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L'UNIVERSITÉ DE BORDEAUX**

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**SPÉCIALITÉ ÉCOLOGIE ÉVOLUTIVE, FONCTIONNELLE ET DES
COMMUNAUTÉS**

Par Laura SCHILLÉ

**DIVERSITÉ DES OISEAUX ET RÉGULATION DE L'HERBIVORIE SUR LES
ARBRES : EFFETS DU CLIMAT ET DE L'URBANISATION À DIFFÉRENTES
ÉCHELLES**

Sous la direction de : Bastien CASTAGNEYROL & Luc BARBARO

Soutenue le 04/11/2024

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Titre : Diversité des oiseaux et régulation de l'herbivorie sur les arbres : effets du climat et de l'urbanisation à différentes échelles

Résumé :

Les oiseaux insectivores contribuent activement à la régulation des populations d'insectes herbivores. Ils jouent ainsi un rôle essentiel dans la dynamique des écosystèmes terrestres. La théorie suggère que la diversité des communautés d'oiseaux covarie avec le nombre de fonctions qu'elles remplissent, car des communautés plus diversifiées explorent des espaces fonctionnels plus larges et utilisent ainsi mieux les ressources disponibles. Cependant, les changements globaux pourraient modifier cette relation. La question est alors de savoir s'ils impactent de la même manière la structure des communautés d'oiseaux et les fonctions qu'elles assurent, ou si au contraire ces variables réagissent différemment. De plus, les patrons biogéographiques peuvent être localement altérés par des facteurs biotiques et abiotiques. Ainsi, cette combinaison de facteurs agissant à différentes échelles peut modifier la cascade tri-trophique, en agissant de manière indépendante, antagoniste ou synergique, sur les communautés d'oiseaux, celles des herbivores et les caractéristiques des arbres sur lesquelles ils s'alimentent.

Cette thèse avait pour objectif principal d'explorer les effets de l'augmentation des températures et de l'urbanisation, en interaction avec les facteurs locaux tels que la quantité et la diversité des habitats forestiers, sur la relation entre la diversité et la fonction de prédation des oiseaux insectivores. A cette fin, nous avons travaillé à plusieurs échelles emboîtées, depuis l'arbre et son voisinage immédiat jusqu'à l'échelle continentale. Nous avons employé des méthodes innovantes s'appuyant sur l'écologie acoustique, les sciences participatives et les algorithmes de reconnaissance automatisée pour caractériser les communautés d'oiseaux de manière standardisée et à grande échelle et nous avons développé des approches expérimentales pour évaluer la reproductibilité de ces approches.

Nos résultats indiquent que l'augmentation des températures et l'urbanisation ont un impact significatif, respectivement positif et négatif, sur la diversité taxonomique et fonctionnelle des communautés d'oiseaux insectivores. Cependant, nous avons observé un découplage entre la structure de ces communautés et les fonctions écosystémiques associées, en réponse à ces changements. Ceci plaide pour une reconsidération de la portée générale de la théorie liant la diversité des communautés au nombre de fonctions qu'elles remplissent. De plus, la quantité et la diversité d'habitats forestiers sont des facteurs locaux qui modulent les facteurs climatiques et urbains. Ces derniers structurent les communautés d'oiseaux et les cascades tri-trophiques qu'elles initient à plus large échelle. Enfin, nos travaux ont permis une avancée dans le développement des méthodes permettant l'étude de la dynamique de la biodiversité et de ses fonctions.

Mots clés : Interactions tri-trophiques ; Prédation ; Urbanisation ; Ecologie acoustique ; Ecologie fonctionnelle ; Ecologie des communautés ; Forêt

Title: Top-down control of birds on insect herbivory in trees: effects of climate and urbanization at multiple scales

Abstract:

Insectivorous birds actively contribute to the regulation of herbivorous insect populations, thus playing a key role in terrestrial ecosystem dynamics. The theory suggests that bird community diversity covaries with the number of functions they perform, as communities that are more diverse explore broader functional spaces and utilize available resources more effectively. However, global changes might alter this relationship. The question then becomes whether these changes affect the structure of bird communities and their associated functions similarly, or if these variables respond differently. Additionally, biogeographical patterns may be locally altered by biotic and abiotic factors. Thus, this combination of factors operating at different scales can modify the tri-trophic cascade, acting independently, antagonistically, or synergistically on bird communities, herbivore communities, and the characteristics of the trees they feed on.

The main objective of this thesis was to explore the effects of increasing temperatures and urbanization, in interaction with local factors such as the quantity and diversity of forest habitats, on the relationship between diversity and predation function of insectivorous birds. To this end, we worked at multiple nested scales, from the tree and its immediate surroundings to the continental scale. We employed innovative methods based on acoustic ecology, citizen science, and automated recognition algorithms to characterize bird communities in a standardized and large-scale manner, and we developed experimental approaches to assess the reproducibility of these methods.

Our results indicate that increasing temperatures and urbanization have significant impacts—positive and negative, respectively—on the taxonomic and functional diversity of insectivorous bird communities. However, we observed a decoupling between community structure and associated ecosystem functions in response to these changes. This suggests a need to reconsider the general applicability of the theory linking community diversity to the number of functions they perform. Furthermore, the quantity and diversity of forest habitats are local factors that modulate the effects of climate and urban factors, which structure bird communities and the tri-trophic cascades they initiate on a larger scale. Finally, our work has contributed to advancing methods for studying biodiversity dynamics and its functions.

Keywords: Tri-trophic interactions; Predation; Urbanization; Acoustic ecology; Functional ecology; Community ecology; Forest

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Table des matières

1. Introduction	1
1.1. Biodiversité des communautés d'oiseaux et cascade trophique	2
1.2. Comment les changements globaux affectent la cascade trophique oiseaux insectivores - insectes herbivores - arbres ?	5
1.3. Quelles méthodes standardisées pour la caractérisation des communautés et des interactions trophiques à large échelle ?	9
1.4. Problématique de la thèse.....	13
Références	16
2. Chapitre 1 : Décomposition des facteurs influençant l'insectivorie avienne : effets à grande échelle du climat, de l'habitat et de la diversité des oiseaux.....	24
Abstract	25
2.1. Introduction	26
2.2. Materials and Methods	29
2.3. Results	38
2.4. Discussion.....	42
References	48
Supplementary materials.....	56
3. Chapitre 2 : La diversité des arbres en ville favorise l'insectivorie malgré une diminution de la diversité des communautés d'oiseaux due à l'urbanisation.	65
Abstract	66
3.1. Introduction	67
3.2. Material and Methods.....	69
3.3. Results	76
3.4. Discussion.....	81
References	85
Supplementary materials.....	90
4. Chapitre 3 : Evaluation par pièges photographiques de la méthode des chenilles en pâte à modeler pour quantifier la prédation des oiseaux.....	93
Abstract	94
4.1. Introduction	95
4.2. Material and Methods.....	98
4.3. Results	105
4.4. Discussion.....	109
References	116
Supplementary materials.....	120

5. Chapitre 4: La variabilité intraspécifique des traits acoustiques des oiseaux affecte-t-elle la performance de l'algorithme BirdNET?	127
Abstract	128
5.1. Introduction	129
5.2. Material and methods.....	132
5.3. Results	143
5.4. Discussion.....	145
References	149
Supplementary material	154
6. Discussion	155
6.1. Vers une compréhension détaillée des cascades trophiques par la caractérisation de l'ensemble des niveaux trophiques impliqués	157
6.2. Quelles sont réellement les espèces d'oiseaux qualifiées d'ennemies naturelles et sont-elles différentes selon les habitats considérés?.....	163
6.3. Les risques inhérents à l'utilisation de <i>proxys</i> en sciences	167
6.4. Les enjeux de la reproductibilité en écologie	173
6.5. Conclusion	177
Références	179
7. Annexes	186
7.1. Annexe A1. Évaluer le potentiel de BirdNET pour caractériser les communautés d'oiseaux européennes à partir de données écoacoustiques à grande échelle.	187
7.2. Annexe A2. Évaluation des performances des algorithmes de reconnaissance automatisée des chants d'oiseaux dans divers paysages sonores anthropisés.....	198
7.3. Annexe A3. Bande dessinée « Les gardiens des arbres ».....	214

1. Introduction

1.1. Biodiversité des communautés d'oiseaux et cascade trophique

1.1.1. La biodiversité des oiseaux en déclin

Les populations d'oiseaux déclinent à l'échelle globale (Bowler et al., 2019; Rosenberg et al., 2019; Spiller & Dettmers, 2019). Cette érosion de la biodiversité avifaunistique se manifeste à plusieurs niveaux. L'abondance des oiseaux en Europe a chuté de 25% en près de 40 ans, soit une perte d'environ 800 millions d'individus depuis 1980. Leur distribution est également affectée, leur déclin étant plus prononcé aux hautes latitudes qu'aux basses latitudes, et pour les milieux agricoles que pour les milieux forestiers ou urbains (Rigal et al., 2023). La diversité taxonomique est touchée, certaines espèces subissant un déclin allant jusqu'à 75%, comme le *Moineau friquet*, le *Tarier des prés* ou le *Pipit farlouse* (Rigal et al., 2023). Cela entraîne également une diminution concomitante de diversité fonctionnelle (Devictor et al., 2008). Enfin, une étude récente a mis en évidence une perte généralisée de diversité acoustique en Europe et en Amérique du Nord au cours des 25 dernières années (Morrison et al., 2021). **Cette érosion de la biodiversité des oiseaux est multifactorielle, les causes principales étant les changements globaux, notamment l'augmentation des températures** (Both et al., 2006; McClure et al., 2012), **l'intensification agricole** (Donald et al., 2001) **et l'urbanisation croissante** (Devictor et al., 2007; Lim & Sodhi, 2004).

La biodiversité, notamment celle des oiseaux, a une valeur intrinsèque qui mérite d'être considérée indépendamment de toute utilité pour les humains (Silvertown, 2015). **Toutefois, pour mieux illustrer leur importance au sein des écosystèmes, les oiseaux sauvages sont aussi souvent cités pour la multitude de services écosystémiques qu'il fournissent**, et qui s'inscrivent dans les quatre catégories définies par l'Évaluation des écosystèmes pour le millénaire (*Millenium Ecosystem Assessment*, Reid & Raudsepp-Hearne, 2005). Ils contribuent aux services d'approvisionnement par leur chair, qui est consommée, et leurs plumes, utilisées comme isolant dans la literie et les vêtements (Whelan et al., 2008). Ils fournissent également des services culturels, l'observation des oiseaux étant une activité récréative très populaire à travers le monde (Sekercioglu, 2002). Plusieurs études ont montré que le chant des oiseaux, particulièrement lorsqu'il provient de plusieurs espèces, améliore le bien-être humain

(Ferraro et al., 2020; Hedblom et al., 2014). Enfin, les services de régulation et de soutien incluent la pollinisation, la dispersion des graines, la régulation des ravageurs, et celle des cycles biogéochimiques notamment via l'élimination des carcasses (Whelan et al., 2015). En raison de leur contribution aux services de régulation et de soutien, en plus de leur sensibilité aux changements environnementaux et de leur présence répandue, les oiseaux sont considérés comme de bons bioindicateurs, leur présence ou leur absence reflétant la bonne santé des écosystèmes (Mekonen, 2017; Temple & Wiens, 1989).

1.1.2. Les oiseaux insectivores: des prédateurs essentiels aux écosystèmes terrestres

La prédation est communément définie comme une interaction biologique dans laquelle un organisme, le prédateur, tue et consomme tout ou partie d'un autre organisme, la proie (Taylor, 2013). Les oiseaux insectivores, en consommant annuellement entre 400 et 500 millions de tonnes d'insectes, se classent parmi leurs principaux prédateurs, aux côtés des araignées et des insectes entomophages (Nyffeler et al., 2018; Nyffeler & Birkhofer, 2017). Dans cette thèse, nous nous concentrerons sur les oiseaux insectivores et fonctionnellement insectivores, définis comme des espèces dont une part significative du régime alimentaire peut être constituée d'insectes, particulièrement durant la période de reproduction (Jones et al., 2005; Lopes et al., 2016). Cette définition inclut également les étourneaux, les grives et même les moineaux qui consomment des arthropodes en plus d'autres types de nourriture. Par souci de simplification, ces deux catégories seront nommées *oiseaux insectivores* dans cette thèse. Ces oiseaux jouent un service important de régulation dans l'équilibre de divers écosystèmes terrestres (agricoles, forestiers, urbains) (Barbaro et al., 2017; Faeth et al., 2005; Harris et al., 2020; Jactel et al., 2021; Rey Benayas et al., 2017) en tant que prédateurs naturels d'insectes. **L'abondance** (Roels et al., 2018), **l'activité** (Maas et al., 2015) **et dans une moindre mesure la diversité via la complémentarité fonctionnelle** (Philpott et al., 2009; van Bael et al., 2008) **des communautés d'oiseaux insectivores sont des prédicteurs bien documentés du contrôle descendant qu'ils exercent sur les insectes herbivores.** La biodiversité est étroitement liée au fonctionnement des écosystèmes puisqu'elle favorise leur stabilité écologique et leur

productivité. Cette relation s'explique par la complémentarité des niches écologiques générant une utilisation plus efficace des ressources par des espèces diverses, l'effet de sélection, augmentant les chances de contenir des espèces clés dans des communautés diversifiées et une meilleure résilience face aux perturbations environnementales (Duffy, 2002; Hooper et al., 2005). Cependant, les connaissances sont plus limitées concernant l'influence de la composition fonctionnelle des communautés d'oiseaux insectivores sur la prédation, toutes les espèces ne contribuant pas de manière équivalente aux fonctions de l'écosystème (Barbaro et al., 2017; Philpott et al., 2009).

1.1.3. Oiseaux insectivores, cascades trophiques et santé des arbres

Si le monde est vert, c'est qu'il y a suffisamment de prédateurs pour réguler les populations d'herbivores, les empêchant de surconsommer la végétation. L'hypothèse du monde vert (*Green World Hypothesis*) proposée par Hairston et al., en 1960 est directement liée à la notion de cascade trophique qui décrit la manière dont les changements dans l'abondance, la diversité ou le comportement des prédateurs des niveaux supérieurs affectent les niveaux trophiques inférieurs, et ainsi, en cascade, la structure et la dynamique de l'ensemble de l'écosystème. **Par le biais des interactions trophiques en cascade, les oiseaux insectivores jouent un rôle crucial dans le maintien des équilibres écologiques (Thébault & Loreau, 2005), notamment celui associé aux arbres, l'objet de cette thèse.**

Les arbres fournissent eux aussi, un nombre considérable de services clés tels que l'approvisionnement en produits ligneux, la régulation du climat, des services récréatifs et de loisirs, et le refuge de la biodiversité (mammifères, oiseaux, insectes, champignons), y compris en milieu urbain (Brockhoff et al., 2017; Salmond et al., 2016). Cependant, ils sont vulnérables à une grande variété d'insectes herbivores. Cette vulnérabilité aux stress biotiques dépend de leur état physiologique, de leur capacité à produire des métabolites secondaires pour se défendre et de leur environnement immédiat (Jactel et al., 2019). Les changements globaux amplifient à la fois ces facteurs de vulnérabilité et l'impact des insectes ravageurs. Les oiseaux insectivores, en tant que prédateurs naturels des insectes ravageurs, sont susceptibles d'exercer un biocontrôle particulièrement intéressant pour le maintien de la santé des arbres. Promouvoir la diversité des oiseaux, par exemple en

installant des nichoirs ou en maintenant une diversité arborée, pourrait renforcer leur potentiel de régulation, bien que les preuves à ce sujet soient encore limitées (García et al., 2021; Grass et al., 2017; Olmos-Moya et al., 2022). **Un défi majeur pour la gestion durable des forêts est donc de comprendre la structure des communautés de prédateurs inféodés aux arbres et les interactions biologiques, notamment trophiques, qui en découlent.**

1.2. Comment les changements globaux affectent la cascade trophique oiseaux insectivores - insectes herbivores - arbres ?

1.2.1. Effets du dérèglement climatique et de l'urbanisation sur les arbres, les insectes herbivores et les oiseaux insectivores

La hausse des températures et l'anthropisation croissante exercent des pressions accrues sur les arbres, qu'ils soient en forêt ou isolés dans une matrice urbaine, en altérant progressivement leur physiologie et leur écologie. Le dérèglement climatique entraîne par exemple des modifications phénologiques, comme des débourrements précoces et des sénescences foliaires tardives (Menzel et al., 2006), ainsi que des changements dans les aires de répartition des espèces (Bertin, 2008). Les îlots de chaleur urbains combinés à la compaction des sols et les sécheresses extrêmes augmentent les risques de mortalité des arbres (Hartmann et al., 2018) en limitant leur capacité à réaliser la photosynthèse (Esperon-Rodriguez et al., 2021), en affectant leur croissance (Kirilenko & Sedjo, 2007) et leur accès aux ressources essentielles (Moore et al., 2019). Les stress générés par les changements globaux altèrent également les mécanismes de défense des arbres (Kolb et al., 2019), les rendant plus vulnérables aux ravageurs.

Le dérèglement climatique et l'urbanisation influencent de manière complexe et interactive les populations d'insectes ravageurs associés aux arbres. Les insectes herbivores sont des organismes ectothermes dont l'activité est directement liée à la température extérieure. Les aires de distribution des insectes herbivores sont notamment limitées aux hautes latitudes par les températures basses en hiver, et aux basses latitudes,

par les températures élevées en été. L'élévation généralisée des températures se traduit donc par un déplacement vers les hautes latitudes des aires de distribution des espèces d'insectes herbivores (Bale et al., 2002). Les îlots de chaleur urbains exacerbent ces phénomènes et se traduisent par une accélération des cycles de développement pouvant aller jusqu'à la mise en place d'une nouvelle génération par an (Frank & Just, 2020; Jactel et al., 2019). Par ailleurs, les villes sont des points d'entrée pour les insectes exotiques avec les nombreux échanges commerciaux qui s'y déroulent (Padayachee et al., 2017) et grâce à leur microclimat, elles jouent un rôle majeur à la fois dans l'établissement et la propagation de ces insectes (Dale & Frank, 2018; Tubby & Webber, 2010). Toutefois, les effets des changements globaux diffèrent largement d'une espèce à l'autre (Jactel et al., 2019).

La variabilité du climat à large échelle est connue de longue date pour être un moteur biogéographique de la structuration des communautés d'oiseaux (Blackburn & Gaston, 1996; Fischer, 1960). En revanche, l'effet du dérèglement climatique et notamment des variations de température sur les oiseaux reste moins connu. Une étude récente de Rigal et al., (2023) a toutefois démontré que **les variations de température ont un effet globalement négatif sur l'avifaune, bien que les réponses des oiseaux à ces changements varient considérablement selon les espèces**. Plus précisément et inversement aux schémas observés chez les insectes, les espèces d'oiseaux des climats chauds sont positivement impactées par le dérèglement climatique alors que les espèces des climats froids sont largement négativement impactées. De même, les espèces migratrices sur de longues distances sont plus négativement affectées que les migratrices à courte distance et les espèces résidentes. Il semblerait aussi que les espèces spécialistes et fonctionnellement originales au sein des communautés soient plus vulnérables que les autres (Gaüzère et al., 2015). Au-delà du dérèglement climatique, d'autres perturbations d'origine anthropique peuvent affecter la dynamique des espèces. Par exemple, **l'urbanisation engendre une simplification des communautés, avec des espèces locales progressivement remplacées par des espèces non-natives (McKinney, 2006) et une homogénéisation fonctionnelle, les espèces spécialistes étant plus affectées négativement par l'anthropisation que les espèces généralistes**, qui sont plus tolérantes (Devictor et al., 2008; McKinney & Lockwood, 1999). Ainsi, en milieu urbain, les communautés d'oiseaux sont principalement composées d'espèces omnivores qui

trouvent facilement de la nourriture dans des contextes fortement anthropisés. De plus, en ville, la distribution et l'activité des oiseaux est perturbée par la pollution sonore (Slabbekoorn & Ripmeester, 2008), et lumineuse (Aulsebrook et al., 2020) et le dérangement humain (Price, 2008).

1.2.2. Effets du dérèglement climatique et de l'urbanisation sur la cascade tritrophique oiseaux insectivores - insectes herbivores - arbres

L'ensemble des perturbations générées par les changements globaux tel que décrit ci-dessus modifie les interactions plantes-herbivores (Jactel, 2019; Tubby & Webber, 2010). Ces modifications se manifestent à travers divers mécanismes interconnectés. Les décalages phénologiques entre les cycles de vie des arbres et de leurs herbivores peuvent créer des décalages temporels qui perturbent leurs interactions. Sur le plan physiologique, les dérèglements climatiques peuvent stimuler la croissance des plantes, augmentant les ressources pour les herbivores, mais ils peuvent également réduire la qualité nutritionnelle des tissus végétaux pour ces mêmes herbivores. Ces changements influencent aussi la production de métabolites secondaires impliqués dans les mécanismes de défense des arbres. Le multivoltinisme est favorisé chez certaines espèces, ce qui peut intensifier la pression d'herbivorie (Jactel et al., 2019). Par ailleurs, l'introduction d'insectes ravageurs exotiques dans des environnements où les hôtes indigènes n'ont pas développé de défenses spécifiques accroît les risques de dommages aux arbres, notamment en milieu urbain (Branco et al., 2019; Mech et al., 2019; Tubby & Webber, 2010). Les spécificités du milieu urbain, telles que les pollutions atmosphérique et lumineuse, l'imperméabilisation des sols et les microclimats particuliers, influencent la distribution et l'activité des communautés d'insectes herbivores (voir la méta-analyse de Fenoglio et al., 2020), résultant nécessairement en une modification de leurs interactions biotiques avec les arbres hôtes.

La théorie prédit que les fonctions écosystémiques sont positivement associées à la biodiversité (Philpott et al., 2009; van Bael et al., 2008). Puisque la diversité des oiseaux augmente vers les basses latitudes et les zones les moins urbanisées, on s'attend à ce qu'il en soit de même pour la prédation. **Pourtant, la manière dont les gradient climatiques**

et urbains affectent les fonctions de prédation et de régulation des insectes herbivores par les oiseaux insectivores est encore peu connue (Björkman et al., 2010; Long & Frank, 2020). L'utilisation des clines latitudinaux, considérés comme des laboratoires naturels pour l'étude du climat, génèrent des résultats contradictoires quant à l'intensité des interactions de prédation initiées par les oiseaux (Lövei & Ferrante, 2017; Roslin et al., 2017; Valdés-Correcher et al., 2021; Zvereva et al., 2019). Ces études établissent rarement, voire jamais, de corrélation entre la richesse ou la diversité fonctionnelle des communautés d'oiseaux insectivores et l'insectivorie, à ces échelles. En ville, la fragmentation et la dégradation des habitats naturels (Marzluff, 2001; Pickett et al., 2001; Zipperer et al., 2000) réduisent la disponibilité des niches écologiques pour l'avifaune. De plus, l'homogénéisation des communautés d'oiseaux, caractérisée par une diminution des espèces insectivores, entraîne une faible abondance d'ennemis naturels pour les herbivores, ce qui est propice à leur développement (Bang et al., 2012; Dale & Frank, 2018; Turrini et al., 2016).

1.2.3. Les facteurs locaux agissant comme filtre de la biodiversité et des interactions biotiques associées

Les schémas climatiques et urbains sur la relation diversité-fonction des oiseaux insectivores peuvent être modifiées localement par la structure de l'habitat (Charbonnier et al., 2016; Ferger et al., 2014; Ikin et al., 2014; Kissling et al., 2012). En particulier, l'habitat local agit comme un filtre sur le pool d'espèces régionales et explique parfois une grande partie de la variation spatiale à large échelle de la richesse en espèces d'oiseaux (Ferger et al., 2014). Par exemple, la manière dont les forêts sont composées et structurées influence la diversité fonctionnelle des espèces d'oiseaux le long du gradient climatique en Europe (Charbonnier et al., 2016). Les études sur le lien entre les grands gradients climatiques et l'intensité des interactions biotiques négligent souvent les facteurs locaux, ce qui pourrait expliquer les incohérences observées dans certains résultats.

L'urbanisation est un phénomène multidimensionnel, dont les prédicteurs sont l'imperméabilité des sols, la densité du bâti, la densité de population, la densité du trafic,

etc. Cette complexité génère une forte hétérogénéité au sein d'une même ville (ex. un parc urbain en plein centre-ville peut abriter une biodiversité plus riche qu'une zone résidentielle en périphérie). Le couvert forestier local est considéré comme un bon indicateur de la biodiversité et des interactions trophiques entre les arbres, les insectes herbivores et leurs ennemis naturels en milieu urbain (Long & Frank, 2020; Stemmelen et al., 2020; Valdés-Correcher et al., 2022). La diversité des arbres est particulièrement importante dans la structuration des communautés d'oiseaux et de leur fonction de régulation des insectes herbivores (Staab & Schuldt, 2020; Stemmelen et al., 2020; Xu et al., 2022). Bien que cette idée n'ait eu que très peu de soutien dans la littérature scientifique concernant les écosystèmes forestiers, et ce, seulement récemment (Vázquez-González et al., 2024), la théorie suggère qu'une plus grande diversité d'arbres augmente la complexité de l'habitat, créant ainsi plus de niches écologiques pour les prédateurs susceptibles de contrôler les populations d'insectes herbivores (*l'hypothèse des ennemis naturels*, Root, 1973). La diversité des arbres interfère aussi avec les mécanismes de reconnaissance et de sélection des arbres hôtes par les arthropodes herbivores (Jactel et al., 2021). En conséquence, la prise en compte de la variabilité de l'habitat urbain est nécessaire pour comprendre les variations de biodiversité des oiseaux insectivores et de l'intensité des cascades trophiques associées (Long & Frank, 2020).

Nous allons nous attacher à établir des relations fonctionnelles entre le climat, l'urbanisation, les facteurs locaux (qui varient selon les échelles considérées mais filtrent les espèces régionales à une échelle plus fine), **la diversité des oiseaux insectivores et le contrôle descendant des insectes herbivores. L'un des enjeux pour répondre à cette question est l'obtention de données standardisées à large échelle** sur la structuration des communautés d'oiseaux et sur les interactions trophiques dont elles sont à l'origine.

1.3. Quelles méthodes standardisées pour la caractérisation des communautés et des interactions trophiques à large échelle ?

1.3.1. Les enjeux de la standardisation pour la recherche en écologie

La standardisation des méthodes en écologie joue un rôle crucial pour assurer la rigueur, la reproductibilité dans le temps et l'espace et la fiabilité des recherches. C'est notamment le cas pour l'étude des communautés et des interactions trophiques, où il est essentiel de collecter des données robustes, simples, à large échelle sur les traits des espèces, leurs comportements, leurs interactions, les processus écologiques, et l'importance des facteurs abiotiques dans ces processus. Plusieurs approches standardisées ont été développées pour répondre à ce besoin. Par exemple, le *Tea Bag Index* offre une méthode simple et peu coûteuse pour mesurer la décomposition de la matière organique par les organismes du sol à l'échelle mondiale à l'aide de sachets de thé (Keuskamp et al., 2013). De même, l'utilisation de modèles en pâte à modeler pour quantifier le risque de prédation sur divers organismes est une méthode simple et éthique pour collecter des données standardisées (Brodie III, 1993), notamment le long de gradients climatiques (Roslin et al., 2017), tout en facilitant la participation citoyenne (Castagneyrol et al., 2020). La standardisation des méthodes en écologie fonctionnelle à travers les biomes terrestres est soutenue par des protocoles détaillés (Cornelissen et al., 2003; Moretti et al., 2017), comme ceux du "*Handbook of protocols for standardised and easy measurement of plant functional traits worldwide*" (Cornelissen et al., 2003). Ce manuel fournit des méthodes consensuelles et faciles d'utilisation pour mesurer les traits fonctionnels des plantes en réponse aux changements globaux.

Néanmoins, les méthodes standardisées décrites ci-dessus sont parfois controversées. Les critiques mettent notamment en exergue une simplification excessive des processus écologiques, comme l'incapacité du *Tea Bag Index* à capturer pleinement la complexité de la décomposition liée à la macrofaune (Eggleton et al., 2020); **des imprécisions méthodologiques,** telles que le manque de représentativité des modèles en pâte à modeler en termes de couleur, d'odeur ou d'activité des proies réelles (Nimalrathna et al., 2023; Rodriguez-Campbell et al., 2023; Zvereva & Kozlov, 2023); et **la nécessité d'une mise à jour régulière des protocoles,** notamment pour la mesure des traits fonctionnels des plantes (Pérez-Harguindeguy et al., 2013).

1.3.2. Capteurs et nouvelles technologies : une belle promesse de données standardisées ?

Les capteurs et les nouvelles technologies révolutionnent la collecte de données en écologie. Ils étendent les échelles spatiales et temporelles d'observation, fournissent des données uniformes, de haute précision en réduisant les biais observateurs et facilitent l'accès à des zones reculées (Porter et al., 2009). Grâce à leur capacité à opérer de manière autonome et continue, ils permettent une surveillance constante des écosystèmes, offrant ainsi une vision plus complète et détaillée des processus écologiques. Ils sont par exemple utilisés pour mesurer des facteurs abiotiques, comme la température ou l'humidité (ex. grâce aux HOBO datalogger, Da Cunha, 2015), pour caractériser les comportements des espèces (ex. avec des GPS, Bonnot et al., 2013), ou encore pour surveiller la santé des forêts (ex. grâce à la télédétection via des drones, Dash et al., 2017). Les algorithmes de traitements automatisés basés sur l'intelligence artificielle peuvent ensuite faciliter l'analyse et l'interprétation de ces grandes quantités de données. **Ensemble, ils sont donc un bon moyen de résoudre le défi méthodologique de la caractérisation des communautés à grande échelle tout en tenant compte des facteurs locaux qui façonnent ces communautés. Toutefois, il est essentiel de valider et de calibrer les capteurs pour garantir l'exactitude des données, ainsi que d'assurer des performances suffisantes de l'intelligence artificielle.**

Le développement récent d'outils de surveillance acoustique passive se prête particulièrement à l'étude des communautés pour lesquelles la communication vocale est importante. Les vocalisations animales peuvent être enregistrées au moyen de capteurs acoustique appelés unités d'enregistrement autonomes (Shonfield & Bayne, 2017). Par rapport aux méthodes d'inventaire traditionnelles (ex. les points d'écoute), la surveillance passive constitue un moyen moins coûteux et moins invasifs d'obtenir des données pour l'ensemble des écosystèmes terrestres (Darras et al., 2018). La surveillance acoustique peut-être utilisée pour analyser le paysage sonore d'un environnement donné et/ou pour identifier les oiseaux à l'espèce (Shaw et al. 2021).

L'écoacoustique a pour objectif d'analyser les paysages sonores, afin d'étudier les écosystèmes dans leur ensemble et inclut l'analyse des sons biologiques (la biophonie), abiotiques (la géophonie) et anthropiques (anthropophonie ou technophonie). Dans le cadre de l'écoacoustique, des indices acoustiques peuvent être calculés à partir des enregistrements. Ils visent à quantifier la richesse, l'homogénéité, la régularité, la divergence ou la rareté des espèces, de leurs traits fonctionnels ou de leur phylogénie mais sont aussi intrinsèquement liés à l'environnement local (Sueur et al. 2014, Sueur et Farina, 2015 ; Gasc et al., 2013 ; Stowell et Sueur, 2020).

La bioacoustique est une discipline qui se concentre sur l'étude des sons produits par les organismes vivants pour suivre leurs comportements, surveiller les populations, étudier la communication ou encore les interactions entre les individus ou les espèces. **Elle nécessite souvent une étape d'identification des espèces.** Cette étape peut s'avérer être délicate puisqu'elle requiert un investissement en temps considérable et également une expertise taxonomique qui est parfois rare (Hoefler et al., 2023; Symes et al., 2022). **Une alternative prometteuse réside dans l'utilisation d'algorithmes de reconnaissance automatisée** (Aodha et al., 2018; Kahl et al., 2021; Rowley & Callaghan, 2020). **Cependant, l'adoption de cette approche nécessite une validation rigoureuse préalable pour garantir la fiabilité et l'exactitude des données produites** (Pérez-Granados, 2023). Cette méthode, une fois validée, peut offrir une solution efficace pour la caractérisation de la composition des communautés animales.

Les unités d'enregistrement autonomes, associées aux approches écoacoustiques et bioacoustiques, constituent des outils adaptés pour l'étude à grande échelle des changements environnementaux sur les communautés d'oiseaux. L'écoacoustique est une discipline à l'interface de la caractérisation des habitats, de la détection des perturbations environnementales et de l'évaluation de l'activité vocale des communautés biotiques, pouvant aussi refléter leur composition. La bioacoustique utilise les mêmes capteurs de manière complémentaire pour caractériser précisément la diversité taxonomique et fonctionnelle des communautés d'oiseaux. L'emploi des capteurs autonomes permet l'acquisition de données standardisées sur des étendues spatio-temporelles considérables. Cette combinaison d'outils constitue donc une méthode intéressante pour répondre à la question centrale de cette thèse, à savoir la manière dont

les facteurs climatiques et les caractéristiques de l'habitat affectent la composition des communautés d'oiseaux insectivores et leurs fonctions.

1.4. Problématique de la thèse

Au cours de cette thèse, je me suis attachée à explorer les effets indépendants et interactifs du climat et de l'urbanisation, ainsi que de l'habitat local sur la relation fonctionnelle entre la diversité des communautés d'oiseaux et la prédation qu'elles exercent sur les insectes herbivores. Pour ce faire, il a été nécessaire d'utiliser des outils et des méthodes standardisées afin de (i) quantifier la prédation sur les larves d'insectes herbivores et (ii) caractériser, par l'acoustique, les communautés d'oiseaux à l'origine de cette prédation. Une partie de mes recherches a ainsi été consacrée à l'étude des biais inhérents à l'utilisation de ces méthodes et outils.

Les hypothèses de travail sont les suivantes : (1) il existe une corrélation positive entre la diversité des communautés d'oiseaux insectivores et le taux de prédation des oiseaux sur les insectes herbivores (1a); il existe une corrélation négative entre la diversité des communautés d'oiseaux insectivores et l'herbivorie des insectes sur les arbres (1b); (2) la diversité des oiseaux insectivores augmente vers les climats les plus chauds (2a) et diminue avec l'urbanisation (2b); (3) la prédation des oiseaux sur les insectes herbivores décroît le long de gradients climatiques et d'urbanisation (3a), mais l'habitat local peut jouer un rôle prépondérant dans ces modifications (3b).

Ces hypothèses écologiques s'appuient sur l'utilisation de proies artificielles pour évaluer la prédation, une méthode standardisée récemment critiquée. J'ai donc cherché à évaluer cette méthode en faisant l'hypothèse qu'elle pouvait toujours être utilisée sous certaines conditions (4).

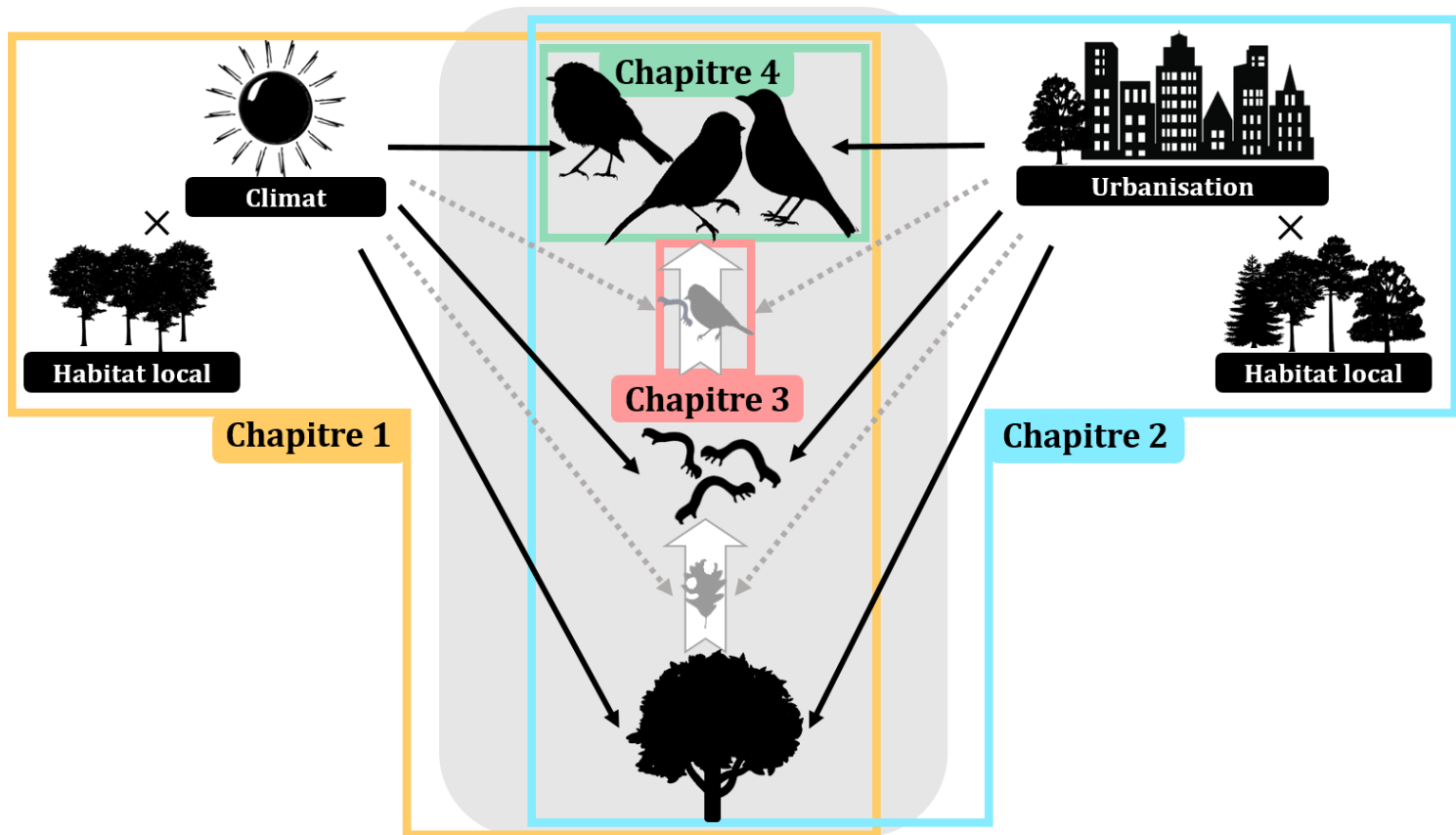
Enfin, j'ai souhaité explorer la capacité des algorithmes de reconnaissance automatisées, associés à l'écologie acoustique, à caractériser la composition des communautés d'oiseaux dans un cadre d'utilisation pour la recherche (5).

La thèse s'articule en quatre chapitres. Deux chapitres répondent à des questions fondamentales en écologie. Deux chapitres méthodologiques développés en parallèle les complètent. Dans le **chapitre 1**, nous caractérisons la diversité taxonomique,

fonctionnelle et acoustique des oiseaux insectivores associés au chêne pédonculé dans 47 sites répartis le long d'un gradient climatique en Europe et évaluons leur activité de prédation. Dans le **chapitre 2**, nous nous intéressons à l'évolution de la richesse spécifique des oiseaux insectivores, de leur activité de prédation et de l'herbivorie des insectes folivores le long de deux gradients orthogonaux d'urbanisation et de diversité en arbres dans la métropole de Montréal, au Canada. Dans le **chapitre 3**, nous menons une expérimentation visant à évaluer les biais systématiques inhérents à l'utilisation de proies artificielles pour quantifier la prédation des oiseaux. Dans le **chapitre 4**, nous nous appuyons sur des enregistrements acoustiques annotés par un ornithologue pour évaluer la fiabilité d'un algorithme de reconnaissance des chants d'oiseaux en fonction des traits vocaux des espèces. Enfin, dans le cadre de deux collaborations, nous analysons la performance de ce même algorithme en fonction de ses paramètres d'entrée (Annexe A1) et du niveau de bruit ambiant (Annexe A2).

Le schéma ci-dessous (Fig.1) récapitule les différentes hypothèses testées ainsi que les chapitres de thèse associés.

Figure 1. Schéma récapitulatif des hypothèses testées et des chapitres associés. Les flèches épaisses à fond blanc représentent les transferts d'énergie dans la cascade tri-trophique oiseaux-herbivores-arbres. Les flèches noires pleines représentent les effets du climat, de l'urbanisation et de l'habitat local sur les trois niveaux trophiques. Les flèches grises en pointillés représentent les effets du climat, de l'urbanisation et de l'habitat local sur l'interaction entre arbres et herbivores d'une part (herbivorie) et entre herbivores et oiseaux insectivores d'autre part (prédation). Les signes "×" représentent les effets d'interactions.



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2. Chapitre 1 : Décomposition des facteurs influençant l'insectivorie avienne : effets à grande échelle du climat, de l'habitat et de la diversité des oiseaux

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Abstract

Aim

Climate is a major driver of large scale variability in biodiversity, as a likely result of more intense biotic interactions under warmer conditions. This idea fuelled decades of research on plant-herbivore interactions, but much less is known about higher-level trophic interactions. We addressed this research gap by characterizing both bird diversity and avian predation along a climatic gradient at the European scale.

Location

Europe.

Taxon

Insectivorous birds and pedunculate oaks.

Methods

We deployed plasticine caterpillars in 138 oak trees in 47 sites along a 19° latitudinal gradient in Europe to quantify bird insectivory through predation attempts. In addition, we used passive acoustic monitoring to (i) characterize the acoustic diversity of surrounding soundscapes; (ii) approximate bird abundance and activity through passive acoustic recordings and (iii) infer both taxonomic and functional diversity of insectivorous birds from recordings.

Results

The functional diversity of insectivorous birds increased with warmer climates. Bird predation increased with forest cover and bird acoustic activity but decreased with mean annual temperature and functional richness of insectivorous birds. Contrary to our predictions, climatic clines in bird predation attempts were not directly mediated by changes in insectivorous bird diversity or acoustic activity, but climate and habitat still had independent effects on predation attempts.

Main conclusions

Our study supports the hypothesis of an increase in the diversity of insectivorous birds towards warmer climates, but refutes the idea that an increase in diversity would lead to more predation and advocates for better accounting for activity and abundance of insectivorous birds when studying the large-scale variation in insect-tree interactions.

Keywords: Acoustic diversity, Climatic gradient, Functional diversity, Insectivorous birds, Plasticine caterpillars, Predation function

2.1. Introduction

Climate is a key driver of biotic interactions (Dobzhansky, 1950). A long held view in ecology posits that warmer and more stable climatic conditions intensify biotic interactions and accelerates speciation (MacArthur, 1984; Schemske, Mittelbach, Cornell, Sobel & Roy, 2009), which should result in large scale positive correlations between biodiversity and biotic interactions. However appealing this idea is, the generality of large-scale climatic clines in biodiversity and biotic interactions as well as the underlying causal links are still widely debated. Yet, insights into the controversy have been dominated by studies on plant-insect interactions (Anstett, Chen & Johnson, 2016; Kozlov, Lanta, Zverev & Zvereva, 2015). Biotic interactions involving higher trophic levels received much less attention. Yet, insectivorous birds are among the predators contributing the most to the control of insect herbivores in terrestrial ecosystems (van Bael et al., 2008; Sam, Jorge, Koane, Amick & Sivault, 2023; Sekercioglu, 2006) and therefore have consequences on both the assembly of ecological communities and the functioning of ecosystems. The omission of predation in theories linking large-scale variability in climate with biodiversity therefore represents a critical gap in knowledge that needs to be addressed.

Bird communities are highly responsive to climate, at both regional and continental scale. There is a large body of literature demonstrating that several dimensions of bird diversity vary with climate, including bird abundance, species richness, phylogenetic or functional diversity (Blackburn & Gaston, 1996; Symonds Christidis & Johnson, 2006; Willig, Kaufman & Stevens, 2003). A well substantiated explanation is that niche opportunities increase with increasing habitat heterogeneity under milder climatic conditions, which increases species coexistence and ultimately species richness through functional complementarity (Hawkins, Diniz-Filho, Jaramillo & Soeller, 2006). The biodiversity and ecosystem relationship theory predicts that both abundance and diversity of birds are crucial predictors of the top-down control they exert upon insect prey (Bael et al., 2008; Nell, Abdala-Roberts, Parra-Tabla & Mooney, 2018; Otto, Berlow, Rank, Smiley & Brose, 2008; Sinclair, Mduma & Brashares, 2003). Numerous studies supported this theory and demonstrated that bird functional diversity in particular --- that is the diversity, distribution and complementarity of predator traits involved in predation --- is a good

predictor of predation (Barbaro, Giffard, Charbonnier, van Halder & Brockerhoff, 2014; Greenop, Woodcock, Wilby, Cook & Pywell, 2018; Philpott et al., 2009). It follows that variation in bird diversity along climatic gradients should be mirrored by consistent variation in avian predation rates.

Local factors can however alter macroecological patterns (Ikin et al., 2014; Kissling, Sekercioglu & Jetz, 2012), by filtering the regional species pool (De la Mora, García-Ballinas & Philpott, 2015; Kleijn, Rundlöf, Scheper, Smith & Tschardtke, 2011) and by influencing the behavior of organisms. The diversity and composition of bird communities heavily depends on local factors that provide niches and food opportunities (Charbonnier et al., 2016). In this respect, multiscale forest cover proved to be a particularly good predictor of composition of birds communities at different spatial scales, as bird foraging activity is ultimately determined by vertical and horizontal habitat heterogeneity, which influences both where prey can be found and caught, and where foraging birds can breed and hide from predators (Vickery & Arlettaz, 2012). Thus, modeling the response of bird communities to large-scale bioclimatic drivers as well as their role as predators would benefit from using a combination of habitat variables and biotic predictors (Barbaro et al., 2019; Speakman et al., 2000). However, cross-continental studies exploring the relationship between large scale climatic gradients and the strength of biotic interactions generally ignore local factors, which may partly explain inconsistencies in their findings (but see Just, Dale, Long & Frank, 2019).

A major challenge to analyze climatic clines in biotic interactions consists in simultaneously characterizing changes in predator biodiversity and experimentally assessing the strength of predation, while considering the effect of contrasting habitats. However, the recent development of passive acoustic monitoring provides a standardized, low-cost and non-invasive approach for ecological studies and biodiversity monitoring (Gibb, Browning, Glover-Kapfer, Jones & Börger, 2019). The acoustic monitoring of a given habitat primarily allows the delayed identification of bird species over large gradients with no need for distributed expertise across study sites. The quantification of bird abundance through passive acoustic monitoring remains a technical challenge, but the calculation of certain acoustic indices based on the physical characteristics of the recorded sounds provides relevant proxies to this end (Gasc et al.,

2013; Sueur, Farina, Gasc, Pieretti & Pavoine, 2014). Should such indices consistently correlate with macro-scales biotic interactions, ecoacoustics would be a promising complementary approach to existing methods in macroecology and in functional ecology.

Here, we addressed the hypothesis of continental north-south clines on insectivorous bird community diversity and their predation function, while controlling for local factors throughout the European distribution range of the pedunculate oak (*Quercus robur* L., 1753), a major forest tree species. Specifically, we predict the following (Fig. 1): (i) bird diversity (including bird acoustic diversity, insectivorous bird species richness and functional diversity) and predation attempts increase with warmer climates; (ii) bird predation attempts increase with bird acoustic activity, species richness and greater functional diversity of insectivorous birds; (iii) bird diversity, acoustic activity and bird predation attempts increase with increasing forest cover at both local (neighborhood) and larger spatial scales; (iv) large-scale variability in bird predation attempts is driven by local changes in the diversity and acoustic activity of birds. To test these predictions, we quantified bird predation attempts on plasticine caterpillars and estimated bird species richness, functional diversity and acoustic activity through simultaneous passive acoustic monitoring. We eventually tested the respective responses of these variables and their relationships at the pan-European scale.

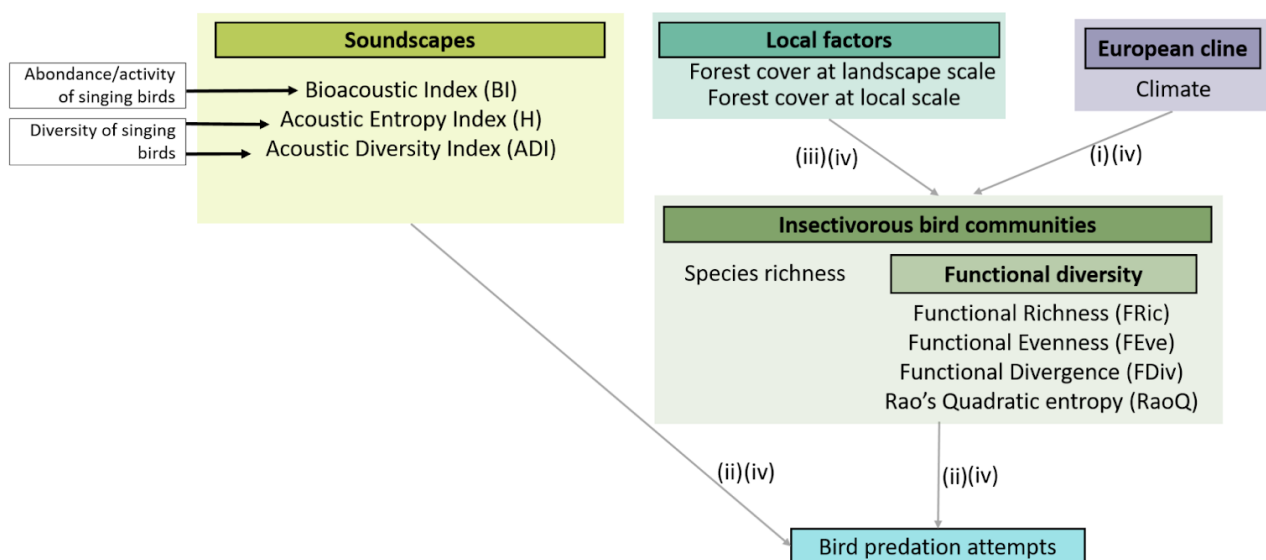


Figure 1. Conceptual diagram of the predictions of this study and the relationships already established in the literature. Boxed elements written in bold correspond to the main categories of variables tested, they are not variables as such. Variables used in models are shown in regular font. Where several variables described the same category (e.g. BI, ADI, H, all describing acoustic indices), we used multi-model comparisons to identify the best variable. Items framed in black on a white

background represent untested variables. Black arrows indicate relationships well supported by the literature (see Gasc et al., 2018; and Fig.2 Sánchez-Giraldo, Correa Ayram & Daza, 2021). Our specific predictions are represented with grey arrows, solid and dashed lines representing positive and negative (predicted) relationships. Numbers refer to predictions as stated in the main text.

2.2. Materials and Methods

2.2.1. Study area

We focused on the pedunculate oak, *Quercus robur*, which is one of the keystone deciduous tree species in temperate European forests, where it is of high ecological, economic and symbolic importance (Eaton, Caudullo, Oliveira & de Rigo, 2016). The species occurs from central Spain (39°N) to southern Fennoscandia (62°N) and thus experiences a huge gradient of climatic conditions (Petit et al., 2002). A widely diverse community of specialist and generalist herbivorous insects is associated with this species throughout its distributional range (Southwood, Wint, Kennedy & Greenwood, 2005).

Between May and July 2021, we studied 138 trees in 47 sites across 17 European countries covering most of the pedunculate oak geographic range (Fig. 2). The sites were chosen with the minimal constraint of being located in a wooded area of at least 1 ha (Valdés-Correcher et al., 2021). We randomly selected three mature oaks per site, with the exception of six sites (three sites with one tree, one site with two trees and two sites with five trees, see Table S1.1 in Appendix S1 in Supporting Information).

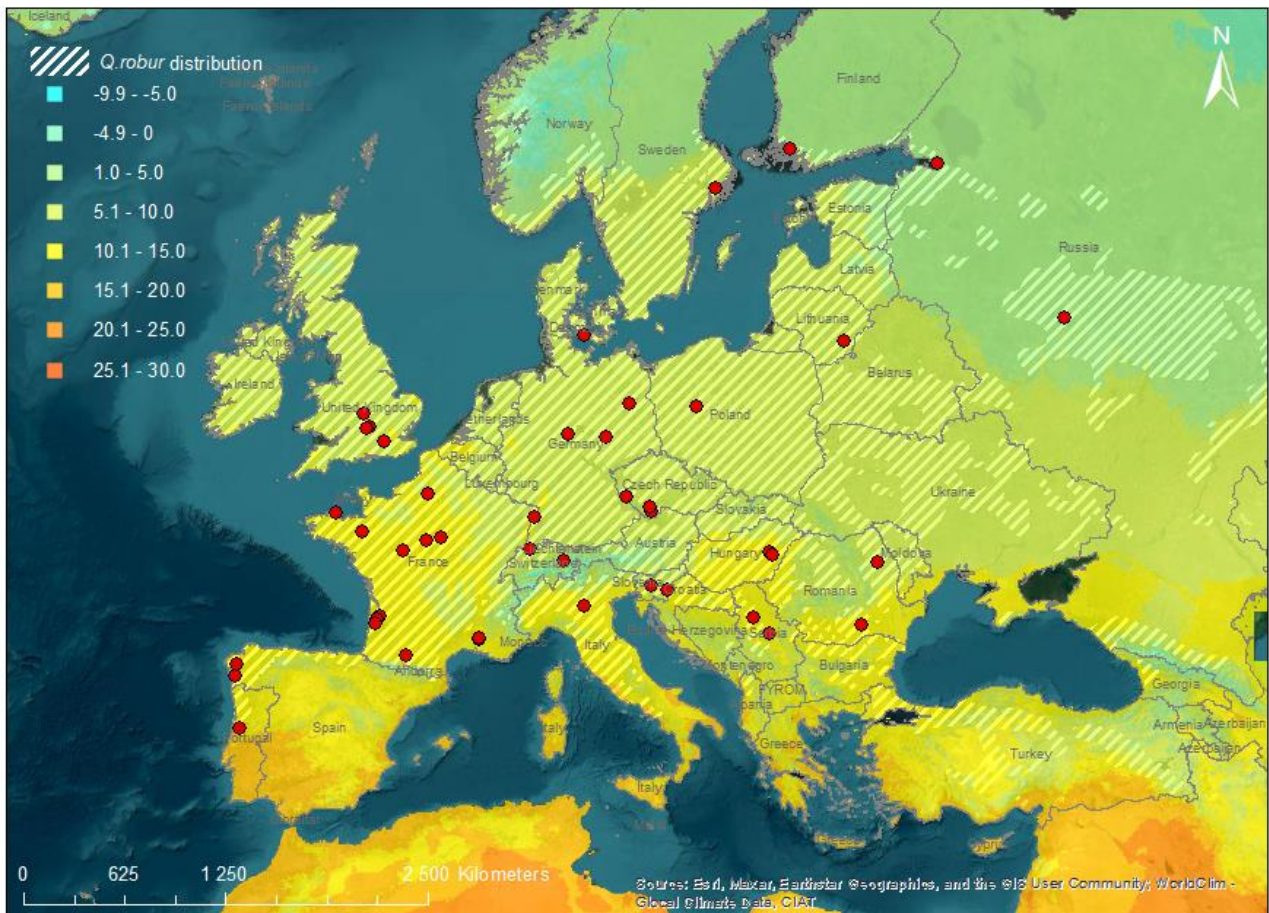


Figure 2. Locations of the 47 sites sampled in spring 2021. Average annual temperature (color scale) according to WorldClim (Hijmans, Cameron, Parra, Jones & Jarvis, 2005) and *Quercus robur* distribution range are indicated.

2.2.2. Bird predation attempts

We measured bird predation attempts in the field by exposing a total of 40 plasticine caterpillars (20 plasticine caterpillars twice) on each individual oak. We made plasticine caterpillars of green plasticine, mimicking common lepidopteran larvae (3 cm long, 0.5 cm diameter, see Low, Sam, McArthur, Posa & Hochuli, 2014). We secured them on twigs with a 0.3 mm metallic wire. We attached five plasticine caterpillars to each of four branches facing opposite directions (i.e., 20 caterpillars per tree) at about 2 m from the ground.

We installed the plasticine caterpillars six weeks after budburst in each study area, thus synchronizing the study with local oak phenology. We removed the plasticine caterpillars after 15 days and installed another set of 20 artificial caterpillars per tree for another 15 days. At the end of each exposure period (which varied from 10 to 20 (mean \pm SD: 14.5 \pm 1.23) days due to weather conditions, we carefully removed the plasticine caterpillars

from branches, placed them into plastic vials and shipped them to the project coordinator. Plasticine caterpillars from six sites were either lost or altered during shipping, preventing the extraction of relevant data.

A single trained observer (EVC) screened the surface of plasticine caterpillars with a magnifying lens to search for the presence of bill marks on clay surface (Low et al., 2014). As we were ultimately interested in linking bird diversity with bird predation attempts, we did not consider marks left by arthropods and mammals.

We defined *bird predation attempts index* as p / d , where p is the proportion of plasticine caterpillars with at least one sign of attempted predation by birds and d is the number of days plasticine caterpillars were exposed to predators in the field. We only considered as attacked those caterpillars that we retrieved; missing caterpillars were not accounted for in the calculation of p . We calculated bird predation attempts for each tree and survey period separately. Because other variables were defined at site level (see below), we averaged bird predation attempts across trees and surveys in each site (total: $n = 41$).

To assess the effect of temperature independently of other variables that could vary with latitude, we also calculated a second bird predation attempts index by standardizing the predation attempts by daylight duration in every site. We ran the same statistical models as for the non-standardized bird predation attempts. The outcomes remained qualitatively the same and the results of this analysis are presented in Table S2.2 in Appendix S2.

2.2.3. Acoustic monitoring and related variables

We used passive acoustic monitoring to characterize the species and functional diversity of bird communities associated with oaks, as well as to serve as a proxy of the abundance and diversity of vocalizing birds (Fig. 2). In each site, we randomly chose one oak among those used to measure bird predation rates in which we installed an AudioMoth device (Hill et al., 2018) to record audible sounds for 30 min every hour. Automated recording started the day we installed the first set of 20 plasticine caterpillars in trees and lasted until batteries stopped providing enough energy. The recording settings were the

following: Recording period: 00.00-24.00 (UTC); Sample rate: 48 kHz; Gain: Medium; Sleep duration: 1800 s, Recording duration: 1800 s.

In all 47 sites, Audiomoths were active on average (\pm S.D.) for 9 ± 3 days (range: 1-24), which corresponded to 5920 h of recordings in total and from 70 to 335 (246 ± 65) 30 min continuous acoustic samples per site. When Audiomoths ran out of battery, the recordings lasted less than 30 min (between 1 and 56 recordings per site were affected).

2.2.3.1. Acoustic diversity indices as proxies of bird diversity and activity

We processed acoustic samples with functions in the “soundecology” v.1.3.3 (Villanueva-Rivera & Pijanowski, 2018) and “seewave” v. 2.1.8 (Sueur, Aubin & Simonis, 2008) libraries in the R environment version 4.1.2 (R Core Team, 2020), and a wrap-up function made available by A. Gasc in GitHub (<https://github.com/agasc/Soundscape-analysis-with-R>). We first divided every acoustic sample (regardless of its length) into non-overlapping 1 min samples.

Acoustic indices capture various dimensions of the soundscape but are not expected to fully reflect any bird biodiversity-related variable. However, several studies have shown that some of them are positively related to the abundance or diversity of vocalizing species (for more details, see Sánchez-Giraldo, Correa Ayram & Daza, 2021, Fig.2 and Gasc et al., 2018), although the strength of this relationships is still poorly understood. We have therefore chosen to consider only those specific indices and we used multi-model statistical inferences to identify those that were the most strongly linked with the response variables of interest (see below).

We calculated the following three acoustic diversity indices for each 1 min sample: the Acoustic Diversity Index (ADI) and the Total Acoustic Entropy (H) which are both based on Shannon diversity index and are therefore close to a proxy for bird diversity (Sueur, Pavoine, et al., 2008; Villanueva-Rivera, Pijanowski, Doucette & Pekin, 2011), and the Bioacoustic Index (BI) which is positively related to bird vocal activity and the occupancy of acoustic signal frequency bands (Boelman, Asner, Hart & Martin, 2007; Gasc et al., 2018). We calculated the median of each acoustic index per day and then averaged median values across days for each site separately. We proceeded like this because 24 h cycles summarize the acoustic activity and account for all possible sounds of a given day.

Furthermore, other studies have previously shown that median values of acoustic indices for a given day are more representative than mean values of the acoustic activity because they are less sensitive to extreme values (Barbaro et al., 2022; Dröge et al., 2021). This procedure resulted in one single value of each acoustic diversity index per site.

2.2.3.2. Bird species richness and functional diversity

We used acoustic samples to identify birds based on their vocalizations (songs and calls) at the species level, from which we further computed functional diversity indices (Fig. 3).

Data processing – For each site, we subsampled the 30 min samples corresponding to the songbird morning chorus (*i.e.*, the period of maximum singing activity), which incidentally also corresponds to the time of the day when anthropic sounds were of the lowest intensity. Specifically, we selected sounds recorded within a period running from 30 min before sunrise to 3 h 30 min after sunrise. We then split each 30 min sample into up to three 10 min sequences, from which we only retained those recorded on Tuesday, Thursday, Saturday, and Sunday. We chose these days on purpose to balance the differences in anthropogenic noises between working days and weekends. For each sound sample, we displayed the corresponding spectrogram with the “seewave” library in the R environment (Sueur, Aubin & Simonis, 2008). We visually sorted sound samples thanks to spectrograms and discarded samples with noise from anthropogenic sources, rain, or wind, which can be recognized as very low frequency noise on the spectrogram. We also discarded samples with noise of very high frequency corresponding to cicada chirps. We then randomly selected one sound sample per site and per day, with the exception of four sites for which the four samples only covered two to three days. In total, we selected 188 samples of 10 min (*i.e.*, 4 samples per site).

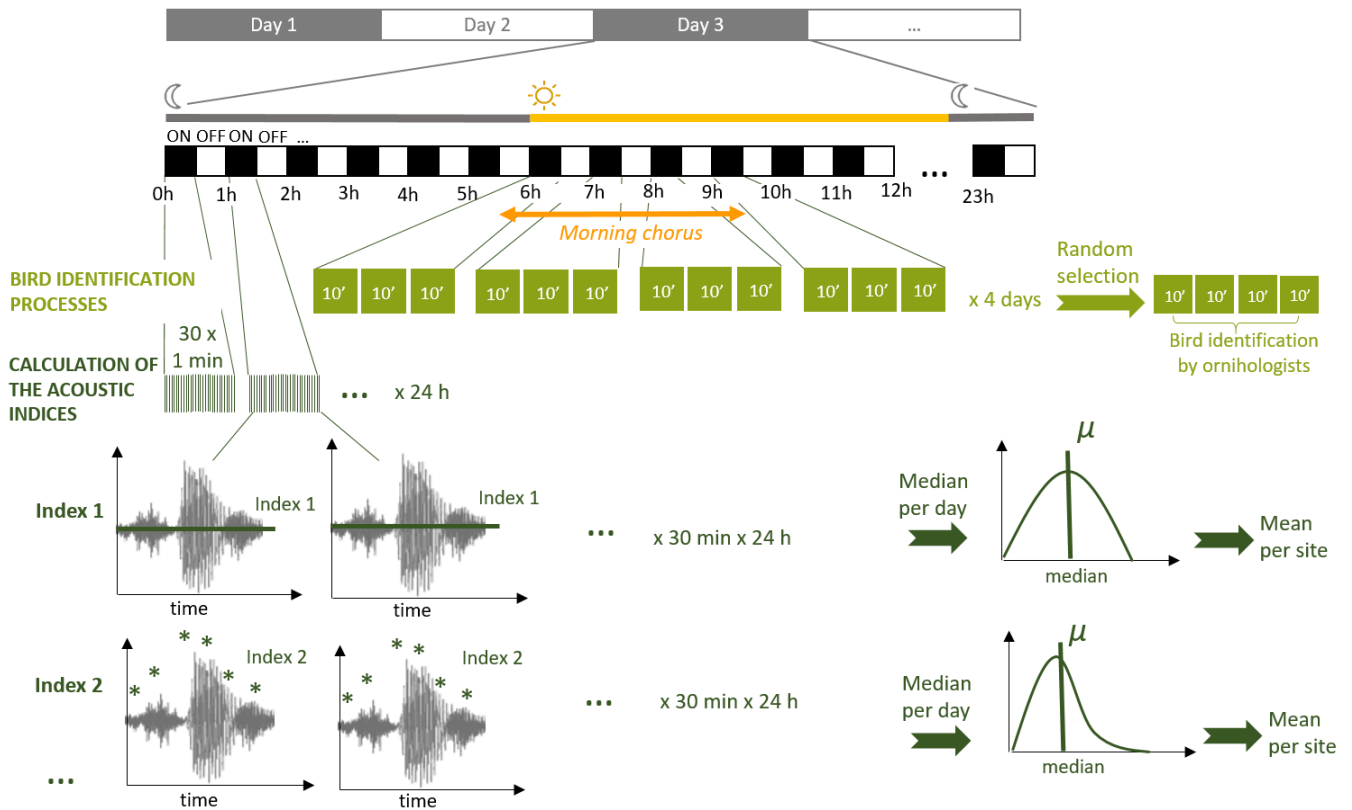


Figure 3. Methodological pathway used to identify bird species (in light green) and calculate acoustic indices (in dark green) from automated recordings (see text for details)

Bird species identification - We distributed the samples among 21 expert ornithologists. Each expert performed aural bird species identifications from 4 (one site) to 52 samples (13 sites), primarily from her/his region of residence, for auditory acoustic detection of bird species. We established a presence/absence Site \times Species matrix, from which we calculated species richness and functional diversity. It is important to note that, there is no possibility to determine the direction and distance at which birds are singing from audio recordings when using a single device for a given site. As a result, there is no standard method for determining whether or not two vocalizations of the same species at two different times come from one single individual or more, which prevents an accurate estimate of bird abundance. However, experienced ornithologists involved in this study consider that, given the territoriality of birds and the range of the recorders, it is unlikely that they recorded the vocalizations of several individuals of the same species. It therefore seems reasonable to assume that among-site differences in bird species richness were also representative of among-site differences in bird abundance.

Functional diversity – We defined 25 bird species as candidate insectivores for attacking plasticine caterpillars (Table S3.3 in Appendix S3) with those bird species meeting the following criteria: be insectivorous during the breeding season or likely to feed their offspring with insects, forage primarily in forested habitats, and are likely to use substrates such as lower branches or lower leaves of trees where caterpillars were attached to find their prey (Barbaro et al., 2021; Brambilla & Gatti, 2022). We calculated the functional diversity of these candidate insectivores by combining morphological, reproductive, behavioral and acoustic traits.

With the exception of acoustic traits, we extracted functional traits from different published sources, listed in Table S3.4 in Appendix S4. Specifically, we used three continuous traits: *body mass*, *mean clutch size* and *bill culmen length* (see Fig. 2 in Tobias et al., 2022) combined with four categorical traits: *foraging method* (predominantly understory gleaner, ground gleaner, canopy gleaner), *diet* (insectivores or mixed diet), *nest type* (open in shrub, open on ground, cavity or open in tree) and *migration* (short migration, long migration or resident).

We derived acoustic traits calculations from the work of Krishnan & Tamma (2016). We first extracted five pure recordings without sonic background for each of the 25 candidate insectivore species from the online database Xeno-canto.org (Vellinga & Planque, 2015). We then calculated the *number of peaks* (i.e., NPIC) in the audio signal (see § Acoustic diversity, above) as well as the *frequency of the maximum amplitude peaks* for each vocal element using the “seewave” library (Sueur, Aubin & Simonis, 2008) and averaged these frequencies for each species. Being based on song and call frequency and complexity, these indices inform the adaptation of the vocal repertoire of these species to their environment.

We summarized the information conveyed by the 9 traits categories into five indices representing complementary dimensions of the functional diversity (FD) of a community (Mouillot, Graham, Villéger, Mason & Bellwood, 2013): functional richness (FRic, i.e., convex hull volume of the functional trait space summarized by a principal coordinates analysis), functional evenness (FEve, i.e., minimum spanning tree measuring the regularity of trait abundance distribution within the functional space), and functional divergence (FDiv, i.e., trait abundance distribution within the functional trait space volume) (Villéger, Mason & Mouillot, 2008), as well as Rao's quadratic entropy (RaoQ, i.e.,

species dispersion from the functional centroid) (Botta-Dukát, 2005). These were calculated for each site with the “dbFD” function of the “FD” library v.1.0.12 (Laliberté, Legendre & Shipley, 2014) in the R environment.

2.2.4. Environmental data

Environmental data refer to local temperature and forest cover. We used the high 10-m resolution GIS layers from the Copernicus open platform (Cover, 2018) to calculate forest cover for all European sites. We manually calculated the percentage of forest cover for the two sites located outside Europe using the "World imagery" layer of Arcgis ver. 10.2.3552. We calculated both the percentage of forest cover in a 20-m (henceforth called *local* forest cover) and 200-m (*landscape* forest cover) buffer around the sampled oaks. We chose two nested buffer sizes to better capture the complexity of habitat structure on the diversity and acoustic activity of birds. Local forest cover is particularly important for estimating bird occurrence probability (Melles, Glenn & Martin, 2003), whereas landscape forest cover is an important predictor of bird community composition in urban areas (Rega-Brodsky & Nilon, 2017). Moreover, both local and landscape habitat factors shape insect prey distribution (Barr, van Dijk, Hylander & Tack, 2021). Preliminary analyses revealed that results were qualitatively the same using 10-, 20- or 50-m buffers as predictors of local forest cover and 200- or 500-m buffers as predictors of landscape forest cover (see Table S4.5 in Appendix S4). Because other variables were defined at the site level, we averaged the percentage of forest cover for the sampled trees per site and per buffer size.

We extracted the mean annual temperature at each site from the WorldClim database (the spatial resolution is $\sim 86 \text{ km}^2$, Hijmans et al., 2005).

2.2.5. Statistical analyses

We analyzed 14 response variables in separate linear models (LMs) (Table S2.2 in Appendix S2): bird predation attempts, species richness of the entire bird community and that of candidate insectivores, functional diversity (each of the four indices) and acoustic diversity (each of the three indices). For each response variable, we first built a full model

including variables reflecting two components of the environment: climate and local habitat. The general model equation was (Eq. 1):

$$Y_i = \beta_0 + \beta_1 \times Forest_{20,i} + \beta_2 \times Forest_{200,i} + \beta_3 \times Climate_i + \varepsilon_i \quad (1)$$

where Y_i is the response variable, β_0 the model intercept, β_1 model coefficient parameters, $Forest_{20}$ and $Forest_{200}$ the effects of the local and landscape forest cover respectively, $Climate$ the effect of mean annual temperature and ε the residuals.

When modeling the response of bird predation attempts (Eq. 2), we added two more variables to the model, being any of the three acoustic diversity indices (*Acoustic diversity*, Eq. 2) and the species richness or any of the four indices describing the functional diversity of candidate insectivores (*Bird diversity*, Eq. 2):

$$Y_i = \beta_0 + \beta_1 \times Forest_{20,i} + \beta_2 \times Forest_{200,i} + \beta_3 \times Climate_i + \beta_4 \times Bird\ diversity_i + \beta_5 \times Acoustic\ diversity_i + \varepsilon_i \quad (2)$$

It has to be noted that the inclusion of the acoustic component in the second set of models does not imply any direct link between avian predation and acoustic diversity. By comparing models including the acoustic diversity or not, we are asking whether residual variance can be explained by this component while controlling for other sources of variation. If so, then acoustic diversity components with non-null coefficients have to be considered as proxies of predation, i.e., relatively easily measurable variables representative of unmeasured (or unknown) variables with a direct effect on predation.

We used logarithmic transformations (for bird predation attempts, acoustic entropy (H) and acoustic diversity (ADI) models) or square rooted transformation (for species richness of the complete bird community) of some response variables where appropriate to satisfy model assumptions. We scaled and centered every continuous predictor prior to modeling to facilitate comparisons of their effect sizes, and made sure that none of the explanatory variables were strongly correlated using the variance inflation factor (VIF) (all VIFs < 5, the usual cutoff values used to check for multicollinearity issues (Miles, 2014)).

For each response variable, we ran the full model as well as every model nested within the full model and then used Akaike's Information Criterion corrected for small sample size (AICc) to identify the most effective model(s) fitting the data the best. We

simultaneously selected the best variable describing the diversity and acoustic component (variable selection) and the best set of variables describing the variability of the response variable (model selection).

First, we ranked each model according to the difference in AICc between the given model and the model with the lowest AICc (ΔAICc). Models within 2 ΔAICc units of the best model (i.e., the model with the lowest AICc) are generally considered as likely (Burnham & Anderson, 2002). We computed AICc weights for each model (w_i). w_i is interpreted as the probability of a given model being the best model among the set of candidate models. Eventually, we calculated the relative variable importance (RVI) as the sum of w_i of every model including this variable, which corresponds to the probability a variable is included in the best model.

When several models competed with the best model (i.e., when multiple models were such that their $\Delta\text{AICc} < 2$), we applied a procedure of multimodel inference, building a consensus model including the variables in the set of best models. We then averaged their effect sizes across all the models in the set of best models, using the variable weight as a weighting parameter (i.e., model averaging). We considered that a given predictor had a statistically significant effect on the response variable when its confidence interval excluded zero.

We run all analyses in the R language environment (R Core Team, 2020) with libraries “MuMIn” v.1.43.17 (Bartoń, 2020), “lme4” v. 1.1.27.1 (Bates, Mächler, Bolker & Walker, 2015). All R codes are provided in Appendix S5 in Supporting Information.

2.3. Results

2.3.1. Bird acoustic diversity

Of the three acoustic diversity indices (see Fig. S6.6 in Appendix S6 for correlation between indices), only Acoustic Diversity Index (ADI) and acoustic entropy (H) were significantly associated with any of the predictors tested, i.e., temperature, local forest cover and landscape forest cover (Table S2.2 in Appendix S2). ADI and H both increased with local forest cover (i.e., percentage of forest cover in a 20-m buffer around recorders).

Landscape-scale forest cover (i.e., percentage of forest cover in a 200-m buffer around recorders) was the only other predictor retained in the set of competing models in a range of $\Delta\text{AICc} < 2$ to explain acoustic entropy variation, but this predictor had little importance ($\text{RVI} < 0.5$) and its effect was not statistically significant (Fig. 5b; Table S2.2 in Appendix S2).

2.3.2. Bird species richness and functional diversity

We identified a total of 87 bird species, among which 25 were classified as candidate functional insectivores. Bird species richness varied from 8 to 23 species per recording site (mean \pm SD: 15.2 ± 3.7 , $n = 47$ sites) and richness of candidate insectivores from 2 to 9 species (5.7 ± 1.5). The null model was among models competing in a range of $\Delta\text{AICc} < 2$ for both total species richness and candidate insectivores (Table S2.2 in Appendix S2).

Among the five bird functional diversity and species richness indices, only functional quadratic entropy (Rao's Q) characterizing species dispersion from the functional centroid was significantly influenced by the predictors tested (temperature, local and landscape forest cover, Table S2.2 in Appendix S2). Specifically, Rao's Q increased with increasing temperature (Fig. 4a and Fig. 5c). Other predictors retained in the set of competing models in a range of $\Delta\text{AICc} < 2$ had little importance ($\text{RVI} < 0.5$) and were not significant (Fig. 5c; Table S2.2 in Appendix S2).

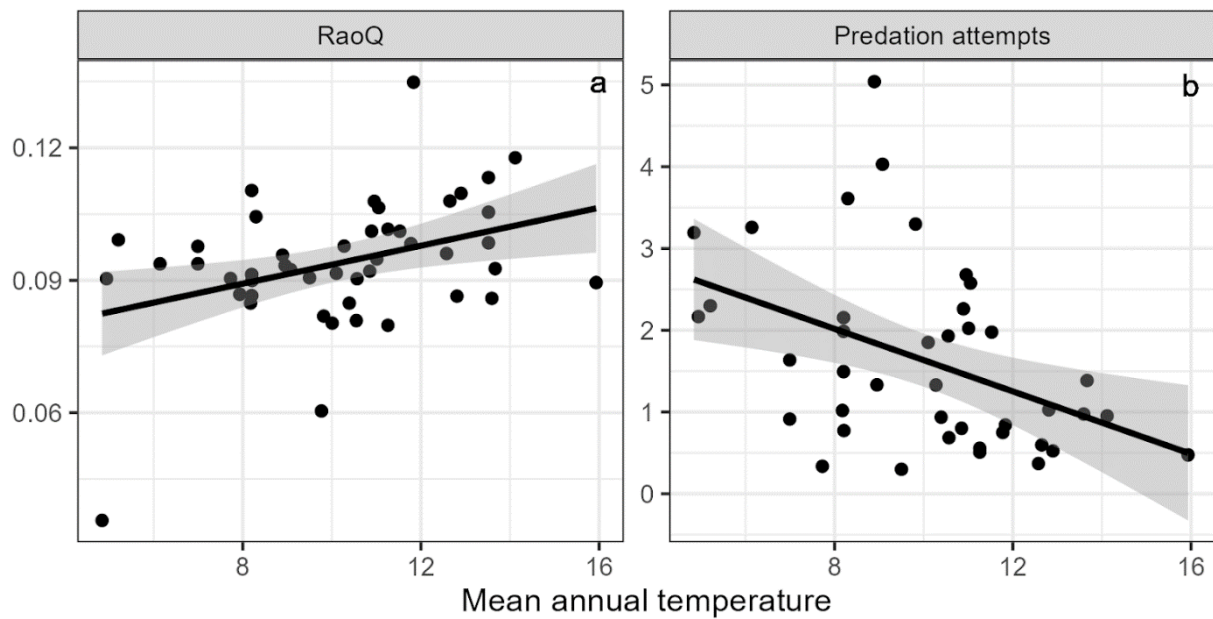


Figure 4. Scatter diagrams showing changes in (a) Rao's quadratic entropy (Rao's Q) and (b) predation attempts with mean annual temperature. These relationships were identified as significant in the linear models tested. A dot represents a site, the prediction line corresponds to a linear regression between the two variables and the gray bands represent the confidence intervals around this regression.

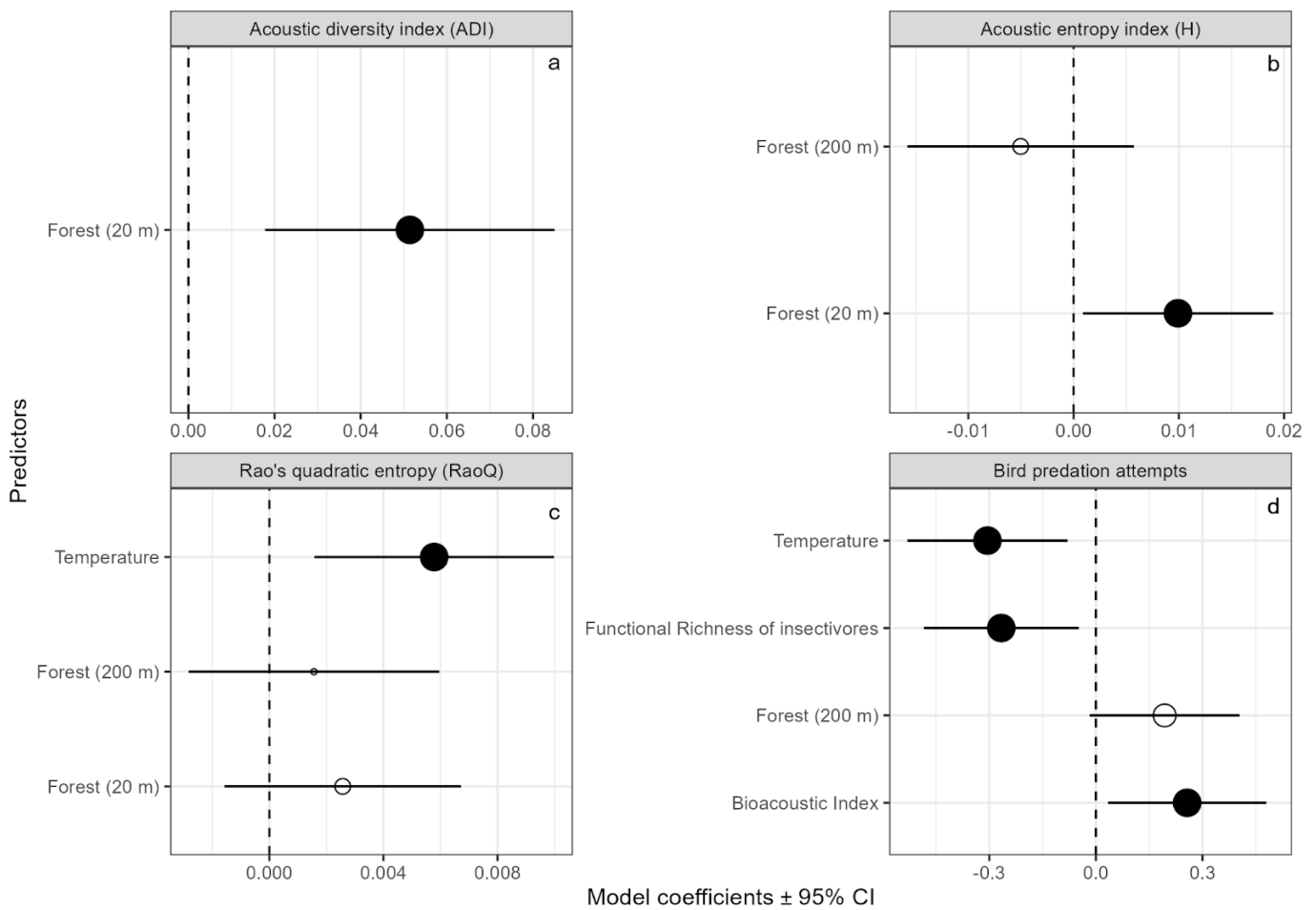


Figure 5. Effects of climate (described by the mean annual temperature) and habitat (percentage of forest cover at 20 or 200 m) on Acoustic Diversity Index (ADI) (a), Acoustic Entropy Index (H) (b), Rao's quadratic entropy (RaoQ) (c), bird predation attempts (d) and effects of acoustic (Bioacoustic Index), bird diversity (Functional Richness) on bird predation attempts (d). Circles and error bars represent standardized parameter estimates and corresponding 95% confidence intervals (CI), respectively. The vertical dashed line centered on zero represents the null hypothesis. Full and empty circles represent significant and non-significant effect sizes, respectively. Circle size is proportional to RVI.

2.3.3. Bird predation attempts

Of the 4,860 exposed dummy caterpillars, 22.8% ($n = 1,108$) had bird bill marks. Model selection retained two models in the set of competing models in a range of $\Delta AICc < 2$ (Table S2.2 in Appendix S2). Bird functional richness (FRic) (RVI= 1.00), bioacoustic index (BI) (RVI = 1.00) and temperature (RVI=1.00) were selected in all models. Landscape forest cover (RVI = 0.62) was also selected in one of the two best models.

Bird predation attempts decreased with increasing mean annual temperature. Bird predation attempts further increased with bioacoustic index (BI), but decreased with bird

functional richness (FRic) (Fig. 4b and Fig. 5d). This finding suggests that the acoustic component captures some features of the habitat that influence predation attempts independently of bird functional diversity. Likewise, the fact that temperature was selected a significant predictor of bird predation attempts suggests that climate has an effect on predation that is not only mediated by its effect on bird communities.

The results were comparable when we incorporated latitudinal changes in diel phenology in the calculation of predation attempts through the standardization with the daylight duration (see Table S2.2 in Appendix S2).

2.4. Discussion

Our study confirms the well documented increase of bird diversity towards warmer regions, a pattern supporting our initial assumption that avian predation would mirror this pattern. Yet, we found the opposite – predation attempts decreased with increasing temperature – which dismissed our prediction that bird diversity and avian predation rate should correlate positively across large geographic gradients. An important result of our study is that even when the functional dimension of bird communities was accounted for, a substantial amount of variability remained to be explained and were only partially accounted for by climate- and habitat-related variables. Altogether, these findings suggest that current theory should be re-assessed, which we discuss below speculating on the main causes of deviation from theoretical expectations.

2.4.1. Functional diversity of insectivorous birds and bird predation attempts are both influenced by climate, in opposite ways

In agreement with our first prediction (i, Fig. 1), we provide evidence for a significant positive relationship between temperature and the functional diversity of insectivorous birds. Despite substantial differences among functional diversity indices, this result suggests that, more functionally diverse assemblages of insectivorous birds are able to coexist locally in oak woods towards the South of Europe (Currie et al., 2004; Hillebrand, 2004; Willig et al., 2003). Of the multiple functional diversity indices commonly used to

describe ecological communities, it is noticeable that only the quadratic entropy index responded positively to temperature, for it is a synthetic index that simultaneously takes into account the richness, evenness, and divergence components of functional diversity (Mouillot et al., 2013).

Contrary to our predictions (i, Fig. 1), bird predation attempts decreased with increasing temperature and were therefore inconsistently linked with bird functional diversity. More bird predation attempts at lower temperatures could be due to longer daylight duration in spring northwards, leading insectivorous birds to have more time per day to find their prey and thus allowing high coexistence of predators during a period of high resource availability (Speakman et al., 2000). Alternatively, as birds require more energy to thermoregulate in colder temperatures, they may need to feed more in order to maintain their metabolic activity (Caraco et al., 1990; Kendeigh, 1969; Steen, 1958; Wansink & Tinbergen, 1994). Moreover, temperature remained an important, significant predictor of bird predation attempts when we controlled for the duration of daylight (Table S2.2 in Appendix S2), which further supports this explanation. However, we cannot exclude the possibility that the lower predation rates at higher temperatures was due to lower prey detectability.

2.4.2. Bird predation attempts are partly predicted by bird functional diversity and acoustic activity

We predicted that bird predation attempts would increase with bird abundance and functional diversity (ii, Fig. 1). The results only partially match these predictions. The relationship between bird functional diversity and predation attempts conflicted with our predictions. Specifically, we found neutral or negative relationship between these variables, depending on the functional index considered. Only functional insectivore richness was negatively correlated to predation attempts. Negative relationships between predation and predator functional diversity can arise from a combination of both intraguild predation --- predators preying upon predators (Mooney et al., 2010) --- and intraguild competition (Houska Tahadlova et al., 2022), although we could not tease them apart in the present study. An important step forward would consist in testing whether

predation patterns revealed using artificial prey are representative of predation intensity as a whole (Zvereva & Kozlov, 2021). For example, functional richness may be a proxy for dietary specialization in such a way that more functionally diverse predator communities would seek more prey of which they are specialized on and thus predate less on artificial caterpillars. It is also possible that a higher diversity of insectivorous birds in warmer regions was linked to higher diversity and abundance of arthropod prey and foraging niches (Kissling et al., 2012) and therefore to greater prey availability (Charbonnier et al., 2016). If so, then the pattern we observed may merely be representative of the 'dilution' of bird attacks on artificial prey among more abundant and diverse real prey (Zeuss, Brunzel & Brandl, 2017; Zvereva et al., 2019). However, the dynamics between herbivore prey abundance and predation activity are complex. A higher abundance of real herbivore prey could also lead to increased predation activity as demonstrated in studies such as Singer, Farkas, Skorik & Mooney (2011), where the presence of abundant herbivorous prey was found to drive higher predation rates by bird predators. This aligns with the notion that predator populations respond to fluctuations in prey density (Salamolard, Butet, Leroux & Bretagnolle, 2000), adjusting their foraging behavior to capitalize on available food resources. A follow-up of the present study should therefore pay special attention to the real prey density pre-existing in each sampling site where artificial prey are to be deployed as a standardized measure of predation rates across sites.

Although passive acoustic monitoring, as most other relative bird sampling methods, does not allow inferring directly bird absolute abundance, our study further brings methodological insights into the usefulness of eco-acoustics into community and functional ecology. We found that among acoustic indices that have been shown to correlate with bird abundance, activity and diversity, the Bioacoustic index was positively correlated with bird predation attempts. Yet, this index was found to be representative of the abundance and activity of singing birds (Boelman et al., 2007; Gasc et al., 2018). It is thus reasonable to infer substantial causality between vocalizing bird abundance, their acoustic activity, and the top-down control they exert upon insect prey. Such an interpretation is in line with previous studies having reported positive relationships between bird abundance and predation attempts on artificial prey (Roels, Porter & Lindell, 2018; Sam, Koane & Novotny, 2015). It is further substantiated by the fact that if a species is recorded in a given site during the breeding season, it indicates that it is

probably feeding on that territory and can potentially affect predation rates. Our study indicates that despite acknowledgeable limitations inherent to the current development of analytical tools, passive acoustic monitoring has the potential to provide acceptable proxies for the characterization of bird biodiversity, the habitat they live in, and, to some extent, the ecosystem services they provide. The present study therefore opens pathways for new research on the link between functional and acoustic ecology.

2.4.3. Local forest cover predicts bird acoustic diversity, whereas landscape forest cover increases bird predation

Acoustic diversity increased with closeness of canopy cover in the immediate neighborhood (20m radius) of sampled trees (iii, Fig. 1). The most responsive indices were the Acoustic Diversity Index (ADI) and the acoustic entropy (H), both designed to predict bird acoustic diversity across different habitats under various ambient sound conditions (Fuller, Axel, Tucker & Gage, 2015; Machado, Aguiar & Jones, 2017). The former is related to a greater regularity of the soundscape and the latter is related to the amplitude between frequency bands and time. They therefore correspond to soundscapes containing multiple vocalizing species (Sueur, Pavoine, et al., 2008; Villanueva-Rivera, Pijanowski, Doucette & Pekin, 2011). Acoustic entropy is also known to respond significantly to local forest habitat (Barbaro et al., 2022), which is generally a good predictor of bird occupancy probability (Morante-Filho, Benchimol & Faria, 2021).

Bird predation attempts were best predicted by forest cover at the landscape level (Prediction (iii), Fig. 1). Indeed, it is likely that forest cover at the landscape level provides structural complexity with a dense understorey and habitat heterogeneity that is both a source of food and niches for predatory birds to exploit (Poch & Simonetti, 2013). As a result, forest cover at the landscape scale is often a key predictor of avian insectivory in various study areas (Barbaro et al., 2014; González-Gómez, Estades & Simonetti, 2006; Valdés-Correcher et al., 2021). This is also consistent with the results of Rega-Brodsky & Nilon (2017) who found greater abundance of insectivorous birds in mosaic urban or rural landscapes including a significant part of semi-natural wooded habitats, such as those we studied here.

2.4.4. Large-scale variability in avian predation is not mediated by large-scale changes in bird communities

We found no evidence that the relationship between climate and bird predation attempts was mediated by changes in bird diversity or acoustic activity (iv, Fig. 1). On the contrary, climate and bird diversity and acoustic activity had independent and complementary effects on predation.

At the European scale, climate may directly drive both bird activity and abundance according to available resources (Pennings & Silliman, 2005). Even changes in the abundance of a single, particularly active, predator species along the European climatic gradient could explain the observed pattern (Maas, Tschardtke, Saleh, Dwi Putra, Clough & Siriwardena, 2015; Philpott et al., 2009). For example, the blue tit *Cyanistes caeruleus* and the great tit *Parus major* are typical and widespread canopy insectivores of European oak forests and are particularly prone to predate herbivorous caterpillars while showing considerable adaptive behavior to prey availability (Mols & Visser, 2002; Naef-Daenzer & Keller, 1999). If the predation attempts on the plasticine caterpillars were to be predominantly due to these species, then it would be their abundance and foraging activity that would play a role in predation attempts rather than the overall diversity of insectivores (Maas et al., 2015). Here, we based our assessment of functional bird composition on candidate insectivore occurrences obtained from standardized acoustic surveys, which on one hand insures that we have no observer, site, or phenological biases on species occurrences, but on the other hand also makes it difficult to precisely account for each species' abundance. Other complementary methods to assess the relative roles of each individual bird species on predation rates should be deployed further to better account for actual predatory bird abundance and activity, including DNA sampling (Garfinkel, Minor & Whelan, 2022), camera traps (Martínez-Núñez et al., 2021) or species-specific bird surveys involving tape calls or capture methods.

2.4.5. Conclusion

We found a positive association between temperature and bird functional diversity, and at the same time, a negative relationship between temperature and avian predation. Our study therefore provides partial support for the climatic clines in biodiversity hypothesis, but demonstrates that predation does not follow the same pattern. As cross-continental studies exploring the large-scale relationship between climate and the strength of biotic interactions generally ignore local factors, we argue that characterizing the contrasting habitats of the study sites is a good way to circumvent some inconsistencies in the results. We identify pre-existing real prey density and single key bird species abundances as two particularly important variables deserving further attention. Furthermore, predicting ecosystem services — here, potential pest regulation service — on a large scale by standardized proxies such as acoustic ecology for predator diversity and plasticine caterpillars for predation function seem to be good ways to reduce methodological biases and strengthen our understanding of the macro-ecology of biotic interactions.

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Data availability statement

The data and codes are available at Schille et al., 2024, « Data and codes for the article "Decomposing drivers in avian insectivory: large-scale effects of climate, habitat and bird diversity" », <https://doi.org/10.57745/0E0JEA>, Recherche Data Gouv.

Supplementary materials

Table S1.1. Cleaned datasets used for all statistical analyses of the manuscript

Site_ID	Index	MedInd	Pred_Daymir	Pred_Day	Lat	Long	MAT	For20	For200	RichSpeTOT	RSpe_Functl	Fric	Feve	FDiv	RaoQ	
and.gal_1	ADI	2,48118239	0,00414209	4,03025794	51,494754	11,948814		9,075	3,8	28,5467929	8	3	0,01891369	0,85139252	0,70994907	0,92397622
and.gal_1	BI	1,39801244	0,00414209	4,03025794	51,494754	11,948814		9,075	3,8	28,5467929	8	3	0,01891369	0,85139252	0,70994907	0,92397622
and.gal_1	H	0,84305843	0,00414209	4,03025794	51,494754	11,948814		9,075	3,8	28,5467929	8	3	0,01891369	0,85139252	0,70994907	0,92397622
and.kav_1	ADI	2,47089193	0,00275585	2,57671958	45,8817333	15,3518333		11,05	46,0732323	30,3990581	13	6	0,1069439	0,87731748	0,77796465	0,10645751
and.kav_1	BI	9,54515976	0,00275585	2,57671958	45,8817333	15,3518333		11,05	46,0732323	30,3990581	13	6	0,1069439	0,87731748	0,77796465	0,10645751
and.kav_1	H	0,93256824	0,00275585	2,57671958	45,8817333	15,3518333		11,05	46,0732323	30,3990581	13	6	0,1069439	0,87731748	0,77796465	0,10645751
and.pio_1	ADI	2,4580626	0,00058424	0,52464495	45,1998873	10,7460803		12,9	72,5272727	66,1178166	16	6	0,19962734	0,89489391	0,85356704	0,10969347
and.pio_1	BI	4,00980414	0,00058424	0,52464495	45,1998873	10,7460803		12,9	72,5272727	66,1178166	16	6	0,19962734	0,89489391	0,85356704	0,10969347
and.pio_1	H	0,86783034	0,00058424	0,52464495	45,1998873	10,7460803		12,9	72,5272727	66,1178166	16	6	0,19962734	0,89489391	0,85356704	0,10969347
and.pri_1	ADI	2,40839817	0,00054408	0,50925926	48,0629752	-1,6067672	11,2583333	42,7962963	57,6757875	19	9	0,21879236	0,93103296	0,81044423	0,10156394	
and.pri_1	BI	6,09843823	0,00054408	0,50925926	48,0629752	-1,6067672	11,2583333	42,7962963	57,6757875	19	9	0,21879236	0,93103296	0,81044423	0,10156394	
and.pri_1	H	0,91494848	0,00054408	0,50925926	48,0629752	-1,6067672	11,2583333	42,7962963	57,6757875	19	9	0,21879236	0,93103296	0,81044423	0,10156394	
ann.mra_1	ADI	2,48351037	0,00035099	0,33730159	48,8341595	14,5114229		7,725	79,45	78,662039	9	5	0,12561421	0,93750419	0,81743883	0,9040685
ann.mra_1	BI	5,23143826	0,00035099	0,33730159	48,8341595	14,5114229		7,725	79,45	78,662039	9	5	0,12561421	0,93750419	0,81743883	0,9040685
ann.mra_1	H	0,87799193	0,00035099	0,33730159	48,8341595	14,5114229		7,725	79,45	78,662039	9	5	0,12561421	0,93750419	0,81743883	0,9040685
ann.pop_1	ADI	2,47240071	0,00211795	2,16666667	55,4418215	37,4643333	4,94166667	86,56	68,7022718	14	8	0,17699259	0,94730458	0,82097196	0,90365801	
ann.pop_1	BI	2,31039562	0,00211795	2,16666667	55,4418215	37,4643333	4,94166667	86,56	68,7022718	14	8	0,17699259	0,94730458	0,82097196	0,90365801	
ann.pop_1	H	0,88475669	0,00211795	2,16666667	55,4418215	37,4643333	4,94166667	86,56	68,7022718	14	8	0,17699259	0,94730458	0,82097196	0,90365801	
aur.sal_1	ADI	2,47998813	0,00239863	2,26190476	47,714	2,0049	10,8916667	81,5969697	83,1294011	15	5	0,07538284	0,88848902	0,76599895	0,10110234	
aur.sal_1	BI	6,85783168	0,00239863	2,26190476	47,714	2,0049	10,8916667	81,5969697	83,1294011	15	5	0,07538284	0,88848902	0,76599895	0,10110234	
aur.sal_1	H	0,90849521	0,00239863	2,26190476	47,714	2,0049	10,8916667	81,5969697	83,1294011	15	5	0,07538284	0,88848902	0,76599895	0,10110234	
bas.cas_1	ADI	2,42712394	0,00067655	0,59739627	44,8085203	-0,5936123	12,65	64	7,52124808	18	6	0,18285103	0,96022123	0,81177241	0,107950271	
bas.cas_1	BI	6,70987132	0,00067655	0,59739627	44,8085203	-0,5936123	12,65	64	7,52124808	18	6	0,18285103	0,96022123	0,81177241	0,107950271	
bas.cas_1	H	0,91672861	0,00067655	0,59739627	44,8085203	-0,5936123	12,65	64	7,52124808	18	6	0,18285103	0,96022123	0,81177241	0,107950271	
ben.let_1	ADI	1,60759506	0,00059472	0,55725624	48,783364	-3,0581587	11,2583333	9,06060606	11,3816375	20	6	0,09244244	0,95646199	0,71001597	0,79796994	
ben.let_1	BI	4,95264101	0,00059472	0,55725624	48,783364	-3,0581587	11,2583333	9,06060606	11,3816375	20	6	0,09244244	0,95646199	0,71001597	0,79796994	
ben.let_1	H	0,85731664	0,00059472	0,55725624	48,783364	-3,0581587	11,2583333	9,06060606	11,3816375	20	6	0,09244244	0,95646199	0,71001597	0,79796994	
car.lop_1	ADI	2,46624026	0,0021948	1,97751323	47,3523307	0,70381899	11,525	59,9185185	51,7232463	17	5	0,07538284	0,88848902	0,76599895	0,10110234	
car.lop_1	BI	6,64963755	0,0021948	1,97751323	47,3523307	0,70381899	11,525	59,9185185	51,7232463	17	5	0,07538284	0,88848902	0,76599895	0,10110234	
car.lop_1	H	0,91848521	0,0021948	1,97751323	47,3523307	0,70381899	11,525	59,9185185	51,7232463	17	5	0,07538284	0,88848902	0,76599895	0,10110234	
chr.bou_1	ADI	2,36669681	0,00282848	2,67857143	47,834317	2,759332	10,9527778	65,9488216	36,8554157	20	8	0,22827892	0,95074327	0,8133498	0,10789081	
chr.bou_1	BI	9,60366712	0,00282848	2,67857143	47,834317	2,759332	10,9527778	65,9488216	36,8554157	20	8	0,22827892	0,95074327	0,8133498	0,10789081	
chr.bou_1	H	0,88320064	0,00282848	2,67857143	47,834317	2,759332	10,9527778	65,9488216	36,8554157	20	8	0,22827892	0,95074327	0,8133498	0,10789081	
csa.eot_1	ADI	2,46521775	0,0020863	1,92982456	47,3097536	21,0150881	10,55	8,15757576	65,0719877	15	6	0,16125395	0,92331245	0,85953213	0,80879153	
csa.eot_1	BI	6,82506136	0,0020863	1,92982456	47,3097536	21,0150881	10,55	8,15757576	65,0719877	15	6	0,16125395	0,92331245	0,85953213	0,80879153	
csa.eot_1	H	0,88547351	0,0020863	1,92982456	47,3097536	21,0150881	10,55	8,15757576	65,0719877	15	6	0,16125395	0,92331245	0,85953213	0,80879153	
csa.eot_2	ADI	2,45411777	0,00074702	0,68650794	47,2032787	21,1893168	10,5666667	0	0	18	6	0,17326608	0,93914102	0,8290676	0,9034529,	
csa.eot_2	BI	6,37756073	0,00074702	0,68650794	47,2032787	21,1893168	10,5666667	0	0	18	6	0,17326608	0,93914102	0,8290676	0,9034529,	
csa.eot_2	H	0,87256495	0,00074702	0,68650794	47,2032787	21,1893168	10,5666667	0	0	18	6	0,17326608	0,93914102	0,8290676	0,9034529,	
deb.har_2	ADI	2,22771067	NA	NA	51,295592	-0,33978	10,0083333	22,3636364	20,1927083	17	6	0,12460155	0,96951584	0,71256843	0,80281348,,	
deb.har_2	BI	9,32792844	NA	NA	51,295592	-0,33978	10,0083333	22,3636364	20,1927083	17	6	0,12460155	0,96951584	0,71256843	0,80281348,,	
deb.har_2	H	0,89497332	NA	NA	51,295592	-0,33978	10,0083333	22,3636364	20,1927083	17	6	0,12460155	0,96951584	0,71256843	0,80281348,,	
dmi.mus_1	ADI	2,34757825	0,00292177	3,19349845	59,9938802	30,3380896	4,84166667	99,7866667	84,2372652	11	2	NA	NA	NA	0,35605934,,	
dmi.mus_1	BI	4,90029619	0,00292177	3,19349845	59,9938802	30,3380896	4,84166667	99,7866667	84,2372652	11	2	NA	NA	NA	0,35605934,,	
dmi.mus_1	H	0,89613048	0,00292177	3,19349845	59,9938802	30,3380896	4,84166667	99,7866667	84,2372652	11	2	NA	NA	NA	0,35605934,,	
ele.val_1	ADI	2,47942356	0,00041568	0,37037037	44,7380393	-0,7775387	12,575	67,0606061	37,0087959	20	7	0,1377694	0,91543444	0,75215062	0,96062065	
ele.val_1	BI	4,28533794	0,00041568	0,37037037	44,7380393	-0,7775387	12,575	67,0606061	37,0087959	20	7	0,1377694	0,91543444	0,75215062	0,96062065	
ele.val_1	H	0,90848439	0,00041568	0,37037037	44,7380393	-0,7775387	12,575	67,0606061	37,0087959	20	7	0,1377694	0,91543444	0,75215062	0,96062065	
eli.flu_1	ADI	2,44783446	NA	NA	46,9666303	9,56965433	7,93333333	13,9023569	21,4857272	10	3	0,07814351	0,84053761	0,79514551	0,8682882,,	
eli.flu_1	BI	6,85109621	NA	NA	46,9666303	9,56965433	7,93333333	13,9023569	21,4857272	10	3	0,07814351	0,84053761	0,79514551	0,8682882,,	
eli.flu_1	H	0,87005604	NA	NA	46,9666303	9,56965433	7,93333333	13,9023569	21,4857272	10	3	0,07814351	0,84053761	0,79514551	0,8682882,,	
eli.man_1	ADI	2,47538867	0,00505104	5,04093567	52,5956667	13,2631667	8,89166667	81,8833333	87,2965924	18	6	0,1391052	0,92851441	0,7616098	0,95695873	
eli.man_1	BI	4,66131561	0,00505104	5,04093567	52,5956667	13,2631667	8,89166667	81,8833333	87,2965924	18	6	0,1391052	0,92851441	0,7616098	0,95695873	
eli.man_1	H	0,89869066	0,00505104	5,04093567	52,5956667	13,2631667	8,89166667	81,8833333	87,2965924	18	6	0,1391052	0,92851441	0,7616098	0,95695873	
fla.bal_3	ADI	2,34023222	0,00087572	0,80128205												

kat.sam_1	ADI	2,45951708	0,00223291	2,15476191	48,975786	14,4251813	8,2	80,1030303	67,6319148	14	6	0,15844048	0,95131016	0,76140667	0,11034143
kat.sam_1	BI	4,95872242	0,00223291	2,15476191	48,975786	14,4251813	8,2	80,1030303	67,6319148	14	6	0,15844048	0,95131016	0,76140667	0,11034143
kat.sam_1	H	0,88849853	0,00223291	2,15476191	48,975786	14,4251813	8,2	80,1030303	67,6319148	14	6	0,15844048	0,95131016	0,76140667	0,11034143
kat.sam_2	ADI	2,48010913	0,00094436	0,91414141	49,3378502	13,0891489	6,99166667	74,7060606	70,0969279	15	4	0,11659095	0,8323709	0,80609571	0,97684669
kat.sam_2	BI	1,99100803	0,00094436	0,91414141	49,3378502	13,0891489	6,99166667	74,7060606	70,0969279	15	4	0,11659095	0,8323709	0,80609571	0,97684669
kat.sam_2	H	0,87756155	0,00094436	0,91414141	49,3378502	13,0891489	6,99166667	74,7060606	70,0969279	15	4	0,11659095	0,8323709	0,80609571	0,97684669
leo.dud_1	ADI	2,46784594	0,00108177	1,01902727	46,8888222	27,0128667	8,175	41,3878788	43,9457879	23	4	0,10737714	0,91203237	0,85438639	0,84820661
leo.dud_1	BI	4,63654225	0,00108177	1,01902727	46,8888222	27,0128667	8,175	41,3878788	43,9457879	23	4	0,10737714	0,91203237	0,85438639	0,84820661
leo.dud_1	H	0,86657843	0,00108177	1,01902727	46,8888222	27,0128667	8,175	41,3878788	43,9457879	23	4	0,10737714	0,91203237	0,85438639	0,84820661
luc.bar_1	ADI	2,48472605	0,00083057	0,75	43,239408	0,820423	11,775	91,6363636	57,419964	16	7	0,15761944	0,91681077	0,8666749	0,98278946
luc.bar_1	BI	2,74059441	0,00083057	0,75	43,239408	0,820423	11,775	91,6363636	57,419964	16	7	0,15761944	0,91681077	0,8666749	0,98278946
luc.bar_1	H	0,87217881	0,00083057	0,75	43,239408	0,820423	11,775	91,6363636	57,419964	16	7	0,15761944	0,91681077	0,8666749	0,98278946
maa.deg_1	ADI	2,46268263	0,00100104	0,93697206	46,0222667	14,4498	10,3916667	67,1691919	42,8859772	13	4	0,10737714	0,91203237	0,85438639	0,84820661
maa.deg_1	BI	4,04031617	0,00100104	0,93697206	46,0222667	14,4498	10,3916667	67,1691919	42,8859772	13	4	0,10737714	0,91203237	0,85438639	0,84820661
maa.deg_1	H	0,85952705	0,00100104	0,93697206	46,0222667	14,4498	10,3916667	67,1691919	42,8859772	13	4	0,10737714	0,91203237	0,85438639	0,84820661
man.bra_1	ADI	2,40734527	0,00054861	0,47619048	40,2116477	-8,449072	15,9333333	75,5357143	32,8695125	11	7	0,13052453	0,94769649	0,79186263	0,89475793
man.bra_1	BI	4,39145977	0,00054861	0,47619048	40,2116477	-8,449072	15,9333333	75,5357143	32,8695125	11	7	0,13052453	0,94769649	0,79186263	0,89475793
man.bra_1	H	0,85008421	0,00054861	0,47619048	40,2116477	-8,449072	15,9333333	75,5357143	32,8695125	11	7	0,13052453	0,94769649	0,79186263	0,89475793
mar.fat_1	ADI	2,44005969	0,00154571	1,63690476	59,2996938	18,0474623	6,99166667	44,6011905	14,7553337	18	5	0,09978709	0,89800096	0,79799054	0,9373859
mar.fat_1	BI	3,16900994	0,00154571	1,63690476	59,2996938	18,0474623	6,99166667	44,6011905	14,7553337	18	5	0,09978709	0,89800096	0,79799054	0,9373859
mar.fat_1	H	0,87579082	0,00154571	1,63690476	59,2996938	18,0474623	6,99166667	44,6011905	14,7553337	18	5	0,09978709	0,89800096	0,79799054	0,9373859
mar.gos_1	ADI	2,48385977	0,00143678	1,33333333	47,4345533	7,74818667	8,95	84,8181818	60,8365341	22	8	0,15095034	0,91880579	0,75323366	0,93351698
mar.gos_1	BI	2,4833887	0,00143678	1,33333333	47,4345533	7,74818667	8,95	84,8181818	60,8365341	22	8	0,15095034	0,91880579	0,75323366	0,93351698
mar.gos_1	H	0,91003389	0,00143678	1,33333333	47,4345533	7,74818667	8,95	84,8181818	60,8365341	22	8	0,15095034	0,91880579	0,75323366	0,93351698
mic.bog_1	ADI	1,71218563	0,00151383	1,49415205	52,4978704	16,9347222	8,2	1,59259259	21,9443796	16	7	0,11938928	0,92552374	0,75105491	0,91326697
mic.bog_1	BI	7,17848122	0,00151383	1,49415205	52,4978704	16,9347222	8,2	1,59259259	21,9443796	16	7	0,11938928	0,92552374	0,75105491	0,91326697
mic.bog_1	H	0,83596592	0,00151383	1,49415205	52,4978704	16,9347222	8,2	1,59259259	21,9443796	16	7	0,11938928	0,92552374	0,75105491	0,91326697
mik.koz_1	ADI	2,46661007	0,00207181	2,2997076	60,4344444	22,1788888	5,20833333	64,5	42,7900263	17	5	0,1545746	0,92208426	0,81862151	0,99159363
mik.koz_1	BI	5,11397647	0,00207181	2,2997076	60,4344444	22,1788888	5,20833333	64,5	42,7900263	17	5	0,1545746	0,92208426	0,81862151	0,99159363
mik.koz_1	H	0,89173326	0,00207181	2,2997076	60,4344444	22,1788888	5,20833333	64,5	42,7900263	17	5	0,1545746	0,92208426	0,81862151	0,99159363
mon.bjo_1	ADI	2,2503773	0,00076767	0,77380952	54,8616853	10,7368673	8,20833333	44,4083333	27,5848077	20	6	0,12605838	0,93602863	0,87884534	0,89947518
mon.bjo_1	BI	3,5092371	0,00076767	0,77380952	54,8616853	10,7368673	8,20833333	44,4083333	27,5848077	20	6	0,12605838	0,93602863	0,87884534	0,89947518
mon.bjo_1	H	0,89074173	0,00076767	0,77380952	54,8616853	10,7368673	8,20833333	44,4083333	27,5848077	20	6	0,12605838	0,93602863	0,87884534	0,89947518
pil.fer_1	ADI	2,19480782	0,00109538	0,97598162	43,9163473	4,87939733	13,5916667	0	3,59160295	8	4	0,05264921	0,87970862	0,85849558	0,85907797
pil.fer_1	BI	2,06770396	0,00109538	0,97598162	43,9163473	4,87939733	13,5916667	0	3,59160295	8	4	0,05264921	0,87970862	0,85849558	0,85907797
pil.fer_1	H	0,85149023	0,00109538	0,97598162	43,9163473	4,87939733	13,5916667	0	3,59160295	8	4	0,05264921	0,87970862	0,85849558	0,85907797
pil.fer_2	ADI	2,1705406	0,00152258	1,3855472	43,962414	4,871011	13,6666667	24,9848485	20,1860185	17	4	0,06887642	0,83967461	0,84849382	0,92648511
pil.fer_2	BI	5,15266783	0,00152258	1,3855472	43,962414	4,871011	13,6666667	24,9848485	20,1860185	17	4	0,06887642	0,83967461	0,84849382	0,92648511
pil.fer_2	H	0,86278648	0,00152258	1,3855472	43,962414	4,871011	13,6666667	24,9848485	20,1860185	17	4	0,06887642	0,83967461	0,84849382	0,92648511
ric.hou_1	ADI	2,45739844	NA	NA	51,8063583	-1,1846495	9,76666667	2,01818182	1,42564754	17	5	0,07399899	0,95857819	0,75634606	0,60402137,
ric.hou_1	BI	4,68987688	NA	NA	51,8063583	-1,1846495	9,76666667	2,01818182	1,42564754	17	5	0,07399899	0,95857819	0,75634606	0,60402137,
ric.hou_1	H	0,87792375	NA	NA	51,8063583	-1,1846495	9,76666667	2,01818182	1,42564754	17	5	0,07399899	0,95857819	0,75634606	0,60402137,
rit.ise_1	ADI	1,38170223	0,00141754	1,33106576	48,5840778	7,9782458	10,275	0	7,2401402	15	6	0,200693	0,92900023	0,92304316	0,97747107,
rit.ise_1	BI	5,53172297	0,00141754	1,33106576	48,5840778	7,9782458	10,275	0	7,2401402	15	6	0,200693	0,92900023	0,92304316	0,97747107,
rit.ise_1	H	0,85976304	0,00141754	1,33106576	48,5840778	7,9782458	10,275	0	7,2401402	15	6	0,200693	0,92900023	0,92304316	0,97747107,
sam.gre_1	ADI	2,40993194	0,00030564	0,30075188	52,287206	-1,520706	9,5	24,3909091	5,34412426	16	6	0,14734582	0,9389891	0,79860957	0,905714
sam.gre_1	BI	6,02719241	0,00030564	0,30075188	52,287206	-1,520706	9,5	24,3909091	5,34412426	16	6	0,14734582	0,9389891	0,79860957	0,905714
sam.gre_1	H	0,89483494	0,00030564	0,30075188	52,287206	-1,520706	9,5	24,3909091	5,34412426	16	6	0,14734582	0,9389891	0,79860957	0,905714
slo.mil_1	ADI	2,44334537	0,00219264	2,02380952	44,1440367	21,0776733	11,0083333	53,7666667	38,3618254	18	5	0,17326608	0,91280493	0,83944247	0,94813186
slo.mil_1	BI	11,93386644	0,00219264	2,02380952	44,1440367	21,0776733	11,0083333	53,7666667	38,3618254	18	5	0,17326608	0,91280493	0,83944247	0,94813186
slo.mil_1	H	0,909377	0,00219264	2,02380952	44,1440367	21,0776733	11,0083333	53,7666667	38,3618254	18	5	0,17326608	0,91280493	0,83944247	0,94813186
slo.mil_2	ADI	2,4786739	0,00090786	0,84249084	44,7394	20,1387767	11,8333333	50,9156566	37,3184143	12	5	0,16834568	0,98950492	0,77750244	0,13486387
slo.mil_2	BI	3,214464	0,00090786	0,84249084	44,7394	20,1387767	11,8333333	50,9156566	37,3184143	12	5	0,16834568	0,98950492	0,77750244	0,13486387
slo.mil_2	H	0,87653732	0,00090786	0,84249084	44,7394	20,1387767	11,8333333	50,9156566	37,3184143	12	5	0,16834568	0,98950492	0,77750244	0,13486387
sof.gri_1	ADI	2,4514967	0,0033353	3,29861111	51,7634984	-1,313708	9,81666667	68,3666667	53,0878437	12	6	0,05877847	0,94647263	0,75002838	0,81878572
sof.gri_1	BI	7,58295683	0,0033353	3,29861111	51,7634984	-1,313708	9,81666667	68,3666667	53,0878437	12	6	0,05877847	0,94647263	0,75002838	0,81878572
sof.gri_1	H	0,89493515	0,0033353	3,29861111	51,7634984	-1,313708	9,81666667	68,3666667	53,0878437	12	6	0,05877847	0,94647263	0,75002838	0,81878572
tho.dam_1	ADI	2,24026822	0,00191667	1,85150376	49,4601177	2,068195	10,1	31,0429293	28,5030425	13	6	0,11938928	0,93980913	0,76637913	0,91597822
tho.dam_1	BI	4,57940581	0,00191667	1,85150376	49,4601177	2,068195	10,1	31,0429293	28,5030425	13	6	0,11938928	0,93980913	0,76637913	0,91597822
tho.dam_1	H	0,89449663	0,00191667	1,85150376	49,4601177	2,068195	10,1	31,0429293	28,5030425	13	6				

Table S2.2. Model selection table for each of the 4 types of linear models to analyze bird predation attempts (a); taxonomic diversity (b); functional diversity (c) (any of the 4 indices) and acoustic diversity (d) (any of the 3 indices). The model selection abis (in grey) corresponds to the model where the bird predation attempts variable is standardized by the daylight duration per day. The results of this model are not presented in the result part of the manuscript. Explanatory variables that cannot be included in the model selection for a given response variable are shaded. Explanatory variables included in each model are indicated by the value of the slope. Those values are in bold if the variation of the response variable as a function of the explanatory variable is significant. *df* is the number of parameters included in the model, *logLik* is the log-likelihood. Model selection is based on the Akaike information criterion adapted to small sample sizes (*AICc*), the difference in *AICc* from the best model ($\Delta AICc$) and the *AICc* weight of each model. The set of models with a $\Delta AICc$ less than 2 are shown. For the same response variable, if only one row is shown, it means that either the null model was selected or the best model had no competition.

	Response variable	MAT	Forest20	Forest200	Specific Richness	FRIC	Bioacoustic Index	df	logLik	AICc	$\Delta AICc$	weight	R ²
a	Bird predation attempts	-0.2808		0.1934		- 0.2747	0.2636	6	-33.722	82.0	0.00	0.141	0.354
	Bird predation attempts	-0.3454				- 0.2524	0.2454	5	-35.615	83.0	1.01	0.085	0.300
a bis	Bird predation attempts/daylight	-0.2312		0.2005		- 0.2698	0.2603	6	-33.376	81.3	0.00	0.118	0.328
	Bird predation attempts/daylight	-0.2983				- 0.2466	0.2415	5	-35.437	82.6	1.34	0.061	0.266
b	Total Specific Richness							2	-31.894	68.1	0.00	0.388	0.000
	Specific Richness of Funct Insect							2	-85.026	174.3	0.00	0.2269	0.000
c	FRic		0.01329					3	76.744	-146.9	0.00	0.328	0.072
	FRic							2	74.987	-145.7	1.22	0.178	0.000
	FRic		0.02129	-0.010510				4	77.238	-145.5	1.42	0.161	0.089
	FEve							2	88.033	-171.8	0.00	0.364	0.000
	FDiv							2	70.156	-136.0	0.00	0.384	0.000
	RaoQ	0.005503						3	135.765	-265.0	0.00	0.406	0.138
	RaoQ	0.006020	0.002570					4	136.583	-264.2	0.76	0.277	0.164
RaoQ	0.006058		0.0015620				4	136.037	-263.1	1.85	0.161	0.145	
d	BI	0.5240						3	-105.395	217.3	0.00	0.252	0.048
	BI							2	-106.581	217.4	0.09	0.242	0.000
	BI			-0.3827				3	-105.956	218.5	1.12	0.144	0.026
	BI		-0.28760					3	-106.230	219.0	1.67	0.110	0.015
	H		0.008646					3	111.793	-217.0	0.00	0.446	0.125
	H		0.012540	-0.005032				4	112.264	-215.6	1.45	0.216	0.139
	ADI		0.05142					3	36.744	-66.9	0.00	0.510	0.171

Table S3.3. Bird species from all study sites heard in recordings and their corresponding diet in breeding season. The 25 functional insectivores are the candidates for attacking plasticine caterpillars. The comment column is used to explain why certain species were or were not considered to as functional insectivores in this study.

Genus.species	Common.Name	Diet in breeding season	Comment
Aegithalos caudatus	Long-tailed Tit	functional insectivore	
Anas platyrhynchos	Mallard	herbivore	
Anser anser	Graylag Goose	herbivore	
Anthus trivialis	Tree Pipit	insectivore	
Apus apus	Common Swift	insectivore	
Ardea cinerea	Gray Heron	carnivore	
Branta canadensis	Canada Goose	herbivore	
Buteo buteo	Common Buzzard	carnivore	
Caprimulgus europaeus	Eurasian Nightjar	insectivore	
Carduelis carduelis	European Goldfinch	granivore	
Certhia brachydactyla	Short-toed Treecreeper	insectivore	
Certhia familiaris	Eurasian Treecreeper	insectivore	
Chloris chloris	European Greenfinch	granivore	
Chroicocephalus ridibundus	Black-headed Gull	carnivore	
Coccothraustes coccothraustes	Hawfinch	granivore	
Columba oenas	Stock Dove	granivore	
Columba palumbus	Common Wood-Pigeon	granivore	
Corvus corax	Common Raven	omnivore	
Corvus cornix	Hooded Crow	omnivore	
Corvus corone	Carrion Crow	omnivore	
Corvus frugilegus	Rook	omnivore	
Corvus monedula	Eurasian Jackdaw	omnivore	
Coturnix coturnix	Common Quail	granivore	
Cuculus canorus	Common Cuckoo	insectivore	<i>Not likely to attack false caterpillars;specialist in eating stinging caterpillars</i>
Curruca communis	Greater Whitethroat	functional insectivore	
Curruca melanocephala	Sardinian Warbler	functional insectivore	
Cyanistes caeruleus	Eurasian Blue Tit	functional insectivore	
Dendrocopos major	Great Spotted Woodpecker	insectivore	<i>We excluded the bark foragers from the functional insectivores category</i>
Dendrocopos syriacus	Syrian Woodpecker	insectivore	<i>We excluded the bark foragers from the functional insectivores category</i>
Dendrocytes medius	Middle Spotted Woodpecker	insectivore	<i>We excluded the bark foragers from the functional insectivores category</i>
Dryobates minor	Lesser Spotted Woodpecker	insectivore	<i>We excluded the bark foragers from the functional insectivores category</i>
Dryocopus martius	Black Woodpecker	insectivore	<i>We excluded the bark foragers from the functional insectivores category</i>
Emberiza citrinella	Yellowhammer	insectivore	
Erithacus rubecula	European Robin	functional insectivore	<i>Ground insectivore but likely to attack false caterpillars attached to low branches</i>
Falco subbuteo	Eurasian Hobby	carnivore	
Falco tinnunculus	Eurasian Kestrel	carnivore	
Ficedula hypoleuca	European Pied Flycatcher	functional insectivore	
Fringilla coelebs	Common Chaffinch	insectivore	
Fulica atra	Eurasian Coot	herbivore	
Gallinula chloropus	Eurasian Moorhen	omnivore	
Garrulus glandarius	Eurasian Jay	omnivore	
Hippolais icterina	Icterine Warbler	functional insectivore	
Hirundo rustica	Barn Swallow	insectivore	
Larus argentatus	Herring Gull	carnivore	
Larus canus	Common Gull	carnivore	
Larus michahellis	Yellow-legged Gull	carnivore	
Luscinia luscinia	Thrush Nightingale	functional insectivore	

Luscinia megarhynchos	Common Nightingale	functional insectivore	
Merops apiaster	European Bee-eater	insectivore	
Milvus migrans	Black Kite	omnivore	
Milvus milvus	Red Kite	omnivore	
Motacilla cinerea	Gray Wagtail	insectivore	
Muscicapa striata	Spotted Flycatcher	functional insectivore	
Oriolus oriolus	Eurasian Golden Oriole	insectivore	<i>Not likely to attack false caterpillars attached low in the branches; canopy predator</i>
Parus major	Great Tit	functional insectivore	
Passer domesticus	House Sparrow	granivore	
Pariparus ater	Coal Tit	functional insectivore	
Phasianus colchicus	Ring-necked Pheasant	granivore	
Phoenicurus ochruros	Black Redstart	insectivore	
Phoenicurus phoenicurus	Common Redstart	functional insectivore	
Phylloscopus bonelli	Western Bonelli's Warbler	functional insectivore	
Phylloscopus collybita	Common Chiffchaff	functional insectivore	
Phylloscopus ibericus	Iberian Chiffchaff	functional insectivore	
Phylloscopus sibilatrix	Wood Warbler	functional insectivore	
Phylloscopus trochilus	Willow Warbler	functional insectivore	
Pica pica	Eurasian Magpie	omnivore	
Picinae sp.	Woodpecker sp.	insectivore	
Picus canus	Gray-headed Woodpecker	insectivore	<i>We excluded the bark foragers from the functional insectivores category</i>
Picus viridis	Eurasian Green Woodpecker	insectivore	<i>We excluded the bark foragers from the functional insectivores category</i>
Poecile montanus	Willow Tit	functional insectivore	
Poecile palustris	Marsh Tit	functional insectivore	
Prunella modularis	Dunnock	functional insectivore	<i>Ground insectivore but likely to attack false caterpillars attached to low branches</i>
Psittacula krameri	Rose-ringed Parakeet	granivore	
Regulus ignicapilla	Common Firecrest	functional insectivore	
Regulus regulus	Goldcrest	functional insectivore	
Serinus serinus	European Serin	granivore	
Sitta europaea	Eurasian Nuthatch	insectivore	
Streptopelia decaocto	Eurasian Collared-Dove	granivore	
Streptopelia turtur	European Turtle-Dove	granivore	
Sturnus vulgaris	European Starling	omnivore	
Sylvia atricapilla	Eurasian Blackcap	functional insectivore	
Troglodytes troglodytes	Eurasian Wren	functional insectivore	<i>Ground insectivore but likely to attack false caterpillars attached to low branches</i>
Turdus merula	Eurasian Blackbird	insectivore	
Turdus philomelos	Song Thrush	insectivore	
Turdus pilaris	Fieldfare	insectivore	
Turdus viscivorus	Mistle Thrush	insectivore	
Upupa epops	Eurasian Hoopoe	insectivore	

Table S3.4. Functional traits of the 25 candidate insectivores for attacking plasticine caterpillars. The colors correspond to the origin of the data specified in the legend.

Genus.species	Common.Name	Bird	Clutch	Bill Length	Foraging		Nest Type	Migration	Number	Frequency
		Mass	Size	Culmen	Method	Diet			Peaks	Peaks
<i>Aegithalos caudatus</i>	Long-tailed Tit	8,6	7	7,6	under	insect	shrub	resid	5,8	5,96
<i>Curruca communis</i>	Greater Whitethroat	15,1	4	13,6	under	insect	shrub	long	11,6	3,79
<i>Curruca melanocephala</i>	Sardinian Warbler	11,7	4,5	13,7	under	insect	shrub	resid	9,4	4,10
<i>Cyanistes caeruleus</i>	Eurasian Blue Tit	11,1	9	9,7	canopy	insect	cavity	short	12,2	5,02
<i>Erithacus rubecula</i>	European Robin	17,7	5	14	under	mixed	ground	short	13,4	4,76
<i>Ficedula hypoleuca</i>	European Pied Flycatcher	13,8	6	12,8	canopy	insect	cavity	long	10	4,21
<i>Hippolais icterina</i>	Icterine Warbler	13,2	4,5	17,5	under	insect	shrub	long	11,8	4,33
<i>Luscinia luscinia</i>	Thrush Nightingale	23,8	4,5	17	under	insect	shrub	long	15,8	4,08
<i>Luscinia megarhynchos</i>	Common Nightingale	19,6	4,5	16	under	insect	ground	long	13,2	3,76
<i>Muscicapa striata</i>	Spotted Flycatcher	15,9	4,5	16,2	canopy	insect	cavity	long	11	5,68
<i>Parus major</i>	Great Tit	16,3	8	12,2	canopy	insect	cavity	resid	12,2	4,53
<i>Periparus ater</i>	Coal Tit	9,2	9	10,7	canopy	insect	cavity	short	7,6	5,12
<i>Phoenicurus phoenicurus</i>	Common Redstart	14,6	8	13,9	canopy	insect	cavity	long	12,4	4,01
<i>Phylloscopus bonelli</i>	Western Bonelli's Warbler	8,7	5	11,5	canopy	insect	ground	long	8,4	4,00
<i>Phylloscopus collybita</i>	Common Chiffchaff	8,3	5,5	11,6	canopy	insect	ground	short	8	4,34
<i>Phylloscopus ibericus</i>	Iberian Chiffchaff	8,3	5,5	12,4	canopy	insect	ground	short	7,4	4,25
<i>Phylloscopus sibilatrix</i>	Wood Warbler	9,2	6,5	13,2	canopy	insect	ground	long	12	4,75
<i>Phylloscopus trochilus</i>	Willow Warbler	8,7	6,5	12,8	canopy	insect	ground	long	10,4	3,93
<i>Poecile montanus</i>	Willow Tit	11,1	7,5	11	canopy	mixed	cavity	resid	7,4	4,27
<i>Poecile palustris</i>	Marsh Tit	11,1	8,5	9,4	canopy	insect	cavity	resid	5,8	4,12
<i>Prunella modularis</i>	Dunnoch	20,2	4	14	ground	insect	ground	short	11,8	4,83
<i>Regulus ignicapilla</i>	Common Firecrest	5,6	8,5	10,9	canopy	insect	tree	resid	7,4	6,58
<i>Regulus regulus</i>	Goldcrest	5,5	8,5	10,6	canopy	insect	tree	short	9,4	6,20
<i>Sylvia atricapilla</i>	Eurasian Blackcap	16,7	4,5	15,2	under	mixed	shrub	short	18,6	3,98
<i>Troglodytes troglodytes</i>	Eurasian Wren	9,7	5,5	13,8	ground	insect	ground	resid	9,2	5,30

Data origin
Barbaro et al. 2021
Barbaro et al. 2019
AVONET2_eBird database (Clements et al. 2021; Tobias et al. 2022)
Storchová & Hořák, 2018
According to experts (L.B.)
Calculated (with data from Vellinga & Planque, 2015)

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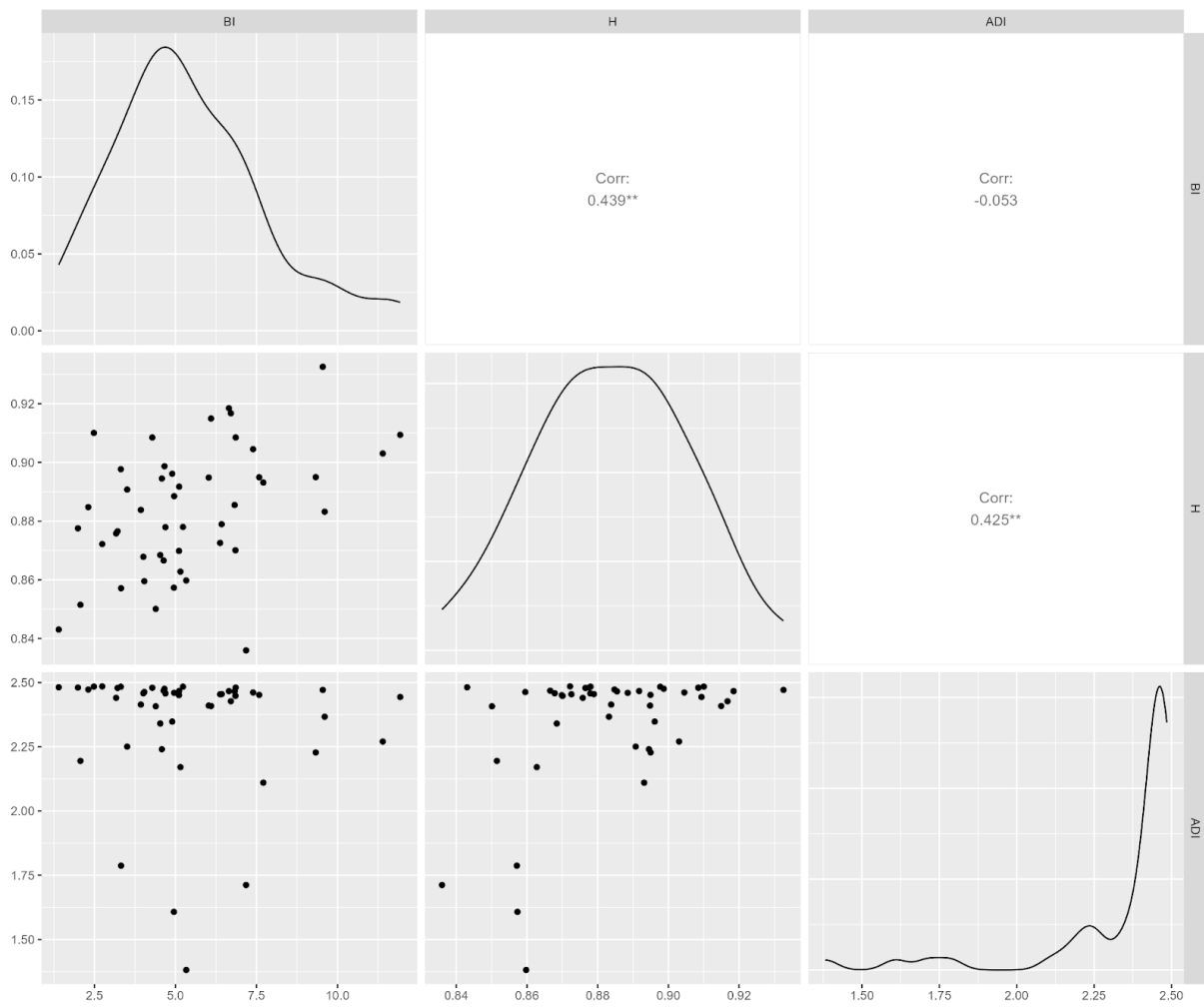
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Table S4.5. Bird predation attempts models are presented with several combinations of predictors of forest cover at the local scale (10 m or 20 m or 50 m) and at the landscape scale (100 m or 200 m or 500 m). The + indicates a positive effect, the - a negative effect, their colour is either black for a significant effect of the predictor in the model averaging (models with $\Delta AICc < 2$) and grey for a non-significant effect of the predictor in the model averaging. We can see that the local forest cover predictors never have a significant effect on bird predation attempts. The landscape scale forest cover predictors give qualitatively identical results with buffers of 200 m and of 500 m. The buffer of 100 m caused multicollinearity issues as it was too close to the local forest cover predictors.

Response variable	Predictors					
	MAT	Forest10	Forest100	Specific Richness	FRIC	Bioacoustic Index
<i>Bird predation attempts</i>	-		+		-	+
	MAT	Forest20	Forest100	Specific Richness	FRIC	Bioacoustic Index
<i>Bird predation attempts</i>	Multicollinearity issues between forest cover predictors					
	MAT	Forest50	Forest100	Specific Richness	FRIC	Bioacoustic Index
<i>Bird predation attempts</i>	Multicollinearity issues between forest cover predictors					
	MAT	Forest10	Forest200	Specific Richness	FRIC	Bioacoustic Index
<i>Bird predation attempts</i>	-	-	+		-	+
	MAT	Forest20	Forest200	Specific Richness	FRIC	Bioacoustic Index
<i>Bird predation attempts</i>	-		+		-	+
	MAT	Forest50	Forest200	Specific Richness	FRIC	Bioacoustic Index
<i>Bird predation attempts</i>	-		+		-	+
	MAT	Forest10	Forest500	Specific Richness	FRIC	Bioacoustic Index
<i>Bird predation attempts</i>	-		+		-	+

	MAT	Forest20	Forest500	Specific Richness	FRIC	Bioacoustic Index
<i>Bird predation attempts</i>	-		+		-	+
	MAT	Forest50	Forest500	Specific Richness	FRIC	Bioacoustic Index
<i>Bird predation attempts</i>	-		+		-	+

Fig. S6.6. Correlation matrix and pairwise graphical representations of acoustic diversity indices



3. Chapitre 2 : La diversité des arbres en ville favorise l'insectivorie malgré une diminution de la diversité des communautés d'oiseaux due à l'urbanisation.

Laura Schillé, Alain Paquette, Gabriel Marcotte, Hugo Ouellet, Swane Cobus, Luc Barbaro[□] & Bastien Castagneyrol[□] (n.d.) - **Urban tree diversity fosters bird insectivory despite a loss in bird diversity with urbanization** – *Landscape and Urban Planning* – Major revision 19.08.2024

Abstract

Urbanization is one of the main driver of biotic homogenization in bird communities worldwide. Yet, only few and inconclusive studies have addressed its functional consequences on the top-down control birds exert on insect herbivores. We hypothesized that such discrepancy among studies might reflect the heterogeneity of the urban habitat for birds, and in particular the distribution and diversity of urban trees.

We monitored tree diversity, bird diversity, avian predation attempts on artificial prey and the effect of bird exclusion on insect herbivory in 97 trees distributed among 24 urban experimental plots in the city of Montreal, Canada. We characterized urbanization levels through a combination of variables related to tree density, impervious surfaces, anthropic noise, and human population density.

Bird diversity decreased with increasing urbanization, but we found no significant relationship between predation and urbanization or between predation and bird diversity. However, tree diversity was positively correlated with predation attempts on artificial prey, irrespective of bird diversity.

Our study advocates for the consideration of intra-urban heterogeneity in the investigation of trophic cascades within cities, and unravels the functional importance of tree diversity in shaping the avian predation function in urban ecosystems.

Keywords: Herbivory; Insectivorous birds; Plasticine caterpillars; Predation function; Urbanization gradient; Tree diversity

3.1. Introduction

Populations of insectivorous birds are declining worldwide (Bowler et al., 2019; Rosenberg et al., 2019). Causes are numerous and likely interacting. They include a sharp decline in the abundance of insect herbivores that are a main source of food for insectivorous birds (Bowler et al., 2019), the intensification of anthropic pressure on ecosystems (Devictor et al., 2007) and climate change (Both et al., 2006). Yet, insectivorous birds provide humans with essential regulation services by reducing insect herbivore pressure on plants through top-down trophic cascades (Nyffeler et al., 2018). The factors influencing the strength of bird-induced trophic cascades have been well documented in natural and cultivated ecosystems (Harris et al., 2020; Jactel et al., 2021). However, whether and to which extent knowledge gained in these ecosystems can be transferred to urban environments remains uncertain.

Both the abundance (Roels et al., 2018), activity (Maas et al., 2015), and diversity (Nell et al., 2018) of insectivorous birds are well-documented predictors of the top-down control they exert on insect herbivores. Insectivory increases with the abundance and foraging activity of insectivorous birds particularly during the chick feeding period (Naef-Daenzer & Keller, 1999). It is also a period during which non-insectivorous species may include insects in their diet to feed their nestlings. Theory predicts that predation pressure increases with increasing diversity of insectivorous birds, as a result of functional complementarity among species within the community (Philpott et al., 2009). Several studies consistently reported positive relationships between the functional diversity of insectivorous birds and the regulation function (Barbaro et al., 2014; Peña et al., 2023). In the same way, any environmental factor influencing the distribution, diversity, or composition of insectivorous bird communities is likely to also affect the trophic interactions they initiate, but the strength and direction of these effects are elusive (McDonnell & Hahs, 2015).

Urbanization alters the composition of bird communities (McKinney, 2006) as well as bird behavior (Fuller et al., 2007). The scarcity of food and nesting opportunities generally reduces the taxonomic and functional diversity of birds (La Sorte et al., 2018) making

urban bird communities dominated by habitat and diet generalists, as well as poorly mobile, generally resident species (Lakatos et al., 2022). In addition, the distribution and activity of birds are disrupted by anthropogenic nuisances such as noise (Slabbekoorn & Ripmeester, 2008), light pollution (Aulsebrook et al., 2020), direct disturbances by humans (Price, 2008) or by their domestic carnivores (Baker et al., 2005). All those disturbances are also likely to modify the ability of bird communities to regulate herbivorous arthropods. However, how urbanization affects predation is still poorly documented and contradictory. Some studies showed an decrease of herbivore regulation in urban ecosystems, when compared to non-urban ones (e.g., Turrini et al., 2016), whereas others highlighted a stronger top-down control of herbivores in urban areas (e.g., Faeth et al., 2005). The same contradictions occur for the arthropod herbivory in urban versus rural environments (Kozlov et al., 2017; Raupp et al., 2010). A possible explanation for these inconsistencies might be the focus on city-to-countryside gradients, and the lack of consideration for intra-urban heterogeneity.

Indeed, cities are heterogeneous environments in which the abundance and distribution of trees jointly contribute to shape biodiversity. Locally, tree diversity has the potential to alleviate the adverse effect of urbanization on avian communities (Da Silva et al., 2021) and on the biocontrol they exert on herbivores (Stemmelen et al., 2020). The diversity of insect herbivores and their natural enemies generally correlates positively with tree diversity (Castagneyrol & Jactel, 2012) as a result of increased habitat complexity and food resources for insectivorous birds (Barbaro et al., 2019). As stated by the natural enemies' hypothesis (Root, 1973), the regulation function provided by birds is thus expected to increase with the diversity of trees. Efforts to restore tree biodiversity in urban areas could therefore allow for the maintenance of higher bird diversity and their biotic interactions, a key issue for managing urban ecosystems.

In this study, we investigated the interacting effects of urbanization and tree diversity on bird diversity and insectivory, to infer their consequences on tritrophic interactions between birds, insect herbivores and trees. To document the ecological functions provided by trees and their diversity in urban environments, we measured tree diversity, insect herbivory, insectivorous bird diversity and the regulation function provided by birds in 24 urban plots distributed along a gradient of urbanization within the city of

Montreal, Canada. We predicted the following : (i) urbanization reduces insectivorous bird diversity and predation and thereby the strength of tritrophic cascade, leading to increased insect herbivory on trees; (ii) local tree diversity is positively associated with insectivorous bird diversity and predation and (iii) local tree diversity mitigates the effect of urbanization.

3.2. Material and Methods

3.2.1. Study area

The study was conducted in the city of Montreal, Canada, where the climate is temperate cold, with 6°C average temperature and 1000mm annual rainfall during the 1985-2015 period (Pierre Elliott Trudeau airport weather station). We used a pre-established network of 24 urban plots called the Urban Observatory of Montreal (<https://paqlab.uqam.ca/tags.php?id=45&lang=fr>, Fig.1) selected to cover the largest range of two gradients: (i) tree density, approximated through the percentage of canopy cover, (ii) human population density, used here as proxy for human disturbance in bird communities.



Figure 1. Locations of the 24 sampled urban plots in the city of Montreal, Canada

3.2.2. Target trees

We selected four deciduous trees (henceforth, focal trees) in each urban plot, with the exception of one plot in which we selected five trees. We chose focal trees among the ten most abundant species in Montreal (namely *Acer platanoides*, *Acer saccharinum*, *Acer negundo*, *Gleditsia triacanthos*, *Tilia cordata*, *Tilia americana*, *Prunus* spp., *Ulmus americana*, *Ulmus pumila* and four *Ulmus x hybrids*). We ensured that focal trees met the following criteria: be within a 100m radius of the plot center (to link with tree richness measured over a 100m radius), have easily accessible branches using a small ladder, and be located in the public domain. We further ensured that each focal tree species was repeated at least three times in three different urban plots. This resulted in the selection of 97 focal trees (Table SA).

Tree diversity of each urban plot was characterized through the prior identification of all trees in both the public and private domains within a 200m radius around the center of the plot. We calculated the species richness of neighboring trees within a 20m radius around each target trees.

3.2.3. Insectivorous bird species richness and functional diversity

We used passive acoustic monitoring to identify all vocalizing bird species and characterize bird communities within the plot, at the species level. We selected a central tree or hedge in each urban plot to conceal an AudioMoth device (Hill et al., 2018). The AudioMoth was parameterized to record audible sounds for 30 minutes every hour. Automated recording began on the day we installed the plasticine caterpillars in trees, for eight consecutive days.

For every urban plot, we only sub-sampled the 30-minute recordings corresponding to the morning chorus of songbirds (from 30 minutes before sunrise to 3 hours and 30 minutes after sunrise). We only retained the subsamples recorded on Tuesday, Thursday, Saturday and Sunday to balance out the impact of human activity between weekends and weekdays. These 30-minutes recordings were then divided into three 10-minutes segments. Each sound sample underwent analysis through the 'seewave' library in the R environment (Sueur et al., 2008), and any sample containing low-frequency noise typical

of human activity, rain, or wind were excluded based on their spectrogram appearance. This process yielded a total of 96 10-minutes recordings (4 recordings per urban plot).

All recordings were listened to by a single expert ornithologist (H.O.), who identified all species heard, the time intervals during which they were heard, and an approximate count of the number of individuals distinguished per time interval. It should be noted that this process provides a vocalization occurrence of each species and, therefore, a form of activity of that species, but it is not a reliable measure of bird species abundance (Schillé et al., 2024). We focused exclusively on functionally insectivorous birds, defined as species that meet the following criteria: being totally or partially insectivorous during the breeding period or feeding their chicks with insects, foraging primarily in trees, and using lower branches of trees to find their prey.

Using the presence/absence Plot \times Species matrix, we computed the species richness of the communities in each urban plot, and we used the vocalization occurrence Plot \times Species matrix to calculate a vocalization-based Shannon index (hereafter referred to as Shannon diversity). Additionally, we integrated morphological, reproductive and behavioral traits (Cornell Laboratory of Ornithology, 2022) to compute the vocalization-based functional dispersion index (hereafter referred to as FDis), an index representing species dispersion in trait space, weighted by their relative vocalization occurrence. This index was calculated for each urban plot using the dbFD function of the FD library (Laliberté et al., 2014) in the R environment.

3.2.4. Urban habitat variables

We integrated information from eight variables representing human activities and habitat characteristics to refine the definition of the urbanization gradients encompassing the 24 urban plots (Table 1). When the data were accurate enough, we used an aggregation level of 200m around the focal trees. Indeed, preliminary analyses revealed that the results were qualitatively identical using buffers of 100, 200, or 500m, as the metrics used were highly correlated at these scales. We chose a buffer size of 200m because several common insectivorous birds in the city of Montreal have vital ranges not exceeding 200m. This is the case, for example, for the black-capped chickadee, whose vital range can go from 1.5 ha to 5.3 ha (equivalent to a circle with a radius of 130m) (Québec center of expertise in

environmental analysis, 2005) or warblers with average vital ranges of 2 ha (Cornell Laboratory of Ornithology, 2022).

Table 1. Summary of the variables used to describe urbanization, their definition, their sources, and their aggregation level.

Used variable	Variable definition	Data source	Aggregation level
Imperviousness	Percentage of the combined surface area of low and high mineral surfaces	Normalized Difference Vegetation Index (NDVI) and city's digital elevation model (Communauté métropolitaine de Montréal, 2017)	200m around focal trees
Building cover	Percentage of high mineral surface area	NDVI and city's digital elevation model (Communauté métropolitaine de Montréal, 2017)	200m around focal trees
Canopy cover	Percentage of high vegetation surface area	NDVI and city's digital elevation model (Communauté métropolitaine de Montréal, 2017)	200m around focal trees
Population density	Average household size from the 2016 census	Population census data (Government of Canada 2016)	200m around focal trees
Light pollution	Night-time radiance	Satellite VIIRS image (National oceanic and atmospheric administration, 2023)	Plot level
Sound intensity		Measured with a sound level meter in the field	Four measuring points per focal tree
Habitat connectivity	Number of high vegetation patches	Derived from NDVI and city's digital elevation model (Communauté métropolitaine de Montréal, 2017)	200m around focal trees
NDSI index	Biophony to anthropophony ratio	Calculated from passive acoustic field recordings	Plot level

Specifically, we used the metropolitan canopy index raster layer and QGIS software (version 3.16 Hannover) to extract the percentage of imperviousness, of building density and of canopy coverage at the tree level. We also calculated habitat connectivity at the tree level. The values were then averaged at the plot to standardize the scale across different urbanization metrics.

Population density was extracted from a vector layer of the 2016 census. We calculated an average estimate of population density around the target trees and then averaged the values at the plot level.

We used the VIIRS night-time radiance raster layer, an annual cloud-free composite with a 450m pixel resolution, to extract light pollution at plot level.

Sound intensity was measured using a digital sound level meter (*TROTEC, SL400, measurement range from 30 to 130 dB, slow sampling rate, i.e., one measurement per second*) for 5 minutes each time we visited focal trees to install or remove material or collect samples at one week interval or more. This resulted in 16 measurements per urban plot (4 dates × 4 trees), which were taken on different week days and times during the day, with no particular sequence to avoid confounding effects. The measurement device was consistently positioned with its back to the tree, pointing towards the nearest road, and placed on a tripod at 1m above the ground with a 60° inclination relative to it. We averaged the data across sampling dates and trees to provide a synthetic estimate of anthropogenic noise in each urban plot.

Finally, we characterized the soundscape of the urban plots using the recordings made with the Audiomoths. To do so, we first cut each recording into 1-minute chunks. We then calculated the ratio between biophony and anthropophony using the Normalized Difference Sound Index (NDSI) thanks to 'soundecology' library in the R environment (Villanueva-Rivera & Pijanowski, 2018). We then calculated the median of NDSIs per day and then averaged median values across days for each urban plot individually.

3.2.5. Bird predation attempts

We assessed the activity of insectivorous birds by counting predation attempts (as revealed by bill marks) on plasticine caterpillars (Low et al., 2014). We made 3 × 0.5 cm caterpillar-shaped cylinders of green plasticine (brand *Staedtler*, model 8421-5). We exposed 20 plasticine caterpillars per tree, on twigs with a 0.3 mm diameter metallic wire.

We attached five plasticine caterpillars to four branches facing opposite directions, about 2.5 m from the ground. We installed them five weeks after the average budburst date for all the selected species, thus synchronizing the study with local tree phenology. They were exposed for 15 days and were removed one week before we collected leaves for herbivory measurements. In the field, a single observer (L.S.) examined each caterpillar, checking for the presence of bill marks on the clay surface. When there were doubts about the type of attack, the caterpillars were brought back to the lab for a second check and to seek advice from colleagues. We approximated bird predation attempts through the number of plasticine caterpillars presenting at least one evidence of bird attack.

3.2.6. Bird exclusion

To assess the strength of the trophic cascade, we prevented insectivorous birds from foraging on one branch per focal tree. To this end, we installed a bird exclusion net around a 1m long branch in April 2023, a few days before expected budburst. Nets were made of green plastic material and had a mesh size of 15 × 15mm to prevent bird access while allowing the passage of herbivorous arthropods). The net was adjusted weekly throughout the budburst process to ensure that leaves remained enclosed within the net.

3.2.7. Insect herbivory

To assess the strength of the trophic cascade, we compared insect herbivory in the bird exclusion treatment with insect herbivory on control branches that were adjacent to those with the exclusion treatment. Specifically, we haphazardly collected 30 leaves in each treatment, totaling 60 leaves per focal tree. We collected leaves eight weeks after budburst, which corresponds to the peak of activity of insect herbivores and to the period during which we assessed bird diversity and activity. We oven dried the leaves for 48 hours at 45°C, and haphazardly selected 20 leaves (out of 30) per treatment and per tree to be processed for further analyses.

Herbivory was visually assessed by a single experimenter (G.M.) and was defined as the percentage of the leaf surface removed or impacted by insect herbivores. The leaves were assigned to 11 different classes based on the amount of damage: 0%, [1%-5%], [6%-10%],

[11%-15%], [16%-20%], [21%-25%], [26%-30%], [31%-40%], [41%-50%], [51%-75%] and >75%. We then used the median values of these classes to calculate an average herbivory rate across the 20 leaves per treatment and per tree. We defined the herbivory regulation function provided by birds as the difference between the herbivory on the netted branch and the herbivory on the control branch.

3.2.8 Statistical analyses

We first summarized the information about urbanization by running a Principal Component Analysis (PCA) on the eight urbanization-related variables. By doing so, we intended to provide a synthetic and reliable description of the degree of urbanization in each urban plot. We extracted the coordinates of the projection of plots onto the first two PCA axes, which together explained 71% of the variance in urban plot descriptors (see *Results*). We used PCA coordinates as proxies for urbanization intensity (PC1) and for urban naturalness (PC2) in further analyses (see below).

We tested the effects of urbanization (PC1 and PC2) and tree diversity on insectivorous birds (species richness, Shannon diversity, and FDis), their activity (predation attempts on plasticine caterpillars) and the regulation function they provide (insect herbivory in control vs. bird exclusion treatments) using separate models (Table SB).

We analyzed diversity related variables with data aggregated at the plot level using Generalized Linear Models (GLMs) and predation attempts, and insect herbivory at tree level using generalized linear mixed effect models (GLMMs). We used GLM with Poisson error distribution to model count data (bird species richness) and GLMs with gaussian error distribution to model bird diversity (Shannon diversity and FDis). We used GLMM with binomial error distribution to analyze predation attempts (i.e., number of attacked vs. number of intact plasticine caterpillars), and GLMM with gaussian error distribution to analyze herbivory regulation function.

In each model, predictors were PC1 and PC2 coordinates along with tree species richness and every two-way interactions. Because we predicted that the effect of urbanization and tree diversity on the tritrophic cascade would be mediated by changes in insectivorous bird diversity, we included insectivorous bird species richness as an additional predictor

when modeling predation attempts and insect herbivory. Urban plots and tree species were considered as crossed random effects in GLMMs.

We scaled and centered every continuous predictor other than PC1 and PC2 prior to modeling to facilitate comparisons of their effect sizes. We made sure that none of the explanatory variables were strongly correlated by examining the variance inflation factors (VIF) (all VIFs < 5, a common cutoff value used to check for multicollinearity issues).

For each response variable, we ran the full model as well as every model nested within the full model and then used Akaike's Information Criterion corrected for small sample size (AICc) to identify the most parsimonious models best fitting the data. Models within 2 Δ AICc units of the best model (i.e., the model with the lowest AICc) are generally considered as equivalent in their ability to fit the data the best. We computed AICc weights for each model (w_i), where w_i is interpreted as the probability of a given model being the best model among the set of candidate models. Eventually, we calculated the relative variable importance (RVI) as the sum of w_i of every model including this variable, which corresponds to the probability a variable is included in the best model.

When several models competed with the best model (i.e., when multiple models were such that their Δ AICc < 2), we applied a procedure of multimodel inference, building a consensus model including the variables in the set of best models. We then averaged their effect sizes across all the models in the set of competing models, using the variable weight as a weighting parameter (i.e., model averaging). We considered that a given predictor had a statistically significant effect on the response variable when its confidence interval excluded zero.

We ran all analyses in the R language environment (R Core Team, 2020) with libraries "MuMIn" v.1.43.17 (Bartoń, 2020), "lme4" v. 1.1.27.1 (Bates et al., 2015).

3.3. Results

3.3.1. Main urbanization drivers

The first two dimensions of the PCA explained 71% of the variance in urbanization related variables (Fig. 2). PC1 was positively associated with sound intensity, human population density, building density and impervious surfaces, with positive values representing urban plots with higher urbanization intensity. PC2 was positively associated with canopy cover and connectivity among forest patches, and negatively associated with NDSI and light intensity. It therefore represented a gradient of urban naturalness whereby positive values represent greener urban plots.

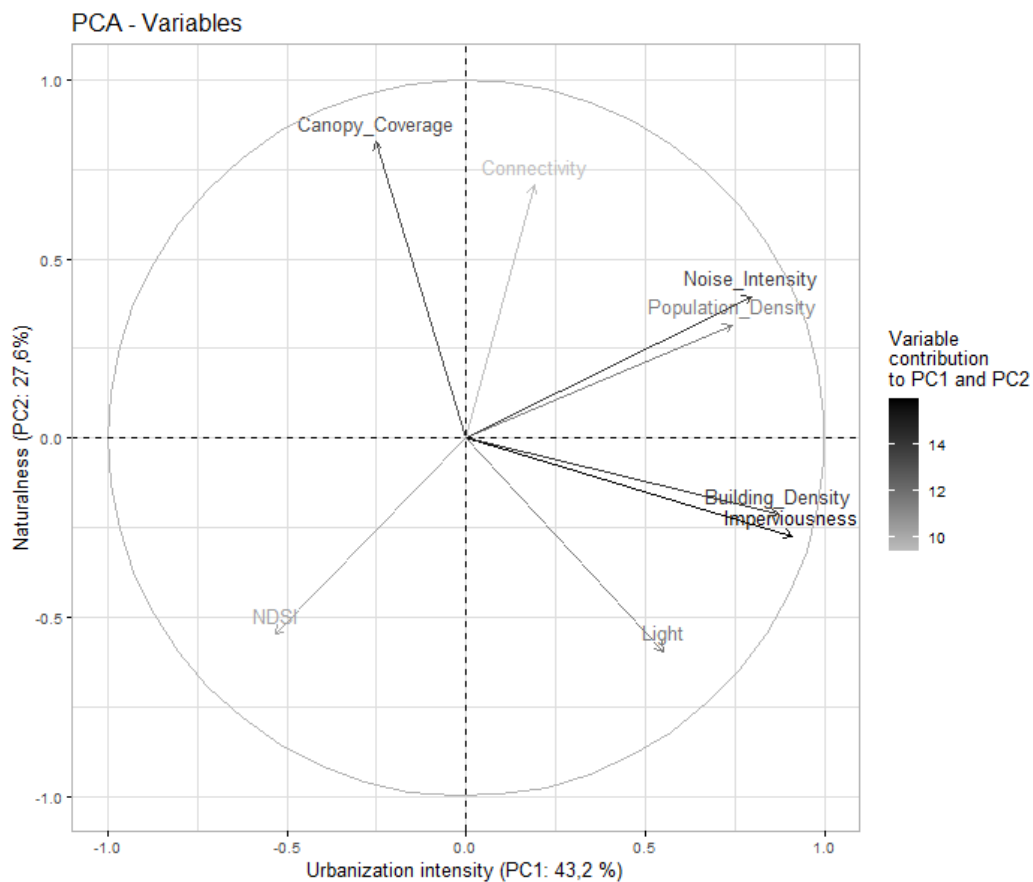


Figure 2. Variables factor map in Principal Components Analyses

3.3.2. Bird species richness and functional diversity

We identified 43 bird species, among which 29 were classified as functional insectivores (Figure 3). The richness of functional insectivores varied from 2 to 14 species per urban plot (mean \pm SD: 7.1 ± 3.3). The sum of occurrences of vocalizations per functional insectivore species varied from 1 to 142 (23.9 ± 38.6).

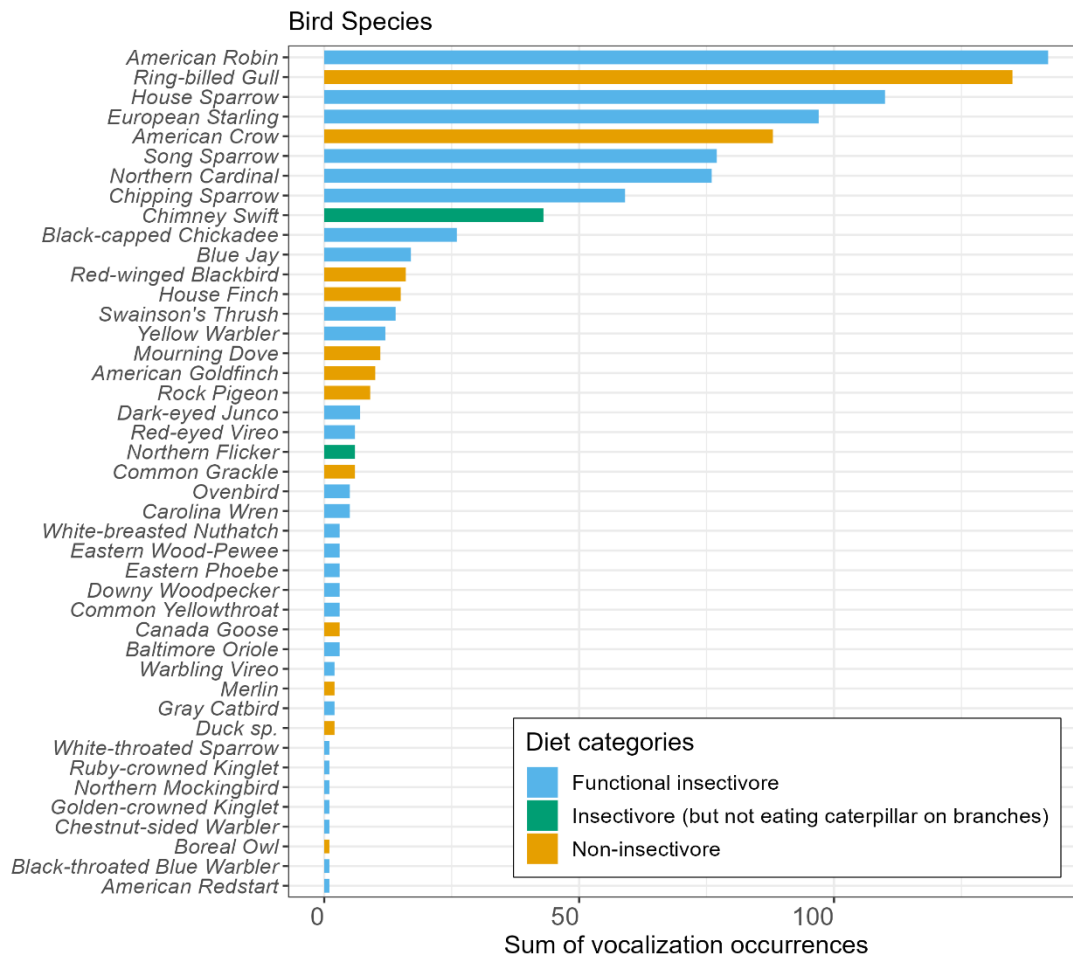


Figure 3. Decreasing total vocalization occurrences of species recorded, all urban plots combined. For this study, functional insectivorous species are the combination of the “strict insectivore” and “insectivore during the breeding season” categories.

Urbanization intensity (PC1) was the most important predictor for both insectivore species richness (RVI=1.00, Fig.4a) Shannon diversity (RVI=1.00, Fig.4b) and FDis (RVI=1.00, Fig.4c). These three variables consistently and negatively decreased with increasing urbanization intensity (Figure 4). Insectivore species richness and Shannon diversity tended to be higher in urban plots with greater tree species richness, while a trend towards decreased FDis tree richness was noticeable. However, this predictor was considered less important than urbanization intensity for the three metrics (RVI=0.33, RVI=0.29 and RVI=0.30 for richness, Shannon diversity and FDis, respectively). FDis tended to positively respond to naturalness, but this predictor was of limited importance (RVI=0.59).

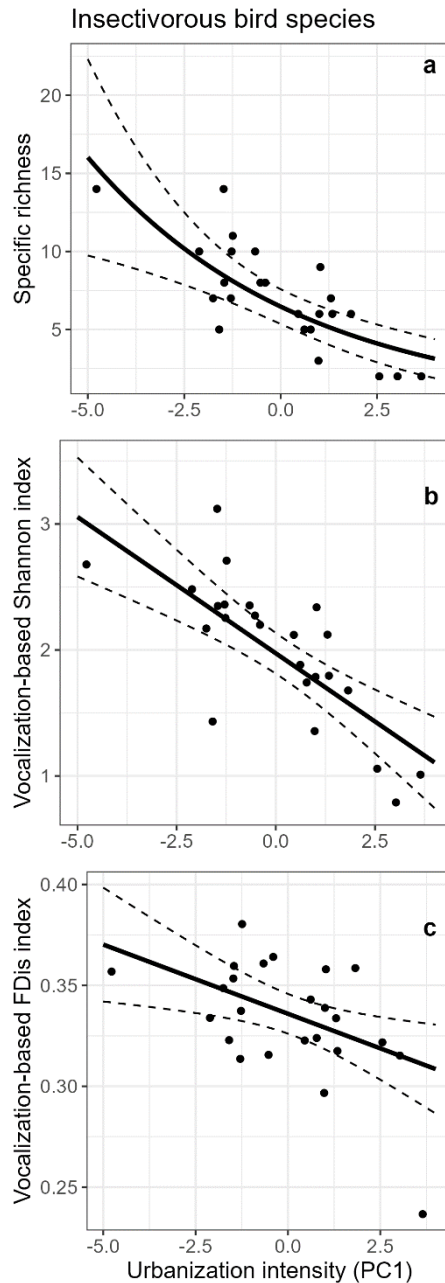


Figure 4. Relationships between (a) functional insectivore richness, (b) Shannon diversity, (c) FDis and urbanization intensity (PC1). Raw data are indicated by dots. The solid line represents the prediction from the models, dashed lines being the corresponding confidence intervals.

3.3.3. Bird predation attempts and herbivory regulation service

Of the 1,940 exposed plasticine caterpillars, 3.0 % (n = 59) had bird bill marks. Model selection retained eight models in the set of competing models in a range of $\Delta AICc < 2$. Of the variables included in the set of competing models, tree species richness was the only significant one and was positively correlated with predation attempts (RVI = 1; see Fig.5). RVI of other predictors were all lower than 0.55 (Table SB).

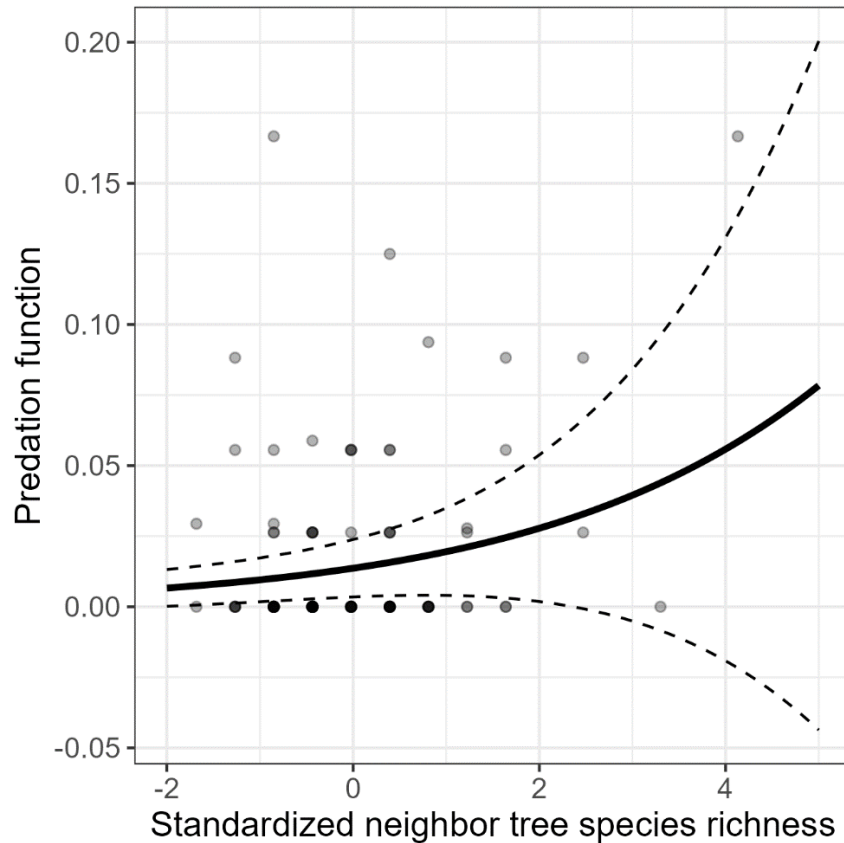


Figure 5. Relationship between bird predation attempts on artificial prey and tree species richness. Raw data are indicated by dots. Solid and dashed lines represent model prediction and corresponding confidence intervals. Grey intensity corresponds to the number of overlaying dots.

Bird exclusion reduced insect herbivory by 0.09 % on average (bird exclusion treatment: 0.90 %, control branches: 0.81 %).

Urbanization intensity (PC1) (RVI=1.00), tree species richness (RVI=1.00) and their interaction (RVI=1.00) were selected as important variables explaining variability in the herbivory regulation function provided by birds. The effect of urbanization intensity *per se* was inconsistent, because it was contingent on tree species richness. Specifically, the regulating service of herbivory significantly decreases with tree species richness, but this relationship becomes positive when urbanization intensity is very low. Bird species richness was retained in the second-best model, showing a positive correlation with the herbivory regulation function but with lower importance (RVI=0.31) (Fig.6).

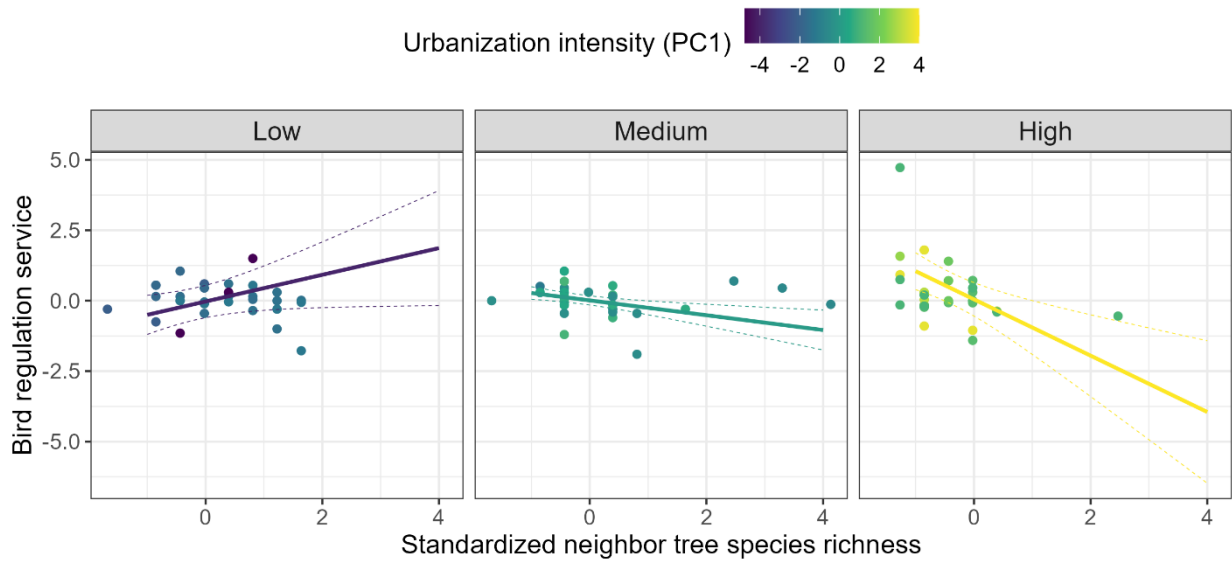


Figure 6. Regression based on model predictions of changes in herbivory regulation function as a function of PC1 and neighbor tree species richness. Raw data are indicated by dots. The dashed lines represent the confidence intervals on the predictions.

3.4. Discussion

Our study unravels the complexity of the effect of urbanization on bird communities and the functions they support along an urbanization gradient. In particular, we found that the distribution and diversity of trees within the city modified the relationship between urbanization and bird insectivory, with important consequences for trophic interactions and ecological functions.

3.4.1. Urbanization intensity reduced bird diversity, with no apparent consequence on avian insectivory

Insectivorous bird species richness and vocalization-based functional diversity decreased with increasing urbanization within the boundaries of the city of Montreal. These findings are consistent with the long-standing theory that urbanization causes a reduction in the complexity of ecological communities (McKinney, 2006) as well as functional homogenization with more generalist species, which display greater resilience to human disturbances (Hahs et al., 2023). Research focusing on birds confirmed this general trend, both locally (Marcacci et al., 2021) and globally (Sol et al., 2020). However, our study is

one of the few (Carvajal-Castro et al., 2019; Yang et al., 2020) having addressed the effect of within-city variability in insectivorous bird diversity in response to local factors related to the intensity of urbanization.

Previous studies have shown that avian insectivory could increase with the functional diversity of insectivorous birds (Barbaro et al., 2014; Philpott et al., 2009). Because insectivorous bird diversity decreased with increasing urbanization intensity, we expected that predation attempts on artificial prey as well as the effect of insectivorous birds on insect herbivory would also decrease along the urbanization gradient. Yet, we found no statistically significant relationship neither between urbanization and predation attempts, nor between insectivorous bird diversity and predation attempts. Literature reviews have questioned the generality of these relationships (see Eötvös et al., 2018 for a meta-analysis). It is however crucial to note that the majority of studies having addressed the effect of urbanization on tri-trophic interactions focused on comparisons between rural and urban habitats (Kozlov et al., 2017; Turrini et al., 2016) or on gradients spanning from these two extremes (Marcacci et al., 2021). The present study differs in that we addressed the effect of within-city variability in urbanization intensity. Still, in a rare comparable study, Long & Frank, (2020) reported higher avian predation attempts on plasticine caterpillars in urban forest remnants as compared to street trees.

Some authors argue that predation attempts on artificial prey might be a poorly reliable proxy of predation (Zvereva & Kozlov, 2023). However, our conclusions remain the same regardless of whether we consider predation through the proportion of artificial prey with bill marks left by birds, or through the effect of bird exclusion on insect herbivory. We are therefore confident that the absence of a clear relationship between urbanization and predation on the one hand, and between predation and insect bird diversity on the other hand is not artefactual and reflects ecological features we did not capture.

A possible explanation is that the patterns were obscured by the disproportionate abundance and foraging activity of some highly generalist species. This was typically the case of the house sparrow that represented 11% of total vocalizations and was the third most frequent species we recorded and observed during our visits to the most urbanized plots (Fig.3 and field observations). House sparrows are particularly known for their opportunistic behavior. They are highly adaptive birds that scavenge on human food

scraps, making them prevalent even in areas where other bird species are not commonly found (MacGregor-Fors et al., 2020). Moreover, the low real prey abundance in urban centers may lead to attack predation rates on plasticine caterpillars compensating the attacks from a higher diversity of birds in less urbanized areas. Another possibility is that local factors such as the present of nesting boxes or human bird feeding behavior interfere with the relationship between urbanization, bird diversity and predation.

3.4.2. Tree diversity promotes bird predation function

Trees promote bird diversity in cities by providing habitats and food for a diverse range of bird species (Dyson, 2020). Contrarily to our predictions, tree density and distribution as well as tree diversity were of little importance to predict bird diversity. It is possible that the distribution of treeless green spaces (Schütz & Schulze, 2015) as well as the vertical stratification of the vegetation (Campos-Silva & Piratelli, 2021) played a substantial role in bird abundance and diversity, which future studies should aim to better capture.

Although tree diversity was poorly related to bird diversity, it was the most important factor influencing bird predation attempts, in a positive way. This finding is in line with the natural enemies' hypothesis that predicts an increase in predation with increasing plant diversity. It must be noted, however, that this hypothesis remains controversial, particularly in forests (Staab & Schuldt, 2020). Adding to the controversy, we found that unlike predation attempts on artificial prey, the trophic cascade whereby birds protect trees against insect herbivores decreased in intensity with increasing tree diversity, especially in highly urbanized areas. This finding has two major implications. First, it indicates that birds may not be the main predators responsible for the top-down control of insect herbivores in urban environments. This idea finds support in the findings by Long & Frank (2020), which demonstrated that in the downtown area of Raleigh, NC, USA, arthropods exhibited a 30% higher predation rate on sentinel prey compared to birds. Conversely, within urban forest fragments, birds displayed a 20% higher attack rate than arthropods. Our study did not account for arthropod predators, which would freely move through the mesh that excluded avian predators. A full understanding of trophic cascades in cities would therefore require that future studies would quantify the relative contribution of vertebrate and invertebrate predation. Second, it highlights that, while

artificial prey may serve as a relevant proxy for bird foraging activity, they may not satisfactorily capture the functional consequences of bird foraging in terms of actual predation (Zvereva & Kozlov, 2023).

3.4.3. Conclusion and implications for future research

In this study, we untied the complex interactions between trees, insect herbivores and insectivorous birds in contrasting urban environments. Specifically, our findings suggest that the abundance, distribution, and diversity of urban trees play a key role in shaping bird communities and influencing the regulation service they provide. While our study revealed trends in this relationship, significance levels were not consistently attained, indicating the need for further investigation to fully elucidate the complex dynamics at play. Importantly, we show that urban biodiversity as well as the ecological functions it supports cannot be fully understood without accounting for within-city heterogeneity in urbanization intensity. Our results were only made possible because we were able to control for urbanization intensity and urban naturalness, two features of urbanization that generally covary.

Our study also has insightful implications for future research. Firstly, we call for more specific description of urbanization in future ecological studies that better account for and disentangle the intertwined factors of urbanization. Secondly, because biodiversity is made of moving organisms, we emphasize the critical need to expand our knowledge of the urban biodiversity beyond the limits of the public domain. This represents a major challenge for future ecological research in cities and for cities that will require strengthened collaborations between the public, researchers and local authorities.

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Data availability statement

For the moment, there is an embargo on data and codes, which will be lifted after open acceptance.

Supplementary materials

Table SA. Identity of focal trees for each urban plot

Plot_ID	Tree_ID	Tree_species
01A	32	<i>Acer saccharinum</i>
01A	91	<i>Acer platanoides</i>
01A	107	<i>Acer platanoides</i>
02A	188	<i>Gleditsia triacanthos</i>
02A	195	<i>Ulmus americana</i>
02A	286	<i>Gleditsia triacanthos</i>
02A	252	<i>Acer platanoides</i>
03A	292	<i>Gleditsia triacanthos</i>
03A	299	<i>Ulmus pumila</i>
03A	300	<i>Acer saccharinum</i>
03A	354	<i>Tilia cordata</i>
04A	522	<i>Gleditsia triacanthos</i>
04A	530	<i>Ulmus americana</i>
04A	525	<i>Gleditsia triacanthos</i>
04A	520	<i>Gleditsia triacanthos</i>
05B	753	<i>Gleditsia triacanthos</i>
05B	762	<i>Gleditsia triacanthos</i>
05B	765	<i>Acer platanoides</i>
05B	773	<i>Acer platanoides</i>
05B	775	<i>Acer platanoides</i>
06C	888	<i>Ulmus pumila</i>
06C	898	<i>Acer saccharinum</i>
06C	887	<i>Acer platanoides</i>
06C	893	<i>Ulmus pumila</i>
07A	1010	<i>Gleditsia triacanthos</i>
07A	1012	<i>Gleditsia triacanthos</i>
07A	1024	<i>Acer platanoides</i>
07A	1019	<i>Gleditsia triacanthos</i>
08A	1089	<i>Gleditsia triacanthos</i>
08A	1090	<i>Ulmus x 'Sapporo Autumn Gold'</i>
08A	1097	<i>Tilia americana</i>
08A	1109	<i>Tilia americana</i>
09B	1217	<i>Prunus spp.</i>
09B	1233	<i>Acer saccharinum</i>
09B	1241	<i>Acer platanoides</i>
09B	1262	<i>Acer platanoides</i>
10A	1366	<i>Prunus spp.</i>
10A	1356	<i>Gleditsia triacanthos</i>
10A	1398	<i>Tilia americana</i>
10A	1407	<i>Gleditsia triacanthos</i>
11B	1487	<i>Gleditsia triacanthos</i>

11B	1481	<i>Gleditsia triacanthos</i>
11B	1499	<i>Ulmus x 'Homestead'</i>
11B	1522	<i>Ulmus americana</i>
12B	1597	<i>Ulmus x 'Homestead'</i>
12B	1624	<i>Ulmus x 'Homestead'</i>
12B	1621	<i>Acer saccharinum</i>
12B	1623	<i>Gleditsia triacanthos</i>
12C	1689	<i>Ulmus americana</i>
12C	1704	<i>Ulmus americana</i>
12C	1710	<i>Gleditsia triacanthos</i>
12C	1706	<i>Ulmus x 'Morton'</i>
13A	1828	<i>Acer saccharinum</i>
13A	1835	<i>Acer negundo</i>
13A	1841	<i>Acer platanoides</i>
13A	1869	<i>Gleditsia triacanthos</i>
14A	1936	<i>Ulmus x 'Morton'</i>
14A	1986	<i>Tilia americana</i>
14A	2028	<i>Tilia cordata</i>
14A	2039	<i>Tilia cordata</i>
15B	2186	<i>Acer platanoides</i>
15B	2204	<i>Gleditsia triacanthos</i>
15B	2206	<i>Gleditsia triacanthos</i>
15B	2201	<i>Ulmus americana</i>
16A	2347	<i>Acer platanoides</i>
16A	2301	<i>Acer platanoides</i>
16A	2362	<i>Acer negundo</i>
16A	2445	<i>Prunus spp.</i>
17C	2521	<i>Acer platanoides</i>
17C	2551	<i>Acer platanoides</i>
17C	2567	<i>Gleditsia triacanthos</i>
17C	2571	<i>Gleditsia triacanthos</i>
18B	2718	<i>Acer saccharinum</i>
18B	B	<i>Ulmus x 'Morton'</i>
18B	2644	<i>Acer saccharinum</i>
19B	2743	<i>Acer negundo</i>
19B	C	<i>Acer negundo</i>
19B	2760	<i>Tilia cordata</i>
19B	2778	<i>Acer saccharinum</i>
21B	2823	<i>Ulmus pumila</i>
21B	2856	<i>Gleditsia triacanthos</i>
21B	2868	<i>Acer negundo</i>
21B	2864	<i>Acer negundo</i>
22A	2980	<i>Gleditsia triacanthos</i>
22A	2983	<i>Acer saccharinum</i>
22A	2990	<i>Tilia americana</i>
22A	3016	<i>Tilia americana</i>

23A	3103	<i>Acer platanoides</i>
23A	3123	<i>Acer platanoides</i>
23A	3093	<i>Acer platanoides</i>
23A	3132	<i>Acer platanoides</i>
24B	3188	<i>Acer platanoides</i>
24B	3200	<i>Ulmus x 'Patriots'</i>
24B	3208	<i>Acer platanoides</i>
24B	3228	<i>Acer saccharinum</i>

Table SB. Summary of model selection for each of the three sets of linear models used to analyze (a) taxonomic or functional diversity (any of the three indices); (b) bird predation attempts and (c) herbivory. Explanatory variables that cannot be included in the model selection for a given response variable are shaded. Values correspond to model coefficients for variables included in a particular model. Values in bold indicate that the coefficient was significantly different from zero. The gray line with white font following each model selection displays the relative variable importance (RVI) of each selected variable in the model selection process (i.e., the sum of weights from each model including that variable).

df: degrees of freedom; logLik: model log-likelihood; AICc: Akaike information criterion adapted to small sample sizes; $\Delta AICc$: difference between model AICc and that of the best model; only models with $\Delta AICc < 2$ are shown; R2 conditional and marginal are also shown for mixed models.

	Response variable	PC1	PC2	Tree Specific richness	Dim.1 : Tree Specific richness	Dim.2 : Tree Specific richness	Specific Richness of Funct Insect	df	logLik	AICc	$\Delta AICc$	weight	R ² _{mar} ginal	R ² _{cond} itional
a	Specific Richness of Funct Insect	-0.1878						2	-52.168	108.9	0.00	0.469	0.59	
	Specific Richness of Funct Insect	-0.1815		0.08169				3	-51.569	110.3	1.43	0.230	0.62	
	RVI	1.00		0.33										
	Vocalization-based Shannon index	-0.2297						3	-9.665	26.5	0.00	0.536	0.57	
	Vocalization-based Shannon index	-0.2164		0.08326				4	-9.099	28.3	1.77	0.221	0.58	
	RVI	1.00		0.29										
	Vocalization-based FDis	-	0.008122					3	55.216	-103.2	0.00	0.280	0.27	
	Vocalization-based FDis	-	0.006853	1.458e-03	-		-0.01114	6	59.778	-102.6	0.62	0.206	0.46	
	Vocalization-based FDis	-	0.008122	4.899e-03				4	56.351	-102.6	0.64	0.204	0.32	
RVI	1.00	0.59	0.30		0.30									
b	Bird predation attempts			0.3156				4	-98.075	204.6	0.00	0.132	0.33	0.87
	Bird predation attempts	0.05565	0.19100	0.2726	-0.3126			7	-94.867	205.0	0.42	0.107	0.33	0.86
	Bird predation attempts	0.06407		0.2857	-0.2055			6	-96.067	205.1	0.49	0.103	0.33	0.87
	Bird predation attempts	0.05750	0.19420	0.3489	-0.2860	0.1234		8	-93.942	205.5	0.95	0.082	0.32	0.86
	Bird predation attempts	0.11080		0.3645				5	-97.529	205.7	1.14	0.075	0.33	0.87
	Bird predation attempts		0.08911	0.4061		0.1854		6	-96.482	205.9	1.32	0.068	0.34	0.87
	Bird predation attempts			0.3633			-0.162700	5	-97.693	206.1	1.46	0.064	0.34	0.87
	Bird predation attempts		0.07120	0.3208				5	-97.906	206.5	1.89	0.051	0.32	0.86
	RVI	0.54	0.45	1.00	0.43	0.22	0.09							
c	Difference in herbivory	-0.035890		-	-0.1869			7	-104.291	223.9	0.00	0.328	0.14	0.14
	Difference in herbivory	0.009583		-	-0.1842		0.111600	8	-103.896	225.5	1.60	0.147	0.15	0.15
	RVI	1.00		1.00	1.00		0.31							

4. Chapitre 3 : Evaluation par pièges photographiques de la méthode des chenilles en pâte à modeler pour quantifier la prédation des oiseaux

Laura Schillé*, Nattan Plat*, Luc Barbaro, Hervé Jactel, Frédéric Raspail, Jean-Baptiste Rivoal, Bastien Castagneyrol[‡], Anna Mrazova[‡] (n.d.) - **Accuracy in bird predation assessment: camera traps testing the efficacy of plasticine caterpillars as prey models** - *PlosOne* - under review - In principle acceptance by *Peer Community In* on 11.06.2024

Abstract

Sampling methods that are both scientifically rigorous and ethical are cornerstones of any experimental biological research. Since its introduction 30 years ago, the method of using plasticine prey to quantify predation risk has become increasingly popular in the field of biology. However, recent studies have questioned the accuracy of the method, arguing that inaccuracy in inferring evidence of predator bite marks and the artificiality of models may bias the results. Yet, bias *per se* might not be a methodological issue as soon as its statistical distribution in the samples is even, quantifiable, and thus correctable in quantitative analyses. In this study, we focus on avian predation of lepidopteran larvae models, which represent one of the most widespread predator-prey interactions in various ecosystems worldwide. We compared bird predation on plasticine caterpillar models to that on dead caterpillars of similar size and color, using camera traps and observer posterior assessment to identify biases and quantify actual predation events. Although camera trap analyses revealed that birds respond similarly to plasticine models and dead caterpillars, suggesting no advantage in using dead prey for assessing avian predation, the results of posterior identification of predation marks showed contradictory results, making the interpretation of the results ambiguous. Observer inconsistencies in detecting predation clues on models highlight potential biases, with camera trap data showing these clues do not reliably indicate actual bird predation. Given the uncertainties and shortcomings of technological character revealed, the development of adequate monitoring methods and further research is essential to refine the assessment approach and better understand the biases in using plasticine models.

Keywords: Artificial prey; Bird predation; Camera trap; Ecological methods; Fake prey; Plasticine caterpillar models; Real caterpillars

4.1. Introduction

The functional role of insectivorous birds in terrestrial ecosystems (1,2) has been the focus of many studies aimed at understanding the predation patterns, feeding behavior, predator control of prey populations and evolutionary ecology (3–6). Traditional methodological approaches to these research topics include direct field observations (7), experimental manipulation in the laboratory (8,9) or in the field (10), and gut or fecal DNA analyses (11,12). Each of these methods has its own set of limitations regarding standardization, logistics, and ethical considerations such as not sparing living prey or handling captive birds. To address these challenges, the use of artificial prey, particularly those made of plasticine, introduced over 30 years ago by Brodie III (13), has become a valuable tool in bird predation research (14). The method is primarily appreciated for its ability to preserve the bite marks of predators, the identification and quantification of which has been used to infer attacks and predation risk from specific predators.

While plasticine caterpillar models are widely employed as simple, standardized prey models to investigate predation activity in diverse ecosystems (15–17), recent studies have raised concerns regarding their limitations and potential inaccuracies (14,18–20). The main concerns relate to the accuracy of inferences of predator identity and activity from the posterior assessment of putative predation marks on prey models.

Inaccuracy of predator identity - Observers may struggle to attribute a considerable portion of attack marks to a specific predator type, e.g., bird, reptile, or arthropod (18,19). For example, Valdés-Correcher et al. (21) found that up to 24% of predation mark identifications were inaccurate when assessed by untrained scientists using photos of attacked plasticine caterpillar models. This was observed in comparison to evaluations conducted by an expert who had access to the actual plasticine caterpillar models. This result shows that the identification of predator marks often relies on subjective human judgment, which can lead to observer bias. This variability is accentuated by the absence of a standardized training system for observers, thus giving them more certainty in recognizing such marks (18,22; but see Low et al. (23), for examples of predator-type classified bite mark images), leading to potential discrepancies in interpretations among researchers.

Inaccuracy in determining real predation events among all identified marks - Even though marks were attributed to birds, questions would remain about what one can infer from them. Incidental contact or non-predatory interactions (e.g., by bird claws, attraction of non-predatory animals, or curiosity) with the plasticine caterpillar models can result in marks that are difficult to distinguish from genuine predation attempts, potentially leading to an overestimation of predation rates (24). The misinterpretation of marks can lead to distorted results on predation pressure and misleading conclusions about predator-prey interactions, especially in areas where the attack rate is low (25).

Furthermore, the artificial appearance and texture of plasticine may not adequately simulate the characteristics of real prey, including smell, possibly affecting the behavior of insectivorous birds and thus the validity of predation assessment (19). The literature contains several studies that compared the attack rates on plasticine larvae to those of real larvae, with the latter being quantified based on missing or partially consumed prey items (19,20,24). As opposed to plasticine caterpillar models, the attack rate on living and dead prey has shown comparable results (19), thus justifying not using living prey for ethical reasons (not to glue or pin them alive). By simultaneously studying predation on dead caterpillars versus plasticine models, it becomes possible to compare the response of predators to both types of prey within the same experimental design with the use of passive monitoring methods. This comparative approach makes it possible to test the assumptions on which the plasticine caterpillar model method is biased and to correct it in relation to observable predation patterns on real dead prey. Quantifying this bias is critical to determining whether plasticine models can reliably mimic real prey, and thus whether the data they provide can reflect an accurate depiction of predation pressure.

Studies comparing predation on both real caterpillars and plasticine models have shown discrepancies, revealing that plasticine models may not be a sufficiently accurate method for assessing predation (19), particularly across large biogeographical ranges (24), varying thermal regimes (26), different seasons of the bird life cycle (20), and for different taxa (19). There appears to be a gap in the literature regarding more detailed analyses that elucidate the origins of the marks found on plasticine models. Moreover, missing plasticine models are usually excluded from the statistical analyses (16,27). Yet, at least part of those missing models can be the result of a predation attempt that was not recorded. On the contrary, studies working with real prey have often assumed that a

missing prey was equivalent to a depredated prey (19,20,24), an assumption that may not always hold true. Without direct observation, the reasons behind the disappearance of the prey remain speculative.

To address these methodological uncertainties, and following recommendations from Bateman et al. (18) and Rößler et al. (22), we employed camera traps. As they have been already used to study bird frugivory (28,29), we suggest their application also to experimentally record predation on plasticine models (hereafter “models”) paired with dead caterpillars (hereafter “corpses”) on the experimental trees. We hypothesized that the integration of camera traps could visually confirm predation attempts, providing a direct and unbiased record of predator interactions with the prey. This visual evidence could enable the differentiation between actual predation marks and those resulting from incidental contact or environmental factors (e.g., rubbing by leaves or branches), therefore increasing the accuracy of predation rate assessment. Ultimately, we believe that the results of this study will help to refine the plasticine caterpillar model method as a tool for ecological research, ensuring that it produces scientifically relevant results.

We used camera traps to quantify predation events on both prey types and possible sources of bias in inferences made from plasticine models. We first assessed bias in the detection of predation clues on plasticine models due to variation among observers (H1). We further hypothesize that observer detection of predation clues leads to an overestimation of predation on plasticine models by attributing unrelated or uncertain marks to actual predation attempts (H2). Taking into account the innate ability of insectivorous birds to recognize suitable prey and the differences in the surface texture of real vs. plasticine caterpillars, we hypothesize that there will be evidence of more predation on corpses than on models, both assessed using camera traps (H3). Finally, we hypothesize that observer detection of predation would lead to an overestimation of the predation on corpses by accounting for missing individuals as a predation event, lacking direct evidence for why the prey disappeared (H4). If we obtain comparable results of the bias between observers and cameras for both models and corpses, and if the test of H3 provides evidence of more predation on corpses than on models, we could conclude that the use of corpses with human post-detection would be a more accurate method than the use of plasticine models with human post-detection.

4.2. Material and Methods

4.2.1. Study area

We carried out this experiment in a pine and oak forest stand of 5ha near Bordeaux, France (44°44'N, 00°46'W). The climate is oceanic, with 12.8°C average temperature and 870mm annual rainfall. We synchronized the start of the experiment as closely as possible with the breeding period of local insectivorous birds, specifically, when the chicks were in the nest and fed by the parents (starting generally mid-April for resident breeders or early migrants). We choose this timing to quantify bird predation by experienced adults rather than later exploratory predation attempts by young, inexperienced birds. The main insectivorous bird species in the study area were Great Tit (*Parus major*), Eurasian Blue Tit (*Cyanistes caeruleus*), Eurasian Blackcap (*Sylvia atricapilla*), Common Redstart (*Phoenicurus phoenicurus*), Eurasian Blackbird (*Turdus merula*), Western Bonelli's Warbler (*Phylloscopus bonelli*), Common Chiffchaff (*Phylloscopus collybita*), Short-toed Treecreeper (*Certhia brachydactyla*), Eurasian Nuthatch (*Sitta europaea*), European Robin (*Erithacus rubecula*), Eurasian Wren (*Troglodytes troglodytes*), and Great Spotted Woodpecker (*Dendrocopos major*) (30).

These bird species have home ranges that vary between 0.3 ha for the Blue Tit (31) and 7.9 ha for the Common Chiffchaff (32), the latter value being extreme as compared to most of the insectivorous species (33,34). It is therefore likely that multiple individuals of the same insectivorous bird species defended separate territories in the study area. Together with the fact that we distributed the experiment across the whole forest stand (see below) and that oak trees host a large density of herbivorous insects (N. Plat, A. Mrazova, and L. Schillé personal observation), we doubt that birds learned to avoid corpses and models during the experiment.

4.2.2. Study design

First, we haphazardly selected 12 pedunculate oaks (*Quercus robur*, the dominant broadleaved species of the area) located at least 10m apart from each other. On one branch accessible from the ground of each of these trees, we glued five plasticine models, and on another branch as far as possible from the first one, we glued another set of five

corpses of *Operophtera brumata* larvae, previously killed by freezing at -80°C . We use this level of prey density because (i) the natural density of caterpillars was high at this time of the year, and (ii) to optimize the use of camera traps by ensuring an adequate number of statistical replicates. The five caterpillars on each branch were spaced at least 5 cm apart to remain in the focus of camera traps.

We used the lepidopteran species *Operophtera brumata* for experimentation, a widespread and often abundant oak-defoliating moth. The caterpillars, whether models or corpses, were directly glued to the branches with two glue drops. We used corpses for ethical reasons, to avoid gluing living caterpillars.

We modeled artificial caterpillars with green plasticine (Staedtler brand, model 8421-5), forming 1.5×0.3 cm cylindrical shapes and mimicking Lepidopteran larvae. They had the same color as most plasticine models commonly used in studies of predation interactions in ecology (15–17,23,35) and the same size as *Operophtera brumata* dead larvae used as corpses.

Corpses darken when exposed in the field; after 48 hours, their color differs from that of live individuals. We cannot exclude that their smell change too. For these reasons, we exposed fresh models and corpses on a new set of 12 trees every two days. After 16 days, this procedure resulted in a total of 480 model- and 480 corpse- caterpillars installed on 96 oaks.

4.2.3. Predation analysis

We took plasticine models collected in the field to the laboratory in plastic vials. Note that none of the plasticine models disappeared during the experiment. All models were examined by three experienced observers who identified marks of attempted predation by birds using a magnifying glass. The models were considered ‘attacked’ if they exhibited at least one attack mark on the plasticine surface. Observers carefully reread the bite mark guide published by Low et al. (23) beforehand. These observations were used to evaluate consistency among the observers. In cases of doubt regarding whether a model was attacked or not, the observers discussed and reached a consensus. Hereafter, we refer to the presence of marks reported by human observers' consensus as ‘predation clues’.

Predation clues on corpses were directly examined in the field. A missing corpse or one with a missing part was considered attacked, as is generally the case in the literature (19,20,24).

4.2.4. Image analysis

Interactions between predators and corpses as well as models were recorded using camera traps (Brand Ltl Acorn model Ltl-5210M). We installed two camera traps on the trunk of each tree facing the two branches holding models and corpses, respectively. The camera was positioned about 1m from the caterpillars to make it easier to focus (without blurring) (Fig 1). The camera traps were active 24 hours a day for the 14 consecutive days of the experiment. They were set to the highest sensitivity and automatically took bursts of three photos when the passive infrared (PIR) sensors detected motion with a 0.5s trigger speed. At each field visit, we changed the SD cards and checked the batteries to replace them if necessary.

We analyzed the images taken by camera traps using the application EcoAssist (36) supporting the MegaDetector learning model (Machine Learning for Wildlife Image Classification, (37)). This learning model automatically detects the presence of animals in images. We used the most conservative detection confidence threshold of 0.01 for the model in the EcoAssist application, as this threshold previously tested showed a 100% success rate (i.e., all birds present in the images were detected). Following this detection process, we carried out a visual examination by an observer of the images. This examination concerned both corpses and plasticine models.

Our camera traps were insufficient to monitor all predation events due to the birds' small size and stealthy behavior. Therefore, we defined 'evidence of predatory bird presence' at the branch level as the presence of at least one image showing a foraging bird on the branch (hereafter 'evidence of bird presence'). These images could show individuals in various contexts: birds looking at the camera (Fig 2d and 2e), flying over the target branch (Fig 2a), engaging in foraging activity on the target branch but with natural prey on the bill (Fig 2c and 2e), foraging on experimental prey (Fig 2f and 2h), standing on the experimental branch (Fig 2b and 2g), or feeding during early morning (Fig 2e).

Subsequently, we statistically compared this evidence of bird presence to the predation clue determined by human observers on the same branch. A branch was categorized as having a predation clue if at least one of its five caterpillars showed a predation clue.

All observed evidence of predator presence, regardless of whether the predator was a bird or not, was also carefully recorded for further discussion. It should be noted, however, that arthropod predators were unlikely to be detected by camera traps. We identified all species associated with the evidence of bird presence.



Figure 1. Photographs of the experimental design in the field. Red arrows point toward the camera traps. Blue and yellow arrows point toward five plasticine models (a) and three corpses (b), respectively.

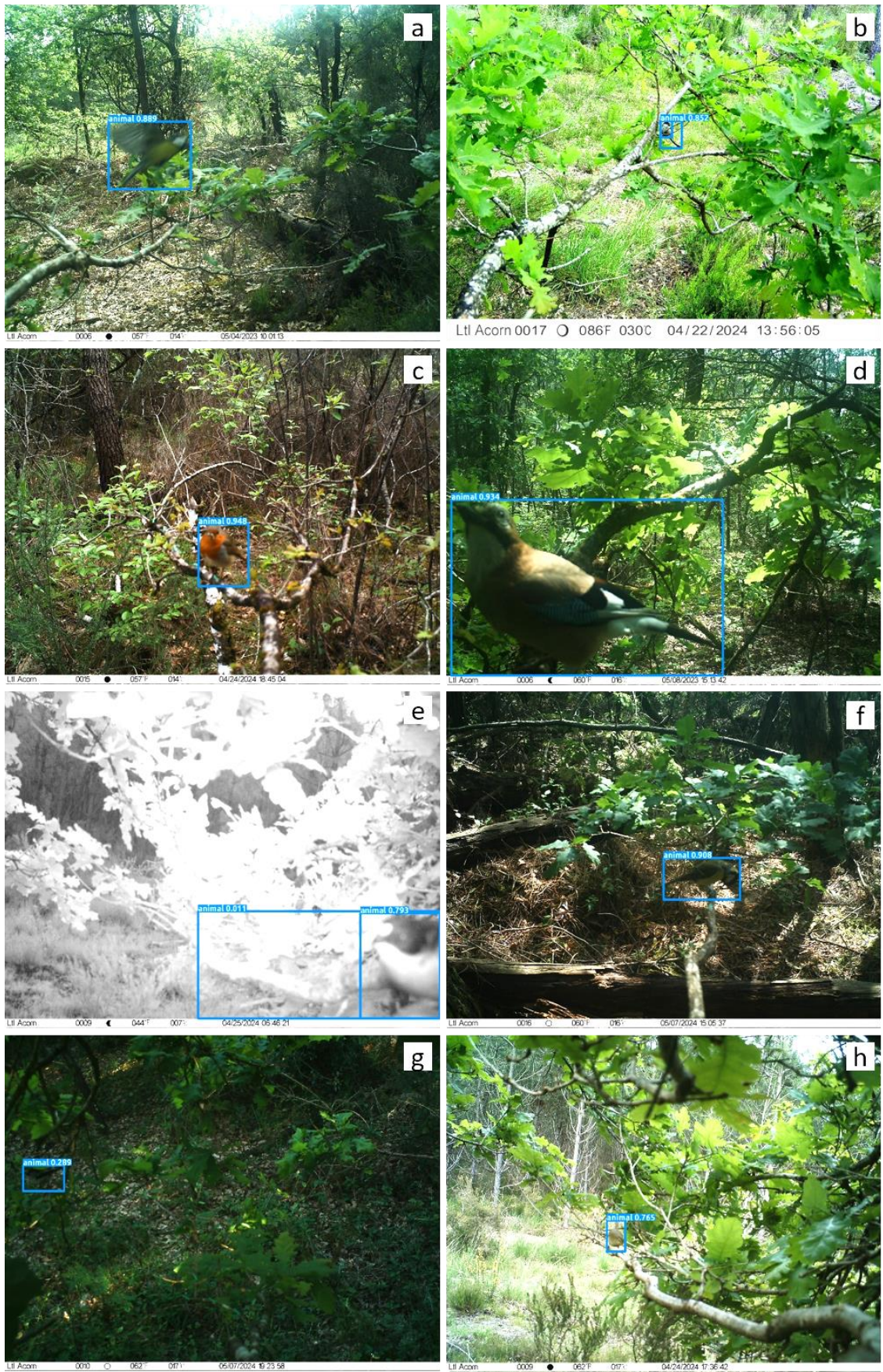


Figure 2. Camera trap photographs of birds taken in various contexts. Birds exhibit different behaviors (perched on a branch, actively foraging, flying, etc., see main text). The blue

squares correspond to MegaDetector detections with the associated confidence level. The bird species included are: the Great Tit (*Parus major*, Figs 2a and 2f), the Long-tailed Tit (*Aegithalos caudatus*, Figs 2b and 2g), the European Robin (*Erithacus rubecula*, Fig 2c), the Eurasian Jay (*Garrulus glandarius*, Fig 2d), the European Pied Flycatcher (*Ficedula hypoleuca*, Fig 2e), and the Common Chiffchaff (*Phylloscopus collybita*, Fig 2h)

4.2.5. Statistical analysis

All analyses were performed in R (38). Fig 3 summarizes all the hypotheses tested using the experimental design.

4.2.5.1. Evaluation of the degree of consistency between observers in the posterior detection of bird predation clues (H1)

We relied on the intra-class correlation coefficient (ICC) to assess the degree of consistency between observers in detecting predation clues on plasticine models. The ICC quantifies the degree of agreement between groups or between observers and is bounded between 0 and 1, where 1 indicates perfect intra-group agreement and 0 indicates no agreement beyond what would be expected by chance. According to Koo and Li (39), an ICC value below 0.50 is considered poor, between 0.50 and 0.75 moderate, between 0.75 and 0.90 good, and above 0.90 excellent. We calculated the ICC using the ‘icc’ function of the *irr* package (40), with a two-way random effect model because each plasticine model was evaluated by the same set of three observers.

4.2.5.2. Comparison between evidence of bird presence assessed by camera traps and predation clues detected by human observers branches with models and corpses (H2 and H4)

We used two generalized linear mixed models (GLMM, *lme4* package; (41)) with a binomial error distribution to evaluate the bias between observer detection of predation clues and evidence of bird presence assessed by camera traps on (i) branches with models (H2) and on (ii) branches with corpses (H4). In both cases, the detection method (predation clues or evidence of bird presence assessed by a camera) was set as a fixed effect, and tree identity nested in temporal permutation was considered a random factor. The model equation was:

$$\text{logit}(P(Y_{ij} = 1)) = \beta_0 + \beta_1 \times \text{Detection}_{clues,ij} + \gamma_j$$

where Y_{ij} is the binary response variable representing detection at each branch (one data point per detection method and branch). Specifically $Y_{ij} = 1$ indicates at least one

predation clue or predation evidence on branches with models (H2) or corpses (H4), while $Y_{ij} = 0$ indicates no predation clue on any model (H2) or corpse (H4) or no evidence of bird presence. β_0 is the model intercept, representing the logit-transformed probability of detection for camera-assessed bird presence evidence (i.e., $Detection_{EvidenceBird,ij}$), β_1 is the coefficient of the fixed effect of the predation clues detected by the observer (i.e., $Detection_{clues,ij}$), γ_j is the random intercept for tree identity nested in temporal permutation.

4.2.5.3. Comparison between the evidence of bird presence on corpses versus models both assessed by camera traps (H3)

We used another GLMM with a binomial distribution to assess the predation bias on models compared to corpses. Fixed effect was the type of prey (model or corpse) and random intercepts were tree identity nested in temporal permutation. The model equation was:

$$\text{logit}(P(Y_{ij} = 1)) = \beta_0 + \beta_1 \times PreyType_{Model,ij} + \gamma_j$$

where Y_{ij} is the binomial response variable indicating bird presence detection at each branch (one data point per type of prey and branch). Specifically, $Y_{ij} = 1$ indicates at least one bird presence evidence, while $Y_{ij} = 0$ indicates absence of evidence of bird presence. β_0 is the model intercept, representing the logit-transformed probability of detecting bird presence for corpses (i.e., $PreyType_{Corpse,ij}$), β_1 is the coefficient of the fixed effect of the plasticine models (i.e., $PreyType_{Model,ij}$), γ_j is the random intercept for tree identity nested in temporal permutation.

For both types of GLMMs, we used the ‘*nlmInbwrap*’ optimizer, which facilitated model convergence and provided results comparable to the default optimizer of the *lme4* package. It should be noted that since the two GLMMs we used are binomial with a *logit* link function, an inverse transformation of the coefficients must be applied to estimate it as a percentage of predation.

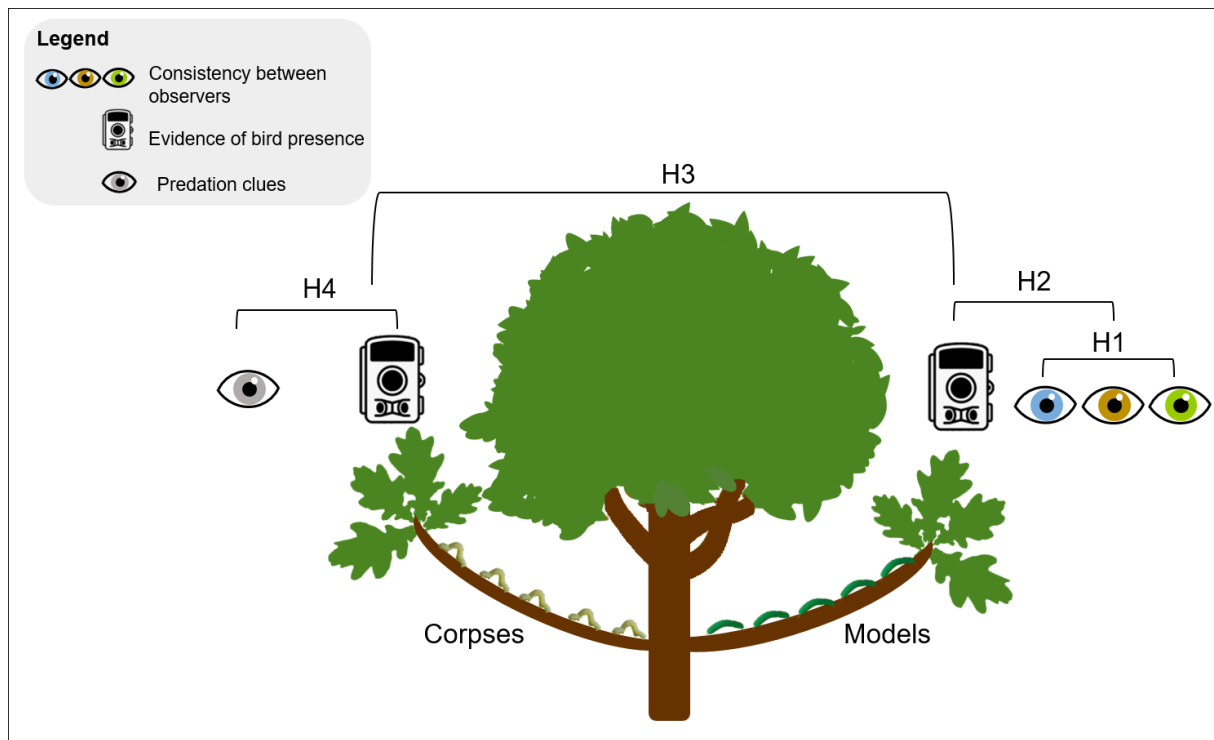


Figure 3. The experimental design testing the four hypotheses. H1: Evaluation of the degree of consistency between observers in the posterior detection of bird predation clues; H2: Comparison between evidence of bird presence assessed by camera traps and predation clues detected by human observers branches with models; H3: Comparison between the evidence of bird presence on corpses versus models both assessed by camera traps; H4: Comparison between evidence of bird presence assessed by camera traps and predation clues detected by human observers branches with corpses.

4.3. Results

4.3.1. Consistency among observers in the detection of bird predation clues (H1)

Observer A detected ten predation clues on 480 plasticine models, whereas Observer B and Observer C detected only three and four predation clues, respectively. At first, the three of them only agreed on two caterpillars (Fig 4a). The intra-class correlation coefficient (ICC) score was 0.47 (CI 95%: 0.41 - 0.52) indicating a poor agreement between the three observers in their assessments of predation clues on the 480 plasticine models ($F_{(479, 960)} = 3.61, P < 0.001$). The three observers therefore re-assessed predation clues to reach a consensus on the attacked vs non-attacked status. The final, consensual status resulting in seven caterpillars with bird predation clues was used in further analyses.

4.3.2. Evidence of bird presence on branches with corpses or models assessed by camera traps (H3)

We obtained 148,157 images from the cameras. The MegaDetector algorithm detected animal presence in 37,495 images (using the lowest detection threshold of 0.01 confidence). After visual evaluation, we ultimately retained only 146 photos showing foraging birds on or around 30 target branches (out of 192). They corresponded to 42 bird individuals belonging to 10 different species (*Aegithalos caudatus*, *Anthus trivialis*, *Phylloscopus collybita*, *Erithacus rubecula*, *Garrulus glandarius*, *Ficedula hypoleuca*, *Cyanistes caeruleus*, *Parus major*, *Fringilla coelebs*, and *Turdus philomelos*). We also detected other potential predators on certain branches, such as rodents of the genera *Mus* or *Eliomys* and a Red Squirrel (*Sciurus vulgaris*) (see Figs S1m and z, respectively).

Evidence of bird presence, defined as the presence on images of a foraging bird on or flying toward a branch, did not differ significantly between branches with plasticine models vs. branches with corpses ($\beta_{1,Corpse} \pm SE = -0.5 \pm 0.4$, $z = -1.3$, $P = 0.20$, Fig 4b). A substantial portion of the variance in bird presence assessment was attributed to random effect (marginal $R^2 = 0.019$, conditional $R^2 = 0.19$)

4.3.3. Evidence of bird presence vs. predation clues on branches with models (H2) and corpses (H4)

We found predation clues on 7 plasticine models (7 branches, Fig 5) and 181 corpses (64 branches). Predation clues on branches with plasticine models were associated with the presence of a bird on the same branches in the case of three branches. We observed the presence of birds on 15 branches with no predation clues on models. Predation clues on models were observed on four branches without the presence of birds being detected by camera traps (Fig 4a). We therefore detected significantly more evidence of bird presence than predation clues on branches with plasticine models ($\beta_{1,Evidence} \pm SE: 1.3 \pm 0.5$, $z = 2.4$, $P < 0.05$, Fig 4c). A substantial portion of the variance in predation assessment on branches with plasticine models was attributed to random effect (marginal $R^2 = 0.08$, conditional $R^2 = 0.34$).

Predation clues on branches with corpses were associated with evidence of bird presence on the same branches in 8 cases. In contrast, we observed evidence of bird presence without predation clues on corpses on 4 branches, and predation clues on corpses without the presence of bird being detected on 56 branches (Fig 4a.). There was therefore significantly less evidence of bird presence than predation clues on branches with corpses ($\beta_{1,Evidence} \pm SE: -2.7 \pm 0.4, z = -6.8, P < 0.001, \text{Fig 4d.}$). The random effect accounted for only a small fraction of the variance (marginal $R^2 = 0.35$, conditional $R^2 = 0.38$).

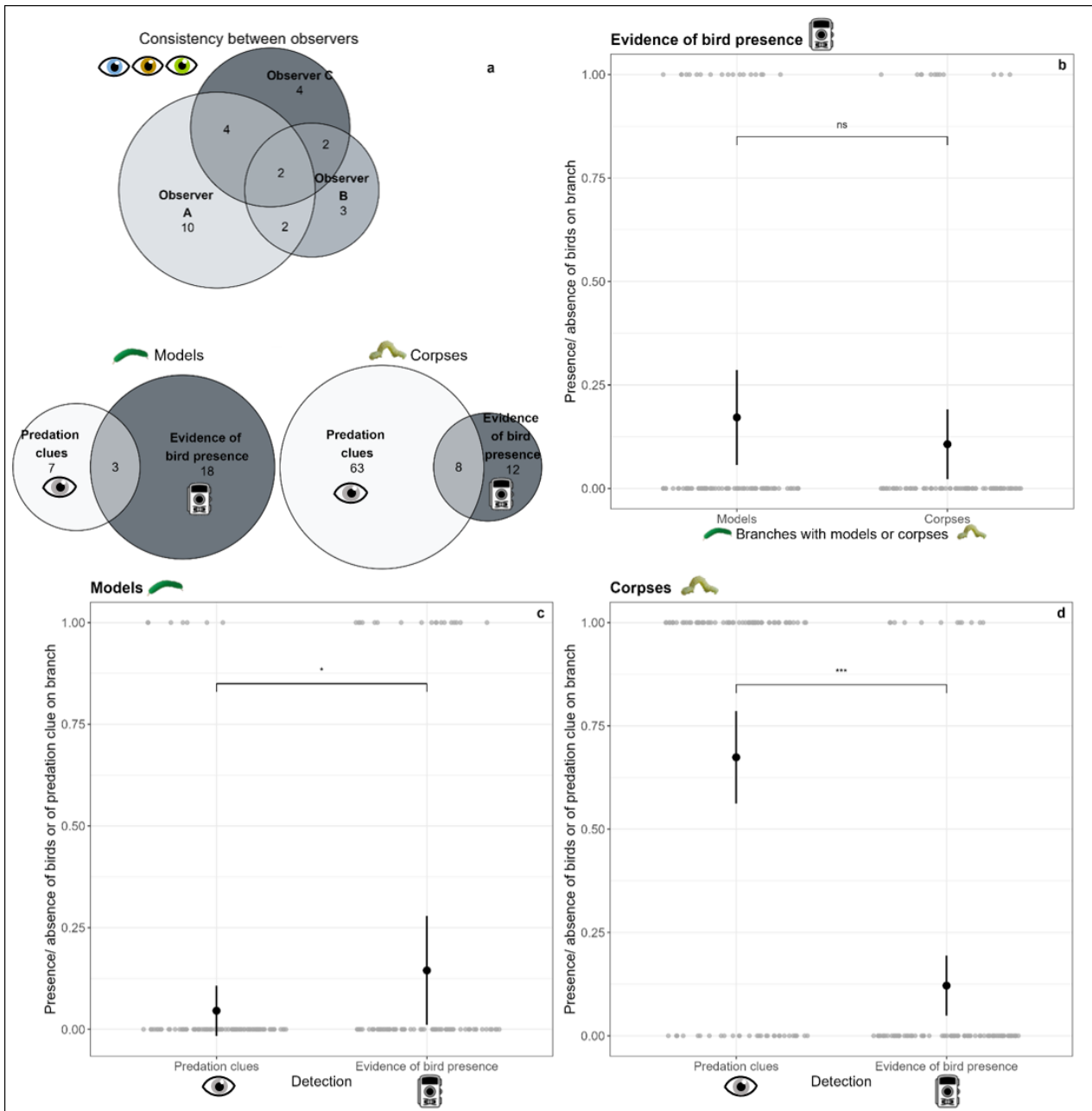


Figure 4. Main results of the study. Euler diagram of consistency between the three observers (a, upper panel), and Euler diagrams of the number of branches with predation clues and with evidence of bird presence for models and corpses (a, lower right and lower

left panels, respectively). Results of the generalized mixed-effects models with binomial distribution for the three hypotheses tested: H2 (c), H3 (b), and H4 (d).

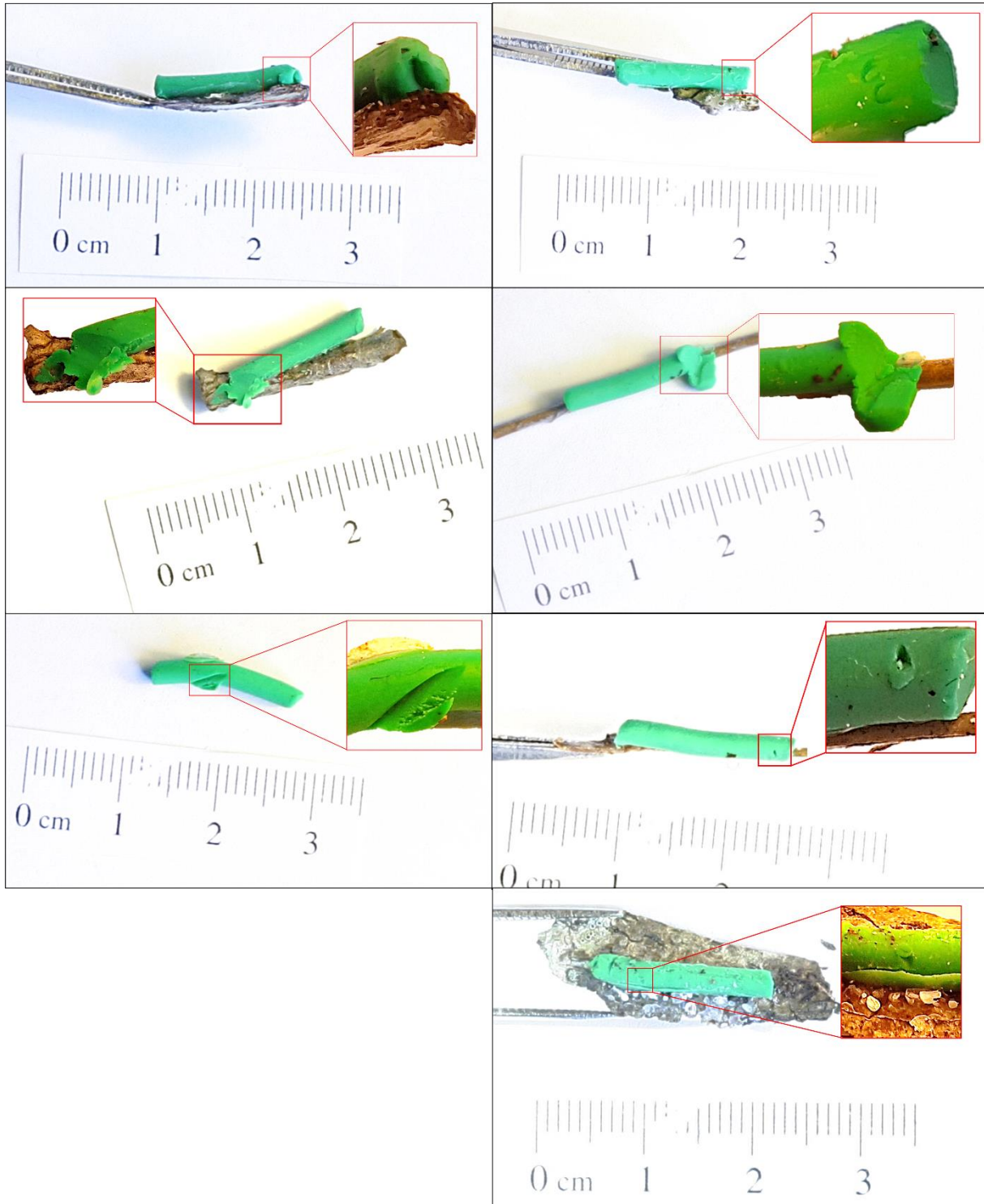


Figure 5. Photographs with mark details. Seven caterpillars that observers considered to have bird predation clues.

4.4. Discussion

4.4.1. Lack of consistency in observations of predation clues on plasticine caterpillar models

Our study confirms the lack of consistency between observers' evaluation of predation marks on plasticine models. Despite all trained observers re-reading the attack mark guide (23), they did not detect the same number of predation clues. Similar results, even among experienced scientists, were reported by Valdés-Correcher et al. (21) and Castagneyrol et al. (42), using a more robust experimental design. In our case, the lack of consistency among observers may have been aggravated by the small size of plasticine models mimicking *Operophtera brumata* caterpillars (1.5 × 0.3 cm). These models were smaller than the artificial prey commonly used in the scientific literature (3 cm on average across the five following studies (16,17,19,23,24)), resulting in a perception of predation marks that differs from what we typically observed on larger models.

To our knowledge, most studies using predation clues on plasticine models rely on a single observer. Information about whether multiple observers could be involved is also rarely provided (e.g., when the primary observer consults one or more colleagues for marks on models that are difficult to assess). Some studies have employed two independent observers evaluating the models by consensus (43,44), which could be a good method to avoid observer bias. It could be also advisable to develop an online standardized training system for identifying bird bill marks on plasticine models, as it is done for insect herbivory (e.g., ZAX herbivory trainer: <https://zaxherbivorytrainer.com/>(45)). This could complement the comprehensive guide developed by Low et al. (23) and be tailored to different biomes, considering the substantial variations in predator and prey sizes and behaviors.

4.4.2. Bird presence assessed by camera traps does not differ between branches with plasticine models and corpses

The main result of our study revealed that the evidence of bird presence assessed by camera traps does not significantly differ between experimental branches. Considering that camera traps caught flying birds and birds foraging under poor light conditions (S1 Figure), we assume that the cameras do not miss birds when they are present. Such an

outcome would suggest that plasticine models can be used to estimate bird predation, as they offer the additional advantage of overcoming the ethical issues associated with the use of real prey, whether dead or alive. This result differs from our findings regarding the number of predation clues assessed by observers and contradicts other studies that find more bird attacks on real prey compared to plasticine ones (19,20).

Specifically, we observed a ratio of 7 predation clues on plasticine models to 181 on corpses. Similar to the findings by Zvereva & Kozlov (20), we believe that the corpses were primarily removed and attacked by arthropods as we found ants crawling around 24 corpses out of 480, but other predators such as spiders or other arthropods could also be involved. These findings are also in accordance with Nimalrathna et al. (24) who found that the attack rate by vertebrate predators was lower on dead prey than on live prey and plasticine models, while invertebrates preyed most on dead prey followed by live prey and plasticine models. Considering our and Nimalrathna et al.'s (24) results, we conclude that our observations of predation on corpses are driven by arthropod consumers.

Although tempting to conclude that birds do not distinguish between real and plasticine caterpillars, and thus claim this method reliable, it must be noted that we cannot rely on the (i) posterior evaluation of clues on corpses; and (ii) the evidence of bird presence assessed by camera traps as evidence of predation. Therefore, the evaluation of the plasticine model method is mostly limited by available technology. To our knowledge, there is currently no reliable, affordable technique for accurately identifying birds preying on insects. Camera traps available on the market have motion detection speeds that are too slow for birds or do not allow for fast sequences of pictures or continuous recording. Cameras that do offer continuous recording have other limitations in data storage, power supply, and encoding time. There is thus a need for advanced cameras, that allow us to observe fast behavioral phenomena of relatively small animals, such as foraging birds. These cameras could be used in various fields such as trophic interaction ecology, conservation ecology, and behavioral ecology. Although some initiatives offering prototypes exist (e.g., (46)), the costs are currently still too high to be affordable for scientific purposes.

The most limiting trade-off is between the camera performance and energy consumption. For scientific research, we need at least 24 hours of endurance, which is currently not possible for continuous recording. The cameras could therefore operate by capturing a

sequence of pictures at intervals of at least 0.5 seconds continuously to maximize the chance of capturing the moment of predation (86,400 pictures/day). At the same time, the batteries must be removable for quick changes in the field. Additionally, the cameras should be affordable, relatively small, light, and waterproof, and finally have programmed a short encoding time.

4.4.3. Predation clues assessed by observers do not correlate with bird presence assessed by camera traps

Predation clues assessed by observers on plasticine models or corpses did not reflect bird foraging activity as revealed by camera traps. Another study comparing camera traps and posterior detection to assess predation on artificial snakes also revealed that predatory birds were underrepresented in the videos triggered after motion detection compared to the number of predation marks on artificial replicates (47). Moreover, O'Brien & Kinnaird (48) demonstrated in 2008 that camera traps were more suitable for larger birds such as pheasants than for functionally insectivorous birds targeted in our study. We acknowledge that modern camera trap technology has significantly improved since 2008, though, to our knowledge, however, no recent studies specifically address this in the context of bird predation.

Contrary to our hypothesis, we found more evidence of bird presence than predation clues on plasticine models suggesting that fake prey underestimates the foraging activity of avian insectivores. Considering the particularly high density of live prey during this time of year (L.S., N.P., A.M. pers. observation), an explanation could be that experienced birds prefer live caterpillars found on the same branch over the models (see also (20)). It is, however, important to consider the low numbers of both observations (clues vs. evidence) (Fig 4c) implying a weak indicative value.

The glue used to attach the prey sometimes caused such small models to harden, potentially preventing the later detection of predation clues. Finally, we could not exclude curiosity-driven behaviors from some individuals, notably Eurasian jays, who seemed to gaze intently at the camera rather than at the available prey. While we anticipated this curiosity behavior, we expected it to manifest more in predation clues on the models (e.g., such as claw marks). We carefully re-checked models on which no predation clues were

initially identified, whereas we obtained evidence of birds foraging on the corresponding branches. The three observers confirmed no predation clue was visible on these models.

We observed more predation clues (181) than presence evidence on corpses (12). As described above, we believe that the effect size is most likely driven by arthropod consumers. This assumption, however, cannot be currently tested as we are not able to distinguish between arthropod and bird clues on corpses and at the same time cannot rely on the evidence of bird presence to be evidence of a genuine predation event. Additionally, we note that photographs from the camera traps revealed potentially predatory rodents on one of the branches with corpses.

Overall, the results discussed here provide only a limited window to the interpretation of whether the use of plasticine models should be regarded as a reliable method. Therefore, we encourage future protocols to explore methods that involve exposing live prey on branches while non-invasively preventing their escape (e.g., applying glue to branch ends) in combination with cameras providing unquestionable evidence of bird predation.

4.4.4. Perspectives

Our study still has not answered the most important question, namely whether plasticine models accurately assess actual predation by birds or not. However, it paves the way for the use of new technologies, such as passive monitoring methods like video surveillance, to obtain real evidence of predation. We, therefore, advocate for their development and use, which will likely refine the widely used plasticine model method in the ecology of trophic interactions.

Taking into account all results and technical difficulties of this study as well as the results of other studies, we summarized the advantages and disadvantages of each method for quantifying bird predation, along with future recommendations in Table 1.

Table 1. Advantages, disadvantages, comments, and recommendations for the three methods of assessing bird predation: plasticine models, real prey, and cameras. Note that cameras must be used in combination with one of the other two methods. If a cell in the third column spans two rows in the first column labeled 'Methods,' it applies to both methods. Literature references supporting our arguments are marked in blue.

Methods	Advantages	Disadvantages	Comments/ recommendations
Plasticine models	<ul style="list-style-type: none"> - Low-cost - Easy method - Standardized - Ethical - Posterior detection possible 	<ul style="list-style-type: none"> - Artificiality: immobile, too bright color resulting in unnatural contrast with branch; non-natural smell; often oversized regarding the size of the species naturally occurring in the habitat - Inconsistency of human detection 	<ul style="list-style-type: none"> - Most models used are too large compared to native European caterpillars ((14); see S2 Figure). Therefore, we recommend adjusting the models' size according to the species likely to be present at study sites. - The vivid green color is not always the most suitable choice for plasticine. We recommend adjusting the color of larvae in a given geography and habitat (e.g., (49)). - We recommend several independent observers (e.g., (43,44)) or an online training system (on the model of (45)) to mitigate the observer detection bias.
Real prey	<ul style="list-style-type: none"> - Really reflects predation 	<ul style="list-style-type: none"> - Expensive and time-consuming rearing - Unethical 	<ul style="list-style-type: none"> - It is necessary to consider a realistic density of models concerning the actual abundance of prey in the study area at any given time (14). - Consider exposing the prey (models or real caterpillars) according to the natural behavior of the species they represent (e.g., petioles of the leaves, inner space of the rolled leaves, tree trunks, etc.) (e.g., (15,17,27)). - Consider the appropriate attachment method regarding the size of the prey, (e.g., the glue may not be the best solution in the case of small prey and could be substituted with pins

			<p>or double-sided adhesive tape) (e.g., (15,17,27,50)).</p> <ul style="list-style-type: none"> - Use live prey to better reflect predation. Develop protocols to utilize live prey without attachment for ethical reasons while preventing their escape from branches (e.g., (19,20,51)). - Combination of real prey and cameras.
<p>Camera traps</p>	<ul style="list-style-type: none"> - Theoretically allows obtaining evidence of predation by birds (but this study showed that current camera traps do not yet allow this) - Identification of bird species - Detection of other vertebrate predators - Knowing the exact time of predation 	<ul style="list-style-type: none"> - Expensive (52) <p><u>Currently:</u></p> <ul style="list-style-type: none"> - Passive infrared sensors are not suitable for small birds (48) - Too slow motion detection speeds for photos and even slower for videos - Only a few photos in burst mode after motion detection decrease the chance of capturing the predation event - Too short video times - Non-existing long-term continuous recording - Low data storage - Short-term power supply - Long encoding time - High power supply (52) - Need for artificial intelligence to process thousands of photos (46) 	<ul style="list-style-type: none"> - We strongly encourage programmers and electronics to use low-cost microcontrollers coupled with small cameras and high-capacity batteries to obtain real evidence of not only bird predation but generally animal behavior under natural conditions. Such a monitoring method could allow us to conduct reproducible experiments on a large geographic scale, in different habitats, and with multiple target larva species to model an overall bias of the plasticine model method.

4.4.5. Conclusion

Our study sheds new light on the evaluation of the plasticine model method for characterizing bird predation. It confirms the existence of an inter-observer consistency bias in the posterior evaluation of predation marks on these models. It also suggests that predation clues do not accurately reflect the presence of predatory birds as assessed by camera traps, neither on the branches bearing the plasticine models nor on those bearing dead natural caterpillars. As we found no differences in the behavioral responses of birds to artificial prey compared with dead natural ones, we would conclude that using caterpillar corpses did not present particular advantages over using plasticine models for assessing avian predation on folivores. However, taking into account predation clues analyzed by observers showing contradictory results indicates a non-accurate monitoring approach for assessing the reliability of this method. Existing technologies do not yet allow this method to be improved and the use of plasticine to assess bird predation cannot be claimed or refused using currently available techniques. Our study suggests it is necessary to be able to evaluate the inherent biases of using plasticine models in field conditions. To this end, we advocate for the development of more precise monitoring devices and more global initiatives building upon our study, as soon as such a reliable monitoring method can be offered.

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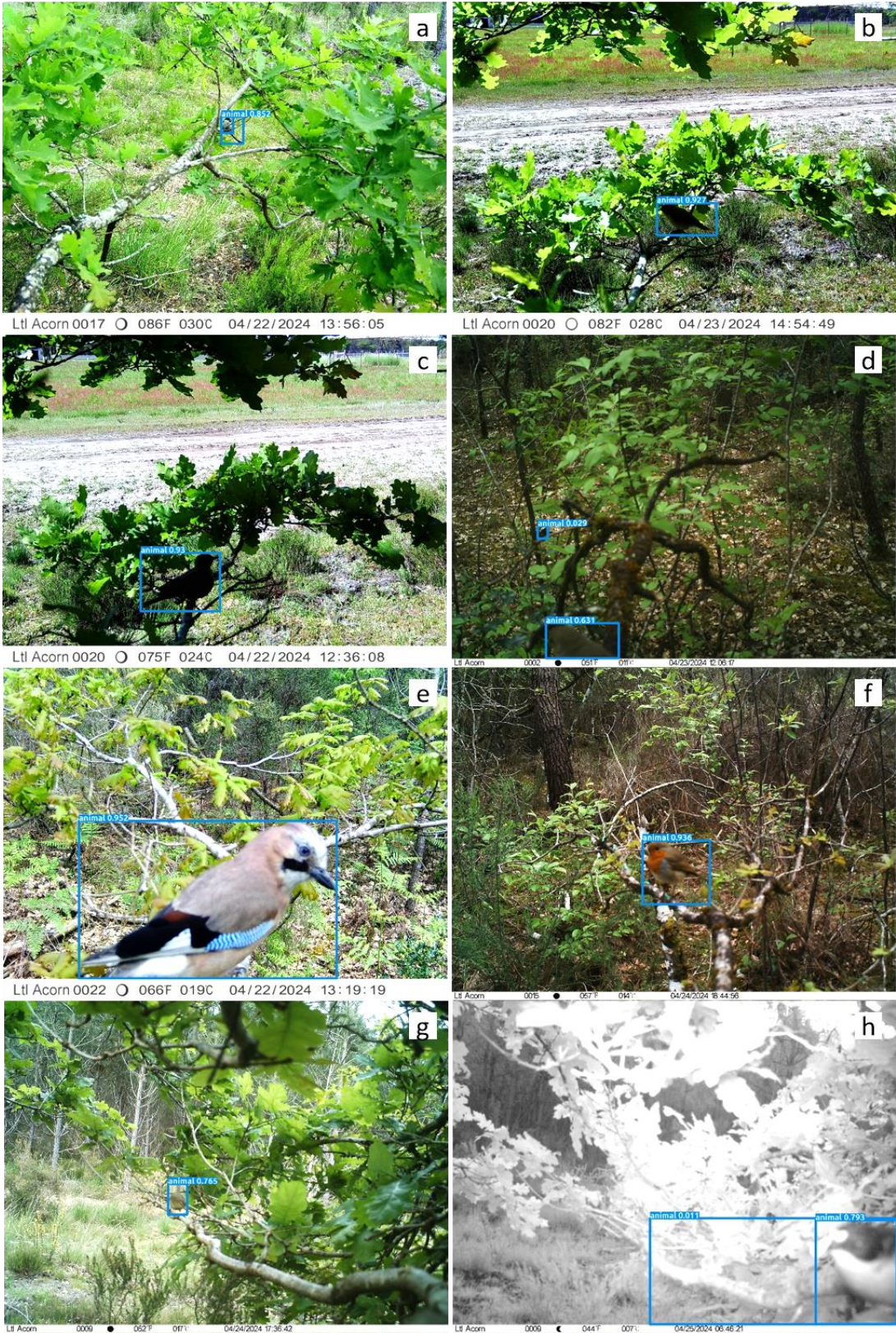
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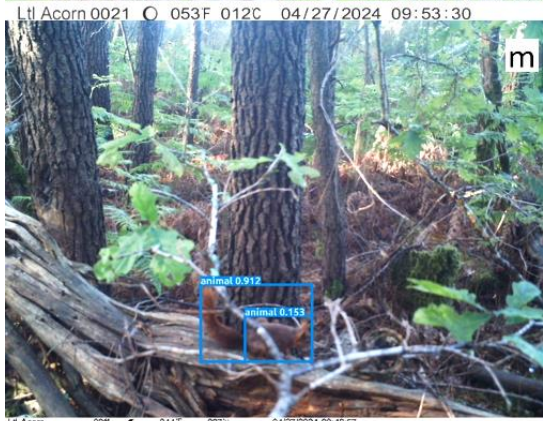
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Acknowledgments

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Supplementary materials







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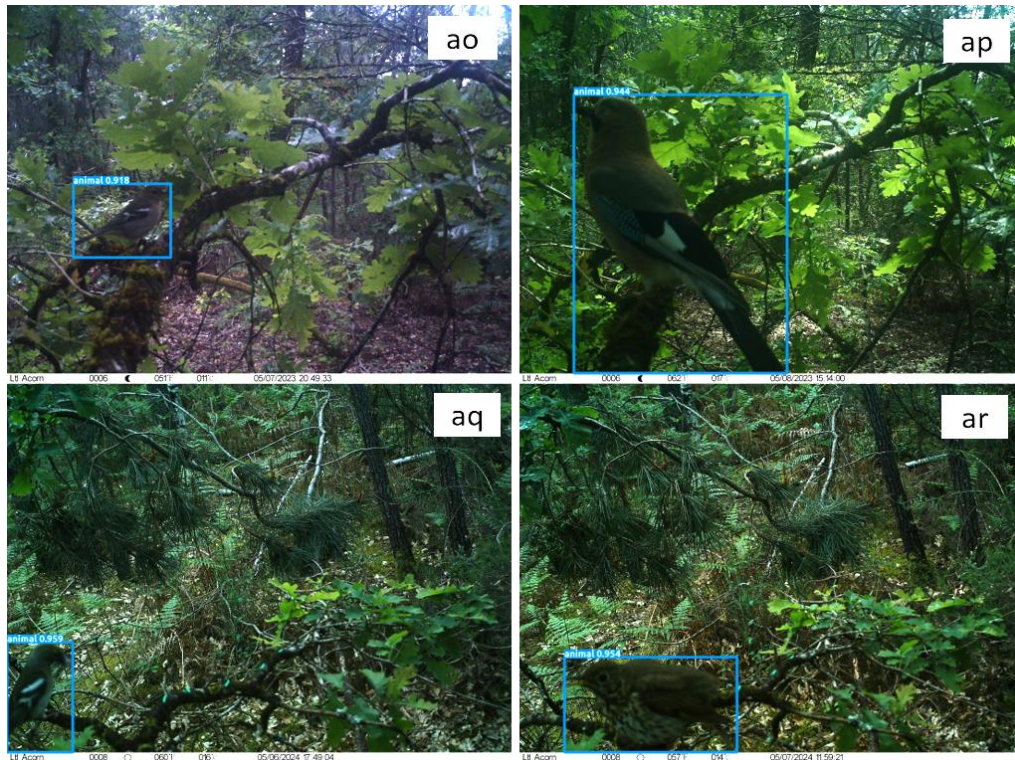


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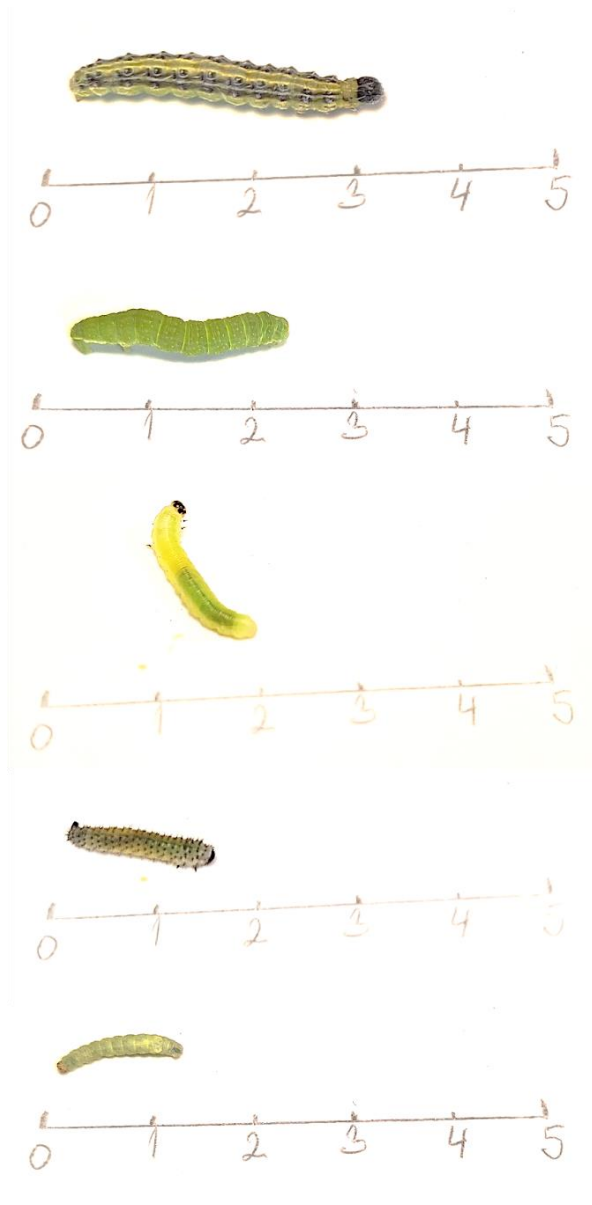


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S1 Figure. All detected birds by MegaDetector AI software. Camera traps photographs of potential predators of caterpillars. The blue squares correspond to MegaDetector detections with the associated confidence level. The animal species included are: the Long-tailed Tit (*Aegithalos caudatus*, S1a, and S1ag Figures), the Tree Pipit (*Anthus trivialis*, Figs S1c, and S1k Figures), the Common Chiffchaff (*Phylloscopus collybita*, Figs S1b, and S1g), the European Robin (*Erithacus rubecula*, Figs S1d, S1f, S1j, S1o, S1p, S1q, S1s, S1ab, and S1ad), the Eurasian Jay (*Garrulus glandarius*, Figs S1e, S1l, S1r, S1y, S1af, S1ak, S1an, and S1ap Figures), the European Pied Flycatcher (*Ficedula hypoleuca*, S1h, and S1i Figures), the Red Squirrel (*Sciurus vulgaris*, Fig S1m), the Eurasian Blue Tit (*Cyanistes caeruleus*, Figs S1n, and S1am), the Great Tit (*Parus major*, Figs S1t, S1v, S1w, S1aa, S1ac, S1ah, and S1ai), the Common Chaffinch (*Fringilla coelebs*, Figs S1u, S1x, S1ae, S1aj, S1al, S1ao, and S1aq), unidentified rodents (Fig S1z), and the Song Trush (*Turdus philomelos*, Fig S1ar).



S2 Figure. Photographs of larvae found in the study area. From top to bottom, the families, genera, or species are: *Cydalima perspectalis* (non-native species), Geometridae family, Tenthredinidae family (likely of *Caliroa* genus), Tenthredinidae family (likely of *Periclista* genus), *Operopthera brumata*. Scale in cm.

5. Chapitre 4: La variabilité intraspécifique des traits acoustiques des oiseaux affecte-t-elle la performance de l'algorithme BirdNET?

Laura Schillé, Ladislav Ptáček, David Funosas, Michela Busana, Maxime Cauchoix, Bastien Castagneyrol & Luc Barbaro (n.d.) - **Does the intra-specific variability in bird acoustic traits affect BirdNET algorithm performance?** *In prep.*

Abstract

Passive acoustic monitoring is a rapidly growing method in biodiversity conservation and ecosystem dynamics studies. This non-invasive approach enables standardized data collection on a large spatiotemporal scale at a relatively low cost. However, the vast volumes of data generated challenge an optimal analysis, as manual processing requires significant time and a high level of expertise. The development of automated recognition algorithms, such as BirdNET, offers new perspectives for data analysis. Nevertheless, biases remain in BirdNET performance, attributed to technical, abiotic, and biotic factors, which limits its direct and large-scale application in ecological research. A relatively unexplored aspect of those biases is the role of inter- and intra-species variability, especially the variability between individual vocalizations of a given species, in the physical characteristics of bird songs and calls.

Our study aims to evaluate the impact of these physical characteristics of bird sounds, or acoustic traits, on the performance of the BirdNET algorithm. We hypothesize that lower-frequency, lower-intensity, shorter, and simpler vocalizations are less likely to be accurately recognized than longer, louder, higher-pitched, and more complex vocalizations. The latter are less likely to be masked by ambient noise or overlapping vocalizations from other individuals, and more likely to be detected on a longer range within a given sound detection range.

We used a large dataset of 180 one-minute recordings, evaluated both by BirdNET and by an expert ornithologist at the vocalization level. This allowed us to categorize each vocalization according to BirdNET performance indicators: true positives, false negatives, and false positives, and to calculate some acoustic traits (others will be added in a subsequent phase) associated with each vocalization.

For confidence thresholds assigned by BirdNET exceeding 0.8, no false positives were detected. In this case, preliminary analyses revealed that vocalization energy was one of the most important predictors of BirdNET performance. These results suggest that BirdNET is more reliable when birds sing loudly and close to the microphone, provided that only sufficiently high confidence thresholds are considered. However, the length of the vocalization was not a key trait in predicting BirdNET performance.

Several research avenues emerge from this work. First, acoustic traits related to the complexity and frequency of vocalizations should be calculated to enable a more detailed analysis of how the physical characteristics of vocalizations affect BirdNET performance. Additionally, calculating acoustic traits for false positive vocalizations, which has been impossible until now, will allow assessing the impact of these traits across the full range of confidence levels in the context of using BirdNET for research. Specifically, we can differentiate between BirdNET use at the community and the species level. For the latter, we propose to test the hypothesis that the effect of acoustic traits on BirdNET performance varies depending on both the species and the confidence levels considered. This research will help optimize the use of automated recognition tools in studying avian biodiversity, with wider applications in the emerging field of conservation ecoacoustics.

Keywords: Acoustic traits of birds; BirdNET algorithm; Vocalization energy

5.1. Introduction

The ability to produce and perceive sounds encompasses a set of traits that are essential for the eco-evolutionary dynamics of individuals and communities (Conner & Corcoran, 2012; Dooling & Prior, 2017; May-Collado et al., 2007; Nottebohm et al., 1990), making sound environments and features a crucial dimension of biodiversity largely overlooked to date (Depraetere et al., 2012; Gasc et al., 2013; Sueur et al., 2014). Over the past decades, passive acoustic monitoring (PAM) has become a valuable tool for studying soundscapes, encompassing all sounds heard in a given environment. First, PAM can be utilized through soundscape analysis using acoustic indices, which summarize specific characteristics of a soundscape by calculating the physical properties of sound signals. This method provides a non-specific measure of biodiversity (Alcocer et al., 2022; Sugai et al., 2019). Second, by identifying the species present—which can be challenging—PAM can also facilitate the study of various levels of biodiversity, including individuals, populations, and communities, as well as their dynamics (Blumstein et al., 2011; Laiolo, 2010).

PAM is particularly well suited to the study of organisms for which vocal communication plays a major role, such as birds. Bird acoustic monitoring is facilitated by the extensive deployment of autonomous recording units (ARUs) (Shonfield & Bayne, 2017) and by the broad appeal of bird vocalizations to the general public (Xeno-canto, 2024). Unlike the traditional point count method, these technologies offer the advantage of obtaining recordings over larger spatial and temporal scales than before, and generally at a lower cost (K. Darras et al., 2018). The data collected is also standardized and its collection is non-invasive and non-destructive for wildlife (K. Darras et al., 2019; Sugai et al., 2019). The ability to gather acoustic information at regular intervals further aids in analyzing variations in vocal activities of multiple species, opening new perspectives for understanding ecological dynamics, including those of cryptic, nocturnal, and endangered species (Budka et al., 2023; Towsey et al., 2014).

As the acquisition of eco-acoustic data becomes increasingly accessible, ecologists face a significant challenge in processing unprecedented amounts of information (Gibb et al., 2019). Manual analyses, though essential, have intrinsic limitations regarding the volume

of data that can be processed, thus hindering the optimal exploitation of the scientific potential offered by the deployment of ARUs (Wimmer et al., 2013). Data processing requires not only a considerable time investment but also a high taxonomic expertise not always available in research projects (Hofer et al., 2023; Symes et al., 2022). However, the emergence of deep learning techniques opens up promising new perspectives (Manzano-Rubio, 2022). These techniques could particularly address the challenges of analyzing and identifying recordings generated by ARUs without taxonomic skills in acoustic-based species identification (Shonfield & Bayne, 2017). To date, scientists have already developed algorithms for the automated identification of bats (BatDetective, Aodha et al., 2018), wolves and coyotes (Sossover et al., 2024), anurans (FrogID, Rowley & Callaghan, 2020), or birds (BirdNET, Kahl et al., 2021), and are currently developing promising tools for many other taxa including orthopterans, cicadas, wild bees as well as fishes and other marine and freshwater wildlife (Darras et al., 2024). Because of its facility to use, BirdNET is one of the most well-known automatic recognition algorithms. Launched in 2019 by the Cornell Lab of Ornithology (USA) and the Technical University of Chemnitz (Germany), it is based on a deep convolutional neural network trained on annotated bird songs from repositories such as Xeno-Canto (Xeno-canto, 2024) and Macaulay library (Macaulay, 2024). The BirdNet and other algorithms represent great potential for biodiversity monitoring at large geographic and spatial scales, provided they are proven reliable.

Several studies have evaluated the potential of BirdNET (see Pérez-Granados, 2023b for a review), revealing that the algorithm performs well when birds sing close to the microphone (Pérez-Granados, 2023a), and without much background noise (Funosas et al., 2024; Ware et al., 2023). However, caution must be exercised when using BirdNET in scientific contexts, as there are still biases to address when using the algorithm under real field conditions to avoid both false positive and negative identification (Pérez-Granados, 2023b). These biases can be attributed to biotic parameters (e.g., the number of species vocalizing simultaneously), abiotic parameters (e.g., the ambient noise of the recordings), or technical parameters (e.g., the volume of training data available online, BirdNET input values, the type of recording device used, etc.). Although precise analyses of these parameters are still needed, recent studies already addressed some of these issues and identified current limitations in the use of BirdNET for biodiversity research. These

include too short durations of recordings (Cole et al., 2022; Funosas et al., 2024), high levels of ambient noise (see in the supplementary material of this thesis: Barlier, 2024; Funosas et al., 2024), and a too long distance (>50m) between the sound source (a vocalizing bird) and the recorder (Pérez-Granados, 2023a). While the cost of the recorder used may not significantly impact the outcomes (Pérez-Granados, 2023a; Toenies & Rich, 2021), there is a need to be stringent with the confidence threshold used to ensure optimal results (Funosas et al., 2024). Consequently, these authors proposed guidelines for the optimal use of BirdNET, properly synthesized for a larger birding audience in Wood and Kahl (2024).

Another critical consideration in BirdNET performance assessment is the ontogenic, ecological, and geographical variability in bird vocalizations. Indeed, bird vocalizations vary not only among species but also among populations of the same species, and even the same individuals can produce different vocalizations depending on their environment (Farnsworth & Lovette, 2008; Irwin, 1988; Podos & Warren, 2007). Additionally, recordings often include multiple birds of the same or different species with overlapping vocalizations. Isolating these vocalizations remains a major technical challenge (Bermant, 2021), despite the clear interest in studying BirdNET performance in various scientific contexts, from intra-specific to community and soundscape levels, to the mutual benefits of soundscape ecology and ornithological science (Gasc et al., 2017). Studies in behavioral ecoacoustics have demonstrated that when exposed to anthropogenic noise, some individuals of certain species are able to shift their vocalization frequencies to higher pitches (Derryberry et al., 2020; Roca et al., 2016), increase the intensity (Brumm, 2004), amplitude (Nemeth & Brumm, 2010), and duration (Francis et al., 2011) of their vocalizations. Yet, this variability is not only overlooked by the BirdNET algorithm—since incorporating it would require an impractically large amount of training data—but it is also not addressed in studies evaluating BirdNET.

Following the recommendation by Pérez-Granados (2023b) we addressed the effect of the physical characteristics of bird vocalization on the performance of the BirdNET algorithm. We hypothesize that vocalizations with lower frequencies or lower intensity are more likely to be masked by ambient anthropogenic noise than louder ones, and thus less likely to be accurately recognized by the BirdNET algorithm. We also hypothesize that

longer and more complex vocalizations are less likely to overlap with those of other individuals or species and are therefore more likely to be correctly recognized. Finally, we hypothesize that the acoustic indices used in soundscape studies as proxies for overall biodiversity (e.g., Acoustic Entropy Index, Number of Peaks) or the abundance of vocalizing species (e.g., Acoustic Complexity Index, Acoustic Diversity Index, Acoustic Evenness Index) (Fuller et al., 2015; Gasc et al., 2013; Sueur et al., 2014) can be adapted at the scale of individual vocalizations to serve as acoustic traits that may be important for evaluating BirdNET performance.

To address current limitations in the use of acoustic traits in the evaluation of an automated recognition algorithm like BirdNET, we used recordings of each vocalization both manually annotated by an expert ornithologist and analyzed by BirdNET algorithm (see data in Funosas et al., 2024). For each vocalization, we compute a set of acoustic traits based on signal characteristics like frequency, amplitude, energy, or duration. By comparing the annotations of BirdNET with those of the ornithologist, we aim to evaluate the ability of acoustic traits to predict BirdNET performance at the vocalization level. We hypothesize that more complex, shorter vocalizations with lower energy will negatively impact BirdNET performance.

5.2. Material and methods

5.2.1. Data acquisition and manual annotation procedure by an ornithologist

The data used consists of 180 one-minute recordings, collected from 2019 to 2022, and distributed across 60 sites (3 recordings per site) in an ecological research area established by the French research institute CNRS, located in the canton of Aurignac in the Occitanie region of southwestern France (within the Zone Atelier Pyrénées Garonne; Barbaro et al., 2022).

An expert ornithologist (DF) identified and annotated all the recordings by ear using the software Audacity (Audacity Team, 2023). Specifically, he delineated areas corresponding to each bird vocalization with frequency and time boundaries on the spectrogram of each recording and assigned them to a specific species.

5.2.2. Analyses by BirdNET

The recordings were analyzed using BirdNET-Analyzer v.2.4 (Kahl et al., 2021). BirdNET segments recordings into three-second intervals and identifies one or more species associated with each segment, providing a confidence score for each identification. Input parameters for BirdNET were left at default settings except for detection sensitivity, which was increased to 1.5, and overlap values between consecutive segments, which were set to 2 seconds, whereas no overlap is the default setting. These choices were informed by preliminary studies (see Funosas et al., 2024) demonstrating improved BirdNET performance with these settings on this specific dataset. BirdNET was also configured to utilize a list of potentially detectable bird species based on the date and geographic coordinates of the recordings.

5.2.3. Comparison between ornithologist and BirdNET identifications

To compare the manual identifications with those of BirdNET, we first concatenated successive and overlapping BirdNET identifications that corresponded to the same vocalization (Figure 1A and 1B, yellow frames). Specifically, if in a given recording the same bird species was recognized in multiple overlapping 3-second segments, we retained only a single identification for that species. This unique identification spans from the first to the last second the species was detected. We assigned this identification the highest confidence level among those returned by BirdNET for the overlapping 3-second segments where the species was identified (Figure 1A and 1B, yellow frames).

We then compared the new intervals in the concatenated BirdNET file with those identified by the bird expert (Figure 1C, blue frame). Note that bird expert's identifications are always considered the reference, as we assume them to be accurate. If, for a given recording, the time interval containing a species identification by BirdNET overlapped with the time interval of the same species identified by the ornithologist, this BirdNET identification was considered a True Positive (TP) (Figure 1D, green frame). If a species was identified by the ornithologist but not by BirdNET, or not within an overlapping time interval, this identification was considered a False Negative (FN) (Figure 1D, green frame). Finally, if a species was identified by BirdNET but not by the ornithologist in a

given recording, or if it was identified by BirdNET in a non-overlapping interval, this identification was considered a False Positive (FP) (Figure 1D, green frame).

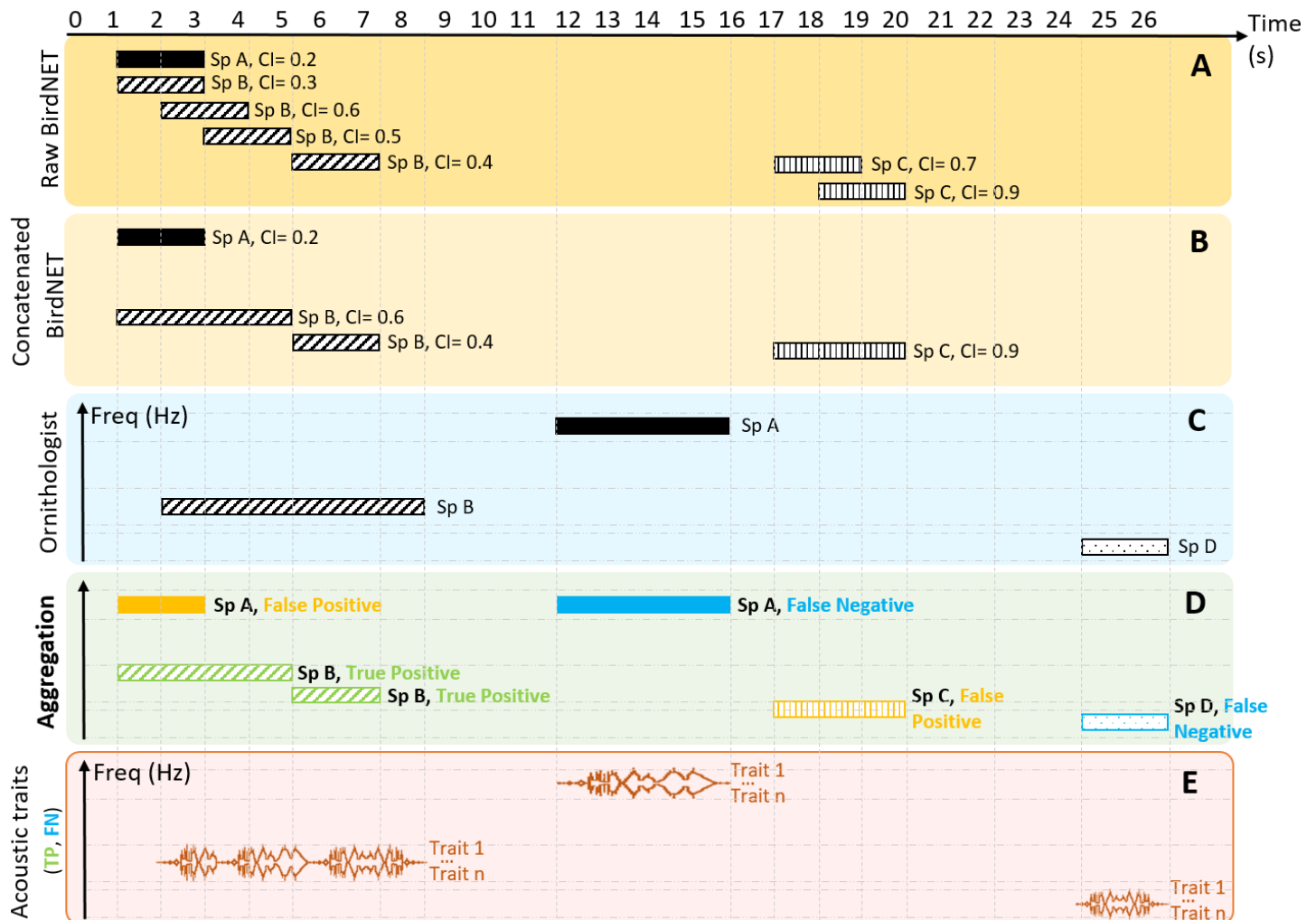


Figure 1. Data aggregation steps. The diagram shows the process for a theoretical individual recording. The yellow frame (A) represents the raw data obtained from BirdNET, which identifies species in 3-second segments with a 2-second overlap. For simplicity, only three species are shown. We combined overlapping identifications of the same species into a single sequence (B, light yellow frame). The blue frame (C) shows the ornithologist's identifications, which vary in duration and are defined by time and frequency ranges. Based on the comparison between BirdNET data and the ornithologist's identifications, we classified each sequence as True Positive, False Positive, or False Negative (D, green frame). In the red frame (E), acoustic traits are calculated for each ornithologist's identification within the corresponding time and frequency ranges. These traits were then associated with BirdNET performance indicators of True Positives and False Negatives.

5.2.4. Calculation of acoustic traits

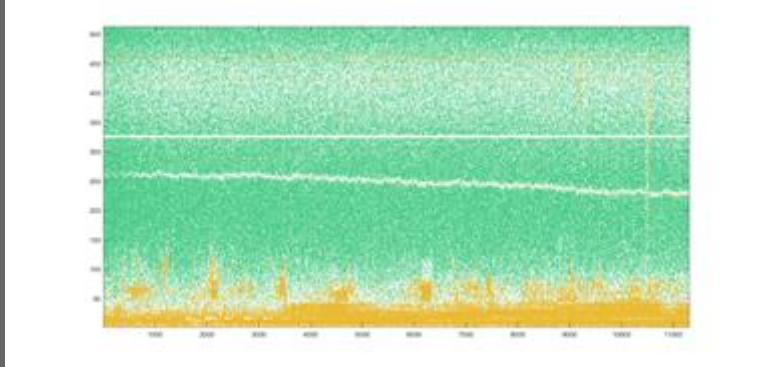
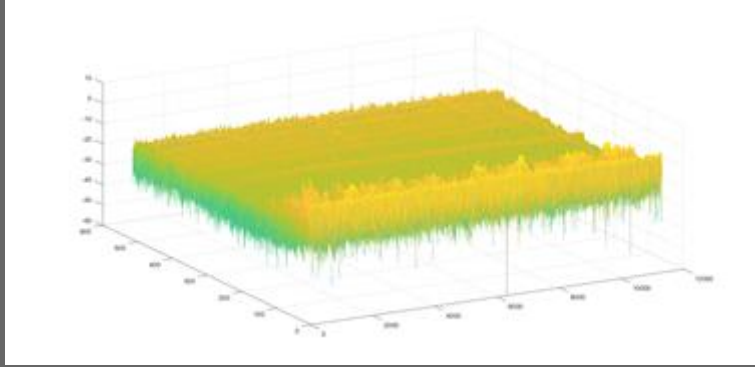
The dataset with manual annotations made by the ornithologist was used to isolate each vocalization within the identified time and frequency ranges. Subsequently, 30 acoustic traits¹ were calculated for each identified vocalization. At the time being, the same procedure could not be applied to the identifications generated by BirdNET. Indeed, while BirdNET identifications are time-bounded, they are not frequency-bounded, making it impossible to calculate acoustic traits without an additional step of isolating the vocalization within a specific frequency range, for example, using the spectrogram². As a consequence, the aforementioned 30 acoustic traits could only be paired with TP and FN BirdNET identifications.

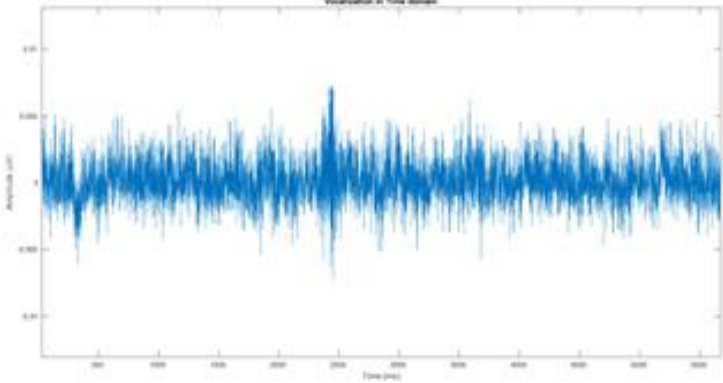
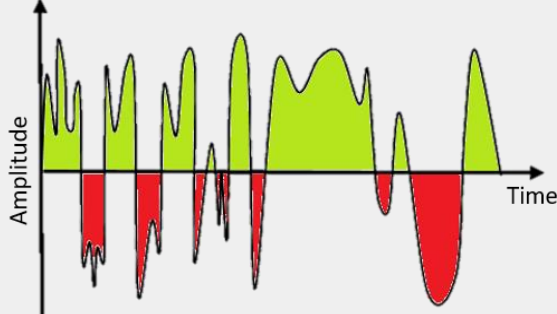
An additional 13 acoustic traits were calculated at the recording level (see Table 1 for a description of the calculated acoustic traits and Fig. 1 for a schematic overview of the traits calculation at the vocalization level). All acoustic traits were calculated by LP, who adapted one of his own codes (Ptacek et al., 2016).

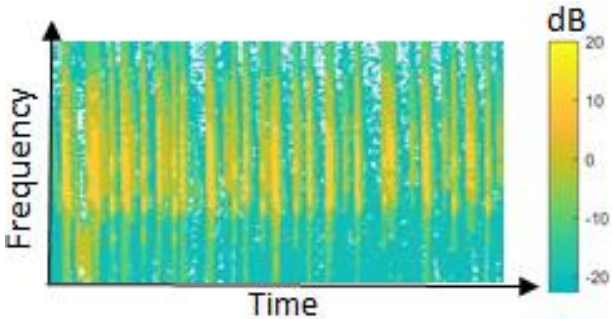
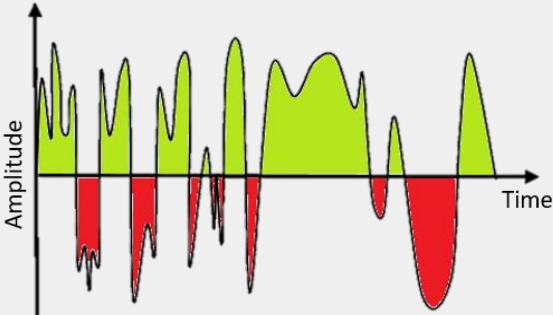
¹Note that in a subsequent processing phase, additional acoustic traits, particularly those related to vocalization complexity (e.g., number of peaks), will be calculated

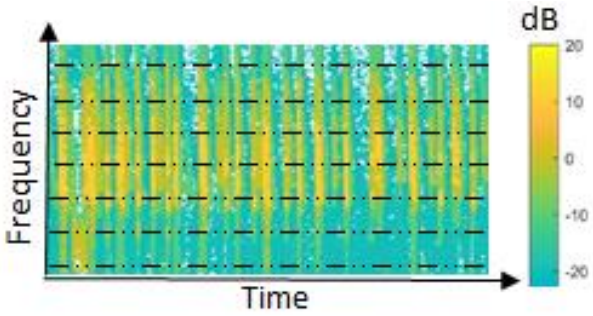
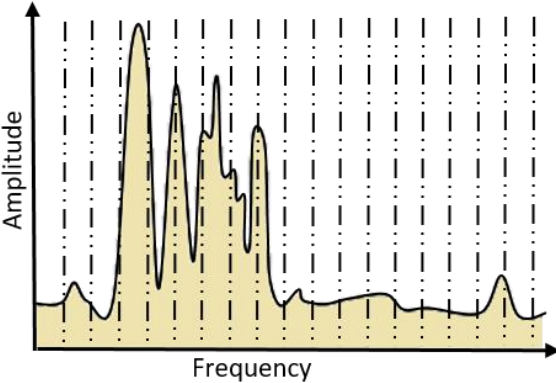
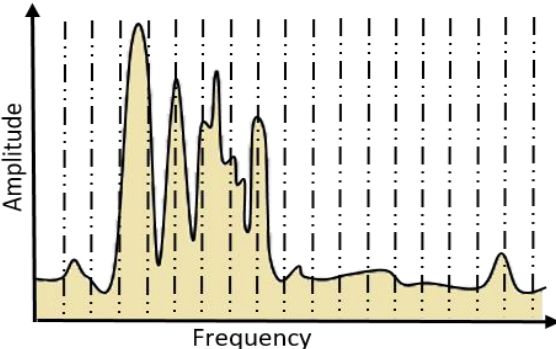

² This step will, however, be feasible in future analyses

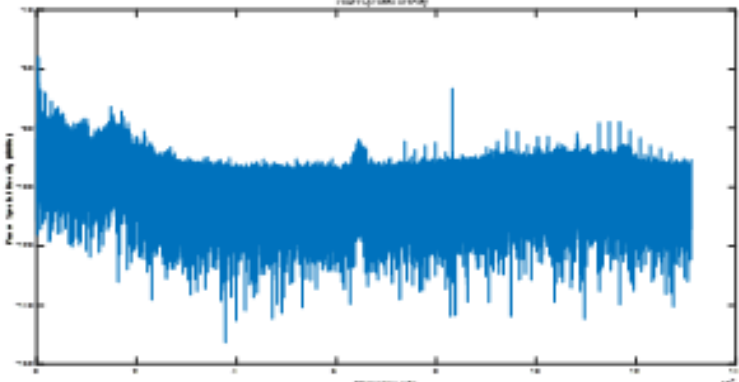
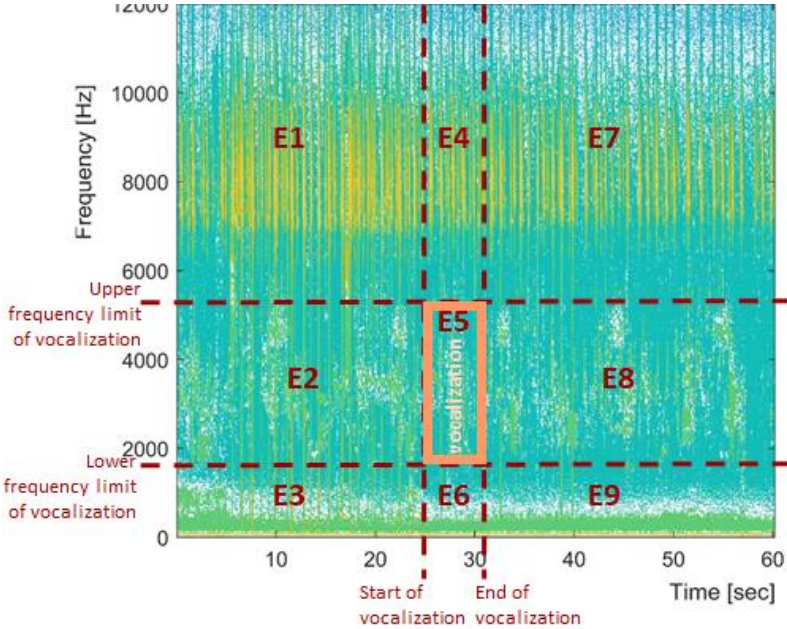
Table 1. Names and definitions of the 43 calculated acoustic traits. In cases where the traits were calculated at the recording level, the cells are shaded grey. If the traits were calculated at the vocalization level, the cells in the table are white. For clarity, the first dark gray row in the table shows a representation of the spectrograms used to better understand how the acoustic traits were calculated.

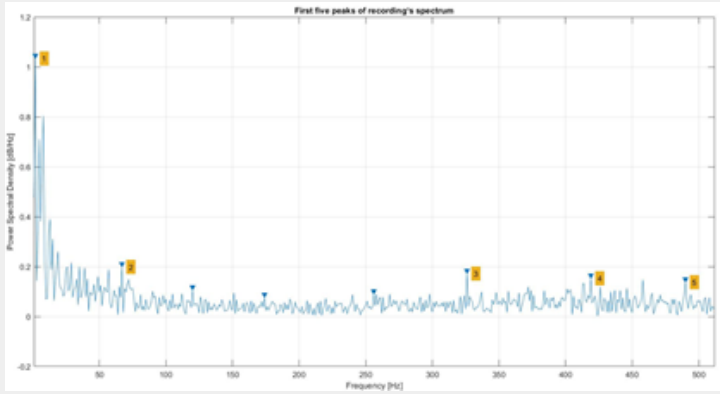
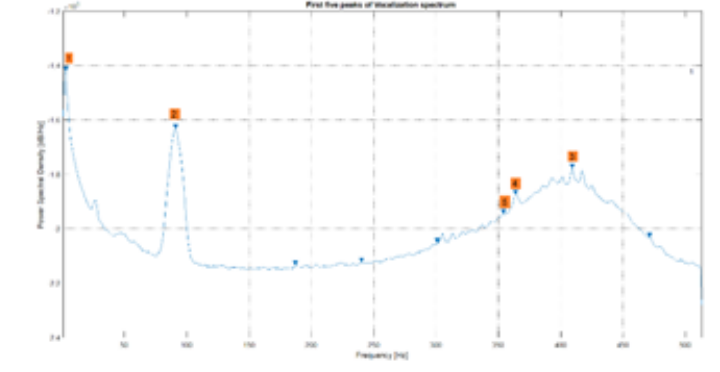
Acoustic Trait	Definition
Spectrogram	<p>Recording or vocalization converted into a frequency domain. 2D or 3D representation can be used. The x-axis represents time, and the y-axis represents frequency.</p> <p>In 2D, the colors express the intensity of a particular frequency for a specific time.</p>  <p>In 3D, the z-axis shows the intensity of a particular frequency for a specific time.</p> 
Vocalization length	<p>Length of the vocalization in seconds.</p> <p>In the time domain, a vocalization is characterized by time (x-axis) and by signal amplitude (y-axis).</p>

	 <p>In the frequency domain, a vocalization is characterized by time and frequency (i.e. Spectrogram) or by frequency and frequency amplitude (frequency components, Fourier transformation).</p> <p>Two or more vocalizations can overlap in time, a phenomenon known as time masking. Additionally, vocalizations can overlap in the frequency band, resulting in frequency masking, which can occur independently of time masking.</p>
Recording length	<p>Length of the recording in seconds.</p> <p>A recording is characterized by time (x-axis) and by amplitude (y-axis).</p>
Energy recording	 <p>The sum of the squares of the absolute values of the signal amplitudes (in red and green on the diagram).</p> $Energy = \sum signal\ amplitudes ^2$

Energy vocalization	 <p>The energy of a vocalization is measured in decibels (dB) and represents the total energy across the vocalization spectrogram, defined by its time and frequency range.</p> <p>Frequency intensity is commonly converted to the decibel scale, a logarithmic scale suited to human hearing. On a linear scale, the graph can be difficult to interpret when peaks are significantly higher than the average values. However, using the dB scale helps to smooth the graph, making it easier to visualize both extremely high and low values.</p>
Energy ratio	Energy Vocalization / Energy Recording
RMS Energy recording	 <p>The square root of the sum of the squares of the absolute values of the signal amplitudes (shown in red and green on the diagram), divided by the signal length.</p> $RMS = \sqrt{\frac{\sum signal\ amplitudes ^2}{signal\ length}}$
RMS Energy vocalization	RMS of Vocalization signal in the time domain
RMS Energy ratio	Energy RMS Vocalization / Energy RMS Recording

<p>Acoustic Complexity Index (ACI)</p>	 <p>It quantifies the sound complexity by estimating the variability of intensities between time samples within a frequency band (Pieretti et al., 2011).</p>
<p>Acoustic Evenness Index (AEI) (vocalization)</p>	 <p>It measures the evenness of the acoustic activity distribution in each 1 kHz band (Sánchez-Giraldo et al., 2021; Villanueva-Rivera et al., 2011).</p>
<p>Acoustic Diversity Index (ADI) (vocalization)</p>	 <p>It is calculated using Shannon's diversity index, applied to the relative proportions of the signal in each 1 kHz frequency band (Sánchez-Giraldo et al., 2021; Villanueva-Rivera et al., 2011).</p>
<p>Acoustic Entropy Index (H)</p>	 <p>It is generated by applying Shannon's diversity index to the</p>

	amplitude envelope (Sueur et al., 2008).
Wiener Entropy	<p>The ratio of the geometric mean of the power spectral density (PSD) to the mean PSD. This is based on the periodogram, which represents the PSD of the vocalization.</p>  <p>The graph is in the frequency domain, with frequency plotted on the x-axis and the power of each frequency component shown on the y-axis.</p>
Spectrum Energy sector E1	 <p>Refer to the section on 'Energy Vocalization' for detailed methods on calculating the spectrogram energy within a specific sector.</p>
Spectrum Energy sector E2	
Spectrum Energy sector E3	
Spectrum Energy sector E4	
Spectrum Energy sector E5	
Spectrum Energy sector E6	
Spectrum Energy sector E7	
Spectrum Energy sector E8	
Spectrum Energy sector E9	

<p>Vocalization energy / band energy</p>	<p>The ratio of energies: $E = \frac{E5}{E2+E5+E8}$</p> <p>It refers to the strength of the vocalization relative to the total vocalization energy within the same frequency band over the vocalization time period.</p>
<p>Vocalization energy / total energy</p>	<p>Ratio of energies: $E = \frac{E5}{E1+E2+E3+E4+E5+E6+E7+E8+E9}$</p> <p>It refers to the strength of the vocalization relative to the total recording energy during the vocalization time period.</p>
<p>Peak 1 to 5 Recording [Hz]</p>	<p>The first five peaks of the recording spectrum. For each detected peak, both the frequency and level were calculated. We limited the analysis to the five most significant peaks.</p>
<p>Peak 1 to 5 Recording [level]</p>	<p>Note that these values are calculated for the entire recording, making them consistent across all vocalizations within that particular recording.</p> 
<p>Peak 1 to 5 Vocalization [Hz]</p>	<p>The first five peaks of the vocalization spectrum. For each detected peak, both the frequency and level were calculated.</p>
<p>Peak 1 to 5 Vocalization [level]</p>	<p>Although in the picture, nine peaks were detected, we limited the analysis to the five most significant ones.</p> 

5.2.5. Analyses

All analyses were performed in R (R Core Team, 2021).

As a preliminary analysis, we used Random Forest (RF) models (*randomForest* package, Cutler & Wiener, 2022) to evaluate the relative importance of acoustic traits in predicting performance indicators, namely TP, FN, and FP, for each confidence threshold set by BirdNET. An RF model is a supervised learning algorithm that, in our case, uses the entire set of calculated acoustic traits to generate decision trees and classify each vocalization into a performance category (TP, FN, FP). The algorithm then aggregates all the decision trees to improve model accuracy.

For this chapter, we decided to perform a single RF analysis, using only the identifications with a BirdNET confidence threshold above 0.8 as the response variable. This threshold was selected because, at confidence levels above 0.8, no vocalizations are classified as FP. Therefore, the lack of acoustic traits for this category does not impact the analysis. The 43 calculated acoustic traits for each TP and FN vocalization were used as explanatory variables in the model.

Because we missed the values of the ratio between vocalization energy and total energy for 20 vocalizations, we used a statistical imputation method based on Random Forest regression trees (*missForest* package, Stekhoven, 2022), to generate estimates for those missing values using information from the existing data.

We used cross-validation to assess model performance. Specifically, we randomly split the complete datasets into training (50%) and testing (50%) sets, with each sub-dataset containing 1,140 vocalizations. We trained an RF model on the training set, configuring it to build 500 decision trees. To evaluate model performance, we applied the trained model to the testing set and compared the predicted classifications with the actual classifications from this set. This comparison was summarized in a confusion matrix, which allowed us to measure the model's accuracy, sensitivity (true positive rate of RF), and specificity (true negative rate of RF). The use of the testing set, which was not involved in the training process, ensured that these metrics reflected the RF model's ability to generalize to new data. Additionally, we extracted variable importance measures from the RF model, specifically the mean decrease in accuracy and the mean decrease in Gini index, to identify

the acoustic traits that contributed most significantly to the RF model's performance and thus were the most influential in predicting BirdNET's performance.

We then extracted the most important acoustic traits, specifically all traits before the inflection point on the mean decrease accuracy and mean decrease Gini curves of the RF model. Subsequently, we generated dot plots with summary statistics for all these traits against the two performance indicators to understand the direction of the effects.

5.3. Results

When predicting the performance of BirdNET identifications with a confidence threshold above 0.8, the RF model results showed excellent accuracy of 97.46% (Confidence Interval: 96.37% - 98.29%) for assessing performance indicators TP and FN. Note that there were no more FP above this confidence threshold. There was a statistically significant difference between the model predictions and the true values (McNemar's test: $P < 0.001$). Although the model sensitivity was very high at 99.73%, the specificity was relatively low at 36.59%, indicating that the model is very good at detecting FN but less effective at detecting TP. The Kappa coefficient of 0.5 reflects a moderate agreement between the predictions and the actual observations (Table S1).

The outcomes of the RF model indicate which traits cause BirdNET to make errors, especially when it fails to detect species that are actually present in a given spectrogram. The *ratio between vocalization energy and total energy*, the *energy of the signal immediately preceding the vocalization (sector E2)*, the *energy of the vocalization*, and the *ratio between vocalization energy and band energy* stood out as the most influential acoustic traits in predicting the model performance, positively affecting both the accuracy (mean decrease accuracy, Fig. 2a) and the nodes purity (mean decrease Gini, Fig. 2b) in decision trees.

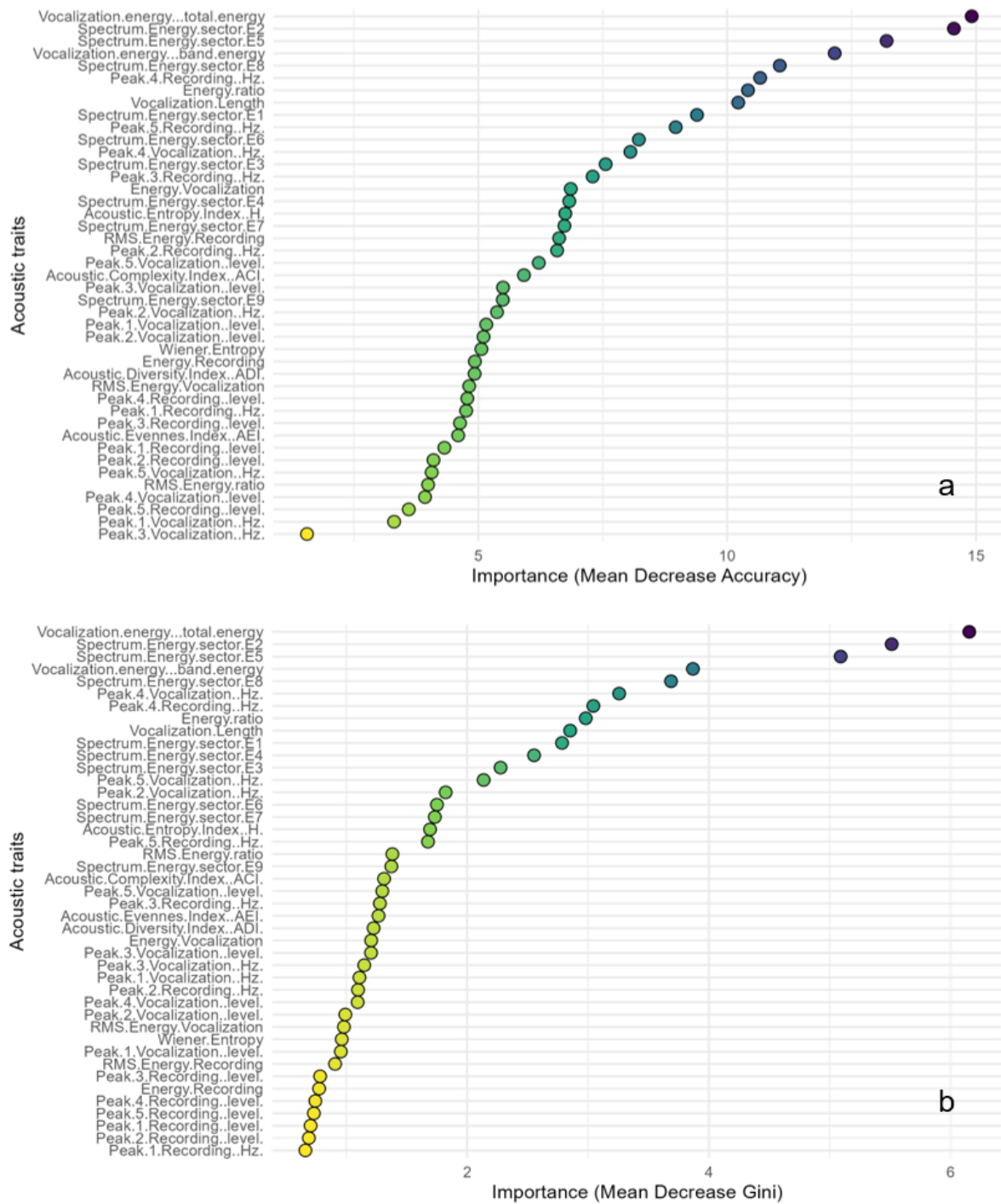


Figure 2. Importance of acoustic traits in BirdNET performance for a confidence threshold above 0.8 according to the mean decrease accuracy (a) and to the mean decrease Gini (b)

For confidence thresholds greater than 0.8, TP identifications were associated with higher values of absolute vocalization energy (*energy of the vocalization*) and relative vocalization energy (*ratio between vocalization energy and total energy and ratio between vocalization energy and band energy*) than FN identifications (Fig.3).

BirdNET was mostly capable of correct identifications when the levels of absolute and relative vocalization energies were high, while the ornithologist was consistent and capable of identifying birds even when the energy of their vocalizations were low. However, there were nearly as many TP as FN when the *energy of the signal immediately preceding the vocalization (sector E2)* was strong (Fig. 3).

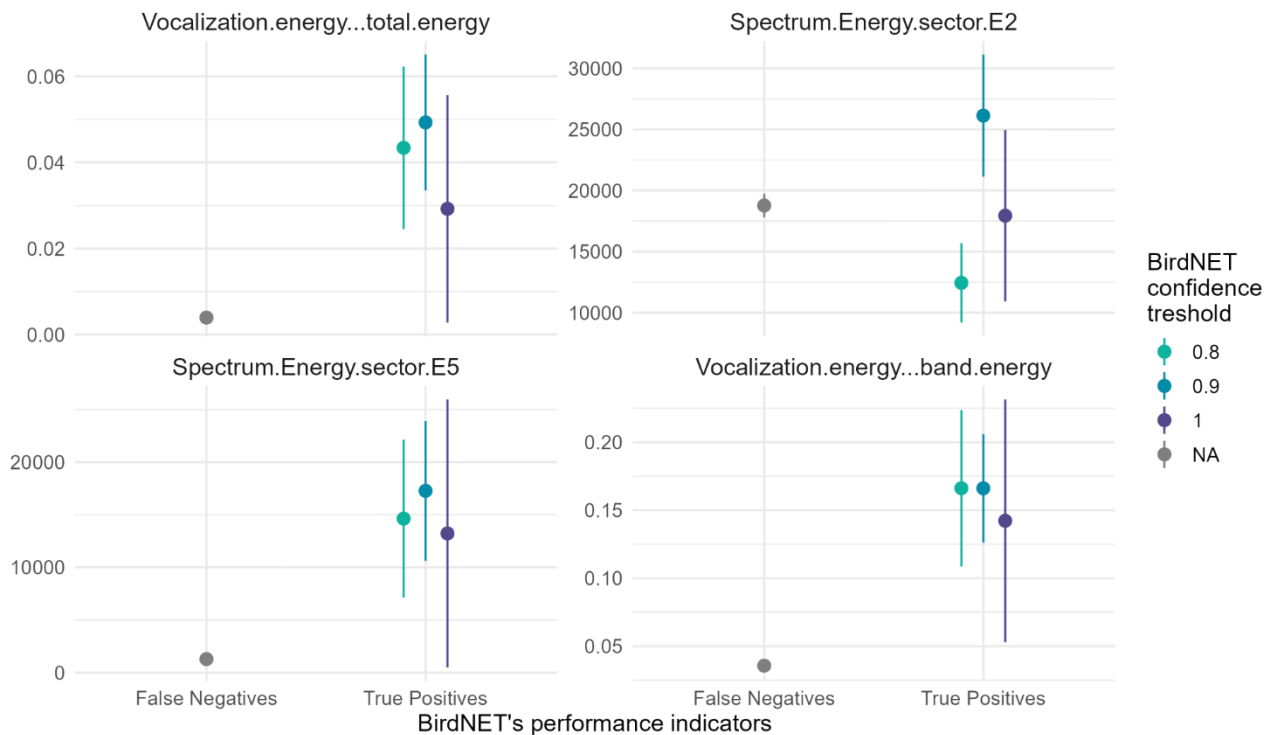


Figure 3. Abundance of False Negative and True Positive identifications according to the acoustic traits selected by the Random Forest model for a confidence threshold above 0.8 assigned by BirdNET.

5.4. Discussion

BirdNET is a promising tool for identifying bird species and communities by enabling the processing of large volumes of recordings generated through passive acoustic monitoring. Our preliminary analyses evaluating the performance of the BirdNET algorithm in identifying bird species highlight the importance of considering some acoustic traits at the vocalization level, such as energy. We can furthermore derive numerous future analytical perspectives from this work. The methodological approach we propose opens new opportunities for evaluating the factors that influence BirdNET performance and for potentially developing guidelines to improve its use in ecological research.

To our knowledge, this is the first study to assess the potential impact of vocalization acoustic traits on BirdNET performance. Consequently, direct comparisons with other studies are not possible, but we can relate our findings to those using different approaches to assess the algorithm. Using Random Forest models, we analyzed identifications for which the BirdNET confidence threshold exceeded 0.8, a level at which no false positives remained in our dataset. The analysis identified key acoustic traits that significantly contributed to predicting the performance indicators, True Positives (TP) and False Negatives (FN). These traits included the energy of the vocalization compared to the energy of the whole recording, the energy of the vocalization itself, the energy of the vocalization over the vocalization time period, and the energy of the signal immediately preceding the vocalization. The high energy of the vocalization, although not directly tested on BirdNET, has already been proven to be a factor enabling the validation of automatic species identification from acoustic recordings (Knight et al., 2020). This implies that an individual singing loudly or close to the microphone is more likely to be accurately recognized by BirdNET with a high confidence threshold. Conversely, although several studies have shown that BirdNET requires long recording periods to match an ornithologist's accuracy (Cole et al., 2022; Funosas et al., 2024; Toenies & Rich, 2021; Wood et al., 2021), our analysis showed that the length of the vocalization itself is not a key trait in predicting TP and FN rates at confidence thresholds above 0.8. It will therefore be valuable to investigate whether this trait becomes important for predicting FP compared to TP at lower confidence levels.

Our results showed that BirdNET is more efficient for high levels of vocalization energy while the ornithologist was fairly consistent in identifying birds regardless of the strength of the energy-related acoustic traits studied. This can be explained by the fact that naturalists typically do not rely on acoustic traits such as energy to identify species, but rather on the rhythm of each song (Emlen, 1972; Roeske et al., 2020). In contrast, our analysis showed that the impact of acoustic traits on BirdNET performance varies slightly across the three confidence levels considered (0.8, 0.9, and 1). This variation could become more pronounced across the full range of BirdNET confidence levels (from 0.1 to 1). These findings, along with those from Cole et al. (2022), Funosas et al. (2024), Singer et al. (2024), and Wood & Kahl (2024) would emphasize the need to be particularly

rigorous when selecting the confidence threshold in BirdNET, as these levels directly influence the presence of False Positive identifications (FP). The cited studies further advocate for adjusting the confidence thresholds for each species considered.

Our next step will be to isolate FP vocalizations within specific frequency bands through spectrogram analysis, followed by calculating the acoustic traits of these FP, which we currently do not have. As previously mentioned, this approach will enable us to evaluate the relationship between BirdNET performance and acoustic traits at various confidence thresholds. Specifically, by analyzing how and which acoustic traits influence the relative proportions of TP, FN, and FP across confidence levels, we aim to identify specific traits that enhance TP rates relative to FN above certain confidence thresholds. Such findings would indicate that these traits are crucial for reducing FN, albeit potentially less effective in minimizing FP, especially at lower confidence levels. In community-based applications of BirdNET, this suggests the need for data filtering at an optimized confidence threshold, which could be determined based on specific acoustic traits. These traits would point out when both FP and FN rates become acceptably low relative to TP across all vocalizations in a given environmental context. This method could significantly enhance the accuracy and reliability of acoustic biodiversity assessments using automated recognition systems. Moreover, as most ecoacoustic studies on bird communities now rely on both automated identifications by AI algorithms and by one or several bird experts conducted independently (Seibold et al., 2024; Sethi et al., 2024; Shaw et al., 2021), it is worth exploring what exactly drives the FP rate in a given acoustic dataset to improve further comparisons between current and future large-scale studies.

Another, even more reliable approach for implementing BirdNET in ecology would involve adopting a species-specific strategy (Singer et al., 2024; Wood & Kahl, 2024). In a subsequent analysis, we propose to test the hypothesis that the effect of acoustic traits on BirdNET performance varies jointly according to the species and confidence levels considered. For instance, species with high-energy vocalizations, such as the Common Blackbird (*Turdus merula*), might be reliably detected at lower confidence thresholds compared to those with less energetic songs. This would be particularly interesting since species with far-reaching, high-energy songs are also those whose abundances are likely to be overestimated by traditional point counts (Nabias et al., 2024). This variability in

detection related to acoustic traits would then reinforce the idea of adapting BirdNET confidence thresholds based on species-specific acoustic traits, thus providing other guidelines for more effective use of this algorithm in large-scale studies (Darras et al., 2024; Sethi et al., 2024).

One of the other future directions of our work is the calculation of additional acoustic traits reflecting the frequency or complexity of vocalizations for further analyses. These additional traits based on sound frequency and complexity (i.e. short-term variation in amplitude and frequency) are likely to better reflect inter-specific differences than traits related to vocalization energy used here, making analyses of how bird acoustic traits affect overall BirdNET performance easier. Yet, several studies have shown that BirdNET precision and recall values vary greatly depending on the species (Funosas et al., 2024; Singer et al., 2024; Wood et al., 2022). However, this variability might not be solely due to differences in BirdNET training between species (Funosas et al., 2024) or to species abundance in the study area (Singer et al., 2024), but also intrinsically related to their vocal traits, such as signal complexity or its average frequency. If this hypothesis is confirmed, it could open new avenues for species identification based on common acoustic traits of bird vocalizations rather than taxonomic-only information, which is in constant progress worldwide (Sangster, 2009) and reveals more and more the existence of cryptic bird species based on vocalization differences, even in well-known and widespread European species (Pavia et al., 2021).

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Supplementary material

Table S1. Confusion matrix and statistics of the Random Forest model of BirdNET performance for a confidence threshold above 0.8. The response variable included only True Positives, and False Negatives because there were no False Positives for this confidence threshold.

		Reference	
		FN	TP
Prediction	FN	1096	26
	TP	3	15
Accuracy		0.9746	
95% CI		(0.9637, 0.9829)	
No Information Rate		0.964	
P-Value [Acc > NIR]		0.02892	
Kappa		0.4974	
McNemar's Test P-Value		4.402e-05	
Sensitivity		0.9973	
Specificity		0.3659	
Pos Pred Value		0.9768	
Neg Pred Value		0.8333	
Prevalence		0.9640	
Detection Rate		0.9614	
Detection Prevalence		0.9842	
Balanced Accuracy		0.6816	
'Positive' Class		FN	

6. Discussion

Les deux premiers chapitres de cette thèse ont mis en évidence une corrélation positive entre la diversité des oiseaux insectivores et les températures moyennes annuelles, et une corrélation négative entre la diversité des oiseaux insectivores et l'urbanisation, conformément à la théorie (Devictor et al., 2008; Rigal et al., 2023). Pour autant, nous n'avons pas trouvé d'effet significatif de ces modifications des communautés d'oiseaux sur les cascades trophiques qu'ils initient. Par ailleurs, dans ces deux chapitres, les facteurs locaux, tels que la surface d'habitat forestier disponible et la diversité spécifique des arbres, étaient plus pertinents pour expliquer la relation entre la diversité et la fonction d'insectivorie des assemblages d'oiseaux que les températures moyennes et l'urbanisation. Ainsi, l'ensemble de ces facteurs sont susceptibles d'agir à des échelles hiérarchiquement emboîtées sur la biodiversité tant taxonomique que fonctionnelle et doivent être considérés de façon synergique, et ce, quelle que soit l'étendue de l'étude, de la ville au continent.

Les deux premiers chapitres ont aussi montré que les diversités taxonomique et fonctionnelle des oiseaux insectivores sont des facteurs essentiels à considérer dans les études des cascades tri-trophiques impliquant les arbres, les insectes herbivores et leurs ennemis naturels. Néanmoins, nos capacités à inférer les mécanismes impliqués dans ces deux chapitres sont limitées par les approches acoustiques employées qui, si elles ont permis un échantillonnage standardisé des communautés d'oiseaux insectivores à l'échelle européenne (voir chapitre 1), ne permettent pas de caractériser directement l'abondance des individus et leur activité de recherche alimentaire, notamment pour les espèces jouant un rôle important dans la prédation des herbivores. De plus, une compréhension plus fine de ces interactions écologiques complexes nécessiterait la caractérisation de la composition des communautés de prédateurs arthropodes potentiellement impliqués.

Pour étudier les communautés d'oiseaux insectivores et leur rôle dans la prédation à large échelle, nous nous sommes appuyés sur des méthodes encore en développement, nous plaçant ainsi à la frontière des savoirs établis au moment où cette thèse a débuté. Nous avons ainsi employé la méthode des leurres en pâte à modeler pour évaluer les taux de prédation, l'acoustique passive pour échantillonner les oiseaux insectivores, et nous avons envisagé d'utiliser les algorithmes de reconnaissance automatisée pour

caractériser la structure de leurs communautés. Conscients de l'importance de la validité de ces méthodes pour obtenir des résultats fiables, nous avons également contribué à leur évaluation afin de déterminer leurs avantages et leurs limites, à l'issue de ce travail de thèse. Le troisième chapitre de cette thèse a ainsi montré qu'en l'absence actuelle de technologies plus performantes pour évaluer les biais inhérents à l'utilisation des leurres en pâte à modeler et pour quantifier plus précisément la prédation, il est plus simple, économique, éthique et tout aussi fiable de continuer à utiliser ces leurres plutôt que de vraies chenilles. Enfin, bien que l'algorithme de reconnaissance automatisé BirdNET soit prometteur, son utilisation systématique sur de larges jeux de données acoustiques acquis par capteurs autonomes passifs demande des ajustements méthodologiques avant de pouvoir être appliquée à grande échelle à des problématiques de recherche en écologie. Des études complémentaires sont par exemple encore nécessaires pour comprendre comment les facteurs biotiques, abiotiques et techniques peuvent influencer les performances de BirdNET.

Dans les paragraphes ci-après, nous explorerons les perspectives ouvertes par ce travail de thèse. Nous nous concentrerons sur quatre axes principaux : deux pistes de recherche en écologie fonctionnelle et des communautés visant à approfondir les interrogations soulevées par les deux premiers chapitres, ainsi que deux pistes de réflexions à visée plus méthodologique transversales aux quatre chapitres.

6.1. Vers une compréhension détaillée des cascades trophiques par la caractérisation de l'ensemble des niveaux trophiques impliqués

La théorie prédit qu'il existe une relation positive entre la diversité des communautés et leurs fonctions écosystémiques (Philpott et al., 2009; van Bael et al., 2008). Cependant, les résultats expérimentaux des deux premiers chapitres de cette thèse montrent le contraire. Nous avons mis en évidence une corrélation négative entre la richesse fonctionnelle des oiseaux insectivores et les taux de prédation pour les sites européens (chapitre 1), avec des taux de prédation plus faibles aux climats les plus chauds. Dans la ville de Montréal, aucune corrélation n'a été constatée entre la diversité des oiseaux insectivores et les taux de prédation ou l'herbivorie. Dans les deux études, l'abondance et

l'activité de certaines espèces d'oiseaux insectivores consommant préférentiellement des larves de lépidoptères et qui s'en servent pour nourrir leurs jeunes, telles que la Mésange bleue (*Cyanistes caeruleus*), la Mésange charbonnière (*Parus major*), ou la Mésange à tête noire d'Amérique du Nord (*Poecile atricapillus*) pourraient être de meilleurs prédicteurs de l'activité de prédation que la diversité globale des oiseaux insectivores. Bien que l'augmentation des températures et l'urbanisation puissent avoir des effets négatifs sur la diversité des communautés d'oiseaux, ces facteurs ne réduisent pas nécessairement l'abondance de l'ensemble des espèces (Chamberlain et al., 2017; Julliard et al., 2006). On peut ainsi s'attendre à des phénomènes de compensation fonctionnelle où la fonction de prédation reste inchangée malgré la modification de la structure de la communauté, car certaines espèces remplacent les fonctions d'autres espèces. Les mésanges, en particulier, sont des espèces omnivores et généralistes, présentes dans des habitats très différents et capables de s'adapter à des environnements fortement anthropisés (Jokimäki et al., 2016; Julliard et al., 2006; Senar et al., 2021; Sinkovics et al., 2021). Par conséquent, connaître l'abondance de ces espèces pourrait permettre une compréhension plus fine des effets des dérèglements climatiques et de l'urbanisation sur la relation entre la composition des communautés d'oiseaux et les interactions trophiques qu'elles initient.

La quantification de l'abondance des espèces d'oiseaux et leur contribution en termes de service de régulation présente de nombreuses contraintes. Les points d'écoute traditionnellement réalisés sur le terrain sont une solution, bien qu'ils ne fournissent pas toujours une mesure absolue de l'abondance, même s'ils peuvent s'en approcher notamment par des méthodes tenant compte des variations dans la probabilité de détection des individus (Hierarchical Distance Sampling, Nabias et al., 2024). Cependant, les observations générées par les points d'écoute peuvent manquer de reproductibilité lorsqu'elles sont effectuées par différents ornithologues et différents protocoles (Fuller & Langslow, 1984; Nichols et al., 2000), rendant difficile l'obtention de données standardisées à large échelle. Plusieurs études ont utilisé une ou des unités d'enregistrements autonomes pour estimer des densités ou des abondances d'oiseaux par diverses méthodes (voir la revue de Pérez-Granados & Traba, 2021). Une approche courante consiste à utiliser les fréquences d'occurrence des vocalisations de chaque espèce comme *proxy* de leur abondance (voir chapitre 2). Si cette méthode constitue une mesure de l'activité vocale des espèces, le nombre de vocalisations varie aussi en fonction

de l'heure de la journée, des conditions météorologiques ou de la territorialité des espèces, rendant l'estimation de l'abondance réelle particulièrement complexe. Une autre approche, prometteuse mais nécessitant des moyens techniques importants et des connaissances approfondies en physique, consiste à déployer des réseaux de microphones dispersés dans l'espace. Ces réseaux permettent de localiser les oiseaux qui vocalisent en se basant sur le décalage temporel d'arrivée des signaux aux différents microphones (Dawson & Efford, 2009; Pérez-Granados & Traba, 2021). BirdNET pourrait également permettre d'identifier l'activité vocale (un indicateur potentiel de l'abondance réelle) des individus de chaque espèce pour lesquels l'algorithme est suffisamment entraîné, en particulier celles dont les traits vocaux sont bien reconnus, et à condition de définir pour chacune de ces espèces un seuil de confiance optimal défini au préalable (Funosas et al., 2024; Knight et al., 2017). Enfin, plusieurs auteurs ont développé des algorithmes de reconnaissance automatisée spécifiques à certaines espèces, souvent dans un cadre d'écologie de la conservation. C'est par exemple le cas pour le Merle à ventre roux (*Turdus rufiventris*) (Souza Filho et al., 2014), le Vanneau téro (*Vanellus chilensis lampronotus*) (Ganchev et al., 2015), le Piauhaus hurleur (*Lipaugus vociferans*) (Ulloa et al., 2016) ou encore le Butor étoilé (*Botaurus stellaris*) (Frommolt & Tauchert, 2014). Si les espèces ciblées par ces algorithmes jouaient un rôle majeur dans la prédation des herbivores, ces outils pourraient s'avérer particulièrement utiles pour quantifier leurs abondances, offrant potentiellement une meilleure efficacité que les algorithmes généralistes (Priyadarshani et al., 2018).

La relation positive observée dans le chapitre 1 entre la richesse fonctionnelle des oiseaux insectivores et les températures pourrait aussi s'expliquer par une plus grande disponibilité de proies dans les climats chauds (Kissling et al., 2012). La corrélation négative entre la richesse fonctionnelle et les taux de prédation pourrait ainsi refléter un phénomène de dilution des ressources, les populations de prédateurs réagissant aux fluctuations des populations de proies. Tester cette hypothèse nécessiterait un échantillonnage des proies réelles afin d'estimer leur densité en fonction des sites étudiés. Si quelques exemples existent le long de gradients altitudinaux ou avec des prédateurs et des proies arthropodes (Mottl et al., 2020; Sam et al., 2017), peu d'études semblent avoir exploré le lien entre la diversité des oiseaux prédateurs, leur fonction de prédation, et les abondances de leurs proies herbivores le long de gradients climatiques (mais voir

Barbaro et al., 2019). Pourtant, la caractérisation du niveau trophique des herbivores aiderait non seulement à élucider les effets des changements globaux sur les communautés d'insectes herbivores elles-mêmes mais aussi sur les interactions biotiques dans lesquelles elles sont impliquées au sein des cascades trophiques.

Les résultats du chapitre 2 ont montré que les communautés d'oiseaux étaient moins diversifiées dans les zones les plus urbanisées, sans que cela ne modifie significativement la pression de prédation ou l'herbivorie. Cela soulève des questions sur l'abondance et la répartition des insectes herbivores dans les paysages urbanisés. Des études empiriques suggèrent que l'abondance des insectes herbivores ravageurs devrait être plus élevée dans les zones fortement urbanisées, bien que cette tendance varie considérablement selon les groupes taxonomiques considérés (voir la revue de Raupp et al., 2010). Couplé à la diminution de la diversité des oiseaux urbains (Matuoka et al., 2020), cette distribution devrait théoriquement entraîner une réduction de la pression de prédation le long des gradients d'urbanisation (Fig. 1a). Cependant, nos résultats montrent une stabilité des taux de prédation le long de ce gradient, contrastant avec nos prédictions. Cette divergence pourrait s'expliquer par les méthodologies employées pour quantifier les taux de prédation qui pourraient ne pas être appropriées (Fig. 1b). A l'inverse, le long du gradient d'urbanisation, il est possible que les zones très imperméables des centres-villes présentent à la fois une faible diversité d'oiseaux et une faible densité de proies herbivores, conduisant à des taux de prédation relativement identiques à ceux observés dans les zones présentant une plus grande diversité de prédateurs et densité de proies (Fig. 1c).

La constance des taux d'herbivorie le long du gradient urbain peut aussi s'expliquer par plusieurs facteurs. Tout d'abord, la diversité des essences d'arbres échantillonnées, en raison des contraintes de disponibilité sur les sites d'étude, limite la comparabilité des résultats. De plus, la technique d'exclusion des prédateurs utilisée présente certaines limites. Les filets ont ainsi parfois été arrachés, et des maillages trop serrés ont pu entraîner la mort de certaines feuilles, réduisant ainsi la taille de l'échantillon (Fig. 1b). La présence accrue d'arbres ornementaux non indigènes dans les centres urbains, comme le *Ginkgo biloba*, pourrait influencer la distribution des herbivores natifs. Ces arbres exotiques sont souvent moins sujets à l'herbivorie (Lin et al., 2022), car leurs herbivores

spécialistes d'origine sont absents en Amérique du Nord, conformément à l'hypothèse de la libération des ennemis (*Enemy release hypothesis*, Keane & Crawley, 2002). La faible densité d'herbivores sur les arbres non indigènes pourrait ainsi expliquer la réduction globale de l'herbivorie observée et, par conséquent, la moindre efficacité du biocontrôle le long du gradient d'urbanisation. Enfin, que ce soit le long de gradients climatiques ou urbains, nos résultats sur l'herbivorie ne devraient pas être généralisés, car notre étude s'est uniquement concentrée sur les insectes défoliateurs, omettant ainsi certains herbivores comme les insectes piqueurs-suceurs, qui peuvent pourtant aussi nuire à la santé des arbres (Parsons et al., 2020).

La divergence observée entre les taux de prédation mesurés par les leurres en pâte à modeler et ceux déduits des différences d'herbivorie entre branches témoins et branches excluant les oiseaux pourrait être élucidée par un échantillonnage direct des communautés d'arthropodes. Cette approche permettrait d'évaluer l'importance de la prédation intragilde dans les cascades trophiques. En milieu urbain, les arthropodes seraient les principaux prédateurs des insectes herbivores (Long & Frank, 2020). Or, les oiseaux insectivores consomment aussi des araignées et des fourmis prédatrices d'insectes herbivores (Gunnarsson, 2007; Mooney & Linhart, 2006). Ainsi, les oiseaux peuvent être considérés comme des consommateurs tertiaires, régulant les prédateurs des herbivores (Mooney et al., 2010; Polis & Holt, 1992, Fig. 1d). Pour quantifier l'effet relatif des oiseaux et arthropodes prédateurs sur les niveaux d'herbivorie, des dispositifs d'exclusion sélective peuvent être mis en place (Mooney et al., 2010). Ces dispositifs, associés à l'échantillonnage des densités et des diversités des arthropodes prédateurs, permettraient de mieux appréhender les interactions multiples qui façonnent la dynamique des écosystèmes en milieu urbain et ailleurs.

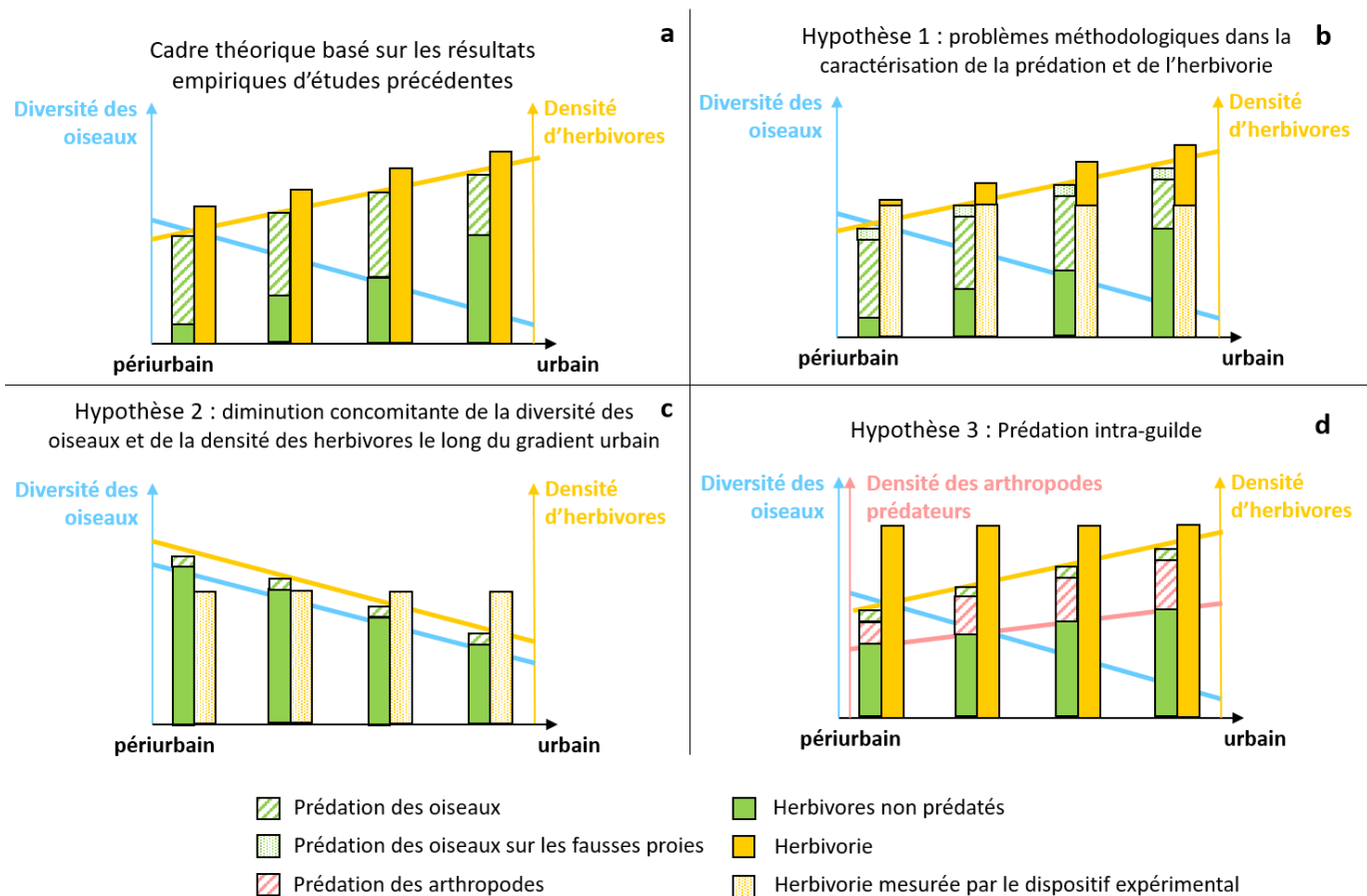


Figure 1. Effets de l'urbanisation sur les communautés d'oiseaux et conséquences pour le service de régulation. Les schémas proposent un cadre théorique construit sur des bases empiriques à partir d'études précédentes et du chapitre 2, expliquant la distribution des communautés d'oiseaux et herbivores le long d'un gradient d'urbanisation et ses conséquences fonctionnels. Dans le cas du schéma (a), conformément aux résultats empiriques des études précédentes, la diversité des oiseaux insectivores diminue en ville alors que la densité des insectes herbivores augmente entraînant une diminution de la prédation et une augmentation de l'herbivorie dans les zones les plus urbanisées. Les schémas (b), (c), et (d) sont trois graphiques théoriques représentant trois hypothèses possibles pour expliquer les résultats du chapitre 2, à savoir la constance des taux de prédation et d'herbivorie le long du gradient urbain malgré la diminution de la diversité des oiseaux insectivores le long de ce même gradient. Soit les méthodes utilisées pour quantifier la prédation et l'herbivorie ne sont pas appropriées (b); soit la densité des proies herbivores diminuent de manière concomitante avec la diversité des oiseaux insectivores, ce qui génère des taux de prédation constants (mais ce qui n'explique pas la constance des taux d'herbivorie) (c); soit la prédation intraguilde augmente le long du gradient urbain mais la prédation des oiseaux sur les herbivores reste constante (d). Dans les trois cas, l'échantillonnage des communautés arthropodes herbivores et prédateurs pourrait permettre de démêler les interactions complexes au sein de la cascade trophique.

6.2. Quelles sont réellement les espèces d'oiseaux qualifiées d'ennemies naturelles et sont-elles différentes selon les habitats considérés?

Dans les deux premiers chapitres de cette thèse, nous avons adopté l'approche simplifiée de considérer l'ensemble des oiseaux fonctionnellement insectivores, comme des ennemis naturels des insectes herbivores (Barbaro et al., 2017; Bereczki et al., 2014; van Bael et al., 2008). Or, toutes les espèces d'oiseaux insectivores fonctionnels ne contribuent pas de la même manière au service de régulation. Par exemple, il existe des spécialisations géographiques de ce service au sein des communautés. Une plus grande implication des espèces spécialistes de l'habitat et des insectivores stricts dans la régulation des ravageurs a été observée dans les agrosystèmes tropicaux, en comparaison avec les agrosystèmes tempérés où les espèces généralistes sont relativement plus impliquées (Boesing et al., 2017). Ces différences pourraient être prises en compte dans les études s'intéressant aux effets des patrons biogéographiques sur la diversité fonctionnelle des oiseaux insectivores et sur l'insectivorie associée.

De plus, certaines espèces d'oiseaux présentent une spécialisation alimentaire pour différents stades de vie de leurs proies au sein d'un même écosystème. On peut par exemple citer la spécialisation marquée des Mésanges bleues (*Cyanistes caeruleus*) pour les chenilles de lépidoptères défoliatrices des chênes, surtout à la période de reproduction (Naef-Daenzer & Keller, 1999). Ceia & Ramos (2016) ont aussi montré que, dans les chênaies méditerranéennes, les espèces se nourrissant au sol (*ground-foragers*) consomment principalement des larves en diapause hivernale, les espèces se nourrissant dans le feuillage et l'écorce (*tree-foragers*) ciblent les oeufs, et les pupes, et les espèces chassant en vol (*aerial-sweepers*) consomment les imagos des mêmes espèces insectes défoliateurs et xylophages.

Cette spécialisation peut aussi se produire pour des espèces de proies bien spécifiques. En Europe, c'est le cas des coucous (*Clamator glandarius* et *Cuculus canorus*), de l'Engoulevent d'Europe (*Caprimulgus europaeus*), de la Huppe fasciée (*Upupa epops*), et de certaines mésanges (*Parus major*, *Lophophanes cristatus* et *Periparus ater*) qui sont les seuls oiseaux capables de prédater les populations de chenilles processionnaires du pin

(*Thaumetopoea pityocampa*), un lépidoptère défoliateur à soies urticantes (Barbaro & Battisti, 2011).

Par ailleurs, une étude australienne a révélé que certaines espèces d'oiseaux insectivores montrent des préférences alimentaires marquées pour des groupes d'arthropodes spécifiques, comme les coléoptères (ex. *Pomatostomus temporalis*), les fourmis (ex. *Climacteris affinis*) ou les diptères (ex. *Myiagra inquieta*) (Razeng et Watson, 2012, Razeng et Watson, 2014). C'est aussi le cas en Europe où les Roitelets huppés (*Regulus regulus*) et les Grimpereaux des bois (*Certhia familiaris*) consomment préférentiellement de petits arthropodes forestiers, en particulier des araignées (Hogstad, 1984; Jäntti et al., 2001).

Ainsi, l'absence de corrélation observée dans nos deux premiers chapitres entre la diversité des oiseaux insectivores et leur fonction de prédation pourrait s'expliquer par le manque de prise en compte des spécialisations alimentaires pour les proies lépidoptères au sein des communautés fonctionnellement insectivores considérées. Pour pallier cette limitation, nous pourrions envisager un système de pondération des espèces d'oiseaux dans le calcul des indices de diversité fonctionnelle reflétant plus fidèlement l'importance relative des larves de lépidoptères dans les régimes alimentaires de chaque espèce. Cette pondération devra s'appuyer sur une analyse détaillée de la variation des régimes alimentaires des espèces par saison, habitat et domaine biogéographique, comme cela a récemment été fait pour les chiroptères européens (Froidevaux et al., 2023).

De même, la variabilité intra-spécifique dans les préférences alimentaires est très rarement considérée, comme en témoigne l'utilisation usuelle de traits moyennés à l'espèce dans les calculs d'indices de diversité fonctionnelle. Pourtant, chez les plantes, il est bien établi que la prise en compte de la variabilité intra-spécifique des traits fonctionnels améliore la capacité à établir un lien entre la diversité fonctionnelle des communautés et les fonctions écosystémiques, tout en permettant une meilleure compréhension des mécanismes d'assemblage des communautés (Albert et al., 2010; De Bello et al., 2011; Jung et al., 2010). Chez les oiseaux, des études ont mis en évidence des comportements de recherche de nourriture adaptés à l'environnement chez certaines espèces, notamment lors de la période de nourrissage des jeunes. En ville, les parents mésanges charbonnières fournissent ainsi davantage de proies non arthropodes, de

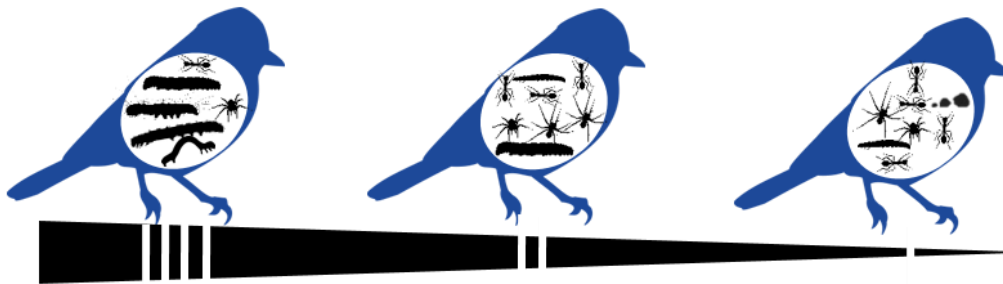
papillons, de guêpes ou d'araignées en comparaison de leurs homologues forestiers qui préfèrent nourrir leur progéniture avec des chenilles de lépidoptères plus nutritives (Naef-Daenzer et al., 2000; Senar et al., 2021; Sinkovics et al., 2021). Cette variabilité intra-spécifique est plus complexe à évaluer chez les oiseaux que chez les plantes car aussi liée à la personnalité des individus (Van Overveld & Matthysen, 2010). Des méthodes telles que l'installation de caméras dans des nichoirs ou l'analyse de fécès pourraient être une manière d'évaluer la variabilité intra-spécifique dans la contribution des oiseaux insectivores au service de régulation.

La méta-analyse de Philpott et al. (2009) montre que la complémentarité fonctionnelle des communautés d'oiseaux dans les systèmes agroforestiers tropicaux joue un rôle important pour la régulation des arthropodes, et que la richesse spécifique est le meilleur prédicteur de cette fonction. Il pourrait être intéressant d'approfondir cette question de manière empirique en identifiant quelles espèces, parmi l'ensemble des oiseaux insectivores en présence dans la communauté, contribuent activement à la prédation des larves d'insectes herbivores défoliateurs, et de déterminer si ces espèces varient selon les types d'habitats (ex. habitats forestiers, agricoles, urbains, soumis à une pression anthropique croissante) et selon leur degré de spécialisation (Fig.2). Pour cela, on pourrait imaginer de combiner l'écologie acoustique, afin de caractériser l'ensemble des espèces insectivores présentes au sein des communautés, avec des expériences de cafétérias (i.e. de choix alimentaires) surveillées par des caméras suffisamment performantes pour identifier les espèces qui s'y nourrissent et observer les proies arthropodes choisies (Darras et al., 2023).

Intensification de l'usage des terres par anthropisation



Spécialisation intra-spécifique pour les larves de lépidoptères en fonction des habitats considérés



Homogénéisation des communautés aviennes



Espèces impliquées dans le biocontrôle des larves de lépidoptères au sein des communautés en fonction des habitats considérés

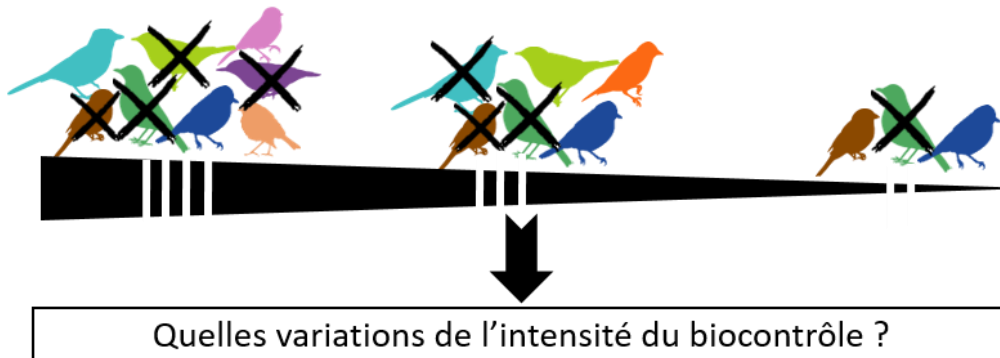


Figure 2. Le gradient d'intensification de l'usage des terres par anthropisation est illustré par des habitats forestiers, agricoles raisonnés et urbains, représentés respectivement par des arbres, du blé et des immeubles. Selon la disponibilité des proies dans ces habitats, certaines espèces insectivores ajustent leur régime alimentaire. Ainsi, les mésanges charbonnières préfèrent les larves de lépidoptères, plus nutritives, dans les habitats forestiers. Cependant, le long du gradient d'anthropisation, ces larves deviennent moins disponibles et sont progressivement remplacées par d'autres arthropodes dans leur régime alimentaire. Les proies consommées sont représentées à l'intérieur du ventre des mésanges, et le nombre de larves consommées est indiqué par le même nombre de lignes blanches dans le gradient. Parallèlement, on observe une homogénéisation fonctionnelle des communautés

d'oiseaux insectivores avec l'augmentation de la pression anthropique. Cette diversité fonctionnelle est représentée par des oiseaux aux silhouettes et aux couleurs différentes. Les mêmes espèces d'oiseaux sont toujours représentées par la même silhouette et la même couleur dans la figure. Dans la partie inférieure de la figure, les espèces d'oiseaux insectivores participant au biocontrôle varient selon les communautés, leur nombre est indiqué par des lignes blanches dans le gradient. Les espèces non impliquées dans le biocontrôle sont marquées d'une croix noire. L'ensemble des phénomènes décrits ont une influence sur l'intensité du biocontrôle exercé par les communautés insectivores le long du gradient d'intensification de l'usage des terres par anthropisation, mais cette influence est difficilement prévisible.

6.3. Les risques inhérents à l'utilisation de *proxys* en sciences

Dans le cas de nombreuses questions en écologie, la complexité des processus impliqués, les échelles spatiales et temporelles auxquelles ces processus se déroulent et les défis pratiques de l'expérimentation liés aux contraintes financières, techniques ou éthiques entraînent la nécessité de recourir à des mesures indirectes, des substituts ou des approximations appelés *proxys* (Petit et al., 2002; Stephens et al., 2015). Le choix des *proxys* utilisés dans les études sur les effets des changements globaux sur les interactions trophiques peuvent en partie expliquer les divergences observées entre les prédictions théoriques et les résultats empiriques, ainsi que les résultats contrastés entre différentes études (Faeth et al., 2005; Lövei & Ferrante, 2017; Roslin et al., 2017; Schillé et al., 2024; Turrini et al., 2016; Valdés-Correcher et al., 2021; Zvereva et al., 2019).

6.3.1. *Proxys* et caractérisation des gradients climatiques

Sans utiliser de *proxys*, l'établissement de corrélations entre les changements globaux et les processus biologiques nécessiterait des études suivies sur des décennies et des mesures directes impliquant un travail considérable. La latitude, l'altitude, les températures moyennes annuelles, le cumul annuel des précipitations ou la productivité primaire nette sont des *proxys* couramment utilisés pour étudier la relation entre les dérèglements climatiques, la biodiversité et les interactions biotiques (Kozlov, Stekolshchikov, et al., 2015; Moreira et al., 2015; Roslin et al., 2017; Valdés-Correcher et al., 2021; Wardle et al., 1998; Zvereva & Kozlov, 2022).

Dans le cas du premier chapitre de cette thèse, nous étions conscients des limites de l'utilisation de la latitude comme *proxy* du climat, en particulier en raison de l'échelle européenne de notre étude (Valdés-Correcher et al., 2021) qui ne couvre pas l'ensemble du gradient latitudinal jusqu'aux tropiques, ainsi que de la répartition non uniforme des sites en Europe. C'est pourquoi nous avons préféré utiliser les températures moyennes annuelles, qui reflètent peut-être davantage les variations dans le transfert d'énergie au sein des cascades trophiques le long des gradients climatiques. Malgré les abus de langage, il est important de noter qu'on ne peut quasiment jamais établir de relations de causalité entre les *proxys* climatiques et les variables biologiques d'intérêt (prédation, herbivorie, etc.); on ne peut établir que des corrélations. C'est la raison pour laquelle nous n'avons pas cherché à trop expliquer les mécanismes sous-jacents à la corrélation négative observée entre la température moyenne annuelle et les taux de prédation le long du gradient climatique européen. Toutefois, si l'on avait les moyens financiers, il pourrait être plus intéressant d'utiliser des mesures directes de la température au niveau des sites d'étude à l'aide de capteurs de précision, qui permettraient de faire un lien plus immédiat avec la composition des communautés d'oiseaux et d'herbivores en présence, ainsi qu'avec leurs interactions. De plus, ces capteurs seraient un moyen de s'assurer que les variations climatiques agissent sur les communautés et les fonctions écosystémiques à la même échelle temporelle que celle à laquelle l'étude a lieu.

Enfin, dans le chapitre 1, malgré la relation statistiquement significative entre la température moyenne annuelle et la prédation, une large proportion de la variance est restée inexplicée en première intention. Ce constat rejoint les observations de Moreira et al., (2015), qui ont montré que la latitude continuait d'exercer un effet significatif sur l'herbivorie des pétunias sauvages, même après avoir pris en compte la température et les précipitations, suggérant l'implication de facteurs non considérés initialement. Face à ce constat, et compte tenu de la résolution parfois limitée des *proxys* climatiques utilisés (dans notre étude, la température moyenne annuelle issue de la base de données WorldClim, avait une résolution spatiale d'environ 86 km², Hijmans et al., 2005), nous avons décidé d'intégrer des facteurs locaux à notre analyse. Ainsi, la couverture forestière à 20m et à 200m autour des sites d'étude, permettaient d'expliquer une grande partie de la variance résiduelle des taux de prédation à l'échelle européenne.

6.3.2. *Proxys* et caractérisation des gradients d'urbanisation

Les gradients d'urbanisation sont associés à la densité croissante des populations humaines des zones rurales vers les zones urbaines (Van Der Merwe & Bekker, 2014). Cependant, l'urbanisation est un phénomène particulièrement complexe à définir (Cloke, 1985) et multidimensionnel, de sorte qu'il est parfois difficile de savoir si les variables utilisées en écologie urbaine sont des moteurs directs de l'urbanisation ou des *proxys*. Dans la littérature, on retrouve des variables aussi différentes que l'imperméabilité des surfaces, la fragmentation des habitats forestiers, les densités de population, le revenu moyen par foyer, la pollution sonore, lumineuse ou encore le réchauffement nocturne (Crooks et al., 2004; Kozlov et al., 2017; Miller et al., 2017; Perillo et al., 2017; Valdés-Correcher et al., 2022). Comme dans le cas des gradients climatiques, ces *proxys* ne varient pas linéairement avec le phénomène qu'ils sont censés représenter, l'urbanisation. Les gradients d'urbanisation ne devraient donc jamais être approximés par un simple transect allant du centre historique, fortement urbanisé, vers une périphérie qui ne le serait pas. Cela est particulièrement vrai étant donné que du fait de leur croissance rapide, de nombreuses villes sont en réalité multicentriques. Il est donc nécessaire de prendre en compte cette non linéarité au travers des *proxys* utilisés (McDonnell & Hahs, 2008) et c'est pour mieux refléter cette hétérogénéité que nous avons choisi d'utiliser plusieurs gradients reflétant l'urbanisation dans le chapitre 2.

La figure 3 montre les variations théoriques de différents *proxys* utilisés par rapport aux gradients climatiques et urbains. Les échelles d'études sont très différentes mais les enjeux inhérents à l'utilisation des *proxys* restent les mêmes : un lien parfois distendu avec la variable d'intérêt, des résolutions différentes, des différences parfois importantes entre les *proxys* et une forte dépendance aux facteurs biotiques et abiotiques locaux.

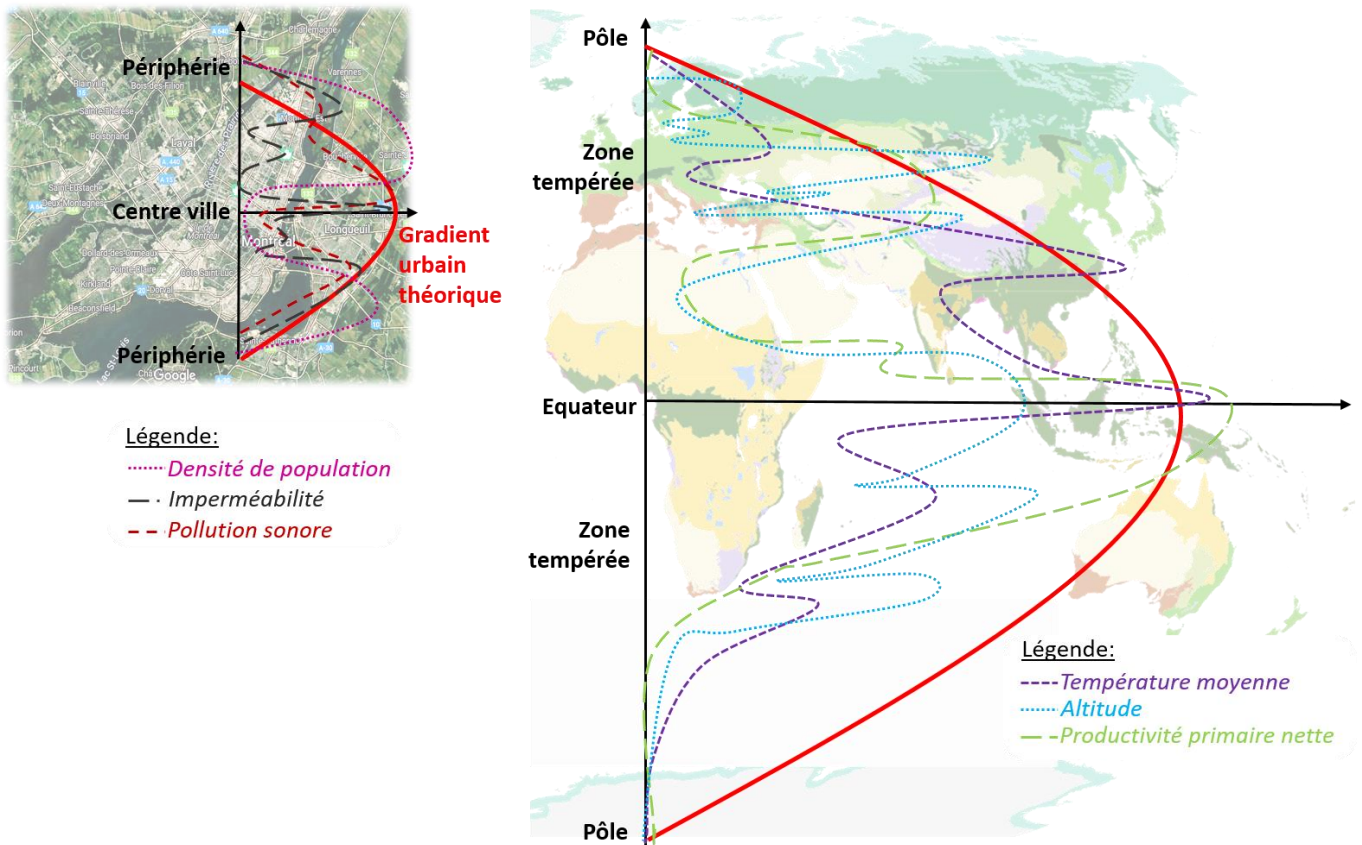


Figure 3. Variations théoriques de divers proxys utilisés pour l'évaluation des gradients urbains (à gauche) et climatiques (à droite) à l'échelle d'une ville (à gauche) ou d'un transect pôle nord-pôle sud (à droite).

6.3.3. Comment utiliser les *proxys* en écologie des interactions trophiques ?

Les *proxys* restent non seulement utilisables mais nécessaires à l'étude des effets des changements globaux sur les interactions trophiques. Une analyse succincte de la littérature m'a permis d'identifier quelques principes directeurs pour leur utilisation adéquate dans ce contexte.

Tout d'abord, il est essentiel d'établir des définitions claires et consensuelles pour les *proxys* utilisés, afin de réduire la variabilité inter-études et d'en faciliter la reproductibilité. Les *proxys* doivent être validés par des modèles ou des études de terrain et adaptés aux contextes et aux questions écologiques. Par exemple, le bruit anthropique est connu pour avoir un effet sur le comportement des oiseaux, en laboratoire et *in situ*

(Dooling & Popper, 2016; Slabbekoorn & Ripmeester, 2008) et est directement corrélé au trafic routier en milieu urbain. Il pourrait donc être un bon *proxy* pour étudier l'impact des perturbations anthropiques sur le comportement et la distribution des oiseaux. Cependant, ce *proxy* n'a peut-être pas d'impact sur le comportement des herbivores ou sur les défenses des arbres, qui conditionnent eux aussi les interactions trophiques. Les *proxys* qui sont les plus à même de décrire l'urbanisation selon que l'on se place du point de vue des oiseaux, de celui des herbivores ou de leurs interactions peuvent ainsi être très différents. Il n'y a pas de solution universelle mais plutôt des compromis à trouver.

Une manière de résoudre ces compromis pourrait être d'adopter des approches multi-*proxy*, combinant plusieurs indicateurs (voir chapitre 2 de la thèse). Ces approches permettent de fournir une image plus complète des gradients climatiques et urbains en dépassant l'opposition entre zones urbaines et zones rurales en intégrant l'hétérogénéité intra-urbaine et ses effets sur les communautés d'oiseaux, sur les communautés d'herbivores et sur leurs interactions biotiques (McDonnell & Hahs, 2008).

Enfin, il est particulièrement souhaitable de bien réfléchir aux résolutions auxquelles on travaille. Les résolutions spatiales plus larges, telles que celles fournies par des bases de données comme WorldClim (Hijmans et al., 2005), sont efficaces pour détecter des variations à grande échelle, par exemple dans les températures moyennes annuelles, et peuvent révéler des tendances générales des gradients climatiques influençant la répartition des espèces et les processus biogéographiques. Cependant, des résolutions plus fines sont nécessaires pour capturer les variations locales dans les interactions trophiques (Stephens et al., 2015). Pour cela, on peut par exemple utiliser des capteurs de température ou d'humidité de haute précision au niveau des sites d'étude. L'intégration d'échelles spatiales emboîtées tenant compte des facteurs locaux s'avère particulièrement utile tant pour les études climatiques à large échelle que pour celles en écologie urbaine. Dans les études climatiques, on gagnerait probablement à tenir compte de la composition et la structuration des habitats des sites étudiés. Inversement, dans les recherches sur les interactions trophiques le long de gradients d'urbanisation, les facteurs locaux non anthropiques, tels que les températures locales ou la disponibilité des habitats forestiers, peuvent s'avérer aussi importants que les facteurs anthropiques pour expliquer la distribution, la diversité des espèces et leurs fonctions (Allen & O'Connor, 2000;

McDonnell & Hahs, 2008). Comme déjà évoqué précédemment, la résolution spatiale des variables écologiques à considérer pour expliquer les interactions biotiques diffère selon les maillons trophiques auxquels on s'intéresse. Ainsi en milieu urbain, les insectes, qui ont une mobilité limitée, sont particulièrement affectés par les surfaces bâties, car celles-ci entravent leurs déplacements. En revanche, les oiseaux, plus mobiles, sont davantage influencés par la structure de la végétation dans les zones boisées, car c'est cette structuration qui leur fournit des habitats (Crocchi et al., 2008). Cela plaide encore une fois pour considérer plusieurs variables *proxys* et à des échelles différentes pour étudier les effets de l'urbanisation sur les interactions trophiques.

Ces principes s'appliquent également aux proies artificielles lorsqu'elles sont utilisées comme *proxys* pour quantifier la prédation. Selon une définition faisant consensus dans la communauté scientifique (Ferrante et al., 2024), les proies artificielles ne visent pas à mesurer la prédation absolue, mais évaluent plutôt la pression de prédation relative entre divers habitats (Howe et al., 2009). Bien que ce *proxy* des proies artificielles soit largement utilisé, il me semble qu'il nécessite encore une validation et une calibration plus approfondies, tant sur le terrain—comme nous l'avons tenté dans le chapitre 3, malgré des moyens techniques limités—qu'en laboratoire, afin d'étudier le comportement des prédateurs face à différents types de proies (artificielles, vivantes, mortes, etc.) (Ferrante et al., 2024). Il est également important de considérer la résolution spatiale à laquelle on travaille lors de l'utilisation de cette méthode. Bien qu'efficace pour comparer les pressions de prédation entre habitats, une étude récente de Rodriguez-Campbell et al., (2023) suggère qu'elle pourrait ne pas être adaptée pour analyser les interactions de prédation à large échelle le long de gradients biogéographiques. Enfin, si Ferrante et al., (2024) affirment que l'utilisation des proies artificielles reste fiable, ils recommandent aussi de combiner plusieurs types de proies sentinelles (vraies vivantes, mortes, ou artificielles) (i.e. approche multi-*proxys*) qui refléterait mieux la prédation de plusieurs sous-ensembles, chevauchants ou non, de prédateurs.

6.4. Les enjeux de la reproductibilité en écologie

6.4.1. Comment obtenir des résultats reproductibles ?

Un autre défi en écologie est d'assurer la reproductibilité des recherches, à plus forte raison dans le cas des études empiriques sur le terrain. La variation significative des résultats obtenus pour une même question constitue un problème fréquent pour la reproductibilité (Filazzola & Cahill, 2021). La question de savoir si et comment l'intensité des interactions biotiques varie le long de gradients latitudinaux a fait l'objet de très nombreuses recherches, à partir de différents modèles. Que ce soit sur les interactions plantes-insectes (Anstett et al., 2016; Kozlov, Lanta, et al., 2015) ou sur les interactions insectes-ennemis naturels (Lövei & Ferrante, 2017; Roslin et al., 2017; Valdés-Correcher et al., 2021; Zvereva et al., 2019), les résultats sont variables et parfois contradictoires (Moles, 2013; Moles et al., 2011). Selon Filazzola & Cahill, (2021), face à ce type de résultats, les écologues tendent à attribuer les incohérences à la variabilité des processus écologiques à large échelle - ce que nous avons d'ailleurs en partie affirmé dans cette discussion- plutôt que de remettre en question la robustesse du cadre théorique de départ (Moles & Ollerton, 2016). La reproductibilité étant l'une des conditions essentielles pour que les gestionnaires, les décideurs, le grand public et les scientifiques eux-mêmes puissent avoir confiance et s'appuyer sur les résultats des recherches, je vais discuter la manière dont les chapitres de cette thèse satisfont ou auraient pu satisfaire davantage aux principes de reproductibilité.

Filazzola & Cahill, (2021) identifient trois niveaux de reproductibilité dans les designs expérimentaux en écologie qui peuvent améliorer la qualité des études. Le premier niveau est la réplication des échantillons, c'est-à-dire le nombre d'observations dans chaque population statistique. Dans le premier chapitre de cette thèse, cela se traduit par un nombre élevé d'arbres échantillonnés par site, facilité par un réseau de partenaires européens mis en place dans le cadre du projet de sciences participatives *Tree bodyguards* (Castagneyrol, 2018). L'expertise des chercheurs impliqués renforce la fiabilité des données collectées et souligne l'importance des réseaux collaboratifs pour la robustesse et la reproductibilité des études. Le chapitre 2 de cette thèse a aussi pu bénéficier d'un réseau préétabli de placettes urbaines sur lesquelles plusieurs chercheurs aux

compétences variées avaient déjà effectué des échantillonnages et dont l'aide a été précieuse pour assurer la réplication des échantillons. De ce point de vue, je pense que nous avons suffisamment de réplifications statistiques pour pouvoir tester nos hypothèses dans ces deux chapitres, nous permettant d'exclure le manque de réplication comme explication possible pour les résultats n'allant pas dans le sens des attendus théoriques.

Le deuxième niveau est la réplication de ses propres méthodes par une même équipe scientifique dans différentes localisations ou à différents moments, tout en restant dans le cadre d'une seule et même étude (Filazzola & Cahill, 2021). Bien que le réseau *Tree bodyguards* ait permis des répétitions temporelles, elles n'ont pas été considérées dans une même étude dans le cadre de ma thèse. La raison principale étant une incompatibilité de temporalité entre la durée d'une thèse et la durée nécessaire pour assurer ce type d'études suivies.

En revanche, ces répétitions temporelles mises en place quatre années de suite avec des partenaires et des protocoles quasiment identiques (voir Valdés-Correcher et al., 2021) et mon chapitre 1 entrent complètement dans le cadre du troisième niveau de réplication cité par Filazzola & Cahill (2021), consistant à reproduire des recherches antérieures dans des conditions expérimentales identiques, en utilisant les mêmes sujets et mêmes matériels. Toutefois, les résultats obtenus par Valdés-Correcher et al. (2021) étaient différents des miens, justifiant l'évocation de l'importance des facteurs locaux dans les discussions de mes résultats. Ainsi, même si l'on pourrait opposer que la répétition d'études quasiment identiques avec des hypothèses de recherche similaires manquent d'originalité, elles sont d'importance pour la reproductibilité scientifique, bien que plus rarement financées ou publiées (Fraser et al., 2020).

Même si la réplication exacte d'études par différentes équipes avec les mêmes protocoles, matériels et sites soit souvent difficile, ne serait-ce que parce que les systèmes naturels qui font l'objet de nos études évoluent dans le temps, il est possible d'améliorer la reproductibilité en écologie en rendant les données, les codes et les protocoles accessibles et en utilisant les systèmes de pré-enregistrement des expériences "*Registered Reports*" (ex. PCI, 2021). Dans le chapitre 3, nous avons mis en œuvre ces pratiques pour garantir des hypothèses et un protocole clairs et reproductibles, évalués par des pairs avant le

début de l'expérimentation. Nous avons également inclus des analyses de puissance pour s'assurer que la taille de l'échantillon statistique soit suffisante pour détecter un effet réel, le cas échéant.

Cette approche a été plus chronophage en termes de rédaction que les autres chapitres de cette thèse, dans la mesure où elle a nécessité l'élaboration en amont de l'expérimentation de l'ensemble des plans d'échantillonnage, des protocoles expérimentaux, des analyses statistiques, ainsi que la rédaction de l'introduction et de la section matériels et méthodes. Cependant, cet investissement initial en temps a été compensé par une rédaction plus efficace du manuscrit final après l'acceptation de principe du *Registered report*. La principale contrainte a été l'anticipation du temps requis pour la rédaction du rapport initial, pour la "prise de rendez-vous" avec les évaluateurs qui s'engagent à rendre leur rapport en deux semaines, et pour l'intégration de leurs révisions afin que l'acceptation de principe soit obtenue avant le début de l'expérimentation, conformément aux conditions établies par les journaux. Malgré cela, je considère que cette approche est très intéressante pour améliorer la qualité, la fiabilité et la reproductibilité de la recherche et j'envisage donc d'y avoir à nouveau recours. Même sans écrire de *Registered Reports*, je pense qu'une utilisation plus systématique des analyses de puissance en écologie pourrait améliorer la qualité des études. De telles approches permettraient d'augmenter la taille des échantillons, réduisant ainsi le risque de tirer des conclusions erronées basées sur un manque de puissance statistique, plutôt que sur une réelle absence d'effet.

6.4.2. Reproductibilité et nouvelles technologies : l'exemple de BirdNET

Pour caractériser les communautés d'oiseaux, des points d'écoute réalisés par des ornithologues sont couramment utilisés et considérés de très longue date comme la méthode la plus efficace (Bibby, 2000). Cependant, cette méthode peut manquer de reproductibilité entre observateurs, en raison d'oiseaux non détectés (Nichols et al., 2000) ou de l'absence de standardisation des protocoles (Fuller & Langslow, 1984). L'utilisation de capteurs acoustiques couplés à des algorithmes de reconnaissance automatisée sont prometteurs dans une perspective de réduction des biais d'observateurs et d'amélioration de la reproductibilité entre les sites d'étude et entre les

études. L'algorithme BirdNET offre par exemple la possibilité d'analyser de très larges volumes d'enregistrements de vocalisations d'oiseaux afin d'identifier les espèces en présence. Il reste que BirdNET présente encore des biais de détection (faux positifs et faux négatifs) lors de son utilisation sur des enregistrements récoltés directement sur le terrain.

Pourtant, des études expérimentales commencent à utiliser cet outil, plus uniquement d'un point de vue méthodologique mais aussi pour répondre à des questions écologiques spécifiques (Biffi et al., 2024; Seibold et al., 2024). Selon moi, cette utilisation est acceptable si elle respecte les conditions d'utilisation décrites dans la littérature méthodologique et si les résultats sont validés par des experts pour assurer leur fiabilité. Par exemple, Seibold et al. (2024) ont utilisé l'algorithme en s'assurant au préalable d'une validation d'un sous-échantillonnage par un ornithologue et en ayant recours à différents seuils de confiance maximisant la précision de l'algorithme pour chacune des espèces rencontrées (voir aussi recommandations de Funosas et al., 2024; Pérez-Granados, 2023).

De manière générale, la standardisation des protocoles d'enregistrements au sein d'une même étude et entre les études, la réplique temporelle des enregistrements pour lisser les variations climatiques, la documentation précise des paramètres d'entrée de BirdNET, le partage des enregistrements, des identifications brutes et des scripts d'analyses et la validation de sous-échantillons par des taxonomistes me paraissent constituer un cadre méthodologique nécessaire à la reproductibilité des études utilisant BirdNET dans un contexte expérimental. A l'inverse, l'utilisation non justifiée et sans test préalable des paramètres par défaut de BirdNET, le filtrage des identifications à des seuils de confiance faibles et l'absence de validation par des experts peuvent nuire à la fiabilité et reproductibilité des études de terrain (Wood & Kahl, 2024). On peut s'inquiéter de la reproduction de protocoles utilisant des nouvelles technologies ou des algorithmes sans une compréhension fine des outils appliqués, sans support méthodologique préalable à leur utilisation et sans validation (Biffi et al., 2024).

Il est important de noter que la fiabilité et la reproductibilité des études utilisant des algorithmes de reconnaissance automatisés sont toujours conditionnées par leurs objectifs et questions scientifiques. Je suppose qu'en l'état actuel de son développement,

BirdNET est plus adapté à la détection de la présence ou l'absence d'espèces communes et pour lesquelles l'algorithme est suffisamment bien entraîné, ainsi qu'à l'estimation générale de l'activité des oiseaux, plutôt qu'au calcul précis de la richesse spécifique ou des indices de diversité fonctionnelle de communautés.

6.5. Conclusion

Cette thèse a mis en évidence deux tendances majeures pour expliquer la corrélation entre les changements globaux et la diversité fonctionnelle des communautés d'oiseaux insectivores, s'ajoutant ainsi au vaste corpus de littérature sur le sujet (Devictor et al., 2007, 2008; McKinney, 2006; McKinney & Lockwood, 1999; Rigal et al., 2023). (i) Le long du gradient climatique européen, nous avons observé une diminution de la diversité fonctionnelle des communautés d'oiseaux du sud vers le nord, corrélée à la baisse des températures. (ii) Dans la métropole montréalaise, la diversité taxonomique et fonctionnelle des insectivores diminuait avec l'augmentation de l'intensité de l'urbanisation. Cependant, contrairement à ce que suggère la théorie sur la relation biodiversité-fonction (Philpott et al., 2009; van Bael et al., 2008), la diversité des communautés d'oiseaux ne présentait pas de corrélation positive avec l'insectivorie, ni le long du gradient climatique européen, ni le long du gradient d'urbanisation à Montréal.

Nous pensons que nos résultats, avec la taille d'échantillon et la reproductibilité dont nous disposons, ne sont pas artefactuels et reflètent bien cette absence de corrélation positive entre la diversité des communautés d'oiseaux et leur fonction de prédation. De plus, l'approche multi-proxy que nous avons utilisée dans le deuxième chapitre semble offrir une perspective intéressante pour appréhender la complexité et l'hétérogénéité du phénomène d'urbanisation. Cette approche pourrait être utile dans les futures études d'écologie des interactions trophiques en milieu urbain.

Nous avons également montré que la densité des habitats forestiers et la diversité des arbres étaient des facteurs tout aussi importants à considérer que les facteurs climatiques et urbains pour expliquer la relation entre la diversité et la fonction des oiseaux insectivores, ainsi que leurs effets en cascade sur l'herbivorie. Ces résultats plaident d'une

part pour considérer des échelles spatiales hiérarchiquement emboîtées pour comprendre les effets des changements globaux sur les interactions trophiques et ce, quelle que soit la résolution des études, qu'elles soient menées à l'échelle locale ou continentale. D'autre part, nos résultats s'ajoutent à la littérature existante qui préconise la conservation et la création de zones boisées diversifiées dans les planifications urbaines (Beninde et al., 2015; Croci et al., 2008; Hobbs, 1988). Ces espaces verts urbains favorisent non seulement la prédation naturelle des insectes ravageurs (Long & Frank, 2020), mais permettent aussi le maintien de la biodiversité, en particulier celle des oiseaux (Croci et al., 2008).

Malgré les critiques récentes sur l'utilisation des proies en pâte à modeler pour caractériser la prédation (Nimalrathna et al., 2023; Rodriguez-Campbell et al., 2023; Zvereva & Kozlov, 2023), nous avons montré qu'elle reste fiable en l'état actuelle des possibilités technologiques permettant de l'évaluer ou de trouver d'autres approches. Associé aux proies sentinelles, l'échantillonnage des arthropodes herbivores et prédateurs, constituerait un moyen (i) d'évaluer la densité des herbivores et donc la manière dont les oiseaux insectivores réagissent aux fluctuations de leurs proies et (ii) d'obtenir des informations sur l'intensité de la prédation intragilde dans les sites d'étude.

L'une des limites de ce travail est la difficulté de quantifier l'abondance des espèces insectivores, en particulier celles spécialisées dans la prédation des larves de lépidoptères. Il est possible que cette abondance soit un meilleur indicateur de la capacité des communautés d'oiseaux à réguler les insectes herbivores que la diversité de ces communautés (Maas et al., 2015; Roels et al., 2018). Les algorithmes de reconnaissance automatisée pourraient être un moyen de quantifier les abondances des oiseaux. Cependant, à ce jour, leur utilisation pour la recherche n'est pas encore optimale en raison de la variabilité de leur performances selon les espèces considérées, l'intensité du signal et la présence de bruit ambiant dans les enregistrements (Funosas et al., 2024; Pérez-Granados, 2023; Pérez-Granados, 2023). Néanmoins, ces outils peuvent déjà être utilisés avec une validation par des experts et devraient rapidement devenir une solution fiable à mesure du perfectionnement des algorithmes (Wood & Kahl, 2024).

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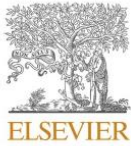
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7. Annexes

7.1. Annexe A1. Évaluer le potentiel de BirdNET pour caractériser les communautés d'oiseaux européennes à partir de données écoacoustiques à grande échelle.

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Original Articles

Assessing the potential of BirdNET to infer European bird communities from large-scale ecoacoustic data

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ABSTRACT

1. Passive acoustic monitoring has become increasingly popular as a practical and cost-effective way of obtaining highly reliable acoustic data in ecological research projects. Increased ease of collecting these data means that, currently, the main bottleneck in ecoacoustic monitoring projects is often the time required for the manual analysis of passively collected recordings. In this study we evaluate the potential and current limitations of BirdNET-Analyzer v2.4, the most advanced and generic deep learning algorithm for bird recognition to date, as a tool to assess bird community composition through the automated analysis of large-scale ecoacoustic data.
2. To this end, we study 3 acoustic datasets comprising a total of 629 environmental soundscapes collected in 194 different sites spread across a 19° latitude span in Europe. We analyze these soundscapes using both BirdNET and manual listening by local expert birders, and we then compare the results obtained through the two methods to evaluate the performance of the algorithm both at the level of each single vocalization and for entire recording sequences (1, 5 or 10 min).
3. Since BirdNET provides a confidence score for each identification, minimum confidence thresholds can be used to filter out identifications with low scores, thus retaining only the most reliable ones. The volume of ecoacoustic data used in this study did not allow us to estimate species-specific minimum confidence thresholds for most taxa, so we instead used and evaluated global confidence thresholds selected for optimized results when consistently applied across all species.
4. Our analyses reveal that BirdNET identifications can be highly reliable if a sufficiently high minimum confidence threshold is used. However, the inevitable trade-off between precision and recall does not allow to obtain satisfactory results for both metrics at the same time. We found that F1-scores remain moderate (<0.5) for all datasets and confidence thresholds studied, and that acoustic datasets of extended duration seem to be currently necessary for BirdNET to provide a reliable and minimally comprehensive picture of the target bird community. We estimate, however, that the usage of species- and context-specific minimum confidence thresholds would allow to substantially improve the global performance benchmarks obtained in this study.

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- We conclude that a judicious use of AI-based identifications provided by BirdNET can represent a powerful method to assist in the assessment of bird community composition through the automated analysis of ecoacoustic data, especially when applied to acoustic datasets of extended duration.

1. Introduction

In recent years, passive acoustic monitoring (PAM) based on autonomous recording units (ARUs) has become an increasingly popular option for monitoring avian populations and communities (Shonfield & Bayne, 2017). Compared to active acoustic monitoring (AAM) methods such as point counts or active searches, ARUs could provide a more cost-effective way of obtaining data (Melo et al., 2021; Darras et al., 2018) and a higher degree of standardization in the data collection process (Darras et al., 2019). Moreover, ARUs offer the possibility of listening to distant, noisy or dubious animal sounds multiple times, potentially facilitating their identification (Sugai et al., 2019). At the same time, ARUs make it possible to collect substantial amounts of ecoacoustic data in a non-invasive way for local wildlife.

ARUs can be especially useful for biodiversity monitoring projects in hard-to-reach areas, where difficult access conditions might hinder frequent data collection through AAM methods, and might improve the detectability of species whose vocal activity patterns do not coincide with the dates and times at which active monitoring is usually conducted (Sebastián-González et al., 2018). This greater facility to collect ecoacoustic data at regular time intervals in a standardized way makes it possible to study the variations in vocal activity patterns of one or more species along a given time gradient (e.g., time of day, week of the year) (Gasc et al., 2013; Towsey et al., 2014). Additionally, the analysis of soundscape variation across time and space allows researchers to study potential correlations between the presence of anthropogenic sounds and the acoustic activity of sound-producing animals (Blumstein et al., 2011). This means that PAM could serve as a reliable way to obtain complementary information to cover the gaps left by traditional monitoring methods (Bradfer-Lawrence et al., 2023). Indeed, recent studies suggest that the combined use of PAM and AAM may provide a more accurate picture of the presence and abundance of target species than the use of only one of the two methods (Bobay et al., 2018; Shaw et al., 2021).

The increased ease of obtaining large amounts of ecoacoustic data—easily within the range of hundreds to tens of thousands of hours for multi-site projects (Dufoucq et al., 2021)—through PAM means that, currently, the main bottleneck in ecoacoustic monitoring is often the time required for the analysis of passively collected data (Symes et al., 2022). Manual analysis of recordings by experts requires time-intensive dedication and therefore severely limits the amount of data that can be processed. Thus, the automated analysis of recordings could represent a potential solution to the current disparity between the efforts required to obtain data through PAM and the efforts necessary to manually analyze these data. In recent years, deep learning techniques have allowed for significant advances in the development of different tools for the automated recognition of biological sounds (Stowell, 2021). However, this field is still in a developing phase, and the use of these algorithms often results in significant numbers of false positives or false negatives, thus requiring subsequent manual validation (Knight et al., 2017) or the use of sophisticated population models to filter out false positives (Clare et al., 2021). Hence, the development of ecoacoustic data processing algorithms that can reliably identify the species recorded without manual supervision could allow for a substantial transformation of the methods through which biodiversity monitoring projects are conducted (Liu et al., 2022).

In this study we evaluate BirdNET-Analyzer v2.4, a deep neural network algorithm developed by the Cornell Lab of Ornithology which is capable of identifying > 6000 bird, mammal and amphibian species worldwide based on their sounds (Kahl et al., 2021). BirdNET, in

addition to detecting and identifying animal sounds present in a given recording, assigns a confidence score between 0 and 1 to each identification, thus providing information about the reliability of its results. If considered sufficiently reliable, BirdNET could partially or even fully automate the analysis of ample amounts of ecoacoustic data that can already be efficiently obtained with ARUs (Stowell, 2021; Borowiec et al., 2022). Moreover, the recently released BirdNET App (Wood et al., 2022) might further contribute to the collection of ornithological data by helping non-experts identify bird vocalizations heard on the field.

Several recent studies have tested the potential and limitations of BirdNET as a tool to assess bird community composition through the automated analysis of environmental soundscapes (Kahl et al., 2021; Arif et al., 2020; Brüggemann et al., 2021; Tolckova et al., 2021; Sethi et al., 2021; Toenies & Rich, 2021; Cole et al., 2022; Höchst et al., 2022; Malamut, 2022; Wood et al., 2021). However, as highlighted in a recent review of these previous studies (Pérez-Granados, 2023), multiple analyses of potential relevance are still lacking. More concretely, the impact of (i) the number of species vocalizing simultaneously, (ii) the recording environment (i.e., the soundscape or acoustic habitat type), (iii) the type of recorder employed, (iv) the volume of species-specific acoustic data available online, and (v) the input values for the overlap and detection sensitivity parameters of the algorithm on BirdNET performance remains to be evaluated. Moreover, the review suggests that BirdNET performance should be studied not only at the entire recording level but also at the level of each single vocalization. Last but not least, BirdNET detection capacity (i.e., recall rate) across a large range of European soundscapes has yet to be investigated.

To help fill this knowledge gap we analyze, both automatically with BirdNET and manually by expert birders, 629 environmental soundscapes collected in 194 different sites spread across a 19° latitude gradient in Europe (Fig. 1) and amounting to a total of 3137 min of recording (Table 1). We then compare the identifications obtained with BirdNET against those made by experts in order to assess the performance of the algorithm in terms of precision and recall (see subsection 2.4.1). Subsequently, we examine how to deal with the existing trade-off between these two metrics and how different features of the acoustic dataset analyzed might influence BirdNET performance. The focus of this study being on the use of BirdNET for the broad characterization of bird communities, our recommendations do not apply to other widespread applications (e.g., occupancy modeling (Cole et al., 2022), bio-acoustic tracking (Verreycken et al., 2021)) of the algorithm. We also suggest caution in the extrapolation of our results to regions with different bird community compositions or geophonic or anthroponic profiles.

2. Methods

2.1. Study area and soundscape collection

The environmental soundscapes analyzed in this study originated from three independent acoustic datasets (Table 1, Appendix S1). Our first dataset, hereafter referred to as ZA-Pygar, consists of a total of 237 1-minute recordings collected from 2019 to 2022 in 79 different sampling sites in the French region of Occitanie (Barbaro et al., 2022). More precisely, the region sampled is part of the Zone Atelier Pyrénées Garonne (Ouin et al., 2021), considered a long-term socio-ecological research site by French research institute CNRS since 2017. Out of the 79 sampling sites from which recordings were obtained, 60 are found in the Aurnignac canton, 16 are found either in alpine meadows or at the edge between alpine meadows and subalpine forests at altitudes between

1400 and 2100 m in the Ariège department, and the remaining 3 are found in lowland agricultural areas in South-West Occitanie (Fig. 1a).

Our second dataset, hereafter referred to as Rambouillet, consists of a total of 204 5-minute recordings collected during the COVID-19 lockdown of 2020 in 68 different sampling sites in the public forest of

Rambouillet (Fig. 1b). This lowland sub-Atlantic broadleaf forest, covering 220 km², is located in South-West Ile-de-France (France), about 70 km from Paris (Barbaro et al., 2023). Finally, our third dataset, hereafter referred to as TreeBodyguards, was inherited from a pan-European citizen science project and consists of a total of 188 10-minute

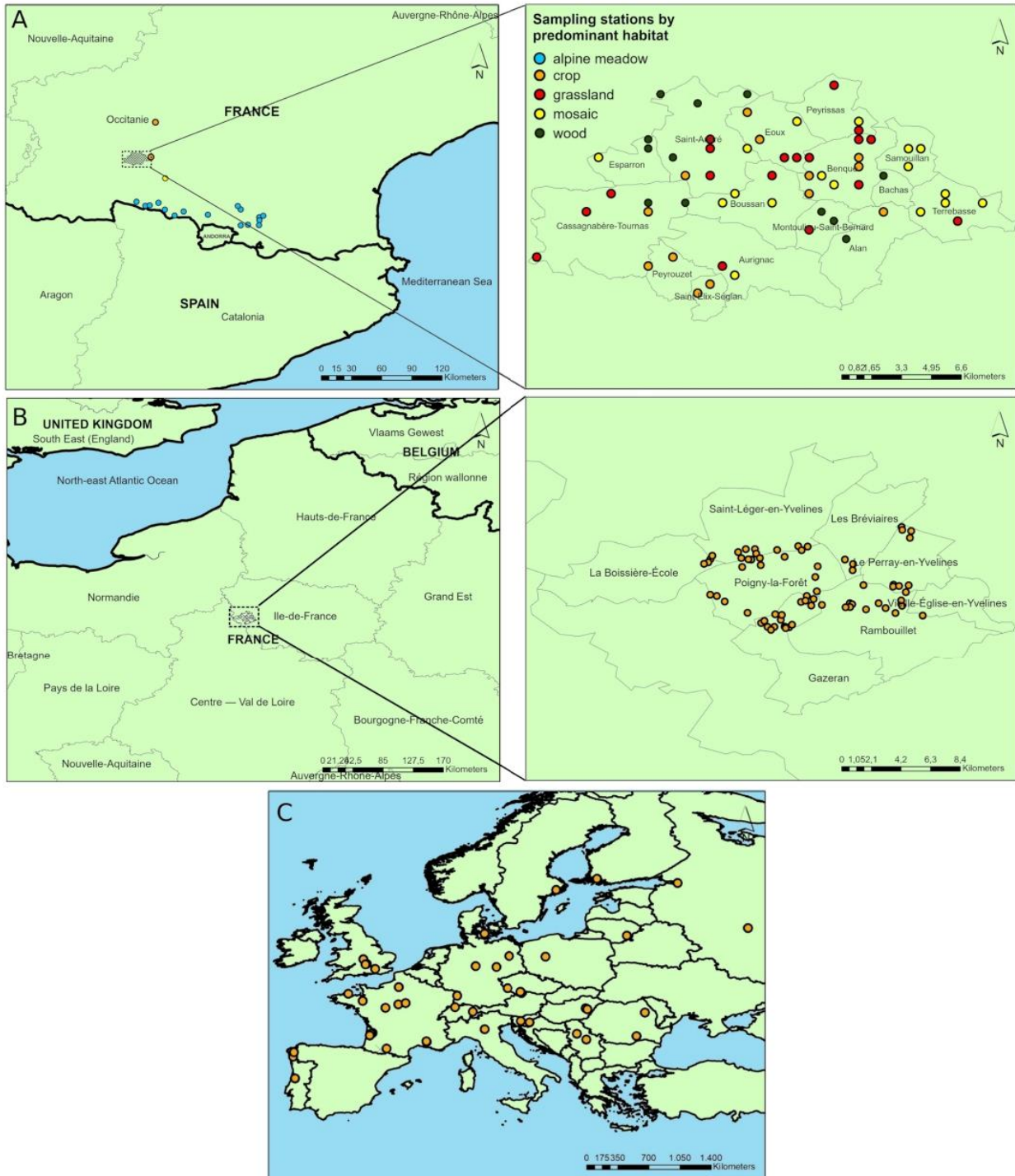


Fig. 1. Maps showing (a) the 79 sampling stations in the ZA-Pygar dataset, (b) the 68 sampling stations in the Rambouillet dataset, and (c) the 47 sampling stations in the TreeBodyguards dataset. The predominant habitat in each station is only specified for the ZA-Pygar dataset.

Table 1
Global description of the three datasets studied along with multiple indicators of BirdNET performance for each dataset.

Dataset Name	ZA-Pygar	Rambouillet	TreeBodyguards
Number of sites	79	68	47
Number of recordings	237	204	188
Recording duration (min)	1	5	10
Total duration (min)	237	1020	1880
Unit of identification	Bird vocalization	Bird presence in the recording	Bird presence in the recording
Number of species	74	44	86
Number of identifications	4101 ¹	2004	1630
BirdNET results at the vocalization level			
Maximal F1-score	0.339	–	–
Optimal confidence threshold ²	0.4	–	–
Precision with optimal conf. threshold	0.584	–	–
Recall with optimal conf. threshold	0.238	–	–
PR AUC	0.432	–	–
ROC AUC	0.054	–	–
BirdNET results at the recording level			
Maximal F1-score	0.401	0.477	0.521
Optimal confidence threshold ²	0.3	0.3	0.45
Precision with optimal conf. threshold	0.59	0.684	0.592
Recall with optimal conf. threshold	0.30	0.312	0.506
PR AUC	0.416	0.37	0.451
ROC AUC	0.157	0.185	0.153

¹ 3340 songs, 754 calls and 7 drumming.

² Confidence threshold with the highest F1-score.

recordings collected in 47 different sampling sites from 17 European countries ranging from Spain to North-West Russia (Fig. 1c) (Schille et al., 2024).

2.2. Manual bird identification by experts

Expert birders identified bird vocalizations in the three datasets. In the ZA-Pygar dataset, all bird sounds found within the first minute of each of the 237 recordings were manually identified and annotated by a single trained birder (DF) by drawing time–frequency bounding boxes around every single vocalization on recording spectrograms (Appendix S2, Fig. S1). In the two other datasets, a list of species present in each recording was generated after the listening, the specific vocalization times of each species remaining unknown. In the Rambouillet dataset, each 5-minute recording selected was manually listened to once, all species detected being listed regardless of their total vocalization time by a single trained birder (LB). As for the TreeBodyguards dataset, given its wide geographical range, we distributed the recordings among 21 expert birders (see Acknowledgements), each of them manually listening to and identifying bird sounds from between 4 (one site) to 52 recordings (13 sites).

2.3. BirdNET-assisted analysis of recordings

The BirdNET version chosen for this study is BirdNET-Analyzer v2.4, the most recent release of the algorithm at the time of publication. BirdNET takes a sound file as input, which it splits into 3-second segments before providing a list of species detected in each segment along with a confidence score assigned to each identification, with values ranging from 0 to 1. By default there is no overlap between consecutive prediction segments, i.e., each segment begins where the previous

segment ends, but BirdNET offers the possibility of allowing a certain degree of overlap (Fig. S2). Another configurable parameter is the detection sensitivity, with potential input values ranging from 0.5 to 1.5. Higher values of this parameter result in a lower threshold for the detection of bird vocalizations in the input recording, thus translating into a greater expected number of bird identifications by BirdNET. In this study we initially performed the same analyses with allowed overlaps of 0 s, 1 s and 2 s between consecutive segments and with detection sensitivity values of 0.5, 1 and 1.5. Despite the increase in BirdNET processing time associated with the use of higher overlaps, the superior performances (as measured by Area Under the Curve scores for both Receiver Operating Characteristic and Precision-Recall curves) obtained with an overlap of 2 s and a detection sensitivity of 1.5 on the ZA-Pygar dataset made us select them as the input values to evaluate BirdNET with in all datasets (Table 2, section 3.1). Finally, we configured BirdNET to filter its list of potentially detectable species based on the approximate date (in the form of week of the year) and geographic coordinates of each recording (Appendix S3).

2.4. Comparing BirdNET and expert identifications

We compared the results obtained with BirdNET against the identifications made by the expert birders in order to evaluate the performance of the algorithm. BirdNET results corresponding to the ZA-Pygar dataset could be analyzed at a higher level of detail (at the vocalization level) than those obtained for the other two datasets, since its temporally annotated identifications make it possible to confront human and BirdNET identifications on each 3 s segment of recording analyzed. For our evaluation we defined 4 possible categories –True Positives (TP), False Positives (FP), True Negatives (TN) and False Negatives (FN)– for each species and acoustic sample, the categorization criteria being slightly variable between the three acoustic datasets analyzed (see detailed explanation in Table S1).

Based on the categorization described, we calculated the precision, recall and False Positive Rate (FPR) of the algorithm for each minimum confidence threshold studied, going from 0.10 to 0.99 with a step of 0.01 (e.g., a minimum confidence threshold of 0.5 implies that all BirdNET identifications with confidence levels lower than 0.5 were filtered out). Each of these thresholds was applied consistently across all species present in the dataset or identified by BirdNET, rather than using variable thresholds on a species-by-species basis.

Precision is a measure of the reliability of BirdNET identifications, i.e., it estimates the probability that a given BirdNET identification will be correct, and is calculated by dividing the number of species correctly detected by the total number of species detected by the algorithm in the acoustic sample analyzed. Recall estimates the probability that a species present in the acoustic sample will be correctly detected by BirdNET, and is calculated by dividing the number of species correctly detected by the total number of species actually present in the acoustic sample analyzed. Finally, FPR estimates the probability that a species absent from the acoustic sample will be detected by BirdNET, and is calculated by dividing the number of species mistakenly detected by the total number of species absent from the acoustic sample analyzed (only considering those featuring in the species lists generated following the procedure explained in Appendix S3). The specific formulas used are the following:

- Precision = TP/(TP + FP)
- Recall = TP/(TP + FN)
- FPR = FP/(FP + TN)

Different conclusions can be drawn from these metrics at different levels of analysis. In the ZA-Pygar dataset, measuring these metrics at the vocalization level provides us with a fine-grained picture of BirdNET performance. However, since the total vocalization time of any given species varies significantly across different recordings, evaluating

Table 2

Area Under the Curve (AUC) scores for both Receiver Operating Characteristic (ROC) and Precision-Recall (PR) curves depending on the detection sensitivity used and the levels of overlap allowed between consecutive prediction segments by BirdNET. The *voc*, *rec*, and *ds* prefixes correspond to precision, recall and FPR being calculated at the vocalization level, recording level and dataset level, respectively. Best results are shown in bold and worst in italics. Only results from the ZA-Pygar dataset are included.

Overlap	Detection sensitivity	voc_PR AUC	voc_ROC AUC	rec_PR AUC	rec_ROC AUC	ds_PR AUC	ds_ROC AUC
0 s	0.5	0.312	0.011	0.177	0.049	0.255	0.084
0 s	1.0	0.384	0.012	0.316	0.051	0.360	0.076
0 s	1.5	0.382	0.023	0.420	0.136	0.449	0.130
1 s	0.5	0.374	0.014	0.213	0.051	0.363	0.038
1 s	1.0	0.408	0.018	0.336	0.060	0.409	0.062
1 s	1.5	0.388	0.031	0.423	0.143	0.428	0.148
2 s	0.5	0.363	0.036	0.246	0.058	0.354	0.057
2 s	1.0	0.428	0.036	0.380	0.062	0.445	0.058
2 s	1.5	0.432	0.054	0.416	0.157	0.446	0.152

BirdNET based on the correctness of each individual identification could result in a small number of recordings with long vocalization times having a disproportionate weight over a greater number of recordings with shorter vocalization times. Thus, calculating precision and recall at the recording level can be an appropriate way of homogenizing the weight of each recording in the final results. Finally, calculating precision and recall at the level of the whole acoustic dataset can inform us about the reliability and exhaustiveness of BirdNET results when using them to provide us with a broad picture of the composition of a bird community recorded over multiple hours or days.

We therefore calculated precision, recall and FPR at all three different levels of analysis: (i) at the vocalization level (only for the ZA-Pygar dataset), (ii) at the recording level and (iii) at the dataset level. The metrics calculated at the first level will be referred to as *voc_precision*, *voc_recall* and *voc_FPR*, the metrics calculated at the second level will be referred to as *rec_precision*, *rec_recall* and *rec_FPR* and the metrics calculated at the third level will be referred to as *ds_precision*, *ds_recall* and *ds_FPR* (Table 3). It is important to note that, since our categorization criteria imply that one correct identification can override any number of incorrect identifications of the same species within the same acoustic sample, the values obtained for these metrics will be highly influenced by the level of analysis chosen. Longer acoustic samples provide more opportunities for BirdNET to detect a given species, either correctly or incorrectly, but the asymmetric weight given to correct identifications over incorrect ones implies that the number of TPs will scale more rapidly with time than the number of FPs. This results in a bias towards more positive results when longer acoustic samples are used.

Once calculated, we used these values to plot the Receiver Operating Characteristic (ROC) and Precision-Recall (PR) curves, both with an estimation of the Area Under the Curve (AUC) (Davis & Goadrich, 2006). The ROC curve consists in plotting recall against FPR for each minimum confidence threshold studied in order to show the trade-off between the two metrics: as the minimum confidence score required to accept BirdNET identifications increases, the number of FPs will decrease, but so will the number of TPs. The PR curve, on the other hand, plots precision against recall for each minimum confidence threshold used, showing the trade-off between these two metrics as well. The AUC is, in both cases, a measure of the predictive power of the algorithm with a range of possible values going from 0 to 1, higher values being indicative of a higher predictive power.

Another metric that we used to evaluate the performance of the algorithm for each minimum confidence threshold studied is the F-score. The F-score measures the overall predictive power of the algorithm by considering both precision and recall scores, the weight assigned to each variable depending on the β coefficient:

$$F\text{-score} = (\beta^2 + 1) * \text{precision} * \text{recall} / (\beta^2 * \text{precision} + \text{recall})$$

An F-score with $\beta = 1$ assigns the same importance to precision and recall, whereas an F-score with $\beta > 1$ weighs recall more heavily than

precision, and vice versa for $\beta < 1$. We performed F-score analyses using three different β values: $\beta = 1$ as a standard value to facilitate the comparison of our results with those of other studies, $\beta = 0.25$ to reflect a clear prioritization of precision over recall and $\beta = 0.1$ to reflect an even more marked asymmetry between the importance assigned to these two metrics. We chose such asymmetrical coefficients because we estimate that ensuring high precision levels is paramount in most biodiversity research projects, i.e., it is usually considered preferable not to detect present species rather than mistakenly detecting non-present ones (Tolkova et al., 2021). Moreover, some types of population models (e.g., occupancy models) can account for the imperfect detection of species in the target study sites (Brunk et al., 2023; Bielski et al., 2024), further underscoring the importance of false negatives with respect to false positives.

2.5. Factors influencing BirdNET performance

Using only the ZA-Pygar dataset, we further analyzed how BirdNET performance might be influenced by factors related to the acoustic dataset analyzed (total duration recorded, habitat recorded, passive recorder used, preponderance of biophony over anthropophony and geophony as measured by NDSI (Bradfer-Lawrence et al., 2023; Kasten et al., 2012; see Appendix S6), and number of species vocalizing at the same time) as well as the number of recordings available online for each species as a proxy for the size of the training dataset used by BirdNET.

To estimate the influence of the size of the dataset (i.e., total recording duration) analyzed on BirdNET performance, we calculated recall and FPR at the dataset level (*ds_recall* and *ds_FPR*) for 23 different subset sizes going from 10 to 230 recordings using a step increase of 10. For each subset size, we performed 200 random selections of recordings from the whole set of 237 recordings making up the ZA-Pygar dataset and then averaged out their results (i.e., we generated 200 random subsets of 10 recordings and then averaged out the *ds_recall* and *ds_FPR* corresponding to each of these subsets; likewise for all other subset sizes until 230). This number of random selections proved to be sufficient to perfectly replicate the ordinality of the *ds_recall* and *ds_FPR* averages by subset size across 2 iterations of the same analysis.

As for the variability of the predictive power of BirdNET across species, we distinguished between two different types of causal factors: (i) factors related to the difficulty inherent in identifying certain vocalizations, such as some acoustic patterns being easier to identify than others, or bird species with vocalizations highly similar to those of other species being harder to identify than species with more idiosyncratic sounds, and (ii) the size and quality of the acoustic data available for each species on the online platforms used as sources of data for the training of the algorithm. The first type of factor being considered out of scope for this study, we analyzed the influence of species-specific data availability on BirdNET performance. Despite not having direct access to the training datasets used by BirdNET, we know that the Xeno-canto platform (Xeno-canto, 2023) and the Macaulay Library of Natural

Table 3
Description of the different metrics used to evaluate BirdNET performance.

Evaluation Metric	Acoustic sample	Description	Aggregation method
voc_precision ¹	3-second audio segment	Proportion of BirdNET identifications that are correct (match in time and species with an annotation by an expert).	No aggregation: each BirdNET identification is either correct (TP) or incorrect (FP)
voc_recall ¹	3-second audio segment	Proportion of manually annotated bird vocalizations that have been correctly identified by BirdNET	No aggregation: each bird vocalization has either been correctly identified (TP) or not (FN)
voc_FPR ¹	3-second audio segment	Number of species mistakenly detected by BirdNET as a fraction of all species actually absent from the prediction segment ²	No aggregation: each species absent from the 3-second audio segment has either been mistakenly detected (FP) or not detected (TN) by BirdNET
rec_precision	Entire recording ³	Proportion of species detected by BirdNET that are actually present in the recording	Aggregation at the recording level: each species detected by BirdNET has either been correctly detected at least once (TP) or not (FP) in the recording
rec_recall	Entire recording ³	Proportion of species present in the recording that have been correctly detected by BirdNET	Aggregation at the recording level: each species present in the recording has either been correctly identified at least once (TP) or missed (FN) by BirdNET
rec_FPR	Entire recording ³	Number of species mistakenly detected by BirdNET as a fraction of all species actually absent from the recording ²	Aggregation at the recording level: each species absent from the recording has either been mistakenly detected (FP) or not detected (TN) by BirdNET
ds_precision	Acoustic dataset (compilation of recordings)	Proportion of species detected by BirdNET that are actually present in the acoustic dataset	Aggregation at the dataset level: each species detected by BirdNET has either been correctly detected at least once (TP) or not (FP) in the dataset
ds_recall	Acoustic dataset	Proportion of species present in the acoustic dataset that have been correctly detected by BirdNET	Aggregation at the dataset level: each species present in the dataset has either been correctly identified at least once (TP) or missed (FN) by BirdNET
ds_FPR	Acoustic dataset	Number of species mistakenly detected by BirdNET as a fraction of all species actually absent from the acoustic dataset ²	Aggregation at the dataset level: each species absent from the dataset has either been mistakenly detected (FP) or not detected (TN) by BirdNET

¹ Only calculated for the ZA-Pygar dataset.

² Only considering those featuring in the species lists generated following the procedure described in Appendix S3.

³ Corresponding to 1 min in the ZA-Pygar dataset, 5 min in the Rambouillet dataset and 10 min in the TreeBodyguards dataset.

Sounds (Macaulay, 2023) were used as sources of audio data for this purpose (Kahl et al., 2021). Even though recordings from other sources were included in the training of the algorithm and the sampling procedures used to convert archival recordings to training data were not simply 1:1 (personal communication, January 31, 2024), we used the total number of foreground recordings available on both platforms for each species analyzed as a rough proxy for the species-specific availability of recordings during the training phase of the algorithm. More specifically, we examined the correlation between the number of recordings available on these platforms and BirdNET precision, recall and F1-scores across species. This allowed us to roughly estimate the explanatory power of species-specific recording availability over the variability of BirdNET performance across species. Species detected fewer than 10 times were filtered out from the analysis, their sample sizes being too low for results to be minimally reliable. Finally, it is important to note that, unless explicitly specified, all figures and statistical results correspond to the analysis of recordings with BirdNET-Analyzer v2.4, using a detection sensitivity of 1.5 and an overlap window of 2 s between consecutive prediction segments.

3. Results

3.1. Optimizing BirdNET parameters

Our evaluation of BirdNET performance under different input parameter configurations suggests that 1 s overlap windows improve AUC scores on both ROC and PR curves with respect to the default 0-second overlap, and that 2 s overlaps improve these scores even further (Table 2). This improvement seems to arise from the fact that high degrees of overlap facilitate the capture of a substantial part of any given bird vocalization within a single prediction segment (Fig. S1). Since longer vocalization times within a given prediction segment are predictive of higher voc_recall levels (Fig. S3; Spearman, $r_s = 0.956$ and $p < 0.001$), an increase in overlap between consecutive prediction segments should correspondingly result in higher recall scores. Likewise, the predictive power of BirdNET as measured by the ROC and PR AUC scores seems to improve along with higher values of the detection sensitivity parameter (Table 2), suggesting that a detection sensitivity of 1.5 (from a range of possible values going from 0.5 to 1.5) might be the optimal value for overall performance in the specific context of this study.

3.2. Assessing BirdNET performance

We found the confidence scores provided by the algorithm to be positively correlated with the actual probability that the corresponding identification is correct (Figs S4 and S5; Kruskal-Wallis, $H(1) = 5977.7$ and $p < 0.001$). This means that a minimum confidence threshold can be established so that identifications with low confidence scores are filtered out, thus retaining only the most reliable ones. In accordance with this premise, the ROC and PR curves (Fig. 2) reveal a clear trade-off between the precision and recall of the algorithm, as well as between recall and FPR: the higher the minimum confidence score required to accept BirdNET identifications, the higher the precision and the lower the FPR will be. Nonetheless, improvements in these two metrics have to be weighed against the lower recall associated with a higher level of selectiveness. Average precision scores by species improve considerably by setting higher minimum confidence thresholds (Fig. S6), recall scores by species following the opposite trend (Fig. S7).

When analyzing BirdNET results at the recording level for the ZA-Pygar dataset, we found that the optimal minimum confidence thresholds for maximizing global F-scores for β -values of 1, 0.25 and 0.1 are 0.3, 0.55 and 0.65, respectively (Fig. 3). The results obtained for each of these thresholds show that, as the minimum confidence score required to accept BirdNET identifications becomes stricter, both TPs and FPs decrease while FNs rise sharply (Fig. 4). This causes both the number of species correctly detected and the number of species mistakenly

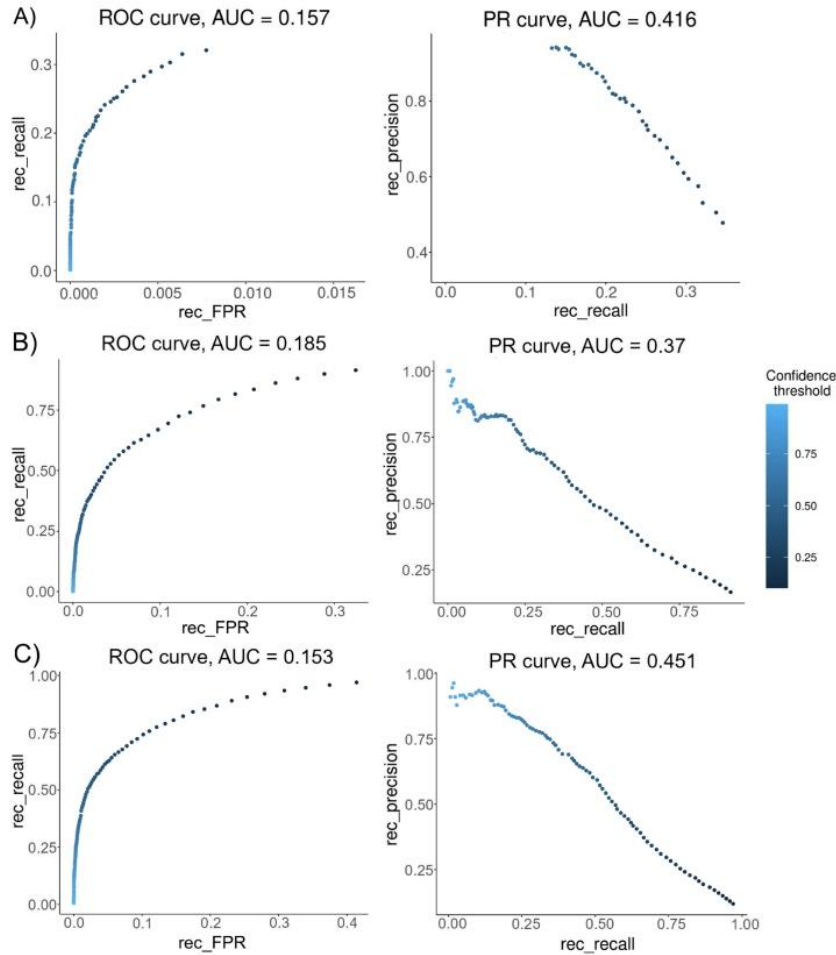


Fig. 2. Receiver Operating Characteristic (left) and Precision-Recall (right) curves of BirdNET-Analyzer. The three plots correspond to results obtained at the recording level for the (A) ZA-Pygar, (B) Rambouillet and (C) TreeBodyguards datasets.

detected to vary considerably depending on the minimum confidence threshold used. While a minimum confidence threshold of 0.3 allows for a ds_recall of 0.65 (i.e., the correct detection of 65 % of the species present in the dataset), a threshold of 0.55 reduces this figure to 0.55 and a threshold of 0.65 reduces it further to 0.5. On the other hand, ds_FPR (i.e., the proportion of species absent from the dataset that are mistakenly detected by the algorithm) varies even more strongly along with the confidence threshold used, with respective values of 0.41, 0.07 and 0.03. In absolute terms, this translates into 48, 41 and 37 species correctly detected and 85, 15 and 6 species mistakenly detected, respectively.

It is important to note that a non-negligible number of species have only been manually detected in fewer than 10 recordings per dataset (47, 15 and 53 species in the ZA-Pygar, Rambouillet and TreeBodyguards datasets, respectively) (Fig. S8). Hence, we deem our estimations of the predictive power of the algorithm for these species to be highly unreliable. Limiting the analysis to species detected –either by BirdNET or by the expert birder– in a minimum of 10 recordings, while filtering out less common species, results in a substantially higher overall performance of the algorithm. More specifically, when analyzing the ZA-Pygar dataset with a confidence threshold of 0.3, this filtering procedure improves $rec_precision$ from 0.59 to 0.71 without compromising rec_recall , which actually remains stable at 0.32. The results obtained after applying this filter (Fig. 4d) also suggest that the variability in

BirdNET predictive power across species is not as pronounced as what we might infer from the analysis of unfiltered results (Fig. 4a), since the low number of data points available for many species leads to more variable outcomes.

Overall, our analyses yielded highly consistent results across the three datasets studied, with maximal F1-scores (corresponding to minimum confidence thresholds between 0.3 and 0.45) ranging from 0.4 to 0.52 at the recording level (Table 1). This roughly means that, in the best case, we can expect two errors (FP or FN) for each correct BirdNET prediction. BirdNET performance is lower (maximal F1-score of 0.33 for a minimum confidence threshold of 0.4) when results are analyzed at the vocalization level (i.e., 1 correct prediction for every 3 errors).

3.3. Factors influencing BirdNET performance

In order to properly isolate the variables of interest and ensure that the heterogeneous identification procedures and recording durations used in the three datasets do not have a confounding effect, only recordings from the ZA-Pygar dataset are included in the following analyses.

Regarding the influence of sample size on BirdNET performance, there appears to be a positive linear correlation between ds_F1 -scores and the logarithm of the number of recordings sampled (Fig. 5; linear regression, adjusted $R^2 = 0.539$, $p < 0.001$). The same seems to be true

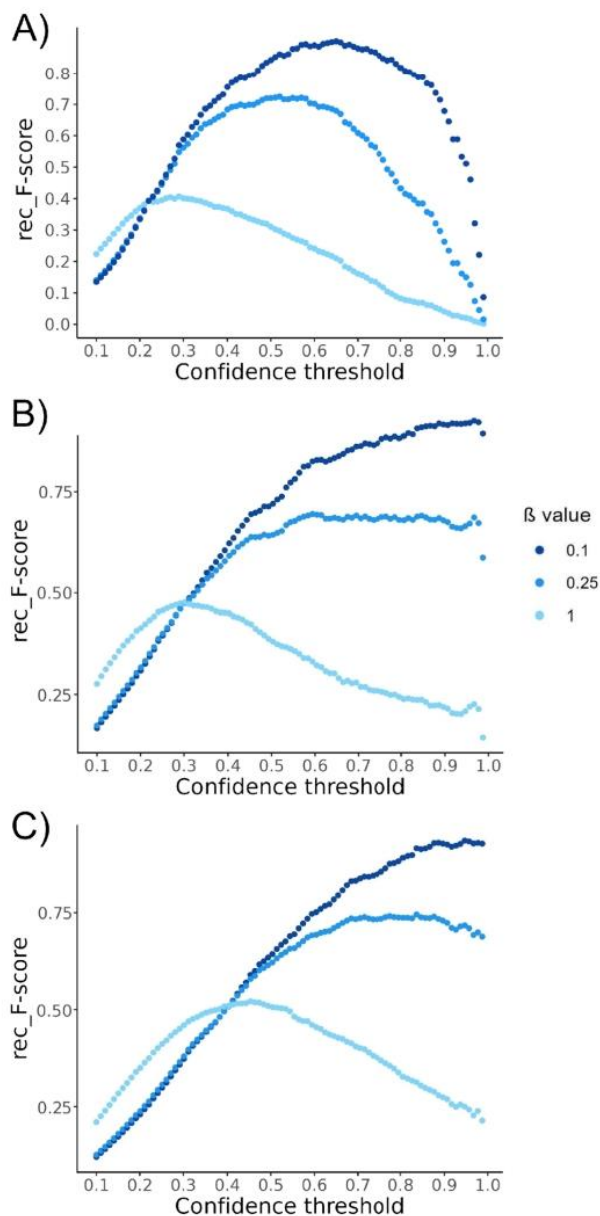


Fig. 3. F-score curves of BirdNET-Analyzer for β values of 0.1, 0.25 and 1. The three plots correspond to results obtained at the recording level for the (A) ZA-Pygar, (B) Rambouillet and (C) TreeBodyguards datasets.

for ds_TPR (adjusted $R^2 = 0.376$, $p < 0.001$) and ds_recall (adjusted $R^2 = 0.095$, $p < 0.001$) as well, in all cases after controlling for the minimum confidence threshold used. ds_FPR shows a pronounced decrease when higher confidence scores are required whereas ds_recall , while following the same trend, shows differences of more moderate proportions as a response to increased minimum confidence thresholds (Fig. 5). This suggests that a given global recall target can be reached either by setting a low enough minimum confidence threshold or by setting a high minimum confidence threshold and procuring a large enough acoustic dataset, the latter approach resulting in substantially lower ds_FPR values.

The correlation tests performed between the number of different bird species vocalizing simultaneously and BirdNET performance metrics

suggest that vocalization superposition has a significant influence on $voc_precision$ (Fig. S9; Spearman, $r_s = 0.122$ and $p < 0.001$) but not on voc_recall and voc_F1 -scores (Spearman, $r_s = -0.051$ and $p = 0.285$ for voc_recall , $r_s = 0.017$ and $p = 0.72$ for voc_F1 -score). In contrast, neither the recorder used nor the predominant habitat sampled seem to affect BirdNET performance (Fig. S10), since neither $rec_precision$, rec_recall nor rec_F1 -scores show significant differences across different habitats (Kruskal-Wallis, $H_4 = 1.11$ and $p = 0.775$ for $rec_precision$, $H_4 = 0.79$ and $p = 0.852$ for rec_recall and $H_4 = 1.24$ and $p = 0.744$ for rec_F1 -score) or recorders (Kruskal-Wallis, $H_3 = 4.08$ and $p = 0.130$ for $rec_precision$, $H_3 = 8.92$ and $p = 0.116$ for rec_recall and $H_3 = 2.04$ and $p = 0.36$ for rec_F1 -score). Finally, the number of foreground recordings available on Xeno-canto and the Macaulay Library for each species studied appears to have a significant influence on species-specific $rec_precision$, rec_recall and rec_F1 -scores. More concretely, the logarithm of the number of recordings available seems to correlate positively with $rec_precision$ and rec_F1 -score but negatively with rec_recall (Fig. 6; Spearman, $r_s = 0.506$ and $p < 0.001$ for $rec_precision$, $r_s = -0.484$ and $p = 0.002$ for rec_recall and $r_s = 0.599$ and $p < 0.001$ for rec_F1 -score).

4. Discussion

BirdNET appears as a promising tool to assist in the assessment of bird community composition through the automated processing of large-scale eacooustic data. Our analyses reveal that BirdNET can provide us with reasonably high levels of precision or recall, at least in the regions studied, but the inevitable trade-off between these two metrics prevents satisfactory results for both at the same time (maximal $F1$ -score < 0.5). Despite BirdNET still having considerable room for improvement in both precision and recall scores, it is important to note that identifications by field observers are not exempt from errors either. Recent studies suggest that acoustic identifications by highly experienced birders present precision scores no higher than 0.94 and recall scores no higher than 0.89 (Farmer et al., 2012; Campbell & Francis, 2011), implying that BirdNET identifications with exceptionally high confidence scores might prove to be as accurate or more as those made by reasonably experienced birders.

Regarding precision scores in particular, our results are in line with previous studies (Sethi et al., 2021; Cole et al., 2022) showing that BirdNET identifications can be highly reliable, especially for common species (Fig. 6), provided that a sufficiently high minimum confidence threshold is used (Fig. S6). Indeed, confidence scores assigned to each identification by the algorithm are positively correlated with the actual probability (species-agnostic $id_precision$) that the identification in question is correct (Fig. S4). It is important to note, though, that the correspondence between confidence scores and precision is not of 1 to 1, i.e., a confidence score of 0.5 is not equivalent to a 50 % probability that the corresponding identification is correct. This correspondence can also vary across different species and recording settings, i.e., a given confidence score can translate into different levels of precision depending on the species identified and acoustic features such as the sampling rate of the recording (Wood & Kahl, 2024). Moreover, recent findings suggest that thresholds based on the use of contextual information in combination with BirdNET confidence scores can yield higher precision results than thresholds based on BirdNET confidence scores alone. More specifically, the precision of a given BirdNET identification might be less reliably correlated with its own confidence score than with the aggregate quality (average, median, minimum and maximum confidence scores) and quantity of BirdNET identifications obtained for the same species over a certain recording duration within the same site (Singer et al., 2024).

Our results further suggest that BirdNET precision can be improved not only by raising the minimum confidence threshold used, but also by filtering out species not having reached a minimum number of BirdNET detections across the whole dataset (Fig. S6). We found, however, that

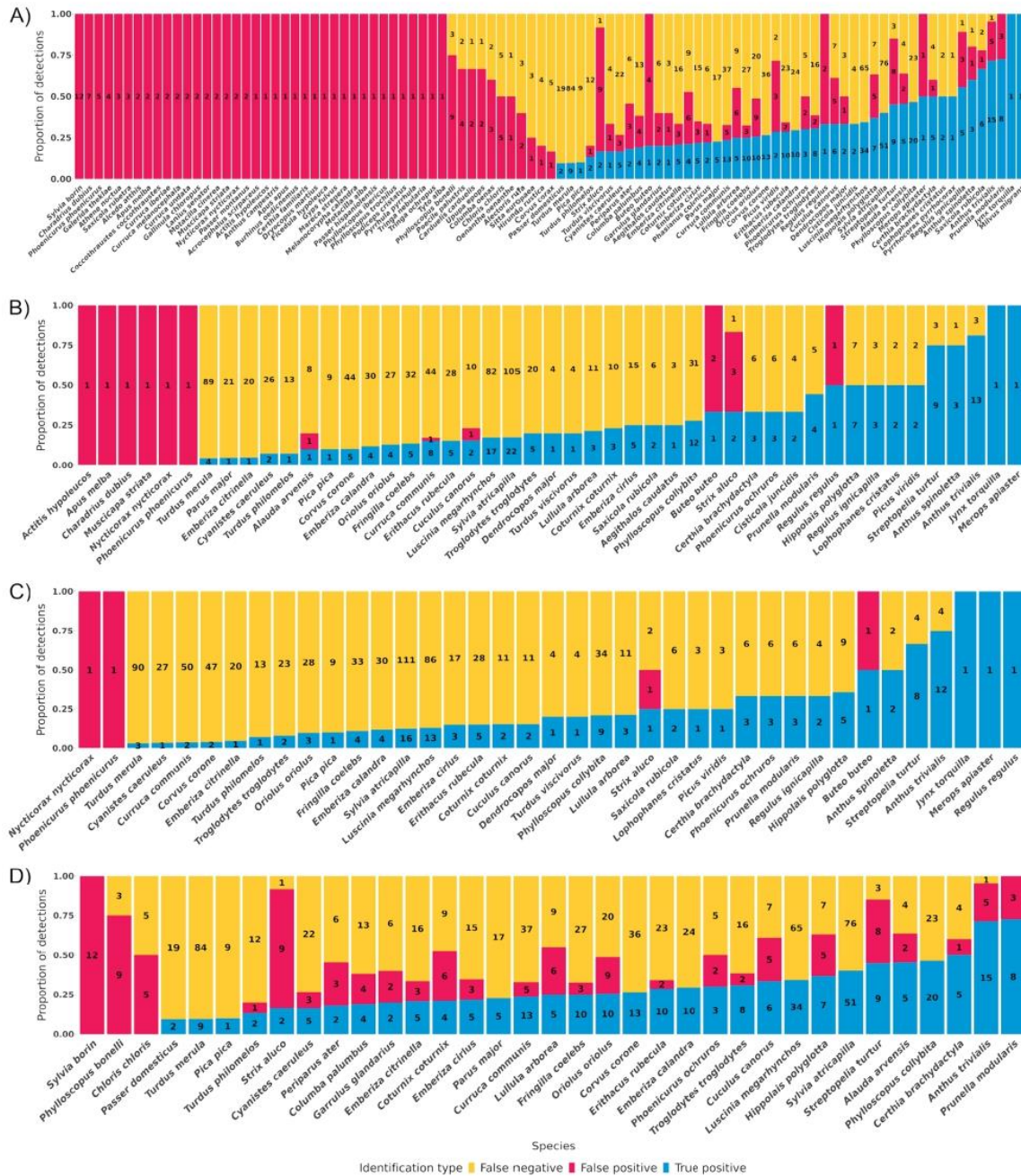


Fig. 4. Proportion of true positives, false positives and false negatives by bird species in BirdNET results with confidence scores (A) ≥ 0.3 , (B) ≥ 0.55 , (C) ≥ 0.65 and (D) ≥ 0.3 , the latter only including species with ≥ 10 detections (either by BirdNET or by an expert). Results are calculated at the recording level and only recordings from the ZA-Pygar dataset are included.

species such as garden warblers (*Sylvia borin*) and Western Bonelli's Warblers (*Phylloscopus bonelli*) were identified by BirdNET on a high number of occasions, always incorrectly, and exceeded our minimum occurrence frequency threshold (Fig. 4d). Non-negligible numbers of FPs for other non-present species suggest caution around their identifications as well. On the positive side, these misidentifications seem to be effectively filtered out by establishing a strict enough global minimum confidence threshold (Fig. 4c), and could probably be filtered out even more effectively with the usage of species-specific thresholds. It is

important to note, though, that background sounds can vary considerably between different locations and times of the year, so the list of problematic species can turn out to be substantially different in other spatio-temporal contexts. We therefore recommend that, prior to its use, a preliminary assessment of BirdNET be conducted with soundscapes from the target study site. This would allow researchers to preemptively identify the species appearing most often as FPs and to pay special attention to identifications of these species when examining BirdNET results. Another possible method to reduce FPs, as suggested by a recent

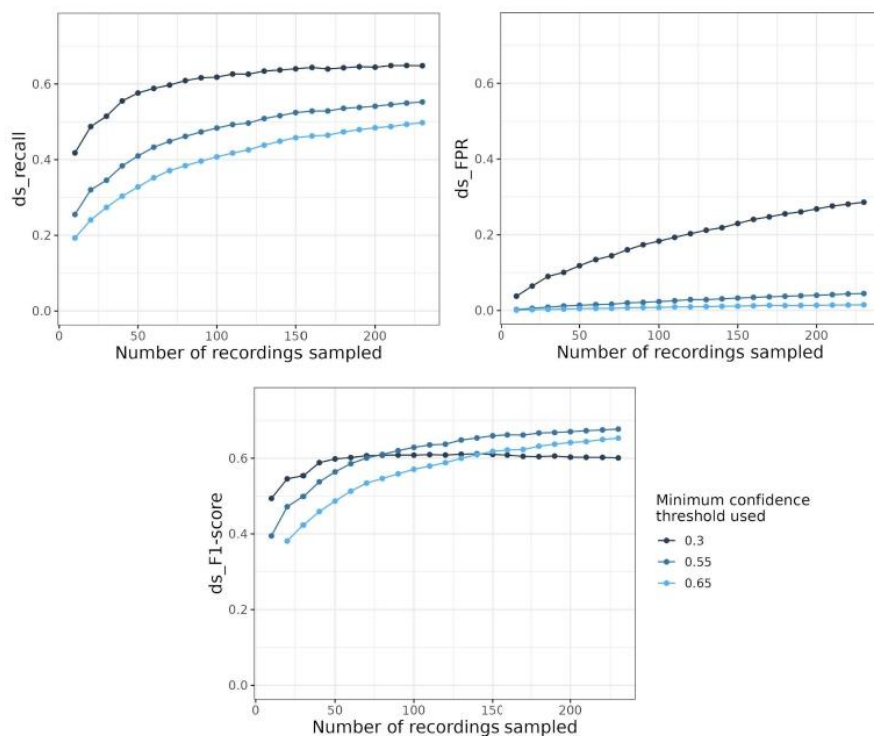


Fig. 5. Dataset performance depending on the number of recordings included in the analysis. ds_recall (top-left), ds_FPR (top-right) and ds_F1 scores (bottom) are shown for virtual datasets of increasing size depending on the minimum confidence threshold required to validate BirdNET identifications. Only recordings from the ZA-Pygar dataset are included.

study (Toenies & Rich, 2021), would be to filter out BirdNET identifications of diurnal species when analyzing nocturnal recordings, thus effectively preventing most dog barks and frog croaks from being misclassified as diurnal waterbird calls.

Our results (Fig. 6, S6, S7), along with those of previous studies (Kelly et al., 2023; Wood et al., 2023; Singer et al., 2024), make it clear that BirdNET precision and recall results can be highly variable across species, even when controlling for the minimum confidence threshold used. We thus recommend that, when using BirdNET for species-specific occupancy modeling, researchers conduct preliminary tests to determine the optimal minimum confidence threshold for the species of interest rather than relying on a threshold optimized for global performance when consistently used across a wide range of species. We estimate that this approach could allow BirdNET users targeting specific species to readily exceed the global performance benchmarks presented in this study. While we expect the use of species-specific minimum confidence thresholds to improve BirdNET performance when applied to the characterization of bird communities as well, the estimation of optimal thresholds for each species potentially present in a given study area represents a much greater challenge for this approach. It is also important to bear in mind that the optimal minimum confidence threshold to be used for any species will always be conditional on recording settings and on the importance that each user or research group assigns to minimizing FPs vs. minimizing FNs.

Despite our study being based on > 600 recordings and > 4000 manually annotated bird vocalizations (Table 1), the number of BirdNET identifications obtained for any given species is quite low, especially in the high confidence range. More precisely, no species has been identified by BirdNET in more than 29 recordings across all datasets (Table S2) or in more than 32 prediction segments in the ZA-Pygar dataset (Table S3) with a confidence score greater or equal than 0.9. This is partly due to the wide bird diversity covered by our acoustic datasets and the short

duration of each recording analyzed, and partly because the vast majority of BirdNET identifications obtained have low confidence scores (Figure S5). More specifically, only 1692 out of 1,047,794 BirdNET identifications obtained across the three datasets have a confidence score ≥ 0.9 , corresponding to 0.16 % of all identifications. Hence, the limited per-species amount of high-confidence BirdNET identifications did not allow for the analysis of BirdNET performance based on species-specific minimum confidence thresholds. We therefore limited our analyses to the estimation of the best possible global threshold for optimized results at the community level. These values, while suboptimal for any given species, might provide researchers seeking to use BirdNET for the general characterization of bird community compositions (Hartig et al., 2023) with a basic picture of the performance that can be expected from the algorithm at different levels of precision exigency.

Another question that arises from our results is the degree to which the cross-species variability in BirdNET performance is due to (i) cross-species differences in the amount or quality of recordings available to train the algorithm with, (ii) the inherent difficulty in identifying vocalizations with certain acoustic patterns, or (iii) the identification difficulty arising from two or more species emitting highly similar sounds. Assuming that the first obstacle is the most tractable among the three mentioned, the higher the percentage of cross-species variation in BirdNET performance that is explained by recording availability, the more optimistic we should be regarding the improvement of the performance of the algorithm over time. In this regard, our results suggesting that 19 % of the variance in F1-scores between species can be explained by online recording availability (Fig. 6) provide ground for optimism about the future reliability of BirdNET. More concretely, this could mean that the diagnostic capacity of BirdNET for less common species could be considerably improved by enlarging the pool of available acoustic data for these species.

We presume that a higher availability of acoustic data could facilitate

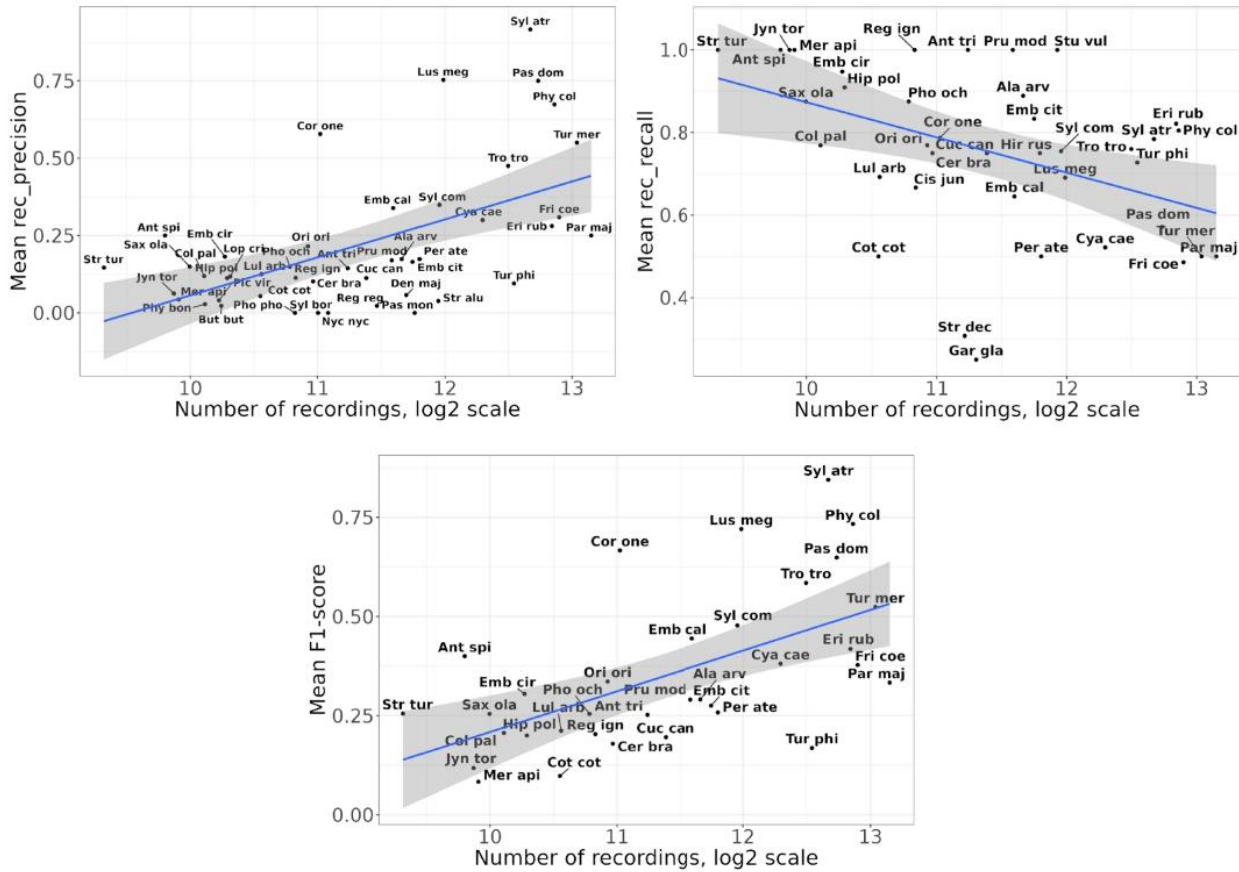


Fig. 6. Relationship between BirdNET performance and the number of foreground recordings available for each species on the Xeno-canto and Macaulay Library platforms. More specifically, the mean rec_precision (top-left), rec_recall (top-right) and rec_F1 (bottom) scores are plotted against the base-2 logarithm of the number of recordings available online for the species in question. Only species having been detected 10 or more times by BirdNET are included in the precision analysis, only species with at least 30 s of (manually annotated) total vocalization time are included in the recall analysis and only species meeting both criteria are included in the F1-score analysis. The minimum confidence threshold used is 0.1, and only recordings from the ZA-Pygar dataset are included.

BirdNET performance through two different mechanisms: (i) by enabling BirdNET to enlarge the size of its training dataset, and (ii) by improving the quality of the recordings comprising its training dataset. Acoustic quality scores are included in the metadata of recordings on Xeno-canto and the Macaulay Library, and higher-quality recordings were prioritized in the selection of training data for the BirdNET algorithm (Kahl et al., 2021). Hence, we would expect the average acoustic quality to be higher in the training datasets of species with larger pools of available recordings to choose from. Inasmuch as both higher-quality recordings and larger training datasets could facilitate a better adjustment of the algorithm to the target bird vocalizations, these factors could provide a plausible explanation to the positive correlation observed between species-specific acoustic data availability and BirdNET predictive power.

We further found a significant linear relationship between the logarithm of the recording time analyzed and the proportion of recorded species having been correctly detected by BirdNET (Fig. 5). A possible explanation to this correlation would be that the short total vocalization time recorded for the least frequent species often results in no correct detections of these species by BirdNET. Thus, insofar as longer recording times contain a greater number of vocalizations per species in expectation, we should expect larger acoustic datasets to provide more chances for the algorithm to correctly detect less frequent species. We therefore hypothesize that a sufficiently high number of recording hours analyzed could partially compensate for the low recall scores obtained when high

minimum confidence thresholds are used. Hence, were the necessary conditions to be met, BirdNET might prove successful in capturing most bird species present in a study site while also ensuring a relatively low number of FPs. These results, in line with recent findings (Toenies & Rich, 2021; Cole et al., 2022; Wood et al., 2021), are encouraging with respect to the potential of BirdNET to reliably and comprehensively describe bird communities in research projects with large amounts of ecoacoustic data at their disposal. Similar results have been obtained in studies targeting specific species and having used highly conservative minimum confidence thresholds (Brunk et al., 2023; Bielski et al., 2024), providing further evidence that ecologically meaningful results can be obtained even with a very strong emphasis on precision over recall when analyzing acoustic datasets of sufficient duration.

Our results also show that the predominance of biophony over anthropophony and geophony in recordings, as measured by NDSI (Kasten et al., 2012), appears to be positively correlated with recall scores (see Appendix S6, Fig. S11). We propose three possible hypotheses explaining this correlation: (i) anthropogenic and geological sounds might hinder the performance of the algorithm by concealing or blurring bird vocalizations, (ii) BirdNET might have mostly been trained with recordings with relatively low levels of background noise, thus being less well calibrated to identify bird vocalizations in noisy recordings, and (iii) high NDSI scores can be indicative of high-amplitude bird vocalizations, which might be easier to identify than low-amplitude bird vocalizations (Pérez Granados, 2023). If the second hypothesis were

correct, we consider it plausible that the application of a noise reduction filter to recordings prior to their analysis with BirdNET could result in an enhanced performance of the algorithm.

Overall, the results of this study may provide valuable information for research groups considering the possibility of using BirdNET for the automated analysis of passively collected environmental soundscapes. However, these results provide an overview of the current potential of BirdNET in a very specific context, and therefore cannot be reliably extrapolated to other regions with different habitats, levels of anthropogenic pressure or bird community compositions. Care must also be taken when extrapolating our results to other areas with similar but geographically distant bird communities, as bird songs and calls can present subtle variations across different regions (Slabbekoorn & Smith, 2002). Likewise, the analyses performed to evaluate the effect of dataset size on BirdNET performance have been conducted with subset sizes of very short durations (on the order of minutes or hours), so our findings might fail to generalize to acoustic datasets of larger scale. The same caveat applies to the optimal values for BirdNET configuration parameters found in this study as well. Higher overlap values between consecutive prediction segments might improve BirdNET performance by facilitating the capture of a substantial part of any given bird vocalization within a single prediction segment (Fig. S1), but they increase processing times as well. In small datasets with few vocalizations of any given species, the improvement in detection capacity might largely compensate for the potential increase in processing time, but the compromise can look very different in large datasets, which provide more opportunities for BirdNET to detect any given species. In these cases, the increased processing time can become a substantial burden without providing much benefit in terms of recall.

Another point that should be borne in mind is that this study starts from the fundamental assumption that all our expert identifications are correct, which is why we used them as the reference to compare BirdNET against. As already mentioned, even highly experienced birders seem to fall short of infallibility (Farmer et al., 2012; Campbell & Francis, 2011), so the possibility that some of the expert identifications included in this study are incorrect cannot be entirely ruled out. As a concluding note, in light of the improvement detected between the recall scores of BirdNET-Analyzer v2.4 and those of older versions of the algorithm –BirdNET-Lite and BirdNET-Analyzer v2.1 to 2.3– that we previously tested with the same data, we consider it plausible that future releases will be capable of identifying bird vocalizations even more reliably and exhaustively. This finding, coupled with the fact that the usage of species-specific minimum confidence thresholds could readily improve the performance benchmarks presented in this study, implies that our results should not be assumed to accurately estimate the best-case performance of BirdNET, but they should rather be interpreted as a lower bound for its potential.

CRedit authorship contribution statement

David Funosas: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luc Barbaro:** Writing – review & editing, Validation, Supervision, Resources, Investigation. **Laura Schillé:** Writing – review & editing, Resources, Investigation, Formal analysis, Data curation. **Arnaud Elger:** Writing – review & editing. **Bastien Castagneyrol:** Writing – review & editing, Resources. **Maxime Cauchoix:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The code used for the analyses performed in this study, as well as both BirdNET and manual identifications/annotations for the three acoustic datasets studied, can be found in the following GitHub repository: https://anonymous.4open.science/r/BirdNET_study_Occitan_ie_2023-8D8F/. The raw acoustic data analyzed is available upon request. We share our code through a link in the “Data availability statement” section

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Appendix A. Supplementary data

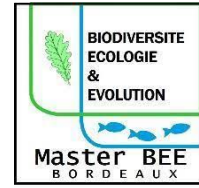
Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112146>.

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7.2. Annexe A2. Évaluation des performances des algorithmes de reconnaissance automatisée des chants d'oiseaux dans divers paysages sonores anthropisés.



Performance assessment of automated algorithms for bird song recognition in diverse anthropogenic soundscapes

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ABSTRACT

To address the challenge of biodiversity conservation and monitoring, it is crucial to leverage all available sources of data and information, including citizen science projects. In this context, BirdNET emerges as a new tool suitable for large-scale bird inventories. However, to effectively use BirdNET, it is important to identify biases in data acquisition. The potential risks these biases pose can be managed, provided they are acknowledged, systematic, and possible to model. This study aims to assess multiple biases, such as distance, signal-to-noise ratio, the biophony/anthrophony ratio, and the type of recorder used.

We selected twenty-two sites in Bordeaux Métropole based on noise intensity levels and analyzed the vocalizations of eight urban bird species using BirdNET on three different smartphones. At each site, we measured the sound intensity and the ratio between biophonic and anthropogenic noise in the surrounding soundscape. We tested two distances (5 meters and 30 meters) between the transmitter and receiver at each site.

Our study demonstrates that the performance of the BirdNET algorithm diminishes as the distance between the sound source and the receiver increases due to a decrease in the signal-to-noise ratio (SNR). In contrast, the ratio of anthrophony to biophony does not affect BirdNET detection capabilities. We also found that different recorders can produce moderately different responses. These findings contribute to the body of research on BirdNET performance, offering insights that improve our understanding of its optimal use in a citizen science framework.

1 | INTRODUCTION

The decline of biodiversity is a worldwide concern (Tittensor et al., 2014). Monitoring biodiversity is essential for implementing conservation efforts as it provides data on population and ecosystem health (De Bello et al., 2010). However, progress in conservation is significantly hindered, if not entirely halted, due to a shortage of qualified personnel, particularly taxonomists, capable of generating this knowledge (Godfray, 2002). This decrease in expertise has created a bottleneck effect, preventing the training of new competent taxonomists for the future. One of the contemporary challenges is to develop multiple sources capable of effectively monitoring biodiversity to complement expert data (Edwards et al., 2021).

To address the challenge of biodiversity conservation and monitoring, it is crucial to leverage all available sources of data and information, including those provided by rapidly advancing tools such as smartphones (Chandler et al., 2017). The widespread adoption of these devices, coupled with the expansion of 5G networks (Davis et al., 2023), has led to a paradigm shift in biodiversity monitoring, as these devices enable easy access to a plethora of tools (e.g., global positioning systems, geographic information systems, microphones, accelerometers, and cameras) allowing for the collection and sharing of environmental data worldwide (Teacher et al., 2013). While these emerging tools are utilized by researchers (August et al., 2015), their user-friendliness also makes them accessible to the general public. Consequently, they enable the expansion of conservation efforts through citizen science, wherein volunteers contribute to the collection and analysis of scientific data (McKinley et al., 2017). Through the production of a huge amount of data, the advancement of scientific knowledge, the shaping of policy, and the encouragement of public engagement, citizen science projects contribute to building social connections and deepening our comprehension of biodiversity (Pocock et al., 2019).

Citizen science represents a valuable approach for acquiring scientific knowledge in the field of biodiversity monitoring and conservation (Pocock et al., 2018). However, legitimate concerns regarding the ability of citizen scientists to accurately identify species and provide reliable biodiversity data still make citizen science controversial (Bonnet et al., 2020). Biases exist and they need to be taken into account to ensure the reliability and validity of the collected data (Callaghan et al., 2021). Among the identified biases, geographical biases are characterized by an increased collection of data in areas with a high concentration of citizen participants, while taxonomic biases involve the underrepresentation of certain species and the overrepresentation of others (Bird et al., 2014). However, the statistical approaches developed to address these biases do not fully resolve the fact that input data may be more or less biased due to differences in the technological tools used (Funosas et al., 2024; Pérez-Granados, 2023b).

In order to address this issue effective tools are being developed in the form of smartphone applications increasingly used worldwide (Wood et al., 2022). They generate considerable amounts of data that are only exploitable through the concomitant development of automated species detection algorithms (e.g., BirdNET, BatDetect and PlantNET). For instance the PlantNET app is an innovative citizen science platform that uses image-based plant identification to engage non-expert contributors and facilitate the collection of botanical observation data (Affouard et al., 2017). However, while photography may be suitable for plants, and, to some extent insect pollinators (Desaegher et al., 2018), it may not be as effective for more mobile animal species such as birds.

To meet this challenge the Ornithology Laboratory at Cornell University (USA) and Chemnitz University of Technology (Germany) launched in 2019 BirdNET, a new analytical approach which is able to identify over 6,000 bird species from around the world using their vocalization (Wood & Kahl, 2024). It can be used for large-scale monitoring while being cost-effective (Clark et al., 2023) and avoiding observer skill differences (Sugai et al., 2019). The BirdNET algorithm is a deep convolutional neural network trained on high-quality recordings from labeled birdsong repositories such as Xeno-Canto (<https://xeno-canto.org>) and the Macaulay Library at the Cornell Lab of Ornithology (<https://www.macaulaylibrary.org>) (Tolkova et al., 2021). Crowdsourcing and machine learning were combined to engage users in bird identification. In 2020, BirdNET was downloaded over one million times (Wood et al., 2022). The BirdNET application enables users to record audio data on a smartphone and transmit it to the BirdNET server. The server then provides species identification accompanied by a qualitative confidence score (Wood et al., 2022). The user also has the possibility to confirm the identification suggested by BirdNET, for the date and the localization of the observation, thereby contributing to biodiversity inventory (Schweizer et al., 2024). Despite the strong performance of BirdNET under optimal conditions—such as comprehensive survey coverage in time and space, high recording durations with multidirectional microphones, and the detection of a single species at a time (Ware et al., 2023)—there still seems to be potential detection biases when used in realistic ecological conditions (e.g., smartphone app directly used in the field, Kaveh et al., 2023). They can include biotic parameters (e.g. number or characteristics of the species' vocalizations) or abiotic parameters (e.g., anthrophony, the total sound produced by human activities within an ecosystem) (Pérez-Granados, 2023b). These biases have the potential to compromise the integrity of the data and mislead participating citizens in their interpretations. Thus, it is crucial to consistently evaluate the quality and uncertainty associated with these emerging tools (Kaveh et al., 2023) in order to ensure the reliability of the information derived from them.

While it is important to identify and eliminate biases in data acquisition, the potential risks they pose to knowledge development can be managed as long as the biases are acknowledged, systematic, and possible to be modeled. In this study, our objective was to assess the accuracy and consistency of bird species identifications generated by the BirdNet algorithm when used across multiple smartphone devices in diverse acoustic settings. Specifically, we predict that (i) The performance of the BirdNet algorithm diminishes as the distance between the sound source and the receiver increases, (ii) due to a decrease in the signal-to-noise ratio. (iii) An increase in the ratio of anthrophony to biophony will result in a decrease in the performance of the BirdNet algorithm. (iiii) Performance of the BirdNet algorithm varies based on the type of recorder used.

2 | MATERIALS AND METHODS

❖ Experimental design

The study was conducted in the city of Bordeaux, and its metropolitan area, SW France, a region characterized by an oceanic climate with mean annual temperature of 12.8 °C and annual precipitation of 873 mm over the last 20 years. We selected 22 urban sites along a SW-NE transect spanning 7 km of the Bordeaux metropolitan area (Fig. 1.), covering a large gradient of noise intensity (Bordeaux métropole. “Carte du bruit de Bordeaux métropole”. 2024. Map. Bordeaux métropole. https://geo.bordeaux-metropole.fr/cartographie_du_bruit/) and various sources of noise (e.g., conversations, cars, tram, etc.). We visited each site once, between March 19 and April 4. In each site, we played a pre-established sequence of bird vocalizations belonging to eight bird species (see *Standard bird songs*, below) with a *Ultimate Ears Wonderboom 3* Bluetooth speaker placed at 5m or 30m from the observers. These distances were chosen considering the auditory capabilities of an average listener and the distance at which a bird can be detected in an urban environment. This ensured that the sound was not too loud at close range but could still be heard at 30 meters. We ran BirdNet version 1.92 on three smartphones (Supplementary material I). We recorded the first 15 s of each vocalization and noted species name(s) and confidence levels as reported by BirdNet. We used the BirdNET application with default settings to simulate standard usage of non-scientific audiences. For each site and each speaker-recorder distance, we characterized the local soundscape and ambient noise (see below). Simultaneously, three AudioMoth devices (autonomous recording units) were positioned at the same distance as the phones to record the entire song. We used Audiomoth recording to characterize the average soundscape at the time the experiment was conducted (see below).



Fig. 1. Location map of the study area showing the 22 sites at the left of the figure, and picture showing site 21, Cenon Palmer park, at the top right, site 20, Cenon train station, at right and site 12, Victoire square, at the bottom right of the figure.

❖ Bird songs

We selected eight bird species, namely the European Robin, *Erithacus rubecula*, the Great Tit, *Parus major*, the House Sparrow, *Passer domesticus*, the Common Swift, *Apus apus*, the Black Redstart, *Phoenicurus ochruros*, the Eurasian Blackbird, *Turdus merula*, the Barn Swallow, *Hirundo rustica*, and the Eurasian Chaffinch, *Fringilla coelebs*, to analyze their vocalizations with the BirdNet application. These species were chosen based on specific criteria: they are common in the study area, prevalent in urban environments, and readily accessible in the Xeno-Canto database (<https://xeno-canto.org>). For each species, we ensured the availability of ten high-quality vocalizations without background noise sourced from Xeno-Canto. We used the Audacity software to compose 22 sequences of eight bird vocalizations chosen at random among the pool of ten high-quality samples per species, all normalized at a -1dB (ensuring that the audio reaches its highest possible volume without distorting or clipping the sound), and assembled in a random order (“song”, henceforth). A typical song consisted of two minutes of silence, up to 30 seconds of vocalization for each of the eight species, and finally another two minutes of silence, totaling a maximum duration of eight minutes. We separated the initial and final silence sequences and each vocalization by a sound beep.

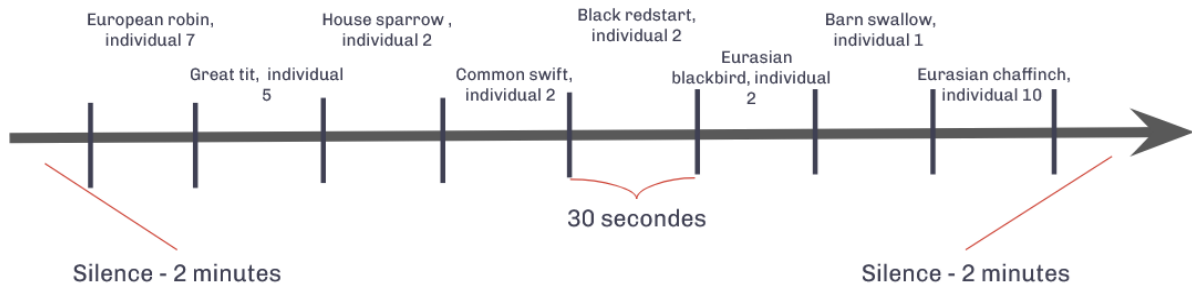


Fig. 2. Example of song design outline. 2 minutes of silence are placed at the beginning and end of the song. The order of the 8 species in the song and the individual chosen to represent the species in the song are determined randomly. A vertical black bar represents a beep.

❖ Normalized difference soundscape index and sound intensity

The three Audiomoth positioned at the same distance as the phones to record the entire song enabled the calculation of the normalized difference soundscape index (NDSI) for the minutes of silence at both distances for each of the 22 sites. The NDSI quantifies the proportion of biological (biophony) to anthropogenic noise (anthrophony) by comparing the sound intensity in the 2-8 kHz range for biophony to the 1-2 kHz range for anthrophony (biophony - anthrophony / (biophony + anthrophony)). Its value ranges from +1 to -1 with higher value corresponding to absence of anthrophony. This index highlights the extent of human presence in an ecosystem (Setyantho et al., 2018). At the same distance as phones and Audiomoth we used a sound level meter (TROTEC, SL400) to measure the sound intensity of each site during the four minutes of silence in the song. The sound level meter is set with a default dBA measurement curve, a sampling frequency per second, in Slow mode, and a measurement range from 30 to 130 dB. It was positioned at a height of 140 cm, facing the speaker at a 60° angle relative to the ground.

❖ Analyse

➤ Signal to noise ratio calculation

Bird vocalizations, like other acoustic signals, gradually deteriorate as they travel from transmitter to receiver (Naguib & Wiley, 2001). To address this correlation, we calculated the actual signal perceived by the receiver in a controlled environment for each species and distance. This involved subtracting the average sound intensity perceived by the receiver for each species and distance from the ambient noise level at the measurement site. The resulting value was then divided by the sound intensity received in the field to determine the signal-to-noise ratio (SNR) for each site, distance and species. The SNR ranges from 0 to 1 and describes the amount of sound actually perceived by the microphone. Thus, the formula for the ratio is : Signal to Noise Ratio = (Signal Intensity - White Noise) / Sound intensity.

➤ Calculation of BirdNET accuracy indicator

We assessed the performance of the BirdNET algorithm by comparing its outputs with the emitted vocalizations. This comparison yielded three identification categories: True Positives (TP, i.e. BirdNET correctly identified the species), False Positives (FP, i.e. BirdNET reported a wrong name), and False Negatives (FN, i.e. BirdNET did not identify any species). These metrics were computed for each BirdNET response, as well as for each confidence level

provided by the BirdNET app, including 'Conjecture,' 'Highly Uncertain,' 'Uncertain,' 'Probable,' 'Very Probable,' and 'Almost Certain.' For instance, applying a minimum confidence threshold of 'Probable' entails filtering out all BirdNET identifications with confidence levels below 'Probable' (e.g., 'Uncertain,' 'Highly Uncertain,' and 'Conjecture') as false negatives.

We defined BirdNet accuracy as the occurrence of TP, for a given confidence level, with values limited to 0 or 1. We completed the information provided by BirdNet accuracy by calculating precision, recall, and F-score for each site, distance, and confidence threshold, adhering to established practices for evaluating automated species detection algorithms (Funosas et al., 2024; Pérez-Granados, 2023a). Precision denotes the proportion of correctly identified bird species out of all identifications made by the BirdNET algorithm (Precision = TP / (TP + FP)). It is determined by the ratio of species correctly identified to the total number of species detected by the BirdNET algorithm within the analyzed acoustic sample. Recall indicates the proportion of actual bird species present that were correctly identified by the BirdNET algorithm (Recall = TP / (TP + FN)). It is computed by determining the ratio of species correctly detected to the total number of species actually present in the analyzed acoustic sample. Quantifying precision and recall provides insights into the accuracy of BirdNET identifications and its ability to detect bird vocalizations accurately. This approach facilitates a nuanced understanding of BirdNET's performance, revealing both the percentage of correct identifications and the accuracy of bird vocalization detection. The F-score, the harmonic mean of precision and recall, offers a single metric that balances both aspects of the algorithm's performance. Its maximum value is 1, indicating that precision and recall are at their maximum (F-score = $(\beta^2 + 1) * \text{precision} * \text{recall} / (\beta^2 * \text{precision} + \text{recall})$). The F- β score belongs to a family of metrics that allow varying the weighting between precision and recall in evaluating the performance of a classification model. The β factor allows adjusting the relative importance given to these two measures (Goutte & Gaussier, 2005). In our study, we conducted F-score analyses using $\beta = 0.10$, to reflect a pronounced asymmetry in the relative importance assigned to these two key classification metrics. We selected these asymmetrical β coefficients based on the premise that maximizing precision is of critical importance in the majority of biodiversity research and monitoring applications. In such contexts, it is generally considered more acceptable for a species detection model to fail to identify a present species, rather than to incorrectly flag a species as present when it is not (Tolkova et al., 2021).

➤ Statistical analysis

The Common Swift (*Apus apus*) had to be excluded from our analyses due to potential bias related to its phenological status. During the first part of our field sampling period, the BirdNET application considered this species as absent from the area, thus generating systematically erroneous responses. Consequently, the data related to the Common Swift (*Apus apus*) are not comparable to other species regarding the effect of soundscape, justifying its removal from subsequent analyses.

The analyses were conducted using R software, version 4.3.2. First we analyzed the impact of SNR on BirdNET algorithm performance. In this regard, a valid binomial model was retained to describe Accuracy as a function of SNR, including species, sites, and recorders as random variables. To evaluate Precision, Recall, and $F_{0.1}$ score, sites and recorders were considered as crossed random effects. Although several types of models were explored, including linear, binomial, negative binomial, and beta regression models, none met the assumptions of normality, homoscedasticity, and independence of residuals, as confirmed by graphical residual analysis against predicted values. Therefore, we only kept the Accuracy model as a more

conservative approach. Similar conclusions were drawn for NDSI models, where included NDSI and distance as independent variables, along with random effects corresponding to the dependent variables mentioned (i.e., only sites and recorders for Precision, Recall, and F0.1 score, while sites, recorders, and species were considered for Accuracy).

Additionally, we performed an Intraclass Correlation Coefficient (ICC) analysis to assess the similarity of recorder responses. The ICC is a statistical measure used to assess the agreement between different measurements taken on the same sample. A high ICC value indicates strong agreement among the measurements or evaluators, suggesting good reliability or reproducibility. Conversely, a low ICC value indicates poor agreement, suggesting poor reliability or reproducibility. To conduct this analysis, we aggregated responses from the BirdNET application that were common across all three recorders, resulting in 279 observations. This sample size adequately meets the minimum requirement of 30 observations for three observers (Koo & Li, 2016).

Finally, to analyze the heterogeneity in BirdNET responses among the tested species, we used an existing dataset comprising 10 acoustic trait variables (median syllable duration, median inter-onset interval duration, song duration, number of syllables per unit time, 90% spectral bandwidth, acoustic fractal dimension, peak frequency, number of frequency peaks and spectral and temporal entropy) for 179 species, including seven selected for our experiment. We conducted a Non-Metric Multidimensional Scaling (NMDS) analysis, which suggested the presence of group differences. To assess the significance of these differences, we initially employed a Permutational Multivariate Analysis of Variance (PERMANOVA). However, due to heterogeneous dispersion among groups, which violated PERMANOVA's assumptions, we subsequently performed an Analysis of Similarity (ANOSIM) accompanied by a Monte Carlo permutation test.

3 | RESULTS

❖ Descriptive analyses

➤ Effect of soundscape and distance on BirdNET responses

The confidence levels associated with BirdNet responses varied with distance and ambient noise levels. In detail, the proportion of "Almost Certain" responses decreased by 59%, from 136 to 12 responses detected at this confidence level, when the transmitter-recorder distance increased from 5 meters to 30 meters and the ambient noise level increased from sites below 50 dB to sites above 60 dB (Figure 3.A). Conversely, the "Conjecture" confidence level responses increased by 53%, from 8 to 121 responses detected at this confidence level, under the same conditions. Additionally, false positives increased by 50%, from 43 to 147 false positives detected, when the distance increased from 5 meters to 30 meters and the ambient noise level rose from below 50 dB to above 60 dB (Figure 3.B).

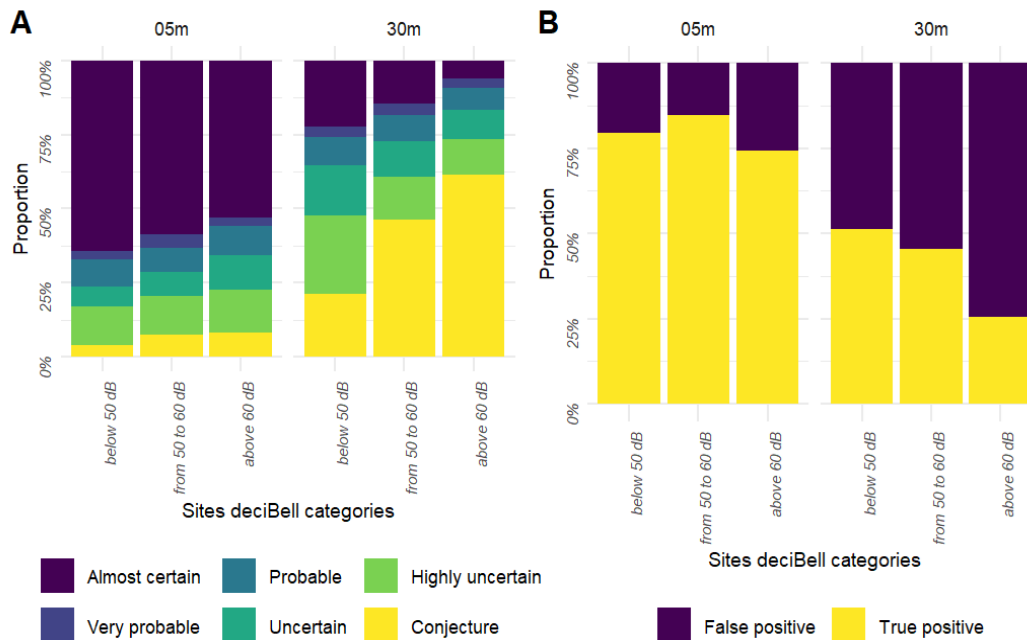


Fig. 3. Distribution of BirdNET response proportions categorized by confidence levels (A) and by true or false positives (B), stratified by site

➤ Performance evaluation of BirdNET across avian species

The level of confidence returned by BirdNET varied among the seven avian species tested, with the Black Redstart (*Phoenicurus ochruros*), Barn Swallow (*Hirundo rustica*), and Great Tit (*Parus major*) being the most frequently identified with high certainty (49%, 49%, and 54% Almost certain responses, respectively), while the House Sparrow (*Passer domesticus*) was the species least frequently identified with a high degree of certainty (24% Almost certain responses) (Figure 4A). A non-metric multidimensional scaling (NMDS) analysis was conducted based on the acoustic traits of the seven studied species, yielding a stress value of 0.2. While this stress value was relatively high, limiting interpretation to general trends, the resulting configuration suggested a division into two distinct sections. One section contained only the House Sparrow (*Passer domesticus*), while the other comprised the remaining six species (Figure 4.B). However, according to the ANOSIM and the Monte Carlo permutation test, the sections did not show significant differences ($R = 1$, $p = 0.135$).

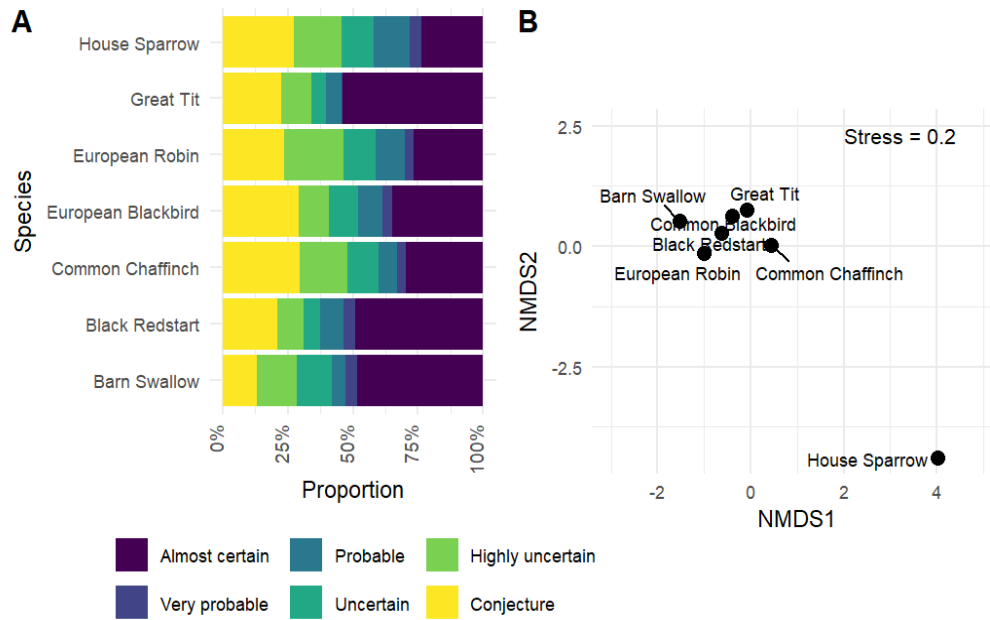


Fig. 4. Proportional distribution of BirdNET response confidence levels by species (A) and Non-Metric Multidimensional Scaling

❖ Impact of SNR and NDSI on BirdNET algorithm performance

The performance of the BirdNET algorithm, as measured by accuracy, increases with an increasing signal-to-noise ratio (SNR) (Table I). The model explains 37.8% of the variance due to the SNR alone (R^2_m of 0.378) and 56.3% of the total variance when considering both SNR and the random effects (Sites, Species, Recorder) (R^2_m of 0.563). Additionally, the BirdNET algorithm's performance decreases as the distance between the recorder and the transmitter increases (Table I, Figure 4B), with 35.4% of the variance explained by the distance alone (R^2_m of 0.354) and 57.1% when considering both the distance and the same random effects as previously mentioned (R^2_c of 0.571). Furthermore, no significant effect of NDSI on the BirdNET algorithm's performance is detected (Table I).

Response	Predictors	Estimate	Std. Error	z value	p-value	
Accuracy	Almost Certain	SNR	14.153	0.938	15.090	0.001
		Distance	-0.132	0.009	-15.049	0.001
		NDSI	0.512	0.629	0.814	0.415
	Probable	SNR	14.038	0.887	15.830	0.001
		Distance	-3.207	0.201	-15.985	0.001
		NDSI	0.429	0.450	0.952	0.341
	Highly uncertain	SNR	14.730	0.970	15.191	0.001
		Distance	-2.833	0.290	-9.902	0.001
		NDSI	0.109	0.270	0.399	0.690

Table I. Summary of binomial GLMER with Sites, Species and Recorder as random effect for estimating the effect of SNR, NDSI and Distance on algorithm performance at three confidence levels (Highly uncertain, Probable, Almost certain). Significant variables are indicated in bold.

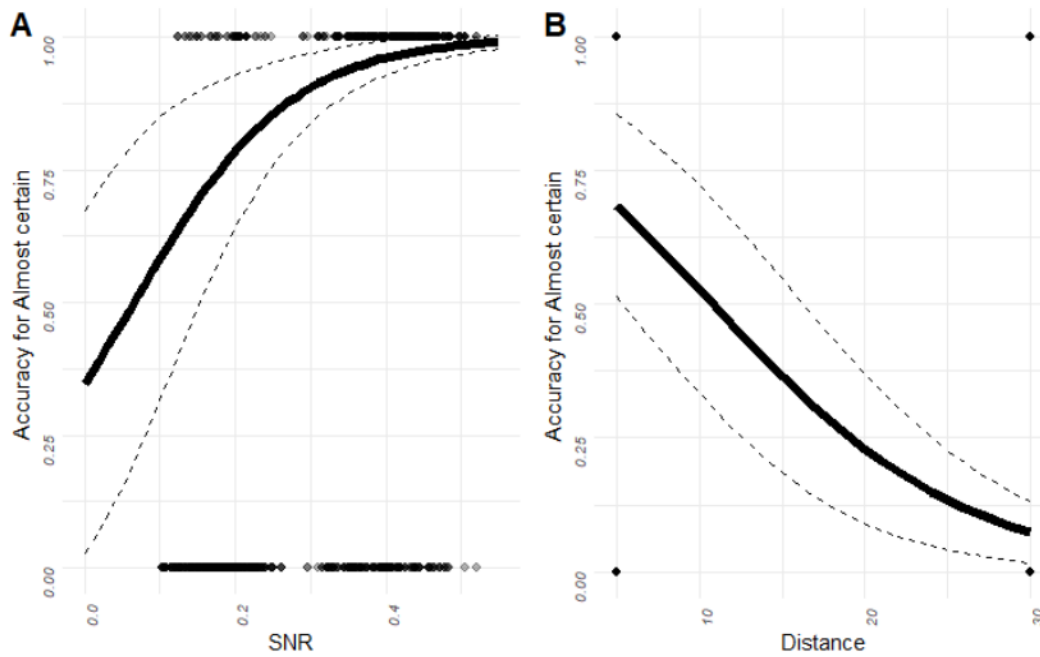


Fig. 5. Logistic regression model of Accuracy values for Almost Certain confidence level as a function of Signal-to-Noise Ratio (SNR) (A) and as

❖ Impact of recorder type on BirdNET algorithm performance

The intraclass correlation coefficient (ICC) was 0.618 ± 0.056 for the responses provided by the three different recorders on a set of 279 common observations. This ICC value indicates a moderate level of agreement, suggesting that the responses proposed by the different recorders are generally similar, although notable divergences may be observed (Koo & Li, 2016).

4 | DISCUSSION

Our study shows that BirdNET can accurately identify the seven species used in this research, but only in calm soundscape and at a close distance. Conversely, the performance of the BirdNET algorithm diminishes as the distance between the sound source and the receiver increases, due to a decrease in the SNR. In contrast, the ratio of anthrophony to biophony does not explain BirdNET detection capabilities. We also found that different recorders can produce moderately different responses. These findings contribute to the body of research on the performance of the BirdNET algorithm, offering insights that improve our understanding of its optimal use in a citizen science framework.

Our results showed that BirdNET species detection performance improves as the Signal-to-Noise Ratio (SNR) increases, while a negative correlation was observed with increasing distance between the recorder and the transmitter. A recent study reported a similar decline in BirdNET performance as the distance between the sound source and the recorder increased (Pérez-Granados, 2023a). However, this study was conducted in a forest environment where the only potentially disruptive sounds were those produced by other birds (i.e., biophony). In contrast, our research took place in an urban environment dominated by human sounds (i.e., anthrophony). We hypothesized that the BirdNET algorithm's performance would be notably

diminished in the presence of anthropogenic noise. However, we found no evidence supporting this hypothesis. On the contrary, our observations revealed no significant effect of the noise singularity index (Normalized Difference Sound Index, NDSI), suggesting that the type of ambient noise (biophonic or anthropogenic noise) does not influence BirdNET performance. These results enable us to distinguish between the effects of distance and noise characteristics on the performance of the BirdNET algorithm. Future research evaluating the application should consider this distinction to obtain the most comprehensive assessment possible of the impact of the noise environment on the BirdNET algorithm.

Observation of the data collected revealed differences in the confidence level distributions of BirdNET predictions for the seven species studied. These results are in line with previous studies evaluating the performance of the BirdNET algorithm (Pérez-Granados, 2023b). These results advance current knowledge by complementing a previous study that suggested interspecific differences could arise from both the inherent difficulty in identifying vocalizations with certain acoustic patterns and the challenge of distinguishing between species with similar vocalizations (Funosas et al., 2024). Our study extends this understanding by demonstrating that these differences are not due to variations in acoustic traits (Figure 4B). Our preliminary observational study should be supplemented with a more systematic evaluation of BirdNET ability to identify vocalizations across a larger sample size. This would enable a more comprehensive assessment of the relationship between the BirdNET algorithm and the vocal traits of different species. Furthermore, if the acoustic traits of the species tested do not explain the difference observed, one possible explanation could lie in the size of the data samples used to train the species recognition models in BirdNet (Funosas et al., 2024). In fact, it is generally accepted that larger sample sizes provide better performance (Knight et al., 2020).

Smartphone applications utilizing automated classifiers like BirdNet can serve as reliable sources of biodiversity data only if different smartphones produce consistent outputs. However, our analysis reveals an ICC value suggesting a moderate level of agreement. This indicates that while the responses from our three different recorders are generally similar, notable divergences exist (Koo & Li, 2016). The small sample size does not allow for a comprehensive understanding of the differences that could be found across the diversity of smartphones used today. Furthermore, a portion of the difference could not be illustrated because we were unable to account for the fact that one phone may provide multiple responses compared to other devices. However, this result can be explained by the fact that the phones are of similar age, for both of them, but different brands and models (Supplementary materials I). Nonetheless, this moderate agreement underscores the necessity to consider the specific characteristics and calibration of different recording devices when interpreting BirdNet results. Variability in recorder sensitivity, frequency response, and microphone type (omni-directional or directional microphones) can lead to inconsistencies in data collection (Brandes, 2008). Standardizing recording equipment and calibration procedures across studies can minimize this variability and enhance the reliability of species detection (Rempel et al., 2013). Future studies should focus on developing and implementing standardized protocols for recorder usage to ensure consistent and accurate data across different devices and environments. Although this may prove difficult in the context of citizen science, where the aim is to involve as many participants as possible, the introduction of an age threshold above which certain phones would not be eligible could be considered. Such an approach would not only improve the comparability of results between different studies but also enhance the overall reliability of BirdNet.

This study presents some limitations. Firstly, the accuracy metric used to evaluate the BirdNet algorithm does not provide as much information as the precision, recall, and F-score metrics,

which are preferred for their ability to reveal both the percentage of correct identifications and the sensitivity of bird vocalization detection. Consequently, our conclusions are limited to a partial perception of the BirdNet algorithm's performance and do not fully demonstrate its sensitivity. Using BirdNet on long-term recordings could enable the application of these metrics in interpretable statistical models, as suggested by some studies (Funosas et al., 2024; Kahl et al., 2021). Furthermore, obtaining more extensive recordings of the sound environment could facilitate the calculation of additional indices, such as the Acoustic Complexity Index (ACI), which measures the acoustic richness of the environment independently of the type of sound sources present (Engel et al., 2023). This would help to better define all sound characteristics and complement the information provided by the NDSI.

5 | CONCLUSION

BirdNET has considerable potential and is already widely used by scientists and the general public (Bota et al. 2023; Wood et al. 2022). The findings of this study provide valuable insights that could further expand BirdNET application in citizen science projects. We have established the importance of the signal-to-noise ratio in BirdNET performance, highlighting the influence of ambient sound intensity and distance. Furthermore, we observed that the type of noise, whether biophonic or anthropogenic, does not significantly affect these performances. In the future, the use of other noise metrics such as the Acoustic Complexity Index (ACI) could complete the characterization of the sound environment and shed light on its impact on BirdNET (Engel et al., 2023). Additionally, including a diversity of species in future studies will allow for a more comprehensive assessment of BirdNET capabilities (Pérez-Granados, 2023b). The use of local recordings could also be considered to reduce intra-species variation related to regional dialects, thereby improving observation accuracy. By continuing these research efforts, we can optimize the reliability of participants' contributions to citizen science projects, ultimately fostering a better understanding and conservation of avian species.

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SUPPLEMENTARY MATERIAL

	Phone brand	Phone modele	Model release year	Operating system	Operating system version	BirNET Version
Recorder 1	Samsung	Galaxy S8	2017	Android	12	1.92
Recorder 2	Iphone	Iphone 8	2017	iOS	16.7.2002	1.92
Recorder 3	Redmi	Redmi Note 12	2023	Android	12	1.92

Supplementary material I. Table of characteristics of the phones used in the study

CONTRIBUTIONS

I was responsible for establishing the protocol, conducting the experiments, acquiring and cleaning the data, as well as performing the analyses and writing the report. At each step, I received support and guidance from my internship supervisor, Laura Schillé, and her thesis director, Bastien Castagnyrol. For the experimentation and data collection phases, I was assisted by the staff of the *Biodiv* team at “Unité Mixte de Recherche BIOGECO” (Biodiversity Genes and Communities) , particularly Jean-Baptiste Rivoal, Olivier Bonard, and Emma Amodeo. Finally, Laura Schillé and Bastien Castagnyrol reviewed the report. Finally, I would like to thank Michela Busana from the ACOUCENE project for providing the dataset regarding the acoustic traits of 179 bird species. This work is part of the WildE project supporting my internship.

ACKNOWLEDGMENTS

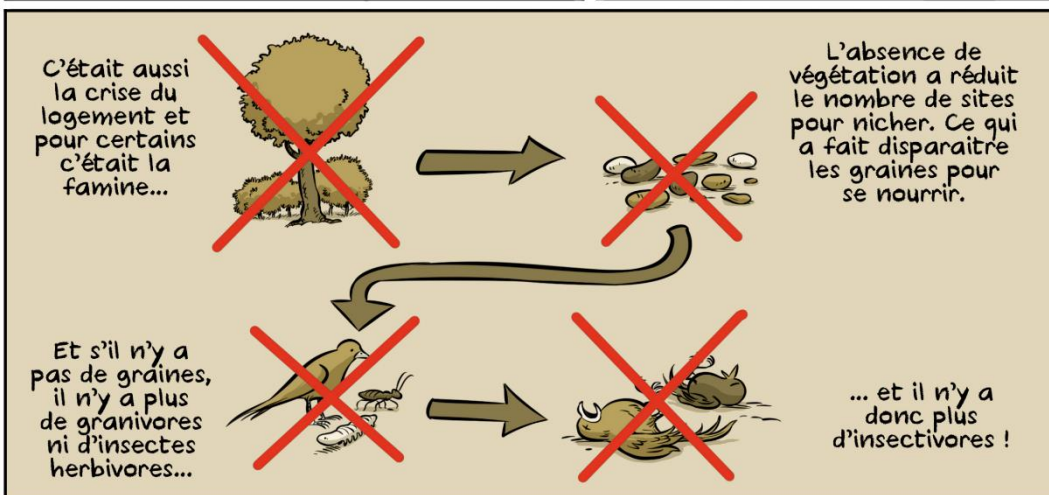
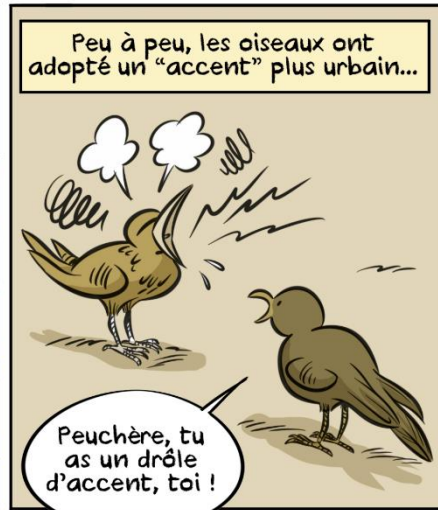
I would like to thank all the members of the Biodiv team at UMR Biogeco for their assistance throughout my internship. I am particularly grateful to Jean-Baptiste Rivoal for his essential material support, which was crucial for the successful conduct of the experiments, as well as to Olivier Bonard and Emma Amodeo for their participation in data acquisition. I would especially like to thank Laura Schillé and Bastien Castagnyrol for the time and effort they dedicated to the success of this internship project and the improvement of this report. Finally, I thank the European WildE project, coordinated by Arndt Hampe, for funding this internship.

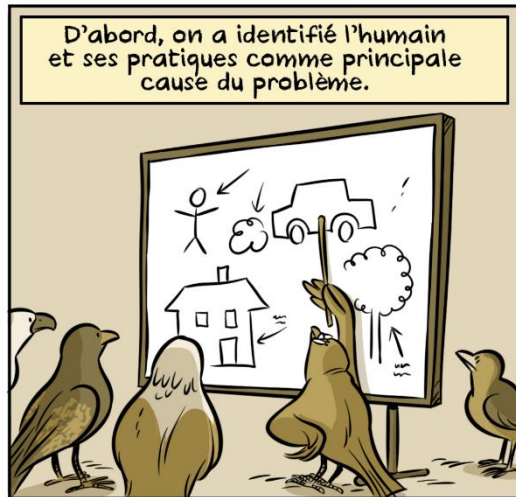
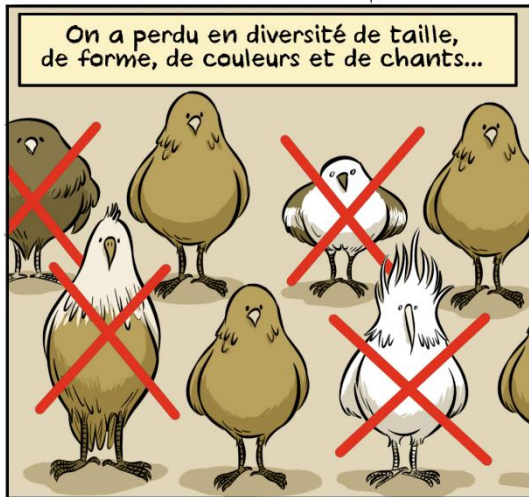
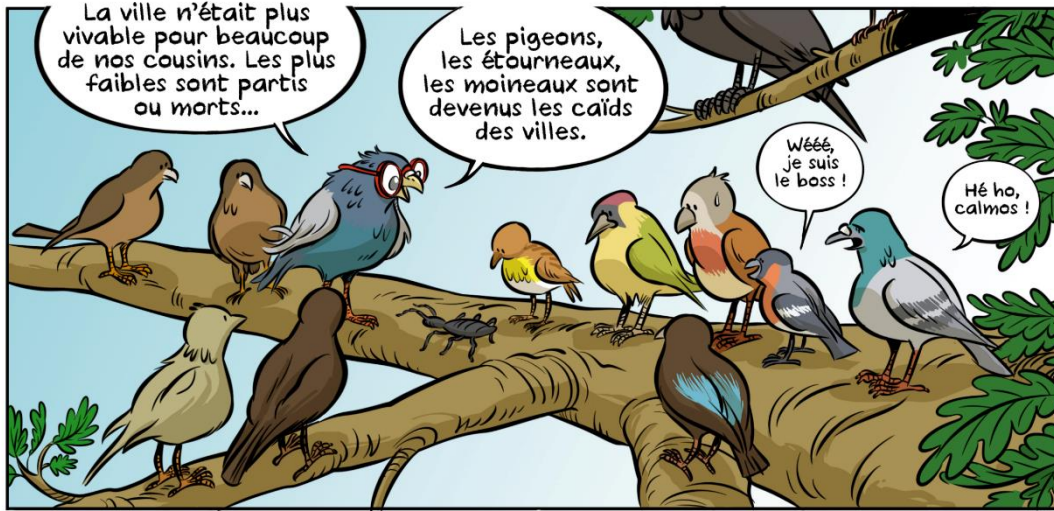
7.3. Annexe A3. Bande dessinée « Les gardiens des arbres »



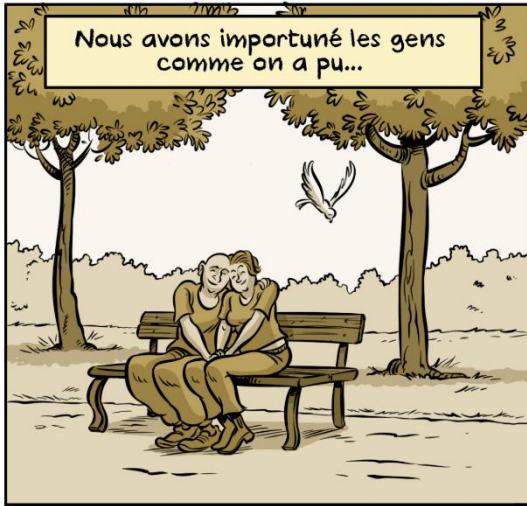


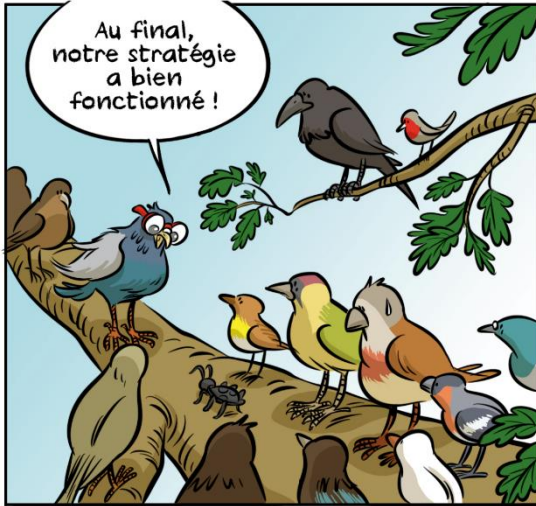








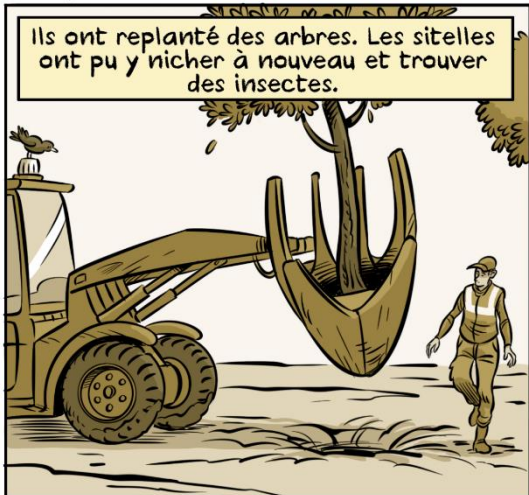




Au final,
notre stratégie
a bien
fonctionné !



Les humains ont cassé le bitume pour
remettre la terre à nu. Les merles ont
pu retrouver les vers !



Ils ont replanté des arbres. Les sittaes
ont pu y nicher à nouveau et trouver
des insectes.



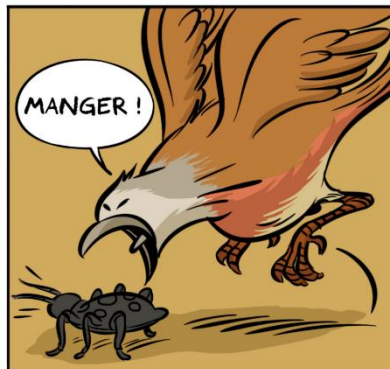
Ils ont créé des zones sans voiture.
Les pinsons des arbres étaient
à nouveau au calme pour chanter
et défendre leur territoire.



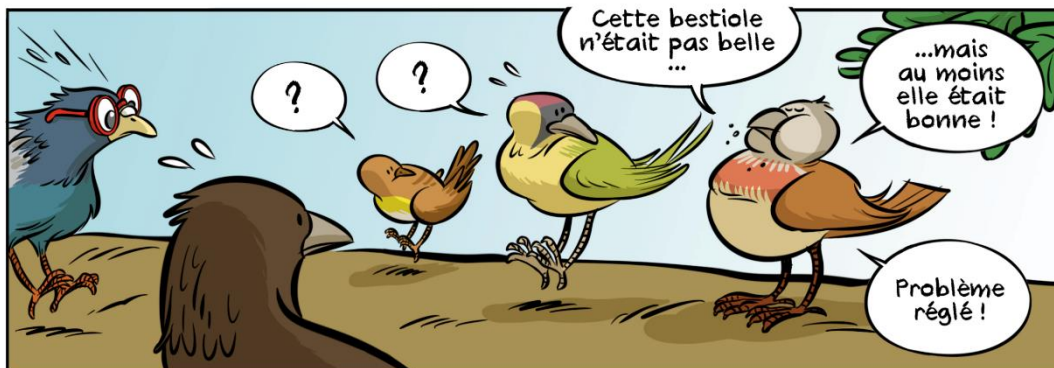
Ils ont éteint les lumières la nuit.
Les chouettes ont pu enfin chasser
en paix !



Grâce
aux efforts
de tous...
...nous avons
pu retrouver
une certaine
tranquillité



CROUNCH



Diversité des oiseaux et régulation de l'herbivorie sur les arbres : effets du climat et de l'urbanisation à différentes échelles

Résumé :

Les oiseaux insectivores contribuent activement à la régulation des populations d'insectes herbivores. Ils jouent ainsi un rôle essentiel dans la dynamique des écosystèmes terrestres. La théorie suggère que la diversité des communautés d'oiseaux covarie avec le nombre de fonctions qu'elles remplissent, car des communautés plus diversifiées explorent des espaces fonctionnels plus larges et utilisent ainsi mieux les ressources disponibles. Cependant, les changements globaux pourraient modifier cette relation. La question est alors de savoir s'ils impactent de la même manière la structure des communautés d'oiseaux et les fonctions qu'elles assurent, ou si au contraire ces variables réagissent différemment. De plus, les patrons biogéographiques peuvent être localement altérés par des facteurs biotiques et abiotiques. Ainsi, cette combinaison de facteurs agissant à différentes échelles peut modifier la cascade tri-trophique, en agissant de manière indépendante, antagoniste ou synergique, sur les communautés d'oiseaux, celles des herbivores et les caractéristiques des arbres sur lesquelles ils s'alimentent.

Cette thèse avait pour objectif principal d'explorer les effets de l'augmentation des températures et de l'urbanisation, en interaction avec les facteurs locaux tels que la quantité et la diversité des habitats forestiers, sur la relation entre la diversité et la fonction de prédation des oiseaux insectivores. A cette fin, nous avons travaillé à plusieurs échelles emboîtées, depuis l'arbre et son voisinage immédiat jusqu'à l'échelle continentale. Nous avons employé des méthodes innovantes s'appuyant sur l'écologie acoustique, les sciences participatives et les algorithmes de reconnaissance automatisée pour caractériser les communautés d'oiseaux de manière standardisée et à grande échelle et nous avons développé des approches expérimentales pour évaluer la reproductibilité de ces approches.

Nos résultats indiquent que l'augmentation des températures et l'urbanisation ont un impact significatif, respectivement positif et négatif, sur la diversité taxonomique et fonctionnelle des communautés d'oiseaux insectivores. Cependant, nous avons observé un découplage entre la structure de ces communautés et les fonctions écosystémiques associées, en réponse à ces changements. Ceci plaide pour une reconsidération de la portée générale de la théorie liant la diversité des communautés au nombre de fonctions qu'elles remplissent. De plus, la quantité et la diversité d'habitats forestiers sont des facteurs locaux qui modulent les facteurs climatiques et urbains. Ces derniers structurent les communautés d'oiseaux et les cascades tri-trophiques qu'elles initient à plus large échelle. Enfin, nos travaux ont permis une avancée dans le développement des méthodes permettant l'étude de la dynamique de la biodiversité et de ses fonctions.

Mots clés : Interactions tri-trophiques ; Prédation ; Urbanisation ; Ecologie acoustique ; Ecologie fonctionnelle ; Ecologie des communautés ; Forêt

Top-down control of birds on insect herbivory in trees: effects of climate and urbanization at multiple scales

Abstract:

Insectivorous birds actively contribute to the regulation of herbivorous insect populations, thus playing a key role in terrestrial ecosystem dynamics. The theory suggests that bird community diversity covaries with the number of functions they perform, as communities that are more diverse explore broader functional spaces and utilize available resources more effectively. However, global changes might alter this relationship. The question then becomes whether these changes affect the structure of bird communities and their associated functions similarly, or if these variables respond differently. Additionally, biogeographical patterns may be locally altered by biotic and abiotic factors. Thus, this combination of factors operating at different scales can modify the tri-trophic cascade, acting independently, antagonistically, or synergistically on bird communities, herbivore communities, and the characteristics of the trees they feed on.

The main objective of this thesis was to explore the effects of increasing temperatures and urbanization, in interaction with local factors such as the quantity and diversity of forest habitats, on the relationship between diversity and predation function of insectivorous birds. To this end, we worked at multiple nested scales, from the tree and its immediate surroundings to the continental scale. We employed innovative methods based on acoustic ecology, citizen science, and automated recognition algorithms to characterize bird communities in a standardized and large-scale manner, and we developed experimental approaches to assess the reproducibility of these methods.

Our results indicate that increasing temperatures and urbanization have significant impacts—positive and negative, respectively—on the taxonomic and functional diversity of insectivorous bird communities. However, we observed a decoupling between community structure and associated ecosystem functions in response to these changes. This suggests a need to reconsider the general applicability of the theory linking community diversity to the number of functions they perform. Furthermore, the quantity and diversity of forest habitats are local factors that modulate the effects of climate and urban factors, which structure bird communities and the tri-trophic cascades they initiate on a larger scale. Finally, our work has contributed to advancing methods for studying biodiversity dynamics and its functions.

Keywords: Tri-trophic interactions; Predation; Urbanization; Acoustic ecology; Functional ecology; Community ecology; Forest