0.466	0.372	0.360	Grass	0.737
<i>Lullula arborea</i>	-0.624	0.228	0.220	0.516	Tree	0.686
<i>Luscinia megarhynchos</i>	0.115	-0.420	0.159	-0.246	Shrub	0.373
<i>Milvus migrans</i>	-0.596	0.510	-0.611	-0.268	Grass	0.500
<i>Motacilla alba</i>	-0.026	0.216	-0.446	0.141	Grass	0.220
<i>Motacilla flava</i>	0.579	0.257	-0.508	-1.069	Grass	0.809
<i>Oenanthe oenanthe</i>	-0.199	0.520	0.617	-0.784	Shrub	0.589
<i>Passer montanus</i>	0.622	0.417	-0.171	-0.433	Grass	0.464
<i>Perdix perdix</i>	0.559	0.544	-0.823	-0.493	Grass	0.739
<i>Phasianus colchicus</i>	0.284	0.326	-0.140	-0.330	Grass	0.336
<i>Picus viridis</i>	-0.114	0.184	-0.297	0.410	Tree	0.026
<i>Saxicola rubetra</i>	-0.956	0.733	-0.646	0.387	Grass	0.910

<i>Saxicola torquatus</i>	-0.255	0.268	0.177	-0.201	Grass	0.797
<i>Streptopelia turtur</i>	0.240	-0.186	0.178	-0.266	Shrub	0.177
<i>Sturnus vulgaris</i>	0.337	-0.125	-0.442	0.242	Tree	0.183
<i>Sylvia borin</i>	0.406	-0.083	0.309	-0.194	Shrub	0.035
<i>Sylvia communis</i>	-0.045	-0.352	0.189	-0.497	Shrub	0.611
<i>Sylvia curruca</i>	0.370	-0.158	0.362	-0.659	Shrub	0.537
<i>Turdus pilaris</i>	0.923	0.745	0.516	0.113	Grass	0.448
<i>Upupa epops</i>	0.486	-0.262	-0.196	0.466	Tree	0.351
<i>Vanellus vanellus</i>	-0.860	0.291	0.282	-0.237	Grass	0.894

## MANUSCRIT 3

# Forestry impacts bird and bat communities through different processes

Running title: Bird and bat responses to forestry

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## **Abstract**

The conservation value of sustainably exploited forests is now well established. But the forestry practices optimising biodiversity conservation in these habitats are still poorly defined. Here, we focused on forest bird and bat communities in Western France where forests undergo heterogeneous forestry practices. We studied habitat parameters being both strongly dependent from forester's management and known to influence bird and bat populations: stand age, stand evenness, conifer introduction and canopy openness. The abundance of 44 birds and 11 bats species was sampled on respectively 117 and 260 forest points. Species responses to each of the four forestry parameters were then estimated and correlated to species degrees of habitat specialization. Major forestry parameters predicting abundance and community composition differed for bats and birds. Responses were especially contrasting for conifers which were strongly negative for bat abundance and community composition, though they were able to conserve high numbers of forest bird specialists. Inversely, canopy openness had a strong negative impact on forest bird community by favouring generalist species with respect to specialists, though it seemed not to affect forest bats. In addition, bird species negatively affected by stand evenness were those facing long-term population declines at the national scale, while stand evenness has been increasing for several decades in France because of changes in forestry practices. This suggests that ongoing changes of forestry are causing the decline of many bird species. Regarding our results, we also predict (i) that forest bird species decline would be accelerated by a shortening of silvicultural rotations and by more intense thinning increasing openness and (ii) that forest bats would decline subsequently to the spread of conifers in temperate lowland forests. All these forestry changes are actually conceivable with the expected marked increase of both roundwoods and wood fuel production in the next decades.

## **Key-words**

Silviculture, conservation strategy, biotic homogenization, global change, cross-taxa congruence, uneven-aged management, plantations, Chiroptera.

## Introduction

Most forest ecosystems are under increasing anthropogenic pressures as global wood demand is expected to increase as fast as global food demand (Alexandratos and Mernies 2000; FAO 2009). Until recently, most forest conservation concerned deforestation, i.e. the conversion of native woodland to farmlands or urban settlements (Jha and Bawa 2006). From now on, the interest of both conservationists and wood industry is moving towards secondary forests and plantations, as such forests are spreading in all continents (Imbeau et al. 2001; Wright 2005). Almost all European forests have been exploited for centuries (Wesolowski 2005), yet they still retain a large terrestrial biodiversity (Cantarello and Newton 2008). While the conservation value of these exploited forests is well established (Barlow et al. 2007; Brockhoff et al. 2008), the forestry practices optimising biodiversity conservation in such habitats are still poorly defined (Freer-Smith and Carnus 2008). In this study, we aimed at identifying key forestry parameters that could impact biodiversity compartments. We focused on forest birds and bats communities in Western France where forests undergo very heterogeneous forestry practices. To infer on the relationship between biodiversity conservation and forestry practices, we studied habitat parameters being both strongly dependent from forester's management and known to influence bird and bat populations: stand age (Donald et al. 1998; Loeb and O'Keefe 2006), stand evenness (Chesson and Pantasticoaldas 1994), fast-growing conifer introduction (Dejong 1995; Lopez and Moro 1997) and canopy openness (Moning and Muller 2008). We tested whether these parameters influence bird and bat species abundance and community composition. Species responses to these parameters is predicted to depend on the species degree of habitat specialization as forestry pressure on communities would likely result in biotic homogenization (Devictor et al. 2008a). We aimed at comparing the relative effects of the four forestry parameters to identify the major drivers of bird and bat populations and communities, and to test their congruence. We finally investigated the correlation between recent bird population trends in France (Jiguet et al. 2007) and species response to forestry parameters, to identify more thoroughly potential causes of forest bird declines. We especially expected a correlation between recent species trends and species response to stand evenness as this parameter has been sharply increasing these last decades in France and other parts of western Europe (National Forest Inventory 2005; Van Calster et al. 2007).

## Material and Methods

### Sampling

The study was carried out from 2006 to 2008 in the Ille-et-Vilaine administrative department of France. This area is in an homogeneous oceanic climate (mean annual rainfall from 660 to 730 mm). It is dominated by farmlands with high hedgerow density and the forest cover is 12.3 %, of which 80% is under private ownership. Main native tree species are *Quercus petraea* (20 % of the total basal area), *Quercus robur* (13 %), *Fagus sylvatica* (12 %), *Castanea sativa* (7 %) and *Betula pubescens* (4 %). Main introduced conifers are *Pinus pinaster* (20 %), *Pinus sylvestris* (15 %) and *Abies alba* (4 %). Both *Pinus* species were introduced in XIX<sup>th</sup> century and *Abies alba* was probably introduced in XVIII<sup>th</sup> century. Within this area, 117 sampling points were randomly selected within forest areas (>100 m from forest edges) and surveyed once during the study period (43 were surveyed in 2006, 47 in 2007 and 27 in 2008, see Fig. 1). Birds were sampled by a single trained observer (YB) using a point count method (Bibby et al. 1992). Sample points were grouped (by four to six) according to their physical proximity. Each group was visited in the same morning, during the first four hours after sunrise. Each point group was visited twice in the year: once between 10<sup>th</sup> and 25<sup>th</sup> May and again between 26<sup>th</sup> May and 12<sup>th</sup> June. Point groups were sampled in a random sequence for the first visit, and this order was reversed for the second visit. Similarly, within-group order of points was reversed from the first visit to the second visit. We avoided unfavourable weather conditions for sampling birds (rain or strong wind - Beaufort > 4, i.e. wind speed > 28 km/h). On a point, a visit consisted of 25-minute count as five consecutive periods of 5-minute counts. During these counts, each detected bird was identified to species and located within one of four distance classes: 0-10 m, 10-25 m, 25-50 m, >50 m. The observer was trained for auditory distance measurement, and used a laser range finder to get the distance of reference points preliminarily to each visit. According to Alldredge et al. (2007c), we considered that individuals were correctly allocated to distance classes as the last class limit (50 m) lied within the range of reliable auditory distance measurement for trained observers. Attention was focalised on auditory detections, and purely visual detections are not considered in this analysis, since there were rare and likely to induce a detectability bias. Abundance per species was finally measured as the sum of all counts on each site.

The habitat surrounding each point was sampled with five circular quadrats of 10-m radius: one centred on the point, the four others 100 m from the point in the four cardinal points direction. In each quadrat, all trees were counted, identified to species and their



circumferences at human-breast height were measured. Non-commercial shrubs were not considered. Four forestry parameters were extracted from these data. First, the maximum circumference measured among the five quadrats of each site whatever the tree species was taken as a measure of stand age. Then, stand evenness was measured as the proportion of basal area occupied by dominant trees, i.e. trees whose circumference was superior to half of the maximum circumference in the quadrat. Despite its high simplification of the stand structure to only a dichotomy, this measure had the advantage to be much less correlated to stand age than usual indices of stand structural heterogeneity (Pommerening 2002). Thirdly, introduced conifer proportion was measured as the proportion of basal area occupied by coniferous species. Finally, hemispherical photography performed on the centre of each quadrats, allowed to measure canopy openness (Weiss 2000). Photos were taken with a Nikon Coolpix 4500 coupled to a fisheye adaptor. Canopy openness was measured as the proportion of pixels covered by sky on each photo.

During year 2008, we also sampled bat activity on the centre of each of the five quadrats in 52 of the 117 points: during six minutes on the central quadrat and during three minutes on each of the other four quadrats. Similarly to bird sample design, we grouped points to be visited the same night (between 0.5 h and 3.5 h after sunset) and, to avoid any bias, we visited each point twice: during May and between 15<sup>th</sup> August and 12<sup>th</sup> September. Order of point sampling was also reversed both between groups and within groups. Bat sampling followed two different methods between the two periods because of a change of bat sampling material. In May, bat sampling followed time expansion method (MacSwiney et al. 2008) and was performed with a Tranquility Transect bat detector (Courtpan Design Ltd). Abundance of each species was then measured as the number of echolocation sequences divided by the total recording time (Menzel et al. 2005). During August and September, bats were sampled with direct recordings performed with a Zoom H2 field recorder (Zoom Corporation) at 96 kS/s rate. Abundance of each species was then measured as the sum of the time length of all echolocation sequence divided by the total recording time.

We standardized both abundance measures by dividing it by the corresponding average total abundance per site. Abundance per species per sites was then calculated as the sum of the two standardized measure. All echolocation sequences were identified using Syrinx 2.6 (Burt 2006) and SCAN'R 1.4.2 (Binary Acoustic Technology 2007). Relative sound pressure level (SPL) of all calls were also computed on direct recordings, using SCAN'R and the SPL of the loudest call ( $SPL_{max}$ ) of all echolocation sequences of the second period were determined.

Data were selected from the 44 bird species and the 11 bat species which were detected on at least five sites (see Appendix S1). We finally aimed at measuring the degree of specialization to forest habitats for each birds and bats species. For that purpose, we used data from the French Breeding Bird Survey and from the French Common Bat Monitoring Program (Kerbiriou et al. 2006; Jiguet et al. 2007). Species specialization to forest was then calculated as the degree of preference for forest habitats:

$$(d_{\text{for}} - d_{\text{nfor}})/\max(d_{\text{for}}, d_{\text{nfor}})$$

with  $d_{\text{for}}$  the average density of the species on forested sites and  $d_{\text{nfor}}$  the average density of the species on non-forested sites (see Appendix S1). We acknowledge that negative values of this index could indicate a specialization to non-forest habitats, however, since only five bird and two bat species had negative values and that all of them had a specialization index superior to  $-0.5$ , we considered that this measure truly discriminated specialist species from generalists.

## Statistical analysis

We analysed the effect of forestry parameters on detectability by fitting two generalized mixed models, one for birds and one for bats. Models were fitted to account for “quasipoisson” distribution of errors, differing from Poisson distribution by allowing over and under-dispersion, with log as a link function (McCullagh and Nelder 1989).

The fixed formula was for both models:

Abundance  $\sim$  specialization +  $F_1$  +  $F_2$  +  $F_3$  +  $F_4$  + specialization:( $F_1$  +  $F_2$  +  $F_3$  +  $F_4$ )

where  $F_s$  are the four forestry parameters (stand age, stand evenness, conifers and openness).

For the models respectively performed for birds and bats, random effects were species and species and site (as we had five samplings per site for bats). Forestry parameters effects and interactions with species specialization were tested using t-tests. Openness was log-transformed to satisfy normality assumption. Given that the detection range of most bird songs exceeded 50 m, stand evenness, conifers proportion and openness were averaged for the five quadrats around each point for the bird analysis (Schieck 1997). On the contrary, the detection range of the bat signals studied here did not exceed 50 m, thus we used stand evenness, conifers proportion and openness measured on the corresponding quadrat for the bat analysis (Holderied and von Helversen 2003). All explanatory variables were z-transformed to allow comparisons of effect magnitude between forestry parameters and between birds and bats.

To identify more thoroughly potential effect of forestry on species trends, we investigated the correlation between recent bird population trends in France (Jiguet et al. 2007) and species responses to the four forestry parameters fitted by the model. To assess potential biases on this correlation, we also tested the correlations between these species responses and three life history traits already known to influence French bird trends (thermal maximum, overall habitat specialization and brood number, see Jiguet et al. 2007).

The residuals of the two models did not exhibit any spatial autocorrelation as the two semi-variograms produced both a flat pattern (see Appendix S2). Our data were then assumed to be spatially independent. We also assessed potential detectability biases due to variations in vegetation structure (Patriquin et al. 2003; Pacifici et al. 2008) using

variations in the ratio between distant detections (DD) and close detections (CD) as a surrogate (Efford and Dawson 2009). In doing so, we assume that for a given spatial distribution of individuals, this ratio will be constant regardless the forestry parameters - for an observer with homogeneous detectability. Instead, if abundance responses to forestry parameters are biased by heterogeneous detectability, DD to CD ratio should vary with some of the forestry parameters. For that purpose, we defined a DD (i) for birds, by individuals detected beyond 50 m, (ii) for bat passes by sequence for which  $SPL_{max} < 41.2$  dB (the median value of all passes in the dataset). We used  $SPL_{max}$  as a proxy for distance between recorder and individual. We are aware of the fact that  $SPL_{max}$  is probably biased by vegetation cover, but if vegetation cover decreases sound wave intensity then this effect should increase with distance and the ratio between DD and CD decrease nonetheless. We further analysed the effect of forestry parameters on detectability by fitting two generalized mixed models accounting for the binomial distribution of errors, one for birds and one for bats. These models were fitted on the whole dataset of contacts: 40415 bird auditory contacts and 876 bat echolocation sequences. The fixed formula was for both models:

$$DD \text{ probability} \sim F_1 + F_2 + F_3 + F_4$$

For the models respectively performed for birds and bats, random effects were species, site and period and species and site. We accounted for period in the bird model as deciduous trees were leaf-off in the first two periods, thus reducing potential vegetation effect on detectability (Pacifici et al. 2008). Forestry parameters effects on detectability were tested by Z-tests. All fits and tests were performed with the lmer function of the lme4 package of R 2.5.1 (R Development Core Team 2005; Bates 2007).

## Results

Overall abundance of birds and bats responded significantly to respectively one and two of the four forestry parameters. Stand age had a significant positive effect on overall abundance of both birds and bats (Table 1, Fig. 2). This effect had a similar magnitude for the two groups. For birds, none of the three other forestry parameter had a significant effect on overall abundance, but conifers had a strong negative effect on overall bat abundance (Fig. 3). This effect had a more than twice higher magnitude than stand age effect. Stand evenness had also a marginally significant positive effect on overall bat abundance.

Interactions between the four forestry parameters and degree of habitat specialization of bird species were all significant (Table 1, Fig. 2). Stand age and conifers favoured forest specialists with respect to generalists. Openness and stand evenness favoured generalists with respect to specialists. The openness effect had the largest magnitude, and stand evenness effect the smallest.

Interaction between conifers and bats degree of specialization was significant (Table 1, Fig. 3). Conifers favoured generalists with respect to specialists. Other interaction effects were not significant on bats.

Recent trends of forest specialist birds were significantly and positively correlated with their response to stand evenness ( $r = 0.40$ ,  $p = 0.038$ , Fig. 4). The response of forest habitat specialist birds to stand evenness was not correlated to other major traits explaining recent trends (thermal maximum :  $r = 0.12$ , habitat specialization index:  $r = 0.00$ , brood number:  $r = 0.00$ ). Recent trends of forest specialist birds were not significantly correlated with their response to stand age, conifers and canopy openness.

In birds, distant detection probability increased significantly with openness ( $p = 0.005$ ). Model fit estimated that distant detection probability varied between 0.74 for the most closed sites to 0.84 for the most open sites. Assuming that detectability of close individuals were constant across sites, global detectability of individuals was thus estimated to increase by 62 % across the whole gradient of openness. Distant detection probability in birds did not vary significantly with any of the three other forestry parameters ( $p > 0.2$ ). In bats, distant detection probability did not vary significantly with any of the four forestry parameters ( $p > 0.15$ ).

## Discussion

Major forestry parameters predicting overall abundance and community composition differed for bats and birds. Responses were especially contrasting for conifers which had a strong negative effect for bats, decreasing both overall abundance and community specialisation (i.e. the relative abundance of habitat specialist species within the whole bat community). The unsuitability of introduced conifers for forest bats was previously reported for a few species (Dejong 1995; Goiti et al. 2003), and appears here as the most important forestry parameter impacting bat communities. Inversely, bird overall abundance was not significantly impacted by conifer introduction which even favoured significantly the abundance of forest specialists with respect to generalists. This can be explained by the proximity of the native range of the most widely introduced species in the study area (*Pinus sylvestris*, *Pinus pinaster* and *Abies alba*) which probably allowed colonization of lowland temperate forest by a specific set of conifer-adapted birds (Fuller et al. 2006; Archaux and Bakkaus 2007). Inversely, conifer-adapted populations of less vagile taxa such as bats would be unable to colonize lowland temperate forests (Paritsis and Aizen 2008). Moreover, it seems that introductions of more exotic tree species could also have a detrimental effect on birds (Bibby et al. 1989; Drapeau et al. 2000).

Similarly, our study revealed different responses of birds and bats to stand evenness. Evenness had a negative impact on forest bird community by favouring generalist species with respect to specialists, though it tended to increase overall bat abundance. A possible positive effect of even-aged management on bats could be explained by lower understorey density facilitating hunting activities (Zahn et al. 2005). Inversely, negative effect of even-age management could be explained by the importance of understorey for many forest birds (Donald et al. 1998; Camprodon and Brotons 2006).

Likewise, openness had a strong negative impact on forest bird community by favouring generalist species with respect to specialists, though it seemed not to affect forest bats. Actually, openness is the major parameter influencing forest bird communities (Sallabanks et al. 2006), though an important part of forest bats prefers low clutter forest to hunt (Menzel et al. 2005; Lloyd et al. 2006). It has however been suggested that open forest could have high conservation value as refuge for formerly farmland bird specialists (Paquet et al. 2006). Paquet *et al.* (2006) studied forest birds in a context of extremely intensified farmlands which could explain that local conservation of some farmland birds could be better achieved in forest than in farmlands, yet considering a larger scale, these species showed a very low specialization to forest (see Appendix S1), revealing that farmland was still the main habitat of these species. This suggests that open temperate forest should have limited conservation value for birds.

Nonetheless, birds and bats overall abundance showed similar positive responses to stand age. Interestingly, the positive effect of stand age is very well-documented, touching a wide variety of taxa, e.g. spiders (Buddle and Shorthouse 2008), carabids (Paquin 2008), lichens (Nascimbene et al. 2009), etc. This global effect is probably related to increasing global biomass in the ecosystem, but may also be related to increasing cavity density in old trees (Michel and Winter 2009). This could explain that (i) stand age increased overall bats abundance regardless of species specialization as even some generalist species depended on tree cavities and (ii) that stand age favoured specialist bird species with respect to generalists as cavity-nesting concern mostly forest specialists.

In addition, results showed that bird response of forest specialists to stand evenness were correlated to species recent long-term trends, while stand evenness has been increasing for several decades in Europe and especially in France because of changes in forestry practices (National Forest Inventory 2005; Van Calster et al. 2007). The strength of the correlation was comparable to major life-history traits explaining bird species responses to global change (Jiguet et al. 2007). This strongly suggests that ongoing changes in forestry practices are causing the decline of a part of forest bird specialists, even if stand evenness was the least important of the four forestry parameters to explain abundance variations and community composition. As a result, curbing the decline of European forest birds needs the maintenance of a high proportion of uneven-aged lowland forest (Berges 2003). Regarding our results, we also predict (i) that forest bird declines would be accelerated by a shortening of silvicultural rotations and by more intense thinning increasing openness and (ii) that forest bats would decline subsequently to the spread of conifers in temperate lowland forests. All these forestry

changes are actually conceivable in the current context of an expected marked increase in both roundwoods and wood fuel production in the next decades (FAO 2009).

We finally argue that the conclusions drawn here can be valuable for important conservation issues in other regions where temperate forests are rapidly becoming heavily exploited (e.g. Zhang et al. 2000; Lantschner et al. 2008).

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Table 1. Results of log-linear models explaining species abundance (for birds and bats) with four parameters related to forestry practices. Slope responses to forestry parameters are given, while the level of significance of the performed t-test is given by the star number: \*\*\* for  $p < 0.001$ , \*\* for  $p < 0.01$ , \* for  $p < 0.05$  and · for  $p < 0.1$

		Birds		Bats	
<i>Overall effect</i>					
	STAND AGE	0.243	***	0.210	*
	STAND EVENNESS	-0.060		0.212	·
	CONIFERS	-0.012		-0.529	***
	OPENNESS	-0.030		0.018	
<i>Interaction with specialization degree</i>					
	STAND AGE	0.311	***	0.052	
	STAND EVENNESS	-0.160	*	0.121	·
	CONIFERS	0.262	**	-0.395	***
	OPENNESS	-0.560	***	0.077	

Figure 1. Map of the 117 sampled sites. Black circles show the sites where both birds and bats were sampled whereas white circles show the sites where only birds were sampled.

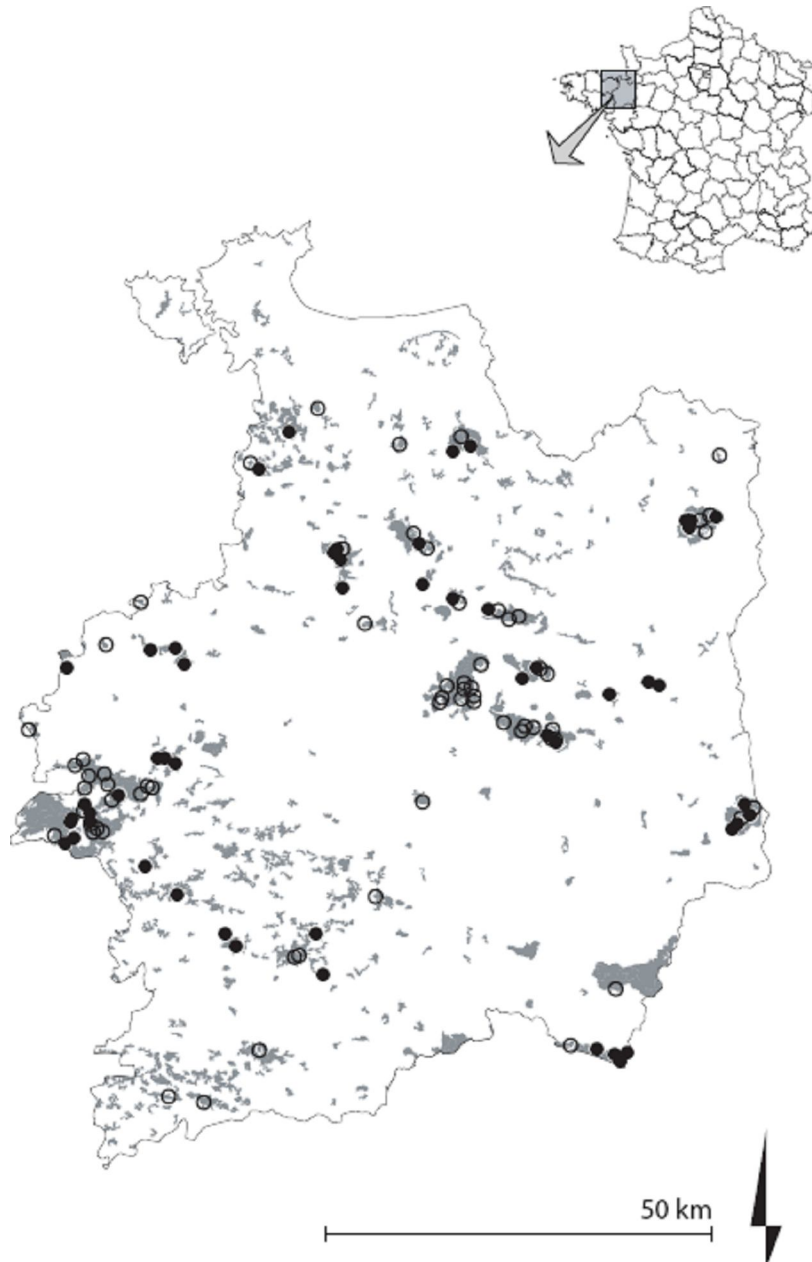


Figure 1. Bird species response to stand age according to their specialization degree to forest. Each dot represents a bird species, and the dotted line shows the correlation slope.

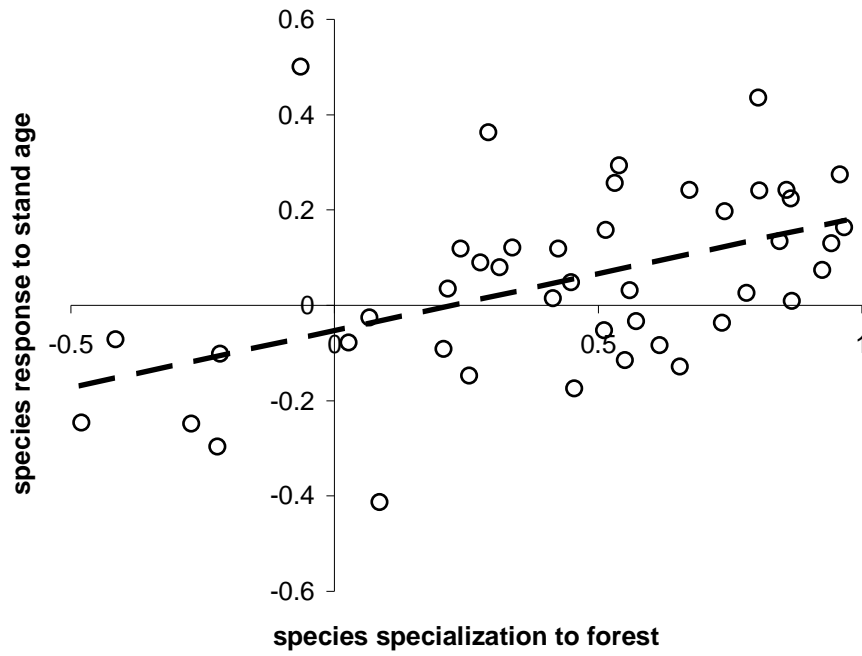


Figure 2. Bat species response to conifers according to their specialization degree to forest. Each dot represents a bat species, and the dotted line shows the correlation slope.

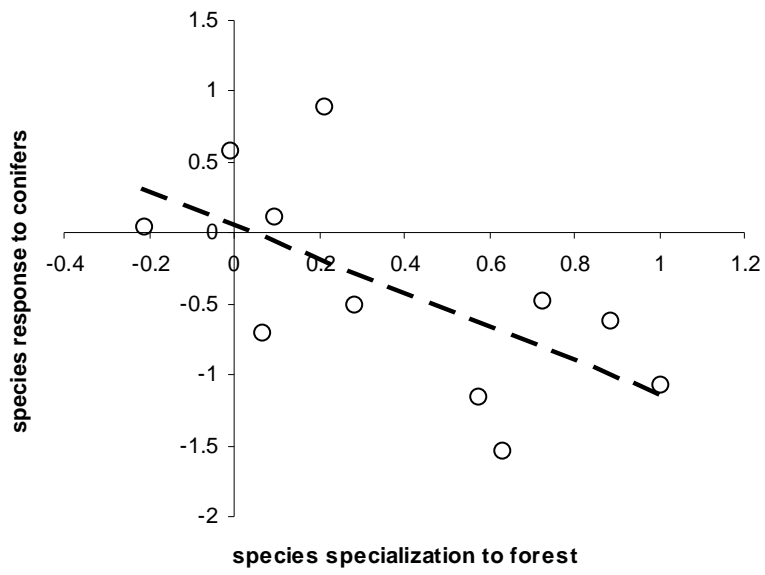
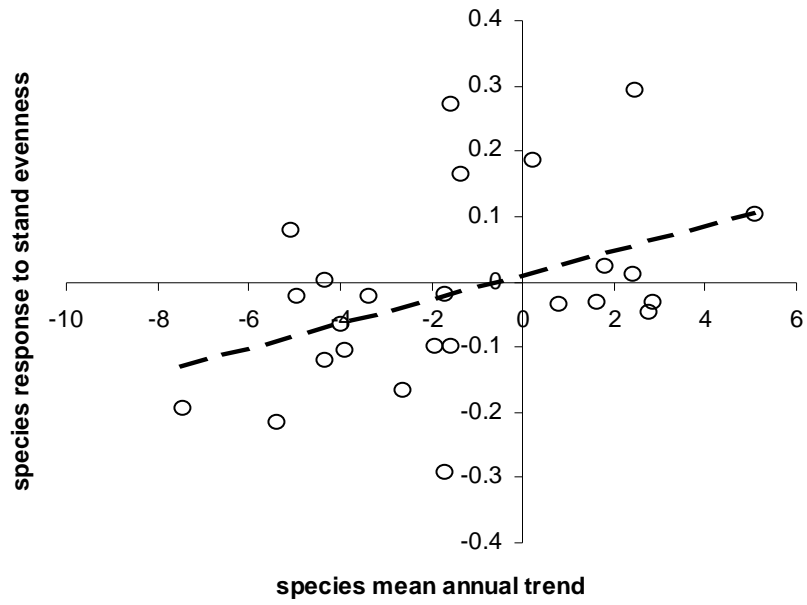


Figure 3. Forest specialist bird response to conifers according to their French mean annual trend. Each dot represents a specialist bird species, and the dotted line shows the correlation slope.



Appendix 1. List of the 46 bird and 11 bat species studied in this analysis. The last column shows their degree of specialization to forest.

	Species name	degree of specialization
<i>Birds</i>		
	Accipiter nisus	0.540
	Aegithalos caudatus	0.511
	Anthus trivialis	0.560
	Buteo buteo	0.256
	Carduelis cannabina	-0.480
	Certhia brachydactyla	0.673
	Coccothraustes coccothraustes	0.868
	Columba oenas	0.292
	Columba palumbus	0.067
	Corvus corone	-0.217
	Cuculus canorus	0.449
	Dendrocopos major	0.740
	Dendrocopos medius	0.959
	Dendrocopos minor	0.514
	Dryocopus martius	0.942
	Emberiza citrinella	-0.222
	Erithacus rubecula	0.617
	Fringilla coelebs	0.277
	Garrulus glandarius	0.655
	Hippolais polyglotta	0.086
	Loxia curvirostra	0.857
	Lullula arborea	0.215
	Muscicapa striata	0.539
	Oriolus oriolus	0.531
	Parus caeruleus	0.313
	Parus cristatus	0.925
	Parus major	0.239
	Parus palustris	0.781
	Phoenicurus phoenicurus	-0.064
	Phylloscopus collybita	0.572
	Phylloscopus sibilatrix	0.966
	Picus canus	0.804
	Picus viridis	0.338
	Prunella modularis	-0.271
	Pyrrhula pyrrhula	0.735
	Regulus ignicapillus	0.845
	Regulus regulus	0.865
	Sitta europaea	0.805
	Streptopelia turtur	0.207
	Sylvia atricapilla	0.425
	Sylvia borin	0.455
	Troglodytes troglodytes	0.414
	Turdus merula	0.027
	Turdus philomelos	0.551
	Turdus viscivorus	0.585



<i>Bats</i>		
	Barbastella barbastellus	0.574
	Myotis bechsteini	1.000
	Myotis daubentoni	0.094
	Myotis mystacinus	0.285
	Myotis nattereri	0.886
	Nyctalus leisleri	0.632
	Nyctalus noctula	0.068
	Pipistrellus kuhli	-0.008
	Pipistrellus pipistrellus	-0.214
	Plecotus auritus	0.726
	Plecotus austriacus	0.214

Appendix 2. Responses of forest specialist birds to the four forestry parameters, together with their French mean annual trend estimated by the French Breeding Bird Survey. The last two columns show the species thermal maximum and brood number, two traits known to influence recent trends of French birds.

Species name	stand age	conifers	stand evenness	openness	mean annual trend	thermal maximum	brood number
<i>Accipiter nisus</i>	0.140	0.077	-0.194	-0.359	-7.44	20.3	1
<i>Aegithalos caudatus</i>	-0.035	-0.202	-0.021	0.252	-1.71	20.3	1
<i>Anthus trivialis</i>	0.020	0.458	0.164	0.859	-1.37	18.6	2
<i>Certhia brachydactyla</i>	0.237	-0.254	-0.034	-0.209	1.63	20.9	2
<i>Coccothraustes coccothraustes</i>	0.056	-0.330	0.102	-0.300	5.09	20.3	1
<i>Dendrocopos major</i>	0.189	-0.087	0.024	-0.067	1.79	19.8	1
<i>Dendrocopos medius</i>	0.280	-0.923	0.293	-0.243	2.47	18.9	1
<i>Dendrocopos minor</i>	0.136	-0.291	0.003	-0.073	-4.34	19.0	1
<i>Dryocopus martius</i>	0.095	0.125	-0.049	0.217	2.74	18.2	1
<i>Erithacus rubecula</i>	-0.081	0.004	-0.032	-0.182	2.83	20.2	2
<i>Garrulus glandarius</i>	-0.103	0.000	-0.034	-0.121	0.78	20.5	1
<i>Loxia curvirostra</i>	0.131	0.866	-0.067	0.120	-4.00	18.8	1
<i>Muscicapa striata</i>	0.189	-0.078	-0.120	0.106	-4.34	20.7	1.2
<i>Oriolus oriolus</i>	0.262	-0.350	0.187	-0.158	0.21	20.6	1
<i>Parus cristatus</i>	0.069	0.576	-0.166	-0.193	-2.65	20.2	2
<i>Parus palustris</i>	0.030	-0.060	-0.105	-0.287	-3.90	18.6	1
<i>Phylloscopus collybita</i>	-0.035	0.131	-0.101	0.211	-1.93	19.4	2
<i>Phylloscopus sibilatrix</i>	0.142	0.009	-0.215	-0.158	-5.38	18.2	1
<i>Picus canus</i>	0.224	-1.015	-0.024	0.914	-4.97	18.4	1
<i>Pyrrhula pyrrhula</i>	0.011	0.022	0.079	0.260	-5.10	17.8	2
<i>Regulus ignicapillus</i>	0.166	-0.070	0.272	-0.484	-1.57	20.1	2
<i>Regulus regulus</i>	0.192	0.675	-0.292	-0.184	-1.71	17.9	2
<i>Sitta europaea</i>	0.237	-0.156	-0.023	-0.185	-3.38	20.0	1
<i>Turdus philomelos</i>	-0.106	-0.098	0.011	0.061	2.40	18.8	2.5
<i>Turdus viscivorus</i>	-0.045	0.054	-0.098	-0.216	-1.57	20.2	2

## MANUSCRIT 4

# Hedgerows influence woodland birds community dynamics but do not favour their conservation

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## Introduction

Habitat loss threaten the persistence of many species and are well-known as the most important member of the “Evil Quartet” (Diamond 1989; Fischer and Lindenmayer 2007). The major effects of habitat loss on population dynamics are to increase the temporal instability and spatial isolation of individuals in the remaining patches (Fahrig 2003). To mitigate these effects, conservationists commonly advocate for interventions that enhance movements of individuals between remnant patches of habitats (Hanski 1994; Bennett 1999). Although there is now strong evidence that habitat corridors can enhance individuals movements of a target species (Tewksbury et al. 2002; Gillies and Clair 2008), their ability to truly enhance persistence of populations remains questioned (Dunning et al. 1992; Simberloff et al. 1992). Evidence of positive population effects of corridors remains anecdotal (Davies and Pullin 2007) and a previous study on community dynamics showed that connectivity can even increase species extinction rates, thus counteracting the supposed mitigation effect (Werner et al. 2007). In this context, conservation benefits from promoting corridors such as hedgerow planting need to be investigated. Here, we asked whether and how hedgerows, commonly considered as woodland corridors, influence woodland bird community dynamics. However community dynamics is silent on which species are positively or negatively affected by corridors. Therefore, we Additionally, tested hedgerows effects on community composition. In particular, one expect specialist species to be more negatively affected by habitat loss and fragmentation than generalists (Boulinier et al. 1998; Devictor et al. 2008b). Therefore, we tested whether hedgerows have a positive effect on woodland birds species richness and particularly on specialist species (Julliard et al. 2006). These questions were investigated using data from the French Breeding Bird Survey and French Forest National Inventory datasets on broad gradients of forest landscape fragmentation and of hedgerow density. Hedgerow effect on community dynamics and composition was controlled for landscape context (forest amount, fragmentation *per se* and isolation), and, as corridors efficiency depend on the availability of source and receiver patches (Falcu and Estades 2007), hedgerow effect was expected to interact with forest amount and isolation.

## Methods

## Bird data

Data on breeding birds was obtained by a national Breeding Bird Survey (BBS) scheme launched in France in spring 2001 (Jiguet et al. 2007). In this scheme, volunteer ornithologists counted all visible and singing individual birds at permanent points. Surveyed sites are 2 x2 km squares randomly selected for each observer within a ten km radius around a locality specified by the volunteer. Observers carried out ten point counts of five minutes each per square, twice per spring, i. e. once before and once after the 8<sup>th</sup> May, with four to six weeks between sessions, with points separated by at least 300m. To be validated, counts must be repeated yearly by the same observer at the same points, on about the same date, and at the same time of day. We considered the 5691 points which were in forest habitats. Among these points, we selected the 3983 points of the 698 squares which were surveyed at least two consecutive years and contained at least two points in forest habitats. Non-woodland birds contacts were discarded by considering only the 78 species which were more abundant in forest than in non-forest habitats according to the BBS database (see Supplementary Materials S1).

The set of woodland birds was considered as a community. We then calculated woodland bird community local species richness, local extinction and colonization rates using the method proposed by Nichols *et al.* (1998) and the software COMDYN (Hines et al. 1999) which allows imperfect detections and account for heterogeneity in detectability between species. Community dynamics parameters were calculated using annual replicates of the counts.

To investigate woodland birds community composition, we also calculated a Community Specialization Index (CSI) as in Julliard *et al.* (2006). The CSI of a given community is the average of each Species Specialization Index (SSI) of species recorded in the community weighted by species abundance. The SSI of each species was considered only with respect to forest and calculated as follows:

$SSI = (d_{for} - d_{nf})/d_{for}$ , where  $d_{for}$  is the species density averaged on forest points from the BBS database and  $d_{nf}$  the species density averaged on non-forest points. This index is thus varying from 0 for most generalist species to 1 for most specialist species. CSI was then calculated as the average SSI of all woodland bird individuals contacted on each square. We were not able to account for imperfect detections of individuals in this calculation. However, we see neither

methodological reasons nor ecological meaning for the interaction between specialization, landscape factors and detectability which could bias our results (Devictor et al. 2008b).

## Landscape data

Forest landscapes were described with four factors: forest area, fragmentation *per se*, isolation and hedgerow density. To measure forest area and fragmentation, each BBS squares were divided in 256 squares of 125 m side which formed the unit cells describing the landscape within BBS squares. Aerial photo interpretation allowed identifying each of these units as forest or non-forest. We deduced from these data the forest area within each BBS squares, as well as a measure of fragmentation independent of forest area, the Normalized Landscape Shape Index (nLSI, see Leitao et al. 2006). Isolation was measured as the ratio between forest area within the BBS square and the surrounding forest area contained in a five km radius buffer around the BBS square centre. Therefore, this index was also independent of forest area. Forest area in the five km buffer was extracted from Forest National Inventory GIS data. Finally, hedgerow density was calculated thanks to Forest National Inventory data collected between 2004 and 2006 (Bélouard et al. 2005). These data contained counts of intersections of hedgerows along 1-km transect on aerial photography. Hedgerows were defined as an alignment of more than 25 m length and less than 20 m width with at least one tree every 10 m. Centre of these transects were arranged in a systematic sampling design, with one transect every 1.4 km, but only 30% of these transects were sampled at the time of this analysis. Direction of transects were randomised to avoid any sampling bias. To measure hedgerow density surrounding each BBS squares, we divided the sum of hedgerows counted on all transects whose centre were less than five km from BBS square centre ( $n \approx 24$ ) by the length of non-forest habitats covered by these transects.

These four landscape indices were weakly correlated to each other (maximum :  $r = -0.38$  for forest area and hedgerow density), to forest habitat composition (12 variables, see Appendix 1 for details; maximum :  $r = -0.31$  for forest area and proportion of mix of broad-leaved timbers and coppice) and to proportion of artificial habitats in non-forest area (maximum :  $r = 0.17$  for hedgerow density). Habitat composition variables were extracted from Forest National Inventory GIS data and aerial photo interpretation.

## **Statistical analysis**

To test the hypothesis that landscape structure and composition influence community dynamics and composition, the analysis was performed using one mixed model for each community index (richness, turnover and CSI). The modelling accounted for the possibly confounding effects of biogeographical gradients within the study area. Thus, the fixed formula contained (i) four basic climatic variables: maximum temperature of the hottest month, minimum temperature of the coldest month, precipitations of the wettest and the driest months (BIOCLIM variables 5, 6, 13 and 14, downloaded at [www.worldclim.org](http://www.worldclim.org), see Hijmans et al. 2006), (ii) the four landscape indices and (iii) the interactions between forest area and hedgerow density and between isolation and hedgerow density:

Index ~ (climate variables) + forest area + forest fragmentation + forest isolation + hedgerow density + (forest area:hedgerow density) + (forest isolation:hedgerow density)

BBS square was incorporated as a random effect. Each of the community indices and landscape variables were z-transformed to allow comparisons of effect magnitudes. Landscape effects and interactions were all tested by a t-test on slope response. Fits and tests were performed with the lmer function of the lme4 package of R 2.5.1 (R Development Core Team 2005; Bates 2007).

## Results

We found a strong positive effect of forest area on both species richness and CSI (Table 1). These two community indices did not respond significantly to the other landscape variables (Table 1). There was also a negative effect of forest area on extinction and colonization rates, but forest effect had a lower magnitude on these rates than on species richness and CSI (Table 1). Moreover, hedgerow density had a significantly positive effect on extinction and colonization rates. Hedgerow density and forest area interacted negatively on these rates (Table 1). In other words, hedgerow density effect was lower for highly forested sites than little forested sites, but hedgerow density effect on dynamic rates remained positive even for maximal forest area (0.092 on colonization rate and 0.065 for extinction rate).

## Discussion

Results showed that hedgerows have no strong effect on richness and composition of woodland bird communities though they strongly enhance turnover rates in these communities. Moreover, our results confirmed that (i) forest area influences woodland species richness positively and favours habitat specialist species compared to habitat generalists (Boulinier et al. 1998; Bennett et al. 2004) and (ii) fragmentation *per se* has little effect on woodland bird communities (Fahrig 2003). We also found a negligible effect of isolation on all community indices, suggesting that woodland birds can cope with the forest mosaic in our study region (Krauss et al. 2003). Moreover, our study region is characterized by a much older deforestation than in the other continents (Williams 2008), thus the resulting extinction debt has probably been paid (Tilman et al. 1994) and could not explain this lack of isolation effect.

More importantly, this study showed that forest area and hedgerows have opposing effects on turnover rates. Indeed, as expected, forest area decreased turnover rates, indicating that woodland bird community dynamics are stabilized in more forested landscapes (Boulinier et al. 1998). Inversely, hedgerows significantly increase community dynamics parameters so destabilized community composition, particularly when forest area was low. This finding invalidates the hypothesis that increasing connectivity enhances population persistence (Davies and Pullin 2007; Gillies and Clair 2008). It also suggests that hedgerows enhance competition among woodland species via increasing movements of individuals between forest patches. However, it remains unclear whether hedgerows could have a negative effect on forest communities since this strong speeding-up of turnover rates did not express any variations in community richness or composition. More fundamentally, this is questioning whether these dynamic rates could be considered as indicators of communities health (Boulinier et al. 1998; Doherty et al. 2003; Devictor and Jiguet 2007).

It has previously been suggested that hedgerows favour woodland specialists birds (Bennett et al. 2004). Nonetheless, Bennett et al. (2004) focused on a much smaller scale than the present study. Thus it seems that hedgerows could enhance species richness of woodland birds on small forest patches but not at the landscape scale. Interestingly, Bennett et al.'s (2004) study did not reveal an increase in turnover rates with hedgerow density as in our study. This may be because hedgerow density was measured on a smaller scale in their study than in ours.

To conclude, our study showed that there is no positive effect of hedgerows on woodland birds. Thus, forest connectivity through hedgerows may be of poor relevance for conservation of woodland bird communities. Hedgerows may still be supposed to act as efficient corridors for other taxa like invertebrates (Bowne and Bowers 2004), but evidence of population level effect is still lacking (Davies and Pullin 2007). Consequently, hedgerows management and incentive schemes should be more driven by conservation needs either of farmland taxa (Gillings and Fuller 1998; Merckx et al. 2009) or of woodland taxa other than birds (Bowne and Bowers 2004).



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Table 1. Slope responses of community indices (in columns) to landscape parameters (in lines). Significant responses are bold typed and level of significance is given by number of stars : \* for p < 0.05, \*\* for p < 0.01, \*\*\* for p < 0.001

	Species richness	Community Specialization Index	Extinction rate	Colonization rate
AREA	<b>0.390</b> ***	<b>0.453</b> ***	<b>-0.117</b> **	<b>-0.091</b> *
nLSI	-0.054	-0.007	-0.059	-0.053
PROXIMITY	-0.015	-0.056	0.029	0.024
HEDGEROWS	-0.028	0.033	<b>0.113</b> *	<b>0.154</b> **
AREA*HEDGEROWS	0.088	0.001	<b>-0.125</b> *	<b>-0.162</b> **
PROXIMITY*HEDGEROWS	0.014	0.016	-0.021	-0.014

Appendix 1. List of the 12 variables of forest composition whose correlation with landscape variables were controlled.

Proportions of forest made of :

- 1) Timber forest dominated (>75% of basal area) by oaks (*Quercus spp.*)
- 2) Timber forest dominated (>75% of basal area) by beeches (*Fagus sylvaticus*)
- 3) Other timber forest dominated (>75% of basal area) by broad-leaved trees
- 4) Timber forest dominated (>75% of basal area) by pines (*Pinus spp.*)
- 5) Other timber forest dominated (>75% of basal area) by coniferous trees
- 6) Timber mixed forest (>25% of broad-leaved and >25% of coniferous trees)
- 7) Mix of broad-leaved timbers and coppice
- 8) Mix of coniferous timbers and coppice
- 9) Coppice
- 10) Mediterranean scrub forest dominated by broad-leaved species
- 11) Mediterranean scrub forest dominated by conifers
- 12) Poplar plantation

## MANUSCRIT 5

# Comparing the performance of wildlife-friendly farming and farmland reserves scenarios for farmland birds

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## Introduction

Humanity's increasing demand for food and fuel puts pressure on ecosystems and makes conservation more and more difficult (Millennium Ecosystem Assessment 2005). To balance food production and biodiversity conservation, it has been proposed to increase farm yields in order to reduce the pressure to convert land for agriculture (Balmford et al. 2005). This "land sparing" strategy may be effective to conserve species linked to pristine habitats such as forests, but it is obviously the wrong choice for the many species which have evolved in and adapted to traditional farmland landscapes such as farmland birds in Europe (Stoate et al. 2001). It is thus also important to identify the most effective strategies to conciliate food production and conservation of the characteristic farmland biodiversity. Green et al. (2005) already provided a framework comparing competing strategies aimed to conciliate food production and biodiversity conservation. The present study proposes transposing their framework to the specific conservation of farmland birds. We thus modified the "land sparing" strategy from sparing land by not farming to sparing land by very low intensity farming, supposedly traditional and optimal for the adapted biodiversity. Green et al.'s (2005) framework allows to determine how to mitigate agricultural intensification, either by moderate exploitation practices over the whole available farmland or by allowing most intensive practices to be applied on one part of available farmland in order to implement low intensity practices on the remaining part. Here we investigated two independent factors of agricultural intensification influencing farmland birds: land consolidation (Gillings and Fuller 1998) and within-field practice intensification (Bas et al. in press).

We thus defined a wildlife-friendly farming strategy, where all farmland would be exploited with moderate-intensity practices. This wildlife-friendly farming strategy was compared to two "land sparing" strategies: one on the land consolidation issue, namely "field margin sparing" and one on the within-field practice intensification issue, namely "extensive farmland sparing". Field margin sparing strategy involved a mix of field margin rich farmlands and of highly consolidated farmlands. Extensive farmland sparing strategy involved a mix of farmland with most intensive practices and of farmland with low intensity practices.

The relative performance of these strategies was tested on bird species with high degree of habitat specialization to farmland since these species are much more likely to be the conservation targets of farmland conservation (Gregory et al. 2005), as being reported as recurrently declining across Europe (Jiguet et al. 2009). The abundance of each species was predicted under competing scenarios representing each conservation strategy. We then tested the difference in predicted abundance between the wildlife-friendly scenario and the land sparing scenarios. If possible, general patterns across species were eventually identified.

## Methods

### *Bird data*

Data on breeding birds was obtained by a national Breeding Bird Survey (BBS) scheme launched in France in spring 2001 (Jiguet et al. 2007). In this scheme, volunteer ornithologists counted all visible and singing individual birds at permanent points. Surveyed sites are two-by-two km squares randomly selected for each observer within a 10 km radius around a locality specified by the volunteer. Observers carried out 10 point counts of five min each per square, twice per spring, i.e. once before and once after the 8th May, with four to six weeks between sessions, with points separated by at least 300m. Counts were repeated yearly by the same observer at the same points, on about the same date, and at the same time of day. Within BBS scheme, 1033 of the sites surveyed between 2001 and 2006 contained 7307 points which were localized on farmlands. We then selected data from these 7307 points for the analysis.

For each species and each point, the yearly count with the maximum number of individuals detected among the two sessions was retained. Only individuals detected within a 100m radius around the observer were considered so that the birds were actually seen in their habitat. Yearly counts were averaged for squares that were monitored over several years between 2001 and 2006.

Observers were also asked to classify land use/habitat within 100 m of each point into nine types, i.e. maize, other cereals, rape, root crop, sunflower, other temporary crop, permanent crop, wet meadow and pasture. The frequencies of the nine farmland habitat types per point were then calculated by averaging yearly frequencies. Non-farmland habitat frequency was not used in the statistical modelling because it was a simple linear combination of the nine frequencies of farmland habitat types ( $1 - \text{sum of them}$ ). Thus, species response to non-farmland habitats was accounted for by the mean of the nine farmland frequencies. The species which were specialized to farmland habitat were considered, i.e. the 25 species which were detected on at least 50 different points and which were twice more abundant in farmland than in other habitats according to the French Breeding Bird Survey (Jiguet et al. 2007).

### *Agricultural data*



An estimate for each BBS site of the local agricultural production intensity (PI) was developed using yields for the different crops and livestock density for pastures. These metrics were standardized thanks to European reference values. Thus, PI measured the local agricultural production intensity as the standardized difference between local yields and European reference yields (see Bas et al. in press for details).

Landscape features delimiting fields and pastures were sampled thanks to interpretation of 1/4000 aerial photos. A 7.66 km transect allowed line-intersect sampling of field boundaries on each BBS site, following de Souza & Batista's (2004)'s design (Fig. 1), and performed by a single trained interpreter (YB). Each field boundaries were then counted along the transect and classified either as "Tree" if it contained at least a tree, "Shrub" if it instead contained shrubs, or "Grass" if it contained neither tree nor shrub. Field boundaries of more than 25 m width were not considered as those are not directly linked to farming management.

This interpretation of aerial photos led to exclude data from BBS sites which contained farmlands which were not divided into plots (128 sites, essentially highland extensive pastures) and BBS sites which contained less than 20% of farmland (23 sites). We further estimated the density of each of the three field margin types by dividing their number by the length of farmland area covered by the transect, for the 880 sites with available data.

### *Statistical analysis*

To compare the competing conservation strategies performance, local abundance of each 25 species was modelled by a multiple regression with quadratic functions of PI and field boundaries density as independent variables associated with further variables controlling for potential habitat and climate effects. Climatic requirements were controlled by using quadratic functions of four basic climatic variables from the WorldClim database: maximum temperature of the hottest month, minimum temperature of the coldest month, precipitations of the wettest and the driest months (BIO5, BIO6, BIO13 and BIO14 at a 2.5 arc-minutes precision, see Hijmans et al. 2006). Quadratic functions allowed the model to account for optima in species climatic requirements.

Each of the 25 models was formulated as follows:

$$\text{Abundance} \sim F_1 + F_2 + \dots + F_9 + C_1^2 + C_1 + C_2^2 + C_2 + C_3^2 + C_3 + C_4^2 + C_4 \\ + PI^2 + PI + PFM^2 + \text{Tree} + \text{Shrub} + \text{Grass}$$

where Fs are the nine farmland habitat frequencies, Cs are the four climatic variables, PI the Production Intensity index, PFM the density of the preferred field margin type of the corresponding species (see Appendix 1), Tree, Shrub and Grass the density of the three field boundary types. In this way, the model allowed concave or convex

response of each species to PI and to the field margin density of the type which is the most likely to be favourable for the corresponding species.

To construct the scenarios, we assumed that both PI and PFM were linearly correlated to yield (yield gain for PI and yield loss for PFM). We then use the models fits to predict each species' abundance under a wildlife-friendly farming scenario (WF) by using average value of all parameters (see Table 1). We also predicted each species' abundances under the 5%-quantile and the 95%-quantile values of both farming parameters to calculate other scenarios' performance.

Each species' abundance under field margin sparing scenario (FMS) was the mean of abundance under 95%-quantile PFB ( $Ab_{PFB95}$ ) and of abundance under 5%-quantile PFB ( $Ab_{PFB5}$ ) weighted by their respective land proportion which was adjusted to obtain an equivalent level of field margin density to WF:

$$Ab_{FMS} = Ab_{PFB95} \times \left( \frac{PFB_{average} - PFB_5}{PFB_{95} - PFB_5} \right) + Ab_{PFB5} \times \left( \frac{PFB_{95} - PFB_{average}}{PFB_{95} - PFB_5} \right)$$

where  $PFB_5$ ,  $PFB_{average}$  and  $PFB_{95}$  were respectively the 5%-quantile, the average and the 95%-quantile of the species preferred field margin density as observed in the sampling (see Table 1). The first term represented the contribution of field margin rich farmlands and the second term represented the contribution of highly consolidated farmlands.

Similarly, each species' abundance under extensive farming sparing scenario (EFS) was calculated as follows:

$$Ab_{EFS} = Ab_{IP95} \times \left( \frac{IP_{average} - IP_5}{IP_{95} - IP_5} \right) + Ab_{IP5} \times \left( \frac{IP_{95} - IP_{average}}{IP_{95} - IP_5} \right)$$

The first term represented here the contribution of highly intensive farmlands and the second term represented the contribution of extensive farmlands.

We focused only on species which were negatively affected by the corresponding intensification gradient. Sensitive species were identified as species which were rarer under consolidated or intensive contexts than under field margin rich or extensive contexts. Confidence intervals of predicted abundance under WF were used to test for difference with predicted abundance under FMS and EFS. To quantify the difference in scenarios performance, we calculated the ratio between species abundance predicted under WF and species abundance predicted under FMS and EFS. The geometric mean of these ratios quantified the overall difference in scenarios performance. All fits and tests were performed with the glm function of R 2.9.0 (R Development Core Team 2009).

## Results

Sixteen species were assumed to be sensitive to within-field intensification since they had a decreasing abundance across the production intensity gradient (Table 2). Among these 16 sensitive species, 11 performed better under the extensive farmland sparing scenario (EFS) than under wildlife-friendly farming scenario (WF), of which three did it significantly: *Alauda arvensis*, *Lullula arborea* and *Saxicola rubetra* (Table 2). Of the five sensitive species which performed better under WF, two did it significantly: *Alectoris rufa* and *Saxicola torquatus* (Table 2). Geometric mean of the sensitive species abundance ratio between WF and EFS was equal to 0.61. Yet, *Anthus campestris* exhibited nearly null WF / EFS ratio despite no significant difference in abundance between the two scenarios (Table 2). The model fit was indeed extremely poor for this species as it was contacted only in the most extensive farmlands, so that this species could have biased the geometric mean calculation. Excluding it, the geometric mean of the WF / EFS ratio was equal to 0.89.

Twenty-one species were assumed to be sensitive to land consolidation since they had an increasing abundance across their preferred field margin type gradient (Table 2). Among these 21 sensitive species, 14 performed better under WF than under field margins sparing scenario (FMS), of which only one did it significantly: *Saxicola torquatus* (Table 2). None of the seven sensitive species which performed better under FMS did it significantly (Table 2). Geometric mean of the sensitive species abundance ratio between WF and FMS was equal to 1.02. Moreover, most species had a WF / FMS ratio close to 1 (Table 2) and WF / FMS ratio varied much less among species (standard deviation = 0.18) than WF / EFS ratio (standard deviation = 0.37).

## Discussion

Results indicated a better performance of extensive farmland sparing (EFS) strategy, compared to wildlife-friendly farming (WF) strategy for most farmland birds. On average, farmland bird species would be 39% less abundant under WF than under EFS.

However, one species (*Anthus campestris*) strongly contributed to this difference and its model fit was poor. Indeed, other farmland bird species would be on average only 11% less abundant under WF than under EFS. It remains thus uncertain which strategy should better achieve the conservation of farmland birds. Furthermore it seemed that some species should be better conserved by a WF strategy. However, the two species which exhibited significantly higher abundance under WF than under EFS appear among the few farmland birds to be not declining (Jiguet et al. 2007). Hence, our results point out the importance of maintaining a substantial proportion of extensive farmland at the cost of higher production intensity on the remaining part (Verhulst et al. 2004). Moreover, EFS seems to be less costly than WF (Gabriel et al. 2009; Kleijn et al. 2009).

Competing scenarios on the land consolidation issue performed similarly, being on the whole almost equal and most species did not exhibit strongly different abundance between WF and field margins sparing scenario (FMS). Thus, farmland birds did not support a difference between the two competing strategies.

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Table 1. Descriptive statistics of the farming parameters used to construct the three farming scenarios. The wildlife-friendly farming scenario was based on the average values. Extensive farmland sparing scenario was based on a mix of 5%-quantile production intensity (farmland reserve) and 95%-quantile production intensity (intensive farmland). Field margins sparing scenario was based on a mix of 95%-quantile of the preferred field margin density (farmland reserve) and of 5%-quantile preferred field margin density. Preferred field margin varied among species according to Manuscript 2.

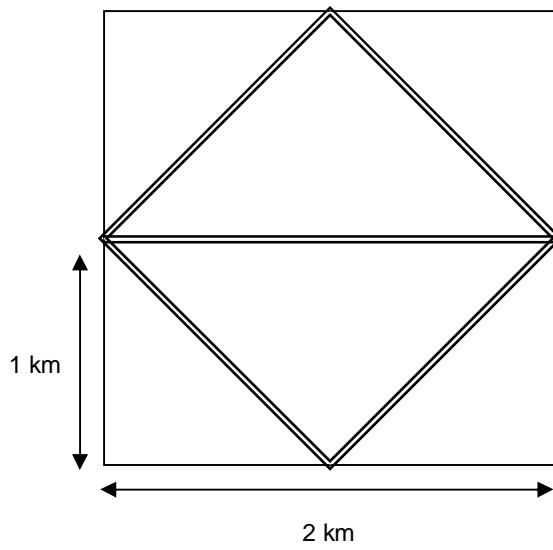
Farming parameters	5%-quantile	Average	95%-quantile
Production intensity	-3.3	59.7	118.3
Grassy strip density	0.93	3.64	7.36
Shrub hedge density	0.32	2.36	5.55
Tree hedge density	0	1.95	4.98

Table 2. Comparisons of the performance of the wildlife-friendly farming (WF) and the farmland reserves scenarios on the 25 farmland specialist species. WF was compared to extensive farmland sparing scenario (EFS) in a within-field intensification context (left part) and to a field margin sparing scenario (FMS) in a land consolidation context (right part). Effect columns indicate the sensitivity of the species to each intensification gradient, either – if the species abundance decreased along the corresponding gradient and + if it increased. Ratio columns indicate the ratio between species abundance predicted under the two competing scenarios. The test column indicates the level of significance of the difference in species abundance between the two scenarios: · for  $p < 0.1$ , \* for  $p < 0.05$ , \*\* for  $p < 0.01$ , \*\*\* for  $p < 0.001$ .

Species	within-field intensification context				land consolidation context			
	effect	WF / EFS ratio	Best scenario	Test	effect	WF / FMS ratio	Best scenario	Test
<i>Alauda arvensis</i>	-	0.88	EFS	***	-	1.01	WF	
<i>Alectoris rufa</i>	-	1.70	WF	***	-	0.97	FMS	
<i>Anthus campestris</i>	-	$3.10^{-3}$	EFS		-	0.74	FMS	
<i>Anthus pratensis</i>	-	0.70	EFS		+	0.80	FMS	
<i>Burhinus oedicephalus</i>	-	0.77	EFS		+	0.94	FMS	
<i>Carduelis cannabina</i>	+	0.92	EFS		-	1.28	WF	
<i>Circus cyaneus</i>	-	1.03	WF		-	0.83	FMS	
<i>Coturnix coturnix</i>	+	0.92	EFS		-	1.39	WF	
<i>Emberiza calandra</i>	-	0.91	EFS		-	1.03	WF	
<i>Emberiza cirius</i>	-	1.02	WF		-	0.96	FMS	
<i>Emberiza citrinella</i>	-	0.90	EFS		-	1.08	WF	
<i>Emberiza hortulana</i>	+	1.07	WF		-	1.10	WF	
<i>Falco tinnunculus</i>	+	0.91	EFS		-	1.03	WF	
<i>Galerida cristata</i>	-	0.77	EFS		-	0.60	FMS	
<i>Lanius collurio</i>	+	1.38	WF	**	-	0.89	FMS	
<i>Lanius senator</i>	-	1.27	WF		+	0.69	FMS	
<i>Lullula arborea</i>	-	0.76	EFS	***	-	1.18	WF	
<i>Motacilla flava</i>	+	0.71	EFS	**	-	1.02	WF	
<i>Oenanthe oenanthe</i>	-	0.88	EFS		-	1.36	WF	
<i>Perdix perdix</i>	+	0.79	EFS		+	0.77	FMS	***
<i>Saxicola rubetra</i>	-	0.44	EFS	**	-	1.04	WF	
<i>Saxicola torquatus</i>	-	1.26	WF	***	-	1.09	WF	**
<i>Sylvia communis</i>	+	1.04	WF		-	1.07	WF	
<i>Sylvia curruca</i>	+	1.53	WF		-	1.08	WF	
<i>Vanellus vanellus</i>	-	0.67	EFS		-	0.99	FMS	



Figure 1.



Scheme of the transect (double line) used to sample intersections with field margins within each Breeding Bird Survey square (delimited by the external simple line)

Appendix 1. Preferred Field Margin (PFM) type of each studied species, according to a linear modelling. We indeed previously modelled each species abundance accounting only for linear response of field margin density, i.e by the same model than presented in Statistical Analysis but without PFM<sup>2</sup> term. PFM was thus determined for each species as the field margin type with the higher linear response.

Species	PFM
<i>Alauda arvensis</i>	Grass
<i>Alectoris rufa</i>	Grass
<i>Anthus campestris</i>	Shrub
<i>Anthus pratensis</i>	Grass
<i>Burhinus oedicnemus</i>	Grass
<i>Carduelis cannabina</i>	Tree
<i>Circus cyaneus</i>	Grass
<i>Coturnix coturnix</i>	Shrub
<i>Emberiza calandra</i>	Grass
<i>Emberiza cirrus</i>	Shrub
<i>Emberiza citrinella</i>	Shrub
<i>Emberiza hortulana</i>	Grass
<i>Falco tinnunculus</i>	Grass
<i>Galerida cristata</i>	Grass
<i>Lanius collurio</i>	Grass
<i>Lanius senator</i>	Tree
<i>Lullula arborea</i>	Shrub
<i>Motacilla flava</i>	Grass
<i>Oenanthe oenanthe</i>	Shrub
<i>Perdix perdix</i>	Grass
<i>Saxicola rubetra</i>	Grass
<i>Saxicola torquatus</i>	Grass
<i>Sylvia communis</i>	Shrub
<i>Sylvia curruca</i>	Shrub
<i>Vanellus vanellus</i>	Grass

## MANUSCRIT 6

# Conciliating forestry and woodland bird conservation: should we promote wildlife-friendly forestry or forest reserves?

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## Introduction

Most forest ecosystems are under increasing anthropogenic pressures as global wood demand is expected to increase as fast as global food demand (Alexandratos and Mernies 2000; FAO 2009). A high priority is thus to identify the most effective strategies to conciliate wood production and conservation. Green et al. (2005) already provided a framework comparing competing strategies aimed to conciliate food production and biodiversity conservation.

The present study proposes transposing their framework to the conciliation of wood production and forest bird conservation in lowland temperate forest of western France. We investigated two independent factors influencing both wood production and forest birds: the length of silvicultural rotation (Hansen et al. 1995) and the introduction of fast-growing exotic conifers (Lopez and Moro 1997). Green et al.'s framework allow to determine how to mitigate these intensification factors, either by moderate exploitation practices over the whole available forest or by land sparing, i.e. allowing most intensive practices to be applied on a part of available forest in order to spare the remaining forests to be spared from exploitation.

Such competing strategies have been both argued as cost-effective ways to conserve biodiversity (Lindenmayer and Franklin 1997; Flueck and Smith-Flueck 2006). We thus defined a wildlife-friendly forestry strategy, where all forests would be exploited with average-intensity practices. This wildlife-friendly forestry strategy was compared to two "land sparing" strategies: one on the silvicultural rotation length issue, namely "old forest sparing" and one on the fast-growing conifer introduction issue, namely "deciduous forest sparing". Old forest sparing strategy involved a mix of intensive short-rotation forestry and of old forest reserves. Deciduous forest sparing strategy involved a mix of intensive pure coniferous forestry and of reserves of pure deciduous forests.

The relative performance of these strategies were tested on the species with high degree of specialization to forest since these species are much more likely to be the conservation targets of forest conservation. The abundance of each species were predicted under competing scenarios representing each conservation strategy. We then tested the difference in predicted abundance between wildlife-friendly scenario and land sparing scenarios. If possible, general patterns across species were eventually identified.

## Methods

### Sampling

The study was carried out from 2006 to 2008 in the Ille-et-Vilaine administrative department of France. Within this department, 117 sampling points were randomly selected within forest areas (>100 m from forest edges) and surveyed once during the study period (43 were surveyed in 2006, 47 in 2007 and 27 in 2008). Birds were sampled by a single trained observer (YB) using a point count method (Bibby et al. 1992). Sample points were grouped (by four to six) according to their physical proximity. Each group was visited in the same morning, during the first four hours after sunrise. Each point group was visited twice in the year: once between 10<sup>th</sup> and 25<sup>th</sup> May and again between 26<sup>th</sup> May and 12<sup>th</sup> June. Point groups were sampled in a random sequence for the first visit, and this order was reversed for the second visit. Similarly, within-group order of points was reversed from the first visit to the second visit. We avoided unfavourable weather conditions for sampling birds (rain or strong wind - Beaufort > 4, i.e. wind speed > 28 km/h). On a point, a visit consisted of 25-minute count as five consecutive periods of 5-minute counts. During these counts, each detected bird was identified to species and located within one of four distance classes: 0-10 m, 10-25 m, 25-50 m, >50 m. The observer was trained for auditory distance measurement, and used a laser range finder to get the distance of reference points preliminarily to each visit. According to Alldredge et al. (2007c), we considered that individuals were correctly allocated to distance classes as the last class limit (50 m) lied within the range of reliable auditory distance measurement for trained observers. Attention was focalised on auditory detections, and purely visual detections are not considered in this analysis. Abundance per species was finally measured as the sum of all counts on each site.

The habitat surrounding each point was sampled with five circular quadrats of 10-m radius: one centred on the point, the four others 100 m from the point in the four cardinal points direction. On each quadrats, all trees were counted, identified to species and their circumferences at human-breast height were measured. Non-commercial shrubs were not considered. Two forestry parameters were extracted from these data. First, the maximum circumference measured among the five quadrats of each site was taken as a proxy for the maturity stage determining exploitation. This is assuming that the largest tree sampled of each site were close to their exploitation. This assumption could be problematic for even-aged managed forest where stands could be at an early stage far from their exploitation. We felt however confident about this approximation because the five sampling quadrats always overlapped several stands of different stage of which at

least one was often close to maturity. We thus assumed our modelling to be robust to this simplification. Finally, conifers proportion was measured as the proportion of basal area occupied by coniferous species.

Data were selected from the 25 bird species which were considered as forest specialists, i.e. at least twice more common in forest than in non-forest according to French Breeding Bird Survey data (Jiguet et al. 2007).

## Statistical analysis

We assessed the relative performance of our scenarios by fitting a generalized linear models incorporating quadratic functions of the two forestry parameters. Models were fitted to account for “quasipoisson” distribution of errors, differing from Poisson distribution by allowing over and under-dispersion, with log as a link function (McCullagh and Nelder 1989).

The fixed formula was for both models:

$$\text{Abundance} \sim \text{species} + \text{MC} + \text{CP} + \text{species}:(\text{MC} + \text{CP})$$

where MC is the maximum circumference linked to silvicultural rotation length and CP the conifer proportion. We assumed that both MC and CP were linearly correlated to yield. It indeed seems that wood productivity of stands decrease approximately linearly after attaining an early productivity peak (10-15 cm diameter for sessile oak, see Pardé 1962; Pardé 1978). Thus MC was assumed to be proportional to yield loss and CP to yield gain since conifers have higher yield than deciduous trees (Vallet et al. 2009).

We then use the model fit to predict each species abundance under a wildlife-friendly forestry scenario (WF) by using average value of both forestry parameters (see Table 1). We also predicted each species abundances under the minimum and the maximum values of both forestry parameters to calculate other scenarios' performance.

Each species abundance under old forest sparing scenario (OFS) was the mean of abundance under minimum MC ( $Ab_{MCmin}$ ) and of abundance under maximum MC ( $Ab_{MCmax}$ ) weighted by their respective land proportion which was adjusted to obtain an equivalent level of wood production to WF:

$$Ab_{OFS} = Ab_{MCmax} \times \left( \frac{MC_{average} - MC_{min}}{MC_{max} - MC_{min}} \right) + Ab_{MCmin} \times \left( \frac{MC_{max} - MC_{average}}{MC_{max} - MC_{min}} \right)$$

where  $MC_{min}$ ,  $MC_{average}$  and  $MC_{max}$  were respectively the minimum, the average and the maximum of maximum circumference observed in the sampling (see Table 1). The

first term represented the contribution of old forest reserves and the second term represented the contribution of short-rotation intensively managed forests.

Similarly, each species abundance under deciduous forest sparing scenario (DFS) was calculated as follows:

$$Ab_{DFS} = Ab_{CP_{max}} \times \left( \frac{CP_{average} - CP_{min}}{CP_{max} - CP_{min}} \right) + Ab_{CP_{min}} \times \left( \frac{CP_{max} - CP_{average}}{CP_{max} - CP_{min}} \right)$$

The first term represented here the contribution of highly productive pure coniferous stands and the second term represented the contribution of pure deciduous stand reserves.

We focused only on species which were negatively affected by the corresponding yield gradient. Sensitive species were identified as species which were rarer under maximum yield than under minimum yield. Confidence intervals of predicted abundance under WF were used to test its difference with predicted abundance under OFS and DFS. To quantify the difference in scenarios performance, we calculated the ratio between species abundance predicted under WF and species abundance predicted OFS and DFS. The geometric mean of these species ratio quantified the overall difference in scenarios performance. All fits and tests were performed with the glm function of R 2.9.0 (R Development Core Team 2009).

## Results

Sixteen bird species were assumed to be sensitive to reduction of silvicultural rotations since they had an increasing abundance across the dominant tree circumference gradient (Table 2). Among these 16 sensitive bird species, 12 performed better under the wildlife-friendly forestry scenario (WF) than under old forest sparing scenario (OFS) scenario, of which seven did it significantly (Table 2). Inversely, of the four bird sensitive species which performed better under OFS, only one did it significantly (Table 2). Geometric mean of the sensitive species abundance ratio between WF and OFS was equal to 1.85.

Nineteen bird species were assumed to be sensitive to conifer introduction since they had a decreasing abundance across the conifer proportion gradient (Table 2). Among these 19 sensitive species, 12 performed better under WF than under deciduous forest sparing scenario (DFS), of which six did it significantly (Table 2). None of the six bird sensitive species which performed better under DFS did it significantly (Table 2).

Geometric mean of the sensitive species abundance ratio between WF and DFS was equal to 1.21.

## Discussion

Results indicated a better performance of wildlife-friendly forestry (WF) strategy, compared to both old forest sparing (OFS) and deciduous forest sparing (DFS) strategies for forest birds. Results were particularly uneven when comparing WF and OFS. The medium rotation length of WF seemed to perform much better than the mix of long and short rotations of OFS. On average, forest bird species would be almost twice more abundant under WF than under OFS. Thus, conservation of most forest birds should be better achieved by a wide implementation of moderate rotation length than by old forest reserves. Few species should certainly be better conserved by old forest reserves (Poulin et al. 2008), but our results point out the importance of negotiating a reasonable silvicultural rotation length to be implemented on most forests.

Most forest birds which prefer deciduous forests seemed also to prefer a wide compromise than the sparing of pure deciduous forest since the scattered introduction of conifers of WF performed better than the mix of pure deciduous and pure coniferous stands of DFS. The overall difference between these two strategies was however relatively low. Hence, forest birds did not provide strong arguments on the choice to promote pure deciduous forests or mixed forests to conciliate conifer introduction and forest bird conservation.

This study focused on two of the main aspects of the relationship between wood productivity and biodiversity, but other management parameters could help to identify the best conservation strategy. Green tree retention indeed seems to be a cost-effective way to maintain high biodiversity in exploited forest (Temesgen et al. 2006). Besides, herbicide use have been argued to enhance wood yields and thus spare more old-growth forest (Flueck and Smith-Flueck 2006).

However, there is now a large body of evidence to suggest that many taxa could recover from forestry intensification with only a little decrease of wood production (Pellens and Garay 1999; Terry et al. 2000; Rolstad et al. 2001; Falk et al. 2008). The reasons put forward for this efficiency of wildlife-friendly forestry is the possibility to maintain relatively intense wood production with a high density of high value microhabitats (Michel and Winter 2009) and with a low level of disturbance (Lindenmayer and Noss 2006; Falk et al. 2008). Yet, wildlife-friendly forestry seems to fail to conserve



highly sensitive taxa, such as spiders (Buddle and Shorthouse 2008), epiphytic lichens (Detki 2003 FEM) or bryophytes (Turner and Pharo 2005). Thus the relative performance of wildlife-friendly forestry and forest reserves seems not to be univocal and probably depends on conservation targets and regional contexts.

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Table 1. Descriptive statistics of the forestry parameters used to construct the three forestry scenarios. The wildlife-friendly forestry scenario was based on the average values. Old forest sparing scenario was based on a mix of maximum dominant tree circumference (old forest reserve) and minimum dominant tree circumference (intensive short-rotation forestry). Deciduous forest sparing scenario was based on a mix of pure broad-leaved forests and pure conifer forests.

Forestry parameters	Minimum	Average	Maximum
Dominant tree circumference	97	180	307
Conifer proportion	0	0.37	1

Table 2. Comparisons of the performance of the wildlife-friendly forestry (WF) and the forest reserves scenarios on the 25 bird forest specialist species. WF was compared to old forest sparing scenario (OFS) in a context of forestry intensification by reduction of silvicultural rotations (left part) and to a deciduous forest sparing scenario (DFS) in a context of forestry intensification by conifer introduction (right part). Effect columns indicate the sensitivity of the species to each intensification gradient, either '-' if the species abundance decreased along the corresponding gradient and '+' if it increased. Ratio columns indicate the ratio between species abundance predicted under the wildlife-friendly forestry scenario and species abundance predicted under the corresponding land sparing scenario. The test column indicates the level of significance of the difference in species abundance between the two scenarios: '·' for  $p < 0.1$ , '\*' for  $p < 0.05$ , '\*\*' for  $p < 0.01$ , '\*\*\*' for  $p < 0.001$ .

Species	Intensification by rotation reduction				Intensification by conifer introduction			
	effect	WF / OFS ratio	Best strategy	Test	effect	WF / DFS ratio	Best strategy	Test
<i>Accipiter nisus</i>	-	2.92	WF		-	14.05	WF	***
<i>Aegithalos caudatus</i>	+	0.87	OFS		-	0.93	DFS	
<i>Anthus trivialis</i>	+	1.79	WF	**	+	0.75	DFS	
<i>Certhia brachydactyla</i>	-	1.60	WF	***	-	0.94	DFS	
<i>Coccothraustes coccothraustes</i>	-	1.64	WF	·	-	1.00	WF	
<i>Dendrocopos major</i>	-	1.26	WF	·	-	1.29	WF	*
<i>Dendrocopos medius</i>	-	0.72	OFS		-	0.69	DFS	
<i>Dendrocopos minor</i>	-	0.86	OFS		-	1.06	WF	
<i>Dryocopus martius</i>	-	0.67	OFS		+	0.68	DFS	
<i>Erithacus rubecula</i>	+	0.83	OFS	**	-	1.02	WF	
<i>Garrulus glandarius</i>	+	1.00	OFS		-	0.94	DFS	
<i>Lophophanes cristatus</i>	-	1.26	WF		+	1.10	WF	
<i>Loxia curvirostra</i>	+	4.99	WF	**	+	0.50	DFS	
<i>Muscicapa striata</i>	-	4.66	WF	***	-	1.56	WF	
<i>Oriolus oriolus</i>	-	9.19	WF	**	-	0.47	DFS	
<i>Phylloscopus collybita</i>	+	0.78	OFS	***	+	1.17	WF	*
<i>Phylloscopus sibilatrix</i>	-	3.77	WF	***	-	1.58	WF	*
<i>Picus canus</i>	-	13.43	WF	*	-	0.43	DFS	
<i>Poecile palustris</i>	+	1.60	WF	**	-	1.26	WF	
<i>Pyrrhula pyrrhula</i>	-	0.35	OFS	**	-	2.57	WF	**
<i>Regulus ignicapillus</i>	-	2.92	WF	***	-	2.21	WF	**
<i>Regulus regulus</i>	-	1.64	WF	**	+	1.86	WF	***
<i>Sitta europaea</i>	-	1.05	WF		-	1.01	WF	
<i>Turdus philomelos</i>	+	1.25	WF	·	-	0.83	DFS	
<i>Turdus viscivorus</i>	+	1.04	WF		-	1.21	WF	

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## Accounting for weather and time-of-day parameters when analysing count data from monitoring programs

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**Abstract** Problems induced by heterogeneity in species and individuals detectability are now well recognized when analysing count data. Yet, most recent techniques developed to handle this problem are still hardly applicable to many monitoring schemes, and do not provide abundance estimates at the point count scale. Here, we show how using simple weather variables can be a useful surrogate to detect variability in species detectability. We further look for a potential bias or loss in statistical power based on count data while ignoring weather and time-of-day variables. We first used the French Breeding Bird Survey to test how each of the counts of the 97 most common breeding species was influenced by weather and time-of-day variables. We assessed how the estimation of each species response to fragmentation could be influenced by correcting counts with such variables. Among 97 species, 75 were affected by at least one of the five weather and time-of-day variables considered. Despite these strong influences, the relationship between species abundance and fragmentation was not biased when not controlling counts for weather and time-of-day variables and further found no improvement in statistical power when accounting for these variables. Our results show that simple variables can be very powerful to assess how species detectability is influenced by weather conditions but they are inconsistent with any specific bias due to heterogeneous detectability. We suggest that raw count data can be used without any correction in case the sources of variation in detectability could be considered independent to the factor of interest.

**Keywords** Breeding bird survey · Detectability · Fragmentation · Point counts · Relative abundance · Time-of-day · Weather conditions

### Abbreviations

BBS Breeding bird survey

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## Introduction

Counts of individuals or species are the result of two processes: a biological process (the true presence or absence of a species or individual), and a methodological filter (the ability of the observer to detect an individual). If variation in detectability among species and/or individuals is not accounted for, an unknown part of the variation in presence or abundance of a given species will result from variation in detectability regardless of its true variation. Therefore, using just the detected bird counts (per unit effort) as an index of abundance is sometimes considered to be neither scientifically sound nor reliable (Burnham 1981). To control the potential bias induced by heterogeneity in detectability, two approaches have been adopted. On the one hand, several methods have been developed to account for the whole detection process and to further directly estimate the probabilities of detection. Yet these methods need either both spatial and temporal replications (Dodd and Dorazio 2004; Royle 2004; Kéry et al. 2005), or temporal replication and marking of individuals (Farnsworth et al. 2002; Ailredge et al. 2007). On the other hand, count data may be corrected with covariables known to be sources of heterogeneity in detectability (Caughley et al. 1976; Link and Sauer 1998, 2002). This approach may be simpler to apply but sources of heterogeneity in detectability may remain unchecked and can still bias the analyses.

Collecting abundance data from incomplete counts may respond to different objectives which involve different strategies to deal with heterogeneity in detectability. First, it is important to note that estimating a species total abundance over an area requires an estimation of detectability even if detectability is constant across sites (Thompson et al. 1998). For these objectives, a direct estimation of detectability seems to perform well (Kéry et al. 2005; Royle et al. 2007). However, most ecological studies do not need an absolute measure of abundance, but rather an index, usually named relative abundance, to infer spatial or temporal variations of species abundance. In these cases, imperfect detection must be accounted for if detectability covaries with the dimension to be compared. Here we focused on the use of count data to infer on abundance variations across spatial variations of an ecological factor, which is a common output of large scale monitoring programs (Jiguet et al. 2006; Julliard et al. 2006; Posthuma and De Zwart 2006; Vaughan et al. 2007). As many ecological factors such as habitat characteristics are measured very locally, these studies often need a measure of relative abundance on a very local scale (e.g. for each point count), which unfortunately precludes using any spatial replication of count data. Thus, in many cases, a direct estimation of detectability is still not possible. In such cases, accounting for factors that potentially affect species detectability could be a valuable proxy in counts analysis (Link and Sauer 1998). Moreover, some of these factors are easily recorded by observers. Here, we focused on time-of-day and weather variables which are more likely directly linked to detection processes rather than to variations in true abundance (Robbins 1981; Verner 1985). We thus provided a framework to test how these simple variables can influence the power of classical analyses based on counts. We specifically addressed two objectives: (i) relating variations in counts to weather and time-of-day factors, (ii) assessing how accounting for these variables could correct bias and/or improve statistical power while testing ecological predictions. For this purpose, we chose to use landscape fragmentation as an ecological factor impacting a wide range of common species (Fahrig 2003; Devictor et al. 2008). Monitoring data came from the French Breeding Bird Survey (Jiguet et al. 2007), which is similar to many classical monitoring programs.



We predict that time-of-day influences detectability of species in either a positive or a negative way depending on the type of activity enhancing detectability (e.g. song activity generally decrease and foraging activities might increase with time after sunrise; Robbins 1981; Lindenmayer et al. 2004). We also predict that weather conditions should affect detectability if they restrain sighting or hearing of individuals or if they influence bird activities (Verner 1985).

## Material and methods

### The French Breeding Bird Survey

A breeding bird survey (BBS) was started in France in 2001 carried out by volunteer skilled ornithologists and following a standardized protocol with the same sites sampled for several years. Each observer provided a locality from which, within a 10 km-radius, a 2 × 2 km plot to be sampled was randomly selected (i.e. among 80 possible plots). Such random selection ensures the survey of representative habitats (including farmlands, woodlands, suburbs and cities). In each site, observers monitored 10 point-counts separated by at least 300 m. Data collected by observer on each permanent point-count stations were the counts and specific identification of all individuals seen and/or heard during a fixed period of 5 min.

We considered all points surveyed in 2005 for this analysis ( $n = 7350$ , i.e. from 735 plots). Birds were counted twice (before and after the 8th of May within April to mid-June) in each plot, with 4–6 weeks between the two counts and within 1–4 h after sunrise. Only individuals detected within 100 m of the observer were considered, to avoid bias due to visual detections strongly depending on landscape structure. Habitats were recorded by observers on their point counts, using a standardized code (Julliard et al. 2006). Finally, we retained species for which at least 30 individuals were counted ( $n = 97$  species, see Appendix) to conduct the analyses.

Observers were also asked for each point count to note the time of the count start (to the nearest minute) and to describe weather conditions for four variables: cloudiness, rain, wind and visibility. Each of these variables was scored as 1, 2 or 3 (see Table 1). The monitoring recommendations stated that counting during rain, strong wind or deep fog should be avoided, so these extreme meteorological conditions are rarely found in the dataset (mostly when conditions changed during the sampling).

### Landscape fragmentation

An estimate of landscape fragmentation within each surveyed plot was obtained using the geographical information system package ArcView 3.2 (ESRI 2000) and the Corine land

**Table 1** Criteria used by observers to assess weather conditions for each point counts

Values	Cloudiness (%)	Rain	Wind	Visibility
1	0–33	Absent	Absent	Good
2	33–66	Drizzle	Light	Moderate
3	66–100	Showers	Medium/strong	Poor

Cloudiness is measured in sky covering percentage

cover database. CORINE is a national geo-referenced land-cover, based on satellite digital images for the whole country. This land cover layer was created in 2000 to classify, by means of remote sensing, landscape units larger than 25 ha as belonging to one of 44 habitat classes (Bossard et al. 2000). The resolution concerning polygon limits is 20 meters. In other words, the difference between two polygons of different habitat types as well as each polygon complex form was precisely represented by CORINE. The edge density (sum of all contact length between polygons) was thus considered as a good measure of habitat fragmentation (Lausch and Herzog 2002; Devictor et al. 2008). The edge density was highly correlated to the number of polygons and to the average polygon size of the different habitat types enclosed in the landscape (Devictor and Jiguet 2007).

### Statistical analyses

We modelled each species counts with two successive statistical models. First, we considered an “uncontrolled model”, i.e. for each species, counts was only a function of period (first or second), habitat type (among 18 classes) and habitat fragmentation using a Generalized Linear Model: Counts vary with Period + Habitat + Fragmentation. Second, we considered a “controlled model” by adding in the previous model the five supplementary predictors supposedly linked to detectability: Counts varies with Period + Habitat + Time + Cloudiness + Rain + Wind + Visibility + Fragmentation.

Time recorded by the observer was converted to time after local sunrise (in min, source: USNO 2007). Time and weather variables were considered as continuous predictors, as we expected the response of each species to each variable to be monotone. These five variables were also standardized by a z-transformation to allow comparisons of their magnitudes. Spearman’s rank correlations between habitat fragmentation, time-of-day and each weather variable were calculated. We found that habitat fragmentation and time-of-day were extremely weakly correlated to other variables (Table 2). As expected, rain, wind and visibility were weakly correlated to each other (Table 2).

We used generalized linear models accounting for “quasipoisson” distribution of errors, differing from Poisson distribution by allowing overdispersion in the count data for a species (McCullagh and Nelder 1989), with log as a link function.

Note that we didn’t account for spatial dependence between point counts (spatial autocorrelation) as statistical models usually run to handle spatial autocorrelation hardly support Poisson regression with large datasets. Despite violating the spatial independence assumption, we assumed that it should impact both models equally (with or without weather variables). Therefore, this problem should not impact the comparison between both models, which is the main focus of our analysis.

**Table 2** Spearman’s rank correlations between variables used in this study

	Fragmentation	Time-of-day	Cloudiness	Rain	Wind
Time-of-day	−0.067				
Cloudiness	0.008	−0.005			
Rain	0.049	0.006	0.310		
Wind	0.023	0.094	0.172	0.119	
Visibility	0.041	−0.031	0.319	0.282	0.028

We analysed the effects of the five variables supposedly linked to detectability in two steps. First, we performed for each species and for each variable, a *t*-test of the corresponding slope fitted in the controlled model, compared to zero, to assess which species respond significantly to each variable. Second, we gathered for each variable, the 97 species response slopes and performed *t*-tests compared to zero in order to test more general patterns of response to weather and time-of-day variables. Time-of-day effects were also tested for the “vocal” activities species subset ( $n = 73$ ; species most often detected because of their territorial vocalizations) as time-of-day effects were mostly expected for vocal activities (Lindenmayer et al. 2004; Woltmann 2005).

We further looked for a possible bias in the fragmentation effect estimation for the uncontrolled model by correlating fragmentation parameters of the two models in a paired *t*-test. Finally, we compared the fragmentation effect estimation’s accuracy in both models. For this purpose, we calculated, for each species, the statistical power gain as follows:

$$\text{Gain} = (\text{SE}_1 - \text{SE}_2) / \text{SE}_1 \times 100$$

where  $\text{SE}_1$  and  $\text{SE}_2$  are the standard errors of the fragmentation parameters of respectively the uncontrolled and the controlled model. This metric gave us a potential gain (or a loss if negative) in accuracy of the fragmentation effect estimation, expressed in percentage of the uncontrolled accuracy.

As the amount of available data was expected to affect model fits, we assessed whether both eventual bias and gain in accuracy were related to the species commonness, measured using the log of total number of individuals recorded in the dataset for each species.

## Results

### Time-of-day and weather effect

Among the 97 species considered, the counts of 38 species were significantly affected by time-of-day (Table 3). These responses were as often positive as negative and the global response of the considered species was not significant (Fig. 1a, b). But, “vocal” species ( $n = 73$ ) responded globally negatively to time-of-day (Table 3). Rain had globally the strongest effect on counts, but only 15 species individually responded significantly (Table 3, Fig. 1c). We also found highly significant negative effects of cloudiness and wind on counts (Table 3, Fig. 1d). However, visibility seemed to affect few species counts, without the expected global positive response (Table 3). Altogether, 75 of the 97 species showed at least one significant response to any of the five variables considered.

### Bias and accuracy in fragmentation effect estimation

Fragmentation effect slope was highly correlated between uncontrolled and controlled models ( $n = 97$ , Pearson correlation coefficient:  $\rho = 0.997$ , see Fig. 2). Paired *t*-test revealed no significant differences between these two estimations ( $t = 1.31$ ,  $df = 96$ ,  $P = 0.194$ ), and these slight differences were not linked to species commonness ( $t = 0.73$ ,  $df = 95$ ,  $P = 0.47$ ).

Moreover there was no gain in accuracy in the estimation of fragmentation effect (average gain =  $-0.7\%$ ,  $t = -1.33$ ,  $df = 96$ ,  $P = 0.186$ ), and there was no significant link between these gains and species commonness ( $t = 0.238$ ,  $df = 95$ ,  $P = 0.812$ ).

**Table 3** Effects of Time-of-day and Weather variables on counts

Variable	Species responses				Total significant	Average slope	P
	–	(–)	(+)	++			
Time-of-day							
Total	22	32	27	16	38	–0.001	0.974
Vocal species	19	28	19	7	26	–0.039	<b>0.014</b>
Cloudiness	21	43	24	9	30	–0.070	<b>&lt;0.001</b>
Rain	9	37	45	6	15	–0.340	<b>0.013</b>
Wind	23	44	26	4	27	–0.072	<b>&lt;0.001</b>
Visibility	5	35	46	11	16	0.041	0.50

The –, (–), (+) and ++ columns refer to the number of species that respectively respond significantly negatively, non-significantly negatively, non-significantly positively and significantly positively to the corresponding variable. Total significant column refers to the total number of species which respond significantly to each factor (either positively or negatively). Average slope column refers to the average response among species to the corresponding variable, and last column refers to the *P*-value from the *t*-test of the Average slope compared to zero

Bold values are significant test with  $P < 0.05$

## Discussion

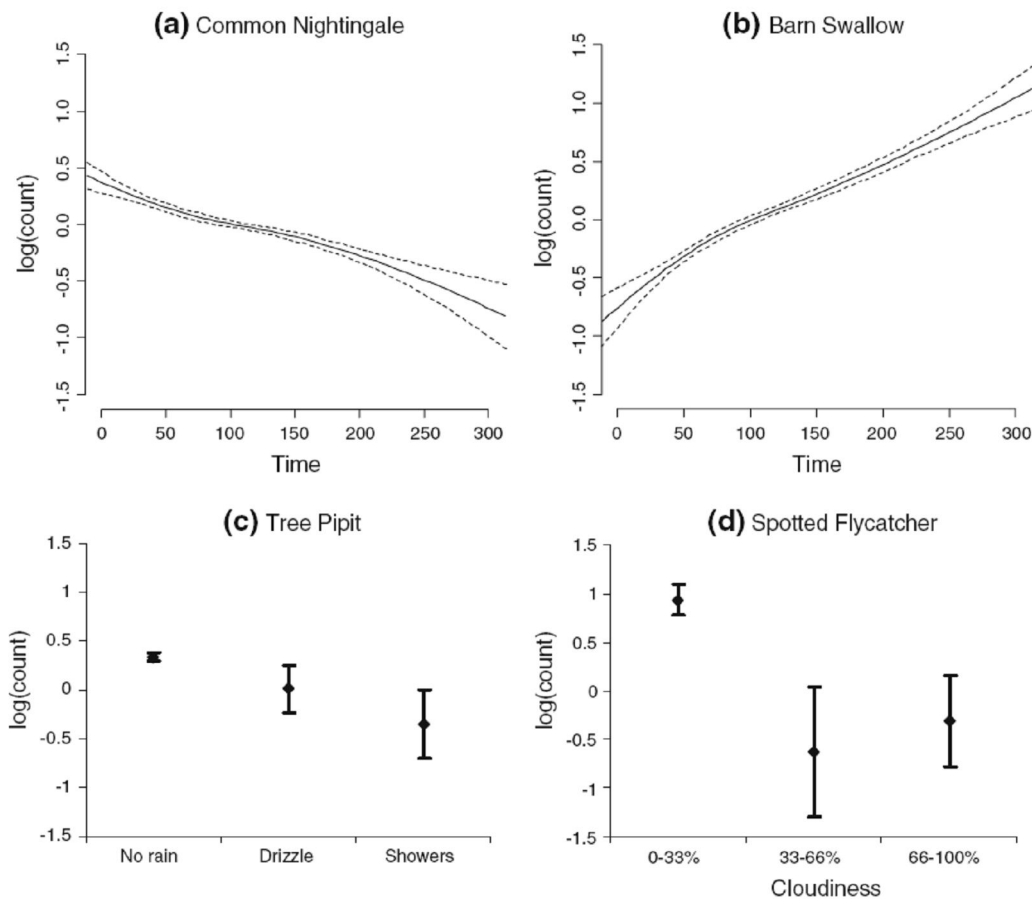
### Weather and time-of-day effects on detection

Among the 97 species we studied, 75 responded at least to one of the five variables potentially linked to detectability. Time-of-day seemed to be the less influential variable but the even distribution and large variability of this variable within the dataset showed many significant responses for individual species and, as expected, a global negative trend for vocal species (Lindenmayer et al. 2004; Woltmann 2005). Conversely, the four weather variables showed stronger global effects but affected fewer species, most likely because there were only three categorical values and very unequal sample sizes, as observers were told to avoid rainy, windy and misty conditions as much as possible. This resulted in only 6% of the counts made in both rainy and strong wind conditions and only 1% in poor visibility. Yet, many species still responded significantly to these variables, showing that standardizing field methods in monitoring programs does not still guarantee a constant detectability across sites (Verner 1985; Thompson 2002).

These results also showed that very easily recorded variables can provide valuable information for practical issues. Similar analyses could help to provide strong recommendations to new monitoring schemes, for example by recording time-of-day and weather conditions to find optimal detection conditions of a targeted species. Such variables could also be useful for more theoretical purposes. For example, these monitoring data could be used to test predictions on the time-of-day specialization of song activities (Cody and Brown 1969; Brumm 2006). In this latter case, we show that one should account for the variation in counts induced by variation in the time of the records.

### Implication for fragmentation effect estimation

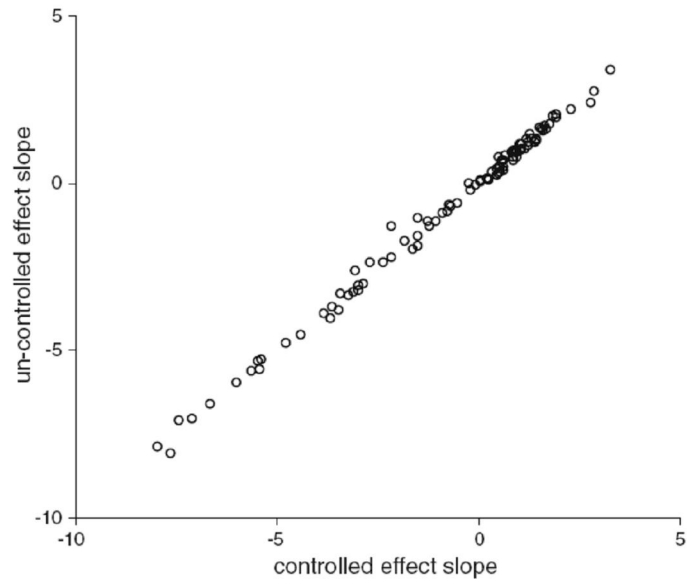
We found no bias induced by weather conditions on the fragmentation effect. Indeed, the fragmentation effect was remarkably robust to time-of-day and weather variables (Fig. 2).



**Fig. 1** Examples for differential detectability under different conditions. (a, b) The relationship between counts and time after sunrise for (a) Common Nightingale (*Luscinia megarhynchos* Brehm), a species detected almost exclusively by its song and for (b) Barn Swallow (*Hirundo rustica* L.) whose detection is linked to its prey activity (dipterans). Fit from a non-parametric spline function with 4 df, adjusted to habitat, count period and weather; dotted lines show  $\pm 1$  SE. (c) The relationship between counts and rain conditions for Tree Pipit (*Anthus trivialis* L.), a species whose detection is linked to territorial display activity which is strongly inhibited by rain. Note that rain was here considered as a discrete variable, its effect was adjusted to habitat, count period, time-of-day and weather; bars show  $\pm 1$  SE. (d) The relationship between counts and cloudiness for Spotted Flycatcher (*Muscicapa striata* Pallas), a species detected mostly when sallying out from vegetation hunting flying insects (Cramp and Perrins 1993). Cloudiness was here considered as a discrete variable, its effect was adjusted to habitat, count period, time-of-day and weather; bars show  $\pm 1$  SE

Thus, this result suggests that when heterogeneity in detectability is not correlated to the process of interest, there should be no bias in ecological correlations using raw counts. However, Gu and Swihart (2004) found strong bias in habitat relationships with simulated occurrence data, even when detectability was independent of habitats. We emphasize that this pattern could be induced when considering occurrence data. Indeed, sites with very few individuals should exhibit critically low detection probabilities which may stronger impact occurrence than abundance potential bias. Thus, we argue that although counts may include more sources of unchecked variations, using counts should be more robust than presence-absence data to detectability heterogeneity.

**Fig. 2** The relationship between uncontrolled and controlled estimation of the fragmentation effect for the 97 species (points)



Moreover, we also found no gain in accuracy when accounting for time-of-day and weather covariates. Thus in this example, there was no need to account for weather and time-of-day covariates to answer our ecological question.

To conclude, we showed that raw counts can be influenced by weather and time-of-day conditions even if the monitoring design intends to standardize field methods. Yet, we also showed that these variations in detectability did not induce any bias nor any lack of statistical power while estimating species response to habitat fragmentation. We suggest that this example is representative of many ecological analyses performed on large raw counts dataset. Obviously, sources of variation in detectability may be more diverse than weather and time-of-day alone (Bart and Schoultz 1984; Schieck 1997; Norvell et al. 2003) and can give wrong ecological messages if not carefully addressed (Moilanen 2002; Mazerolle et al. 2005). We thus strongly recommend to at least list potential bias induced by heterogeneity in detectability. Then, we suggest that counts from classic monitoring scheme may still be used without any correction when relating species abundance to ecological factor, whenever variations in detectability can be safely considered as independent of the ecological factor of interest.

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## Appendix

List of the 97 species used in the analysis

Scientific name	Vocal	Time-of-day	Cloudiness	Rain	Wind	Visibility
<i>Aegithalos caudatus</i>	0	0.118 ± 0.062	0.059 ± 0.068	-0.109 ± 0.076	0.01 ± 0.065	-0.04 ± 0.062
<i>Alauda arvensis</i>	1	0.093 ± 0.018	0.018 ± 0.02	-0.038 ± 0.023	0.015 ± 0.018	-0.024 ± 0.019
<i>Alectoris rufa</i>	1	-0.053 ± 0.08	-0.021 ± 0.084	0.144 ± 0.07	-0.362 ± 0.097	-0.067 ± 0.071
<i>Anthus campestris</i>	1	-0.158 ± 0.083	-0.366 ± 0.114	-5.477 ± 314	-0.075 ± 0.083	5.693 ± 292
<i>Anthus pratensis</i>	1	-0.247 ± 0.08	-0.197 ± 0.089	-0.061 ± 0.094	0.386 ± 0.065	-0.022 ± 0.084
<i>Anthus trivialis</i>	1	0.042 ± 0.037	0.005 ± 0.04	-0.136 ± 0.05	-0.078 ± 0.04	-0.032 ± 0.036
<i>Apus apus</i>	0	0.188 ± 0.094	-0.591 ± 0.162	0.27 ± 0.093	0.089 ± 0.098	-0.088 ± 0.138
<i>Burhinus oedicnemus</i>	1	0.083 ± 0.129	-0.029 ± 0.146	0.167 ± 0.115	-0.47 ± 0.167	-0.144 ± 0.111
<i>Buteo buteo</i>	0	0.158 ± 0.059	-0.059 ± 0.068	-0.15 ± 0.096	-0.094 ± 0.066	0.064 ± 0.074
<i>Carduelis cannabina</i>	1	0.127 ± 0.047	-0.032 ± 0.054	0.04 ± 0.048	0.092 ± 0.045	-0.001 ± 0.05
<i>Carduelis carduelis</i>	1	0.02 ± 0.034	-0.017 ± 0.037	-0.002 ± 0.035	-0.018 ± 0.034	-0.017 ± 0.035
<i>Carduelis chloris</i>	1	-0.096 ± 0.026	-0.006 ± 0.027	-0.003 ± 0.025	-0.015 ± 0.026	0.027 ± 0.027
<i>Certhia brachyactyla</i>	1	-0.092 ± 0.031	0 ± 0.032	-0.013 ± 0.032	-0.103 ± 0.034	-0.023 ± 0.029
<i>Certhia familiaris</i>	1	-0.17 ± 0.111	-0.294 ± 0.134	-0.116 ± 0.151	0.366 ± 0.104	-0.178 ± 0.098
<i>Cettia cetti</i>	1	-0.557 ± 0.086	-0.003 ± 0.085	0.034 ± 0.073	-0.003 ± 0.076	-0.205 ± 0.061
<i>Cisticola juncidis</i>	1	-0.038 ± 0.064	-0.028 ± 0.075	-0.188 ± 0.101	-0.05 ± 0.062	-0.201 ± 0.06
<i>Coccothraustes coccothraustes</i>	0	-0.202 ± 0.093	0.183 ± 0.087	-0.152 ± 0.112	-0.278 ± 0.114	-0.077 ± 0.07
<i>Columba livia</i>	1	-0.208 ± 0.086	-0.369 ± 0.122	0.117 ± 0.075	0.066 ± 0.094	-0.094 ± 0.112
<i>Columba oenas</i>	1	-0.082 ± 0.189	-0.178 ± 0.218	-0.25 ± 0.4	-0.308 ± 0.251	-0.054 ± 0.213
<i>Columba palumbus</i>	1	-0.107 ± 0.021	0.008 ± 0.023	0.015 ± 0.021	-0.074 ± 0.022	-0.006 ± 0.022
<i>Corvus corone</i>	0	0.021 ± 0.036	-0.005 ± 0.039	0.021 ± 0.036	-0.01 ± 0.036	-0.005 ± 0.036
<i>Corvus frugilegus</i>	0	0.207 ± 0.141	-0.442 ± 0.22	0.115 ± 0.186	0.074 ± 0.14	-0.009 ± 0.207
<i>Corvus monedula</i>	0	0.249 ± 0.104	-0.166 ± 0.129	0.116 ± 0.106	-0.216 ± 0.126	-0.118 ± 0.112

## Appendix continued

Scientific name	Vocal	Time-of-day	Cloudiness	Rain	Wind	Visibility
<i>Coturnix coturnix</i>	1	-0.278 ± 0.071	0.031 ± 0.075	-0.036 ± 0.094	-0.007 ± 0.063	-0.26 ± 0.121
<i>Cuculus canorus</i>	1	-0.09 ± 0.035	-0.074 ± 0.038	0.015 ± 0.035	-0.131 ± 0.039	-0.153 ± 0.029
<i>Delichon urbicum</i>	0	-0.073 ± 0.132	-0.338 ± 0.179	-0.425 ± 0.403	-0.207 ± 0.157	-0.104 ± 0.166
<i>Dendrocopos major</i>	1	-0.038 ± 0.032	0.057 ± 0.034	-0.058 ± 0.039	-0.169 ± 0.037	0.036 ± 0.035
<i>Dendrocopos medius</i>	1	0.15 ± 0.073	-0.137 ± 0.081	-0.399 ± 0.18	-0.289 ± 0.105	-0.31 ± 0.051
<i>Dendrocopos minor</i>	1	0.073 ± 0.118	-0.014 ± 0.13	-0.015 ± 0.132	-0.218 ± 0.141	0.004 ± 0.127
<i>Dryocopos martius</i>	1	-0.063 ± 0.121	0.133 ± 0.123	0.012 ± 0.123	-0.019 ± 0.131	0.112 ± 0.141
<i>Emberiza cia</i>	1	-0.291 ± 0.163	0.283 ± 0.157	-0.318 ± 0.226	-0.045 ± 0.164	-0.111 ± 0.135
<i>Emberiza cirulus</i>	1	-0.066 ± 0.039	-0.117 ± 0.043	0.046 ± 0.04	-0.071 ± 0.039	0.003 ± 0.04
<i>Emberiza citrinella</i>	1	-0.047 ± 0.027	-0.013 ± 0.029	-0.028 ± 0.031	0.007 ± 0.026	0.018 ± 0.028
<i>Emberiza hortulana</i>	1	0.234 ± 0.168	-0.19 ± 0.228	-5.607 ± 623	0.213 ± 0.164	-0.081 ± 0.213
<i>Erethacus rubecula</i>	1	-0.08 ± 0.015	0.036 ± 0.016	-0.01 ± 0.015	0.005 ± 0.016	-0.002 ± 0.015
<i>Falco tinnunculus</i>	0	0.116 ± 0.062	0.046 ± 0.068	0.017 ± 0.066	0.068 ± 0.06	0.096 ± 0.075
<i>Fringilla coelebs</i>	1	0.044 ± 0.01	0.02 ± 0.011	0.015 ± 0.01	0.01 ± 0.01	0.021 ± 0.011
<i>Galerida cristata</i>	1	-0.117 ± 0.103	-0.459 ± 0.133	-5.375 ± 265.9	-0.576 ± 0.15	-0.193 ± 0.092
<i>Garrulus glandarius</i>	0	0.041 ± 0.035	-0.089 ± 0.039	0.019 ± 0.037	-0.05 ± 0.038	0.08 ± 0.041
<i>Hippolais polyglotta</i>	1	-0.128 ± 0.036	-0.117 ± 0.043	-0.023 ± 0.047	-0.061 ± 0.037	-0.063 ± 0.041
<i>Hirundo rustica</i>	0	0.341 ± 0.043	0.138 ± 0.048	0.034 ± 0.042	-0.164 ± 0.048	0.076 ± 0.051
<i>Jynx torquilla</i>	1	0.052 ± 0.124	-0.307 ± 0.149	0.062 ± 0.127	-0.125 ± 0.138	-0.093 ± 0.114
<i>Lanius collurio</i>	0	0.17 ± 0.068	-0.108 ± 0.093	-0.006 ± 0.105	-0.136 ± 0.076	0.119 ± 0.125
<i>Locustella naevis</i>	1	-0.123 ± 0.107	0.063 ± 0.106	-0.039 ± 0.101	-0.01 ± 0.104	-0.116 ± 0.084
<i>Lullula arborea</i>	1	0.067 ± 0.048	-0.131 ± 0.055	0.042 ± 0.054	-0.159 ± 0.053	0.058 ± 0.056
<i>Luscinia megarhynchos</i>	1	-0.193 ± 0.023	-0.064 ± 0.024	0.011 ± 0.023	-0.078 ± 0.023	-0.039 ± 0.021
<i>Merops apiaster</i>	0	1.182 ± 0.15	-0.454 ± 0.272	-5.473 ± 629	-0.613 ± 0.287	0.167 ± 0.375
<i>Militaria calandra</i>	1	-0.028 ± 0.039	-0.007 ± 0.043	0.004 ± 0.046	-0.015 ± 0.037	-0.017 ± 0.041



## Appendix continued

Scientific name	Vocal	Time-of-day	Cloudiness	Rain	Wind	Visibility
<i>Mibvus migrans</i>	0	-0.207 ± 0.139	-0.141 ± 0.153	0.142 ± 0.117	0.046 ± 0.128	0.158 ± 0.177
<i>Motacilla alba</i>	1	-0.011 ± 0.041	0.062 ± 0.043	0.047 ± 0.036	0.016 ± 0.039	-0.001 ± 0.041
<i>Motacilla flava</i>	1	-0.031 ± 0.05	0.035 ± 0.054	-0.075 ± 0.068	0.008 ± 0.046	0.055 ± 0.059
<i>Muscicapa striata</i>	0	0.286 ± 0.104	-0.467 ± 0.167	-5.22 ± 299.411	-0.082 ± 0.126	0.067 ± 0.199
<i>Oenanthe oenanthe</i>	0	0.192 ± 0.085	-0.046 ± 0.098	0.065 ± 0.084	-0.073 ± 0.09	-0.216 ± 0.064
<i>Oriolus oriolus</i>	1	-0.017 ± 0.045	-0.051 ± 0.051	0.005 ± 0.054	-0.113 ± 0.049	0.132 ± 0.063
<i>Parus ater</i>	1	0.175 ± 0.041	-0.082 ± 0.051	0.05 ± 0.047	0.09 ± 0.047	0.031 ± 0.047
<i>Parus caeruleus</i>	1	0.03 ± 0.019	-0.018 ± 0.02	-0.015 ± 0.02	-0.037 ± 0.02	0.028 ± 0.02
<i>Parus cristatus</i>	0	0.243 ± 0.061	-0.04 ± 0.077	-0.29 ± 0.144	-0.05 ± 0.079	-0.08 ± 0.071
<i>Parus major</i>	1	-0.025 ± 0.015	0.027 ± 0.016	0.028 ± 0.014	-0.095 ± 0.016	0.041 ± 0.016
<i>Parus montanus</i>	1	-0.045 ± 0.114	0.067 ± 0.128	0.117 ± 0.095	-0.028 ± 0.122	0.141 ± 0.096
<i>Parus palustris</i>	1	0.109 ± 0.062	0.122 ± 0.066	0.019 ± 0.063	-0.274 ± 0.08	0.001 ± 0.062
<i>Passer domesticus</i>	0	0.001 ± 0.021	-0.092 ± 0.024	0.072 ± 0.02	0.028 ± 0.021	0.028 ± 0.025
<i>Passer montanus</i>	0	-0.246 ± 0.104	-0.343 ± 0.125	0.067 ± 0.12	-0.207 ± 0.112	-0.165 ± 0.093
<i>Perdix perdix</i>	0	0.012 ± 0.058	0.074 ± 0.062	0.013 ± 0.065	-0.087 ± 0.057	0.003 ± 0.061
<i>Phasianus colchicus</i>	1	-0.286 ± 0.061	-0.053 ± 0.061	0.02 ± 0.059	-0.085 ± 0.06	-0.009 ± 0.056
<i>Phoenicurus ochruros</i>	1	-0.06 ± 0.031	-0.004 ± 0.033	0.047 ± 0.029	-0.116 ± 0.033	0.118 ± 0.038
<i>Phoenicurus phoenicurus</i>	1	0.027 ± 0.057	-0.13 ± 0.066	-0.085 ± 0.075	-0.062 ± 0.063	-0.001 ± 0.063
<i>Phylloscopus bonelli</i>	1	0.091 ± 0.05	-0.254 ± 0.064	0.034 ± 0.066	-0.249 ± 0.066	0.018 ± 0.061
<i>Phylloscopus collybita</i>	1	-0.006 ± 0.015	0.031 ± 0.016	-0.053 ± 0.016	0.007 ± 0.016	-0.013 ± 0.015
<i>Phylloscopus sibilatrix</i>	1	-0.014 ± 0.108	0.175 ± 0.109	0.118 ± 0.098	-0.348 ± 0.146	0.092 ± 0.118
<i>Phylloscopus trochilus</i>	1	0.223 ± 0.047	0.243 ± 0.05	-0.149 ± 0.059	-0.063 ± 0.054	-0.075 ± 0.044
<i>Pica pica</i>	0	-0.045 ± 0.032	-0.005 ± 0.035	-0.064 ± 0.039	-0.046 ± 0.033	0.003 ± 0.037
<i>Picus viridis</i>	1	-0.002 ± 0.039	-0.001 ± 0.042	0.041 ± 0.036	-0.101 ± 0.042	-0.015 ± 0.038
<i>Prunella modularis</i>	1	-0.058 ± 0.028	-0.048 ± 0.03	0.023 ± 0.026	0.076 ± 0.027	-0.027 ± 0.027

## Appendix continued

Scientific name	Vocal	Time-of-day	Cloudiness	Rain	Wind	Visibility
<i>Pyrrhula pyrrhula</i>	0	0.098 ± 0.077	0.012 ± 0.087	0.02 ± 0.08	0.014 ± 0.082	0.003 ± 0.082
<i>Regulus ignicapillus</i>	1	-0.013 ± 0.051	-0.028 ± 0.056	0.078 ± 0.046	-0.147 ± 0.06	-0.056 ± 0.047
<i>Regulus regulus</i>	1	0.028 ± 0.054	-0.041 ± 0.062	0.061 ± 0.057	-0.157 ± 0.066	0.055 ± 0.06
<i>Saxicola rubetra</i>	1	-0.275 ± 0.113	-0.238 ± 0.129	-0.042 ± 0.139	0.112 ± 0.1	0.072 ± 0.132
<i>Saxicola torquatus</i>	1	0.024 ± 0.039	-0.009 ± 0.042	0.059 ± 0.039	-0.092 ± 0.039	0.028 ± 0.041
<i>Serinus serinus</i>	1	-0.09 ± 0.036	-0.016 ± 0.038	-0.024 ± 0.038	-0.053 ± 0.037	-0.016 ± 0.037
<i>Sitta europaea</i>	1	0.058 ± 0.034	-0.034 ± 0.038	-0.095 ± 0.048	-0.141 ± 0.04	0.052 ± 0.041
<i>Streptopelia decaocto</i>	1	-0.064 ± 0.025	0.029 ± 0.026	0.042 ± 0.022	-0.092 ± 0.026	-0.001 ± 0.025
<i>Streptopelia turtur</i>	1	-0.014 ± 0.032	0.015 ± 0.035	-0.085 ± 0.042	-0.072 ± 0.033	-0.064 ± 0.035
<i>Sturnus vulgaris</i>	1	0.025 ± 0.045	0.117 ± 0.048	0.039 ± 0.04	-0.03 ± 0.045	-0.075 ± 0.043
<i>Sylvia atricapilla</i>	1	-0.019 ± 0.011	0.009 ± 0.011	-0.008 ± 0.011	-0.037 ± 0.011	0.016 ± 0.011
<i>Sylvia borin</i>	1	0.06 ± 0.045	0.125 ± 0.049	-0.175 ± 0.067	0.033 ± 0.046	-0.018 ± 0.052
<i>Sylvia cantillans</i>	1	-0.121 ± 0.093	-0.791 ± 0.158	0.456 ± 0.08	-0.235 ± 0.114	0.236 ± 0.158
<i>Sylvia communis</i>	1	0.004 ± 0.028	-0.004 ± 0.031	-0.069 ± 0.035	0.039 ± 0.027	-0.072 ± 0.028
<i>Sylvia curruca</i>	1	0.029 ± 0.128	-0.282 ± 0.166	0.258 ± 0.111	-0.099 ± 0.135	0.215 ± 0.196
<i>Sylvia melanocephala</i>	1	-0.106 ± 0.067	-0.033 ± 0.072	-0.033 ± 0.072	-0.231 ± 0.079	-0.136 ± 0.059
<i>Sylvia undata</i>	1	0.049 ± 0.097	0.188 ± 0.112	-5.568 ± 383	-0.117 ± 0.116	0.261 ± 0.153
<i>Troglodytes troglodytes</i>	1	-0.138 ± 0.014	0.063 ± 0.014	-0.023 ± 0.014	0.025 ± 0.014	0.013 ± 0.014
<i>Turdus merula</i>	1	-0.062 ± 0.011	0.035 ± 0.011	0.029 ± 0.01	-0.044 ± 0.011	-0.003 ± 0.011
<i>Turdus philomelos</i>	1	-0.141 ± 0.023	0.097 ± 0.023	-0.046 ± 0.023	-0.029 ± 0.024	-0.036 ± 0.021
<i>Turdus pilaris</i>	1	-0.013 ± 0.137	-0.034 ± 0.152	0.072 ± 0.104	0.34 ± 0.122	-0.252 ± 0.097
<i>Turdus viscivorus</i>	1	-0.023 ± 0.05	-0.13 ± 0.056	0.085 ± 0.044	0.029 ± 0.051	-0.131 ± 0.042
<i>Upupa epops</i>	1	-0.237 ± 0.068	-0.252 ± 0.074	0.021 ± 0.065	0.029 ± 0.064	-0.278 ± 0.046
<i>Vanellus vanellus</i>	0	0.396 ± 0.161	-0.301 ± 0.236	0.234 ± 0.164	-0.321 ± 0.2	-0.022 ± 0.197

Vocal column shows which species have been considered as “vocal” (1) or not (0), i.e. whose detections are mainly due to territorial vocalizations. The last five columns show species response slopes ( $\pm$ SE) to the five weather and time-of-day z-transformed variables in the controlled model

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# MANUSCRIT 8

## **A simple method to assess distance-related biases on counts for animal surveys**

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## Summary

1. Methods for estimating probability of detection have recently proliferated. However, they entail disproportionate sampling intensity and force ecologists to study only a few species or to sample only a few sites. Moreover, most of these methods seem unable to correct widespread distance-related biases. In this context, the present study proposes a simple and widely applicable method to measure and correct such biases.
2. The principle is to analyse variations of the ratio between close detections and distant detections against the ecological factor of interest. We tested this method on auditory counts of song birds and counts of bat passes on high sample-rate recordings. We then assessed on these counts the possible bias produced by spatial variations in vegetation density.
3. Understorey cover had a strong effect on birds song detectability, reducing the probability of a contact to be distant (beyond 50m from the observer) from 0.7 for sparse understorey to less than 0.5 for dense understorey.
4. We detected no effect of vegetation cover on detectability of bat passes, and confidence intervals suggest that a strong effect of understorey cover on bats detectability such as observed for birds is unlikely.
5. Synthesis and applications. This analysis shows good evidence of distance-related biases in counts and we give further indications about how to correct the revealed biases. More generally, this article provides a widely applicable method to deal with heterogeneity in detectability in counts, whereas previous approaches seem to fail to correct distance-related biases. We emphasize that the method proposed here does not need any within-site replication, and thus allows ecologists to reallocate their sampling effort to more sites.

## Introduction

Many ecological studies rely on measurements of spatial or temporal variations of species abundance, usually named relative abundance and derived from counts (e.g. Wall et al. 2001; Wheatley et al. 2005; Einum et al. 2008). A recurrent issue of these counts is

that heterogeneity in detectability of individuals in space or time may bias estimates of relative abundance, and lead to erroneous conclusions (Elphick 2008). To circumvent this problem, methods for estimating probability of detection have recently proliferated, and ecologists are under increasing pressure to adapt their sampling design to be able to later implement these methods (Buckland et al. 2001; Royle 2004b; Alldredge et al. 2007a). However, all these methods were built to infer absolute abundance values, whereas only relative abundance estimates are often needed. Looking for unbiased absolute abundance estimates entails excessive sampling intensity in recent study designs and force ecologists to focus on few species and/or to sample few sites (Johnson 2008). These restrictions are frustrating as global change context points out the necessity of monitoring more taxa (Thomas et al. 2004) and the need to do it on a larger scale (Pereira and Cooper 2006). More critically, Efford and Dawson (2009) showed that all these methods except conventional distance sampling were unable to correct widespread biases which are due to heterogeneity in detectability of distant individuals. On that account, ecology is now in need of pragmatic studies determining when and how relative abundance measures can be used for future research (Elphick 2008). In this context, the present study is based on the statement that most heterogeneity in detectability in space or time is distance-related through variations of visual or acoustic properties of habitats, i.e. detectability of individuals close to observers vary much less in space or time than detectability of more distant individuals (Bibby and Buckland 1987; Toms et al. 2006; Pacifici et al. 2008), whereas distance-unrelated heterogeneity is unlikely to bias common ecological studies (Bas et al. 2008). Here we propose a simple and widely applicable method which allows determining if an analysis of abundance variations is biased by distance-related heterogeneity in detectability. The principle is to analyse variations of the ratio between close detections and distant detections against an ecological factor of interest (e.g. time, habitat gradients and types). This method fundamentally differs from conventional distance sampling by using only two distance classes and more importantly by making much fewer assumptions. We used two different case-studies to test our method: (i) auditory counts of song birds and (ii) counts of bat passes on high sample-rate recordings. We used the vegetation density as the ecological factor as it is both a potential factor of interest in forest management and a factor already known to be responsible for heterogeneous detection probability of individuals (at least for song birds: Schieck 1997; Pacifici et al. 2008).

## **Methods**

### **Sampling design**

The study was carried out from 2006 to 2008 in the Ille-et-Vilaine administrative department of France. Within this department, 117 sampling points were randomly selected within forest areas (>100 m from forest edge): 43 in 2006, 47 in 2007 and 27 in 2008. Birds were sampled by a single trained observer (YB) using a point count method (Bibby et al. 1992). We grouped sample points (by four to six) according to their physical proximity. Each group was visited the same morning, during the first four hours after sunrise. Each points group was visited twice in one year: once between the 10<sup>th</sup> May and the 25<sup>th</sup> May and once between the 26<sup>th</sup> May and the 12<sup>th</sup> June. Point groups were sampled in a random sequence for the first visit, and this order was reversed for the second visit. Similarly, within-group order of points was reversed from the first visit to the second visit. We avoided unfavourable weather conditions: neither rain nor strong wind (Beaufort > 4, i.e. wind speed > 28 km/h). A visit consisted of five consecutive periods of 5-minute counts. During these counts, each bird was identified to species and located within one of four distance classes: 0-10 m, 10-25 m, 25-50 m, >50 m. The observer was trained for auditory distance measurement, and used a laser range finder to get the distance of reference points preliminarily to each visit. Attention was focalised on auditory detections, and we distinguished detections which were purely visual, auditory with territorial songs and auditory without territorial songs. For the purpose of this study, we adopted a conservative approach considering only contacts with territorial songs. According to Alldredge et al. (2007c), we considered that individuals were correctly allocated to distance classes as the last class limit (50 m) lied within the range of reliable auditory distance measurement for trained observers.

We sampled the habitat surrounding each point with five circular quadrats of 10-m radius: one centred on the point, the four others 100 m from the point in the four cardinal points direction. We quantified vegetation cover percentage of five horizontal strata (height intervals of 1-2 m, 2-4 m, 4-8 m, 8-16m and >16 m) by estimating vertical projection of leaf area during summer the same year of point bird sampling.

During year 2008, we also sampled bat activity on the center of the five quadrats in 52 of the 117 points. Recordings were performed with a Tranquility Transect bat detector (Courtpan Design Ltd) linked to a Zoom H2 field recorder (Zoom Corporation) at 96 kS/s rate on these 260 quadrats (5x52): during six minutes on the central quadrat and during three minutes on each other quadrats. This high sample rate allowed us to detect echolocation calls of most species because they are emitted below the Nyquist frequency (only three of the 21 local species emit higher calls). Similarly to bird sample design, we grouped points to be visited the same night (between 0.5 h and 3.5 h after sunset) and, to avoid any bias, we visited each point twice: during May and between 15<sup>th</sup> August and 12<sup>th</sup> September. Points sampling orders were also reversed both between groups and within groups. We defined a bat pass as a sequence of echolocation calls supposedly emitted by one individual and not separated by more than one second. We further identified all bat passes on our recordings using Syrinx 2.6 (Burt 2006) and SCAN'R 1.4.2 (Binary Acoustic Technology 2007). Relative sound pressure level (SPL) of all calls were computed using SCAN'R and the SPL of the loudest call (SPL<sub>max</sub>) of all bat passes were determined.



## Vegetation cover indices

For the purpose of this study, we defined vegetation cover with two components which have different ecological effects and management implications: understory cover (UC) and canopy cover (CC). We computed UC as the mean of the cover percentages of the strata 1-2 m and 2-4 m. We computed CC as the mean of the cover percentages of the strata 8-16 m and >16 m. We ignored the vegetation cover measured between 4 and 8 m high because it was strongly correlated to both UC and CC (respectively  $r = 0.53$  and  $r = 0.54$ ). On the contrary, UC and CC were very weakly correlated ( $r = 0.15$ ).

Given that the detection range of most bird songs exceed 50 m, UC and CC were both averaged for the five quadrats around each point for the bird analysis (Schieck 1997). On the contrary, the detection range of the bat signals studied here does not exceed 50 m, thus we used UC and CC measured on the corresponding quadrat for the bat analysis (Holderied and von Helversen 2003).

## Detectability indices

We assessed variations in detectability using variations in the ratio between distant detections (DD) and close detections (CD) as a surrogate. In doing so, we assume that for a given spatial distribution of individuals, this ratio will be constant, regardless the vegetation structure for an observer with homogeneous detectability. Instead, if abundance indices are biased by heterogeneous detectability, DD to CD ratio should be altered by the vegetation structure. For that purpose, we defined a DD (i) for birds, by individuals detected beyond 50 m, (ii) for bat passes by sequence for which  $SPL_{max} < 41.2$  dB (the median value). We used  $SPL_{max}$  as a proxy for distance between recorder and individual. We are aware of the fact that  $SPL_{max}$  is probably biased by vegetation cover, but if vegetation cover decreases sound wave intensity then this effect should increase with distance and the ratio between DD and CD decrease nonetheless. We selected for this analysis the 13 bird species and the two bat species which gathered at least 50 CD and 50 DD (Table 1). For birds, DD proportion varied from 0.22 for the Robin (*Erithacus rubecula*) to 0.86 for the Song Thrush (*Turdus philomelos*) (Table 1). Occurrence among the 117 sites varied between 29% for the Garden Warbler (*Sylvia borin*) to 100% for the Chaffinch (*Fringilla coelebs*) (Table 1).

We further checked whether DD was related to the species-specific song frequency. For each bird species, song minimum frequency and maximum-energy frequency were calculated from a record of a typical song of each species (Roche 2003 - see Table 1). Minimum frequencies and maximum-energy frequencies were strongly correlated ( $r = 0.89$ ), thus we used only maximum-energy frequency as a measure of the species song frequency. A strong correlation between the species maximum-energy frequency and DD proportion ( $r = 0.72$ ) confirms the strong link between this species trait and its song propagation (Schieck 1997). Similarly, we displayed for bats in Table 1 the

average minimum frequencies and maximum-energy frequencies of echolocation calls of both species (Obrist et al. 2004).

## Statistical analysis

We further analysed the effect of vegetation density on detectability by fitting two generalized mixed models accounting for the binomial distribution of errors, one for birds and one for bats. These models were fitted on the whole dataset of contacts: 14602 bird songs and 616 bat passes (Table 1). The fixed formula was for both models:

$$\text{DD probability} \sim \text{species} + \text{UC} + \text{CC} + \text{species:UC} + \text{species:CC}$$

where DD probability was a binomial variable equal to 1 if the corresponding contact fulfilled the Distant Detection criterion (i.e., if the individual was detected in DD range) or 0 if it didn't.

For the models respectively performed for birds and bats, random effects were site and visit nested within site and site and quadrat nested within site. Overall and species-specific effects of UC and CC were tested by Z-tests. Fits and tests were performed with the lmer function of the lme4 package of R 2.5.1 (R Development Core Team 2005; Bates 2007).

## Results

Overall birds DD probability (i.e, the probability of detecting an individual of a given species beyond 50m) significantly decreased with understory cover (UC) (Table 2), from more than 0.7 for sparse understory to less than 0.5 for dense understory (Fig. 1). This effect varied greatly among species. Nevertheless DD probability decreased with increasing UC for 12 out of 13 species (Table 2). There was a weak correlation between these species responses and their song frequency ( $r = 0.19$ ).

Overall birds DD probability did not vary significantly with canopy cover (CC) (Table 2). However, DD probability decreases significantly with canopy cover for four bird species, and increases significantly for two bird species (Table 2). There was a moderate negative correlation between these species responses and their song frequency ( $r = -0.41$ ).

Moreover, there was a moderate negative correlation between species responses to understory cover and species responses to canopy cover ( $r = -0.48$ ).

Overall bats DD did not vary significantly with understorey or canopy cover (Table 2). Confidence intervals suggest that a strong effect of understorey cover on bats DD probability such as observed for birds is unlikely (Fig. 1).

## Discussion

### Vegetation effect assessment

Our results showed that understorey cover decreases the probability of distant detection for birds but not for bats. Results for birds were in accordance with previously shown decreased detectability of broadcasted bird songs in dense vegetation (Schieck 1997; Pacifici et al. 2008). More precisely, Schieck (1997) and Pacifici et al. (2008) found a lower detectability in low dense forests compared to higher mature ones, and this is in further accordance with our results which showed a much more pronounced and univocal effect of understorey cover compared to the canopy cover effect. A first conclusion can be drawn from these results: using bird point counts as relative abundance measure would lead to underestimate the habitat value of forest with dense understorey (e.g. with uneven-aged management) compared to other forest habitats.

We also found that the effect of vegetation on detectability of bird songs was highly variable between species. However the effect of vegetation was not strongly related to the species song frequency, though low song frequencies enhance distant detection probability (Waide and Narins 1988; Schieck 1997). Actually, vegetation could decrease detectability through two physical phenomena : (i) decreased sound intensity through absorption of sound waves and (ii) sound alteration through interference from reflected sound waves (Wiley and Richardson 1982). We suggest that vegetation effect is mainly acting on detection through sound alteration because of two elements in our results. Firstly, vegetational absorption of sound waves should increase with song frequency (Boncoraglio and Saino 2007), thus if sound absorption could explain our results, the vegetation effect on detectability should have been related to species song frequency. Secondly, decreased intensity of sound waves through vegetational absorption should decrease the detectability of both bat signals and bird songs. However, sound alteration could prevent the observer from detecting the determinant elements of complex bird songs without decreasing the detectability of bat signals on recordings. Moreover, this assertion is supported by Patriquin et al. (2003) who found a non-linear effect of vegetation on detectability of broadcasted 25kHz ultra-sounds: thinned forest enhanced detection of these signals compared to clearings and dense forest. We acknowledge that our approach prevent us from detecting such non-linear effect of vegetation on

detectability of bats, and according to them detection radius of these signals should vary  $\pm 6\%$  with vegetation structure.

Besides, the particularly strong vegetation effect found for *Sylvia borin*, a species known to sing in low vegetation (Cramp and Perrins 1994), suggests that the height of song post could explain much of the effect variation between bird species (Mathevon et al. 1996). It leads us to suppose that the availability of high song post could decrease the vegetation effect, and this could explain (i) why the effect of canopy cover was significantly positive for two species and (ii) why the effect of canopy cover was negatively correlated to the effect of understorey cover among the 13 species.

## **A wide applicability**

More importantly, we stress the point that the main goal of this study is not to evaluate vegetation effect on detectability but to provide a widely applicable method to ecologists who want to study variation in abundance across diverse factors. Consequently, we strongly recommend that ecologists preliminarily check if there is any relationship between distant detection probability and their explanatory variables, before analysing their counts as relative abundance measures. This method is here tested for detection involving sound cues but we are confident about its application for visual counts, providing that a range of close contacts can be unambiguously discriminated from more distant contacts. Generally speaking, the only prerequisite of this method is the availability of a criterion distinguishing close detections to more distant ones.

However, we acknowledge that in two particular cases our method can be unable to detect habitat-induced biases on counts. First, habitat can act on elements of the detection process which are unrelated to distance, i.e. the probability of the cues allowing detection to be produced. For example, it seems that bird song rate could be influenced by habitat type (McShea and Rappole 1997). Secondly, our method can be biased by movement responses of individuals to observer presence if these responses vary with the studied ecological factor (e.g. time, habitat gradients or types). These aspects must therefore be cautiously examined before using our method.

If a detectability bias is found through the method proposed, ecologists should either take into account this bias when interpreting their results or attempt to correct this bias by estimating relative detectability of individuals across the studied factor. This could be difficult given the fact that existing methods seem either to not allow effective correction of distance-related bias or to suffer from assumptions too difficult to meet in the field (Efford and Dawson 2009). Yet, we argue that our method can be adapted to estimate relative detectability by doing one additional assumption. When using distance criterion to distinguish close and distant contacts, it is necessary to assume that detectability is constant in time and/or space within the "Close Detection" range. Relative detectability can thus be described as a simple function of the calculated DD probability :  $1 + (\text{DD probability} / (1 - \text{DD probability}))$ . Assuming that detectability is constant in

space within the "Close Detection" range, we can deduce from Table 1 that overall probability of detecting individual birds decrease by 47 % from sparse understorey to dense understorey. The same calculation specifically performed for *Sylvia borin* show that the detection probability of individuals of this species decrease by 83 % along the understorey gradient.

This assumption should be met with a 50 meters distance for most song birds (Schieck 1997), and can be reduced to a closer distance for species with short range songs (Pacifici et al. 2008).

However, when using sound intensity criterion to distinguish close and distant contacts, it should be more difficult to infer true detection probability because sound intensity is not only related to distance but also to habitat structures absorbing sound waves. However, the use of several microphones to locate the individuals should get round this problem (Jensen and Miller 1999).

In conclusion, this article provides a simple framework to deal with heterogeneity in detectability in counts, whereas previous approaches seem to fail to correct distance-related biases (Efford and Dawson 2009). Moreover, we emphasize that the method proposed here does not need any within-site replication: neither temporal replication nor the use of multiple observers. As a consequence, ecologists will be able to reallocate their sampling effort to more sites, therefore increasing the probability of revealing ecological patterns.

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**Table 1. List of the 13 bird species and the two bat species used in this study.** Distant contacts refer for birds to individuals detected beyond 50m from the observer, and for bats to recorded bat passes not containing any call with Sound Pressure Level > 41.2 dB. Occurrence refers to the proportion of sites where the species occurred.

species	Total number of contacts	Proportion of distant contacts	Occurrence	Minimum frequency (Hz)	Maximum-energy frequency (Hz)
<i>Certhia brachydactyla</i>	448	0.38	0.70	4530	6420
<i>Columba palumbus</i>	1097	0.80	0.97	270	470
<i>Erithacus rubecula</i>	2110	0.22	0.99	2010	4280
<i>Fringilla coelebs</i>	2943	0.55	1.00	1620	2880
<i>Parus major</i>	259	0.68	0.67	3090	4220
<i>Phylloscopus collybita</i>	1505	0.48	0.93	2450	4110
<i>Phylloscopus sibilatrix</i>	338	0.54	0.36	2460	6130
<i>Streptopelia turtur</i>	325	0.81	0.46	390	470
<i>Sylvia atricapilla</i>	1349	0.57	0.98	1740	3960
<i>Sylvia borin</i>	134	0.57	0.25	1450	3040
<i>Troglodytes troglodytes</i>	2102	0.49	0.99	2310	5060
<i>Turdus merula</i>	1112	0.79	0.97	1110	2220
<i>Turdus philomelos</i>	440	0.86	0.68	1500	2390
<i>Barbastella barbastellus</i>	179	0.38	0.38	25700	36000
<i>Pipistrellus pipistrellus</i>	437	0.65	0.77	42600	47400

Table 2. Slope responses ( $\times 10^2$ ) of the effects of understorey and canopy cover on distant detection (DD) probability, and their associated p-value.

	Response to understorey cover		Response to canopy cover	
	Slope $\pm$ SE	p-value	Slope $\pm$ SE	p-value
Birds (overall)	<b>-1.52 <math>\pm</math> 0.34</b>	<b>&lt;10<sup>-3</sup></b>	-0.16 $\pm$ 0.24	0.51
Certhia brachydactyla	-0.35 $\pm$ 0.83	0.67	-0.85 $\pm$ 0.69	0.22
Columba palumbus	<b>-1.68 <math>\pm</math> 0.64</b>	<b>0.009</b>	0.09 $\pm$ 0.48	0.85
Erithacus rubecula	<b>-1.11 <math>\pm</math> 0.51</b>	<b>0.032</b>	<b>-0.85 <math>\pm</math> 0.38</b>	<b>0.026</b>
Fringilla coelebs	-0.03 $\pm$ 0.43	0.95	<b>-0.75 <math>\pm</math> 0.32</b>	<b>0.020</b>
Parus major	-1.67 $\pm$ 0.97	0.085	<b>-1.59 <math>\pm</math> 0.78</b>	<b>0.043</b>
Phylloscopus collybita	<b>-1.37 <math>\pm</math> 0.51</b>	<b>0.007</b>	<b>1.13 <math>\pm</math> 0.38</b>	<b>0.003</b>
Phylloscopus sibilatrix	<b>-2.20 <math>\pm</math> 1.02</b>	<b>0.031</b>	-1.23 $\pm$ 0.83	0.14
Streptopelia turtur	-2.10 $\pm$ 1.20	0.079	<b>2.83 <math>\pm</math> 0.87</b>	<b>0.001</b>
Sylvia atricapilla	<b>-1.86 <math>\pm</math> 0.54</b>	<b>&lt;10<sup>-3</sup></b>	-0.12 $\pm$ 0.39	0.76
Sylvia borin	<b>-5.01 <math>\pm</math> 1.56</b>	<b>0.001</b>	1.47 $\pm$ 0.98	0.14
Troglodytes troglodytes	-0.15 $\pm$ 0.48	0.76	0.03 $\pm$ 0.34	0.93
Turdus merula	0.10 $\pm$ 0.68	0.88	<b>-1.86 <math>\pm</math> 0.48</b>	<b>&lt;10<sup>-3</sup></b>
Turdus philomelos	<b>-2.26 <math>\pm</math> 0.99</b>	<b>0.022</b>	-0.74 $\pm$ 0.75	0.33
Bats (overall)	-0.34 $\pm$ 0.81	0.67	0.53 $\pm$ 0.61	0.38
Barbastella barbastellus	-0.46 $\pm$ 1.14	0.69	0.14 $\pm$ 0.97	0.88
Pipistrellus pipistrellus	-0.23 $\pm$ 0.84	0.79	-0.91 $\pm$ 0.06	0.14

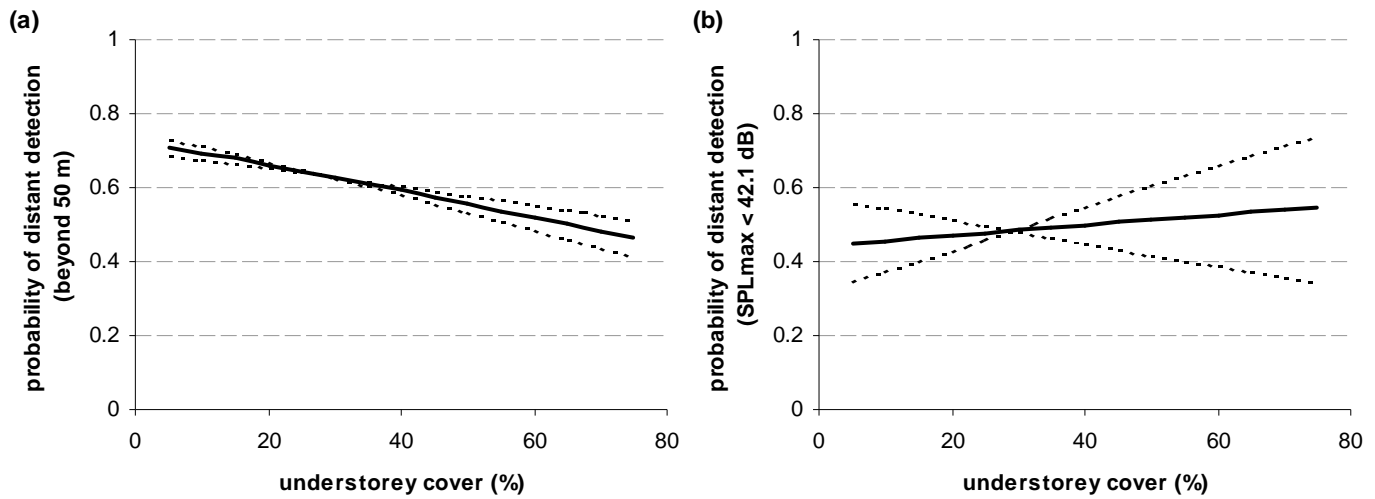


Figure 1. Fitted effect of understory cover on the probability of distant detection (DD), i.e. for birds (a) to be contacted beyond 50m, and for bat passes (b) not to contain a call with SPL > 41.2 dB. This fit is adjusted to the effects of species and canopy cover. Dotted lines show 95% confidence interval of the slope.