Mammal Research Institute
Polish Academy of Sciences
Białowieża

Michał Walesiak

The impact of natural disturbances on bird communities in temperate ecosystems

MRI PAS Doctoral Thesis Series, No. 1

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The impact of natural disturbances on bird communities in temperate ecosystems

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Wpływ naturalnych zaburzeń środowiska
na zespoły ptaków w ekosystemach
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Table of contents

List of publications included in the thesis

Chapter I

Walesiak, M., Mikusiński, G., Borowski, Z., & Żmihorski, M. (2022). Large fire initially reduces bird diversity in Poland's largest wetland biodiversity hotspot. *Biodiversity and Conservation, 31*(3), 1037-1056. https://doi.org/10.1007/s10531-022-02376-y. (Reproduced with permission from Springer Nature)

Chapter II

Walesiak, M., Michielsen, R., Mikusiński, G., & Żmihorski, M. (2024). Salvage logging and subsequent post-windthrow management diminish forest bird communities for two decades. *Journal of Applied Ecology*, *61*(9), 2157-2168. https://doi.org/10.1111/1365-2664.14727. (Reproduced with permission from John Wiley & Sons, Inc.)

Chapter III

Walesiak, M., Bramorska, B., Koprowska, D., Michielsen R., Mikusiński G., & Żmihorski M. Active post-disturbance management in Białowieża Forest shifts bird communities toward farmland assemblages. (manuscript)

Summary in English

Natural disturbances such as windstorms, wildfires, and insect outbreaks are crucial drivers of ecosystem dynamics worldwide, influencing ecological processes at multiple levels. They are important drivers of biodiversity changes in affected ecosystems. This impact depends on a complex interplay of factors, with the most important being pre-disturbance habitat characteristics, the type of habitat affected, and the post-disturbance management strategy.

In my thesis, I focused on three different large-scale disturbances and evaluated their impacts on biodiversity. I used birds as a focal group, as they are sensitive to disturbance-induced changes in ecosystem structure, are frequently prioritized in conservation efforts, and can be surveyed reliably and cost-efficiently.

In the first study, I examined the short-term impacts of a large wildfire (5,500 ha) on open wetland bird communities in the Biebrza Valley, one of the largest Central European wetlands. By comparing post-disturbance bird communities with pre-disturbance data, I was able to isolate the effect of the disturbance from natural spatial and temporal variability. The fire caused an immediate shift in community composition and proved detrimental to several wetland specialists of high conservation concern. It led to the temporary elimination of four species, including the Aquatic Warbler (*Acrocephalus paludicola*), an important species from a global conservation perspective. Three open-habitat generalists benefited from the disturbance, none of them relying on wetlands as their main habitat. I concluded that fire reduced bird diversity in wetlands in the short term. While this effect is likely temporary, I also discussed the potential for adverse long-term outcomes of wetland fires from a conservation perspective.

In the second study, I focused on two decades of forest bird community succession following a windthrow event in a managed forest (Pisz Forest). I compared two post-disturbance management strategies (i.e., no management vs. active management) and contrasted them with control stands unaffected by the disturbance. I showed that bird communities in the unmanaged windthrow were consistently the richest in terms of both abundance and species richness. Unmanaged windthrow maintained forest bird diversity comparable to unaffected production stands throughout the study period, while also supporting a substantial diversity of farmland birds.

Furthermore, I found that managed and unmanaged windthrows followed two distinct successional trajectories and did not converge during the study period. I concluded that refraining from active post-disturbance management sets bird succession on a distinct pathway, leading to unique and diverse bird communities. Hence, natural disturbances may serve as cost-effective ecosystem restoration tools, provided that no active management is implemented.

In the third study, I analyzed the effects of a bark-beetle outbreak in Białowieża Forest, a highly natural lowland forest ecosystem. I quantified bird community shifts caused by both the disturbance and active post-disturbance management, placing these changes in the context of two reference habitats: undisturbed forest and farmland. The bark-beetle disturbance caused a shift in bird community composition, moving from a typical undisturbed forest assemblage toward one more characteristic of farmland, with increased farmland bird richness. Active post-disturbance management led to a further shift in the same direction, resulting in even greater richness of farmland species and closer resemblance to farmland bird assemblages. Notably, active management of the disturbed areas produced a greater deviation from the forest-typical bird communities than the initial bark beetle disturbance. Our results suggest that active post-disturbance management substantially alters bird communities and thus may disrupt natural successional processes in forest ecosystems. Therefore, it should be limited, particularly in forests of high conservation value.

My research demonstrates that natural disturbances cause significant shifts in the diversity and structure of bird communities across temperate European ecosystems. These shifts are strongly influenced by post-disturbance management decisions. Regardless of their overall effect on biodiversity, the impacts of both disturbances and subsequent management are always species-specific and must be evaluated in the context of particular conservation and management goals. When managed appropriately, natural disturbances can serve as effective tools for ecosystem restoration and support objectives prioritized in European environmental policy. As disturbances become more frequent and severe due to climate change, developing management and conservation strategies grounded in strong scientific evidence is essential for our coexistence with natural disturbances in the uncertain future of the Anthropocene.

Streszczenie po polsku

Naturalne zaburzenia, takie jak wichury, pożary czy gradacje owadów, należą do kluczowych czynników kształtujących dynamikę ekosystemów na całym świecie. Wpływają na ich funkcjonowanie na wielu poziomach, między innymi kształtując bioróżnorodność. Wpływ naturalnych zaburzeń na bioróżnorodność zależy od zestawu czynników, spośród których najważniejsze to charakterystyka siedliska sprzed zaburzenia, typ siedliska oraz strategia zarządzania wdrożona po zaburzeniu.

W mojej pracy doktorskiej skupiłem się na trzech wielkoskalowych zaburzeniach środowiska i oceniłem ich wpływ na bioróżnorodność. Jako grupę wskaźnikową wybrałem ptaki, ponieważ szybko reagują na zmiany w strukturze ekosystemu wywołane zaburzeniami, często stanowią priorytet działań ochronnych, a dodatkowo ich monitoring jest stosunkowo prosty i tani.

W pierwszym rozdziale przeanalizowałem krótkoterminowe skutki dużego pożaru w Dolinie Biebrzy (jednego z największych obszarów podmokłych w Europie Środkowej) na zespół ptaków terenów otwartych. Porównując zespoły ptaków przed oraz po pożarze, mogłem oddzielić efekt pożaru od naturalnej zmienności zespołów ptaków w przestrzeni i czasie. Pożar spowodował natychmiastową zmianę w zespole ptaków i miał negatywny wpływ na kilka wyspecjalizowanych gatunków torfowiskowych o wysokim priorytecie ochronnym. Cztery gatunki tymczasowo zniknęły z obszaru dotkniętego pożarem, w tym również wodniczka (*Acrocephalus paludicola*) – gatunek narażony na wyginięcie w skali globalnej. Jedynie trzy gatunki odniosły korzyści z zaburzenia, jednak byli to generaliści otwartych siedlisk, niezwiązani ściśle z mokradłami. Podsumowując, pożar otwartych terenów podmokłych negatywnie wpływa na różnorodność ptaków w pierwszym roku po pożarze. Choć efekt ten jest prawdopodobnie krótkotrwały, w niektórych warunkach może powodować długotrwałe negatywne konsekwencje z punktu widzenia ochrony ekosystemów bagiennych.

W drugim rozdziale przyjrzałem się trwającej dwie dekady sukcesji zespołów ptaków leśnych na wiatrołomie w lesie gospodarczym (w Puszczy Piskiej). Porównałem zespoły ptaków na dwóch typach wiatrołomów (pozostawionym do naturalnego odnowienia oraz odnowionym przez człowieka), a następnie zestawiłem je z zespołami ptaków w pobliskim, niezaburzonym lesie. Wykazałem, że przez cały okres trwania badań wiatrołom pozostawiony do naturalnego odnowienia cechował się największą różnorodnością ptaków spośród wszystkich trzech środowisk (pod względem liczebności i bogactwa gatunkowego). Różnorodność ptaków leśnych była zbliżona do tej z niezaburzonego lasu, a dodatkowo występowały również gatunki terenów otwartych. Stwierdziłem także, że zespoły ptaków na obu typach wiatrołomów podążały dwiema niezbieżnymi trajektoriami sukcesji i pozostały różne od siebie przez cały czas trwania badań. Na podstawie moich wyników doszedłem do wniosku, że rezygnacja z aktywnej gospodarki leśnej po zaburzeniu kieruje sukcesję ptaków na nową ścieżkę, prowadząc do powstania unikalnych i różnorodnych zespołów ptaków. Oznacza to, że naturalne zaburzenia mogą być skutecznym i tanim narzędziem odtwarzania ekosystemów, pod warunkiem że zostaną pozostawione do naturalnego odnowienia.

W trzecim rozdziale przeanalizowałem skutki gradacji kornika drukarza na ptaki w Puszczy Białowieskiej, największym fragmencie nizinnego lasu o charakterze pierwotnym w Europie. Porównałem zmiany w zespołach ptaków wywołane zarówno przez samo zaburzenie, jak i aktywną gospodarkę leśną po zaburzeniu. Odniosłem te zmiany do dwóch siedlisk referencyjnych: lasu nieuszkodzonego przez kornika oraz pobliskich terenów rolniczych. Stwierdziłem, że gradacja kornika drukarza spowodowała przesunięcie w składzie zespołów ptaków – od typowego zespołu ptaków leśnych w kierunku bardziej charakterystycznego dla terenów rolniczych, ze wzrostem liczby gatunków krajobrazu rolniczego. Aktywne zarządzanie po zaburzeniu doprowadziło do dalszego przesunięcia w tym samym kierunku, skutkując jeszcze większym bogactwem gatunków krajobrazu rolniczego. Co istotne, aktywne zarządzanie po zaburzeniu doprowadziło do jeszcze większego odejścia zespołów ptaków od typowych zespołów leśnych niż gradacja kornika drukarza. Moje wyniki pokazują, że aktywne zarządzanie po zaburzeniach powoduje duże zmiany w zespołach ptaków, potencjalnie zakłócając sukcesję w ekosystemach leśnych. Z tych powodów powinno być ograniczane, szczególnie w lasach o wysokiej wartości przyrodniczej, takich jak Puszcza Białowieska.

Podsumowując, moje badania pokazały, że naturalne zaburzenia powodują istotne zmiany w różnorodności i strukturze zespołów ptaków w europejskich ekosystemach strefy umiarkowanej, Zmiany te są kształtowane między innymi przez sposób zarządzania terenem po wystąpieniu zaburzenia. Skutki zarówno samych zaburzeń, jak i strategii zarządzania nigdy nie są jednoznaczne i zawsze muszą być oceniane w kontekście określonych celów zarządzania i ochrony przyrody na danym terenie. Moje badania pokazują, że naturalne zaburzenia mogą stanowić skuteczne narzędzie odtwarzania ekosystemów, co jest istotne z punktu widzenia europejskiej polityki środowiskowej. Coraz częstsze i silniejsze zaburzenia związane ze zmianami klimatu wymagają opracowania strategii zarządzania i ochrony opartych na solidnych podstawach naukowych. Tylko w ten sposób będziemy mogli współistnieć z naturalnymi zaburzeniami w niepewnej przyszłości Antropocenu.

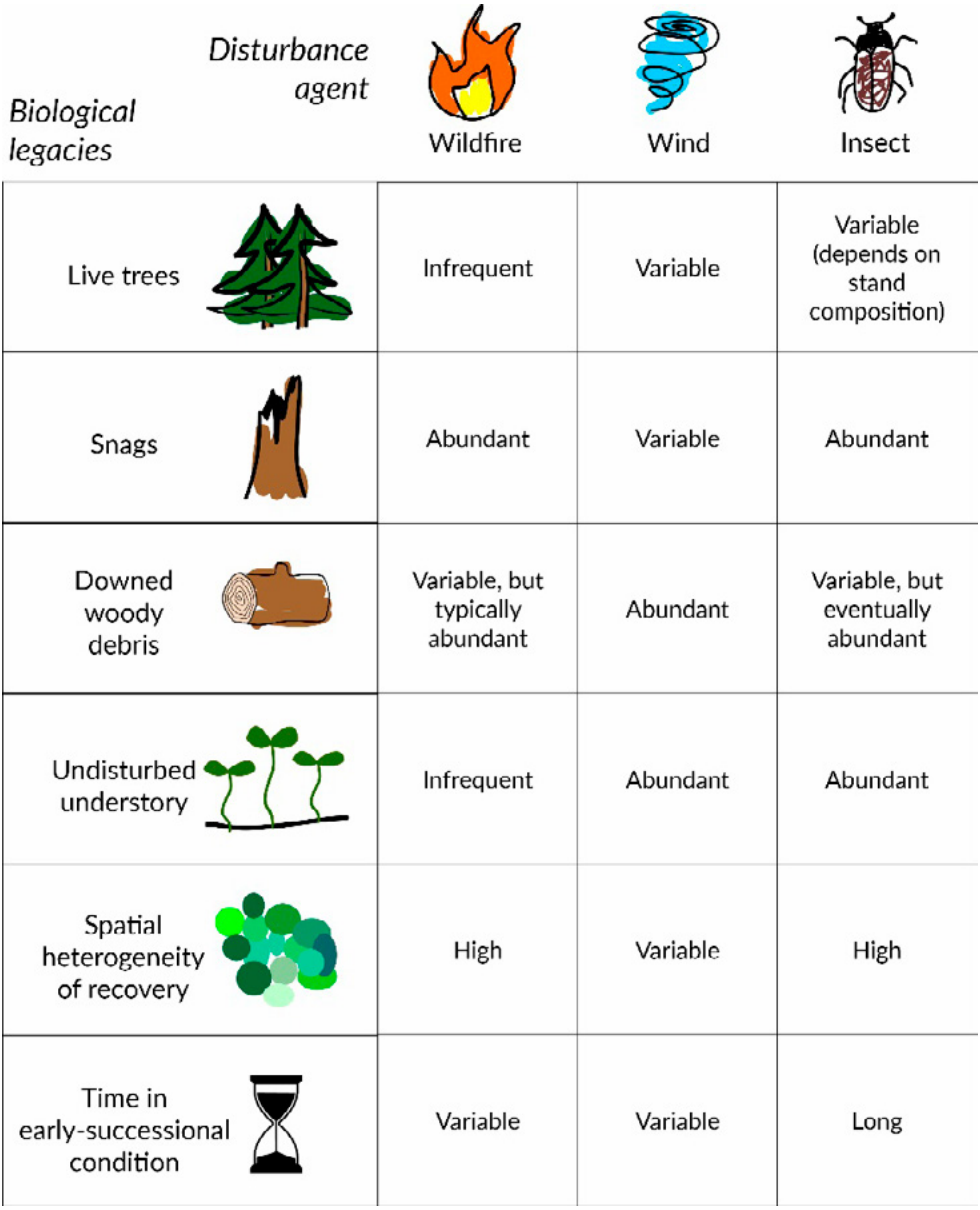
1. Introduction

1.1. Role of disturbances in temperate European ecosystems

Natural disturbances are a key component of terrestrial ecosystem dynamics worldwide (Turner, 2010). They are defined as “any relatively discrete event that disrupts the structure of an ecosystem, community, or population and changes resource availability or the physical environment” (White and Pickett, 1985). These events typically occur over relatively short time periods – for example, wind can drastically disturb thousands of hectares of forest in just minutes. Disturbances vary greatly in scale: volcanic eruptions may affect thousands of hectares, while some wind disturbances impact only individual trees (Kuuluvainen and Aakala, 2011; Turner et al., 1997). They have immediate consequences for ecosystems by altering resource availability, changing physical conditions, and resetting successional processes (Hobbs et al., 2007; Swanson et al., 2011; Turner et al., 2004). Because disturbances often affect specific patches within ecosystems with varying severity (i.e., the degree of damage to pre-disturbance vegetation), they are considered major drivers of spatial and temporal heterogeneity in ecosystems worldwide (Fig. 1; Turner, 2010).

Figure 1. Aerial view of landscape mosaic created as a result of Yellowstone fires in 1988. Photo credit: M. G. Turner (Turner, 2010).

In temperate Europe, the most significant natural disturbance agents are wind, fire, and insect outbreaks (Seidl et al., 2017). Each affects ecosystems in a unique way. Wind is the most impactful disturbance agent in European forest ecosystems, accounting for over 50% of disturbance-induced tree mortality (Schuck and Schelhaas, 2013).



Disturbance agent *Biological legacies*	Wildfire	Wind	Insect
Live trees	Infrequent	Variable	Variable (depends on stand composition)
Snags	Abundant	Variable	Abundant
Downed woody debris	Variable, but typically abundant	Abundant	Variable, but eventually abundant
Undisturbed understory	Infrequent	Abundant	Abundant
Spatial heterogeneity of recovery	High	Variable	High
Time in early-successional condition	Variable	Variable	Long

Figure 2. Differences in biological legacies generated by natural disturbances in temperate European forests (based on Swanson et al., 2011).

By uprooting or breaking trees, wind increases canopy openness and immediately creates large amounts of downed dead wood, while the understory remains largely intact (Fig. 2; Swanson et al., 2011). In contrast, fires primarily affect the surface vegetation layer, although they can also lead to large-scale tree mortality (Swanson et al., 2011; Turner et al., 1997). Fires also impact open habitats, especially peatlands, where they can cause permanent ecosystem transformations across thousands of hectares (Lohberger et al., 2018; Sulwiński et al., 2020; Watts and Kobziar, 2013). Compared to fire and wind, insect outbreaks are the most specific among the three disturbances considered, as they are restricted to forests and typically target a limited set of tree species. Among insect outbreaks, bark beetles form the most important disturbance agent, with the European spruce bark beetle (*Ips typographus*) being responsible for nearly 8% of total disturbance-induced tree mortality in Europe (Schelhaas et al., 2003). Bark beetle outbreaks mainly affect the canopy layer, but leave the majority of the dead wood in form of snags (Swanson et al., 2011). In recent decades, the impact of natural disturbances on temperate ecosystems has increased, largely driven by climate change (Seidl et al., 2017, 2014; Thom and Seidl, 2016). For example, bark beetle damage in European forests increased sixfold, while forest fires increased twofold between 1971–1980 and 2002–2010 (Seidl et al., 2014). As the frequency and severity of natural disturbances are expected to continue rising, these events will play an increasingly important role in shaping the structure of European ecosystems.

1.2. Effect of natural disturbances on biodiversity

Disturbance-induced changes in ecosystem structure have immediate impacts on biodiversity (Dornelas, 2010; Viljur et al., 2022). For example, fires in open habitats reduce vegetation biomass and may alter nutrient cycles, leading to shifts in plant and bird communities (Heim et al., 2019; Mérő et al., 2015). In forests, natural disturbances increase dead wood biomass and sunlight penetration, benefiting taxa such as saproxylic beetles, flowering plants, and pollinators – including species typically associated with open habitats (Cours et al., 2023; Swanson et al., 2011). These disturbances create microhabitats that may otherwise be absent from the ecosystem, supporting rare and protected species (Rachwald et al., 2022; Thorn et al., 2020). On the other hand, disturbances can also result in the loss of ecosystem features important to some species. For instance, fires in open habitats reduce vegetation cover, negatively affecting birds and insects that rely on tall or dense vegetation for nesting or foraging (Curnutt et al., 1998; Swengel, 2001). Similarly, canopy gaps created by disturbances in forests can deter species dependent on closed-canopy conditions (Fuller, 2000). Overall, while disturbances often increase species richness and are generally considered beneficial to biodiversity, their effects vary significantly depending on the taxa involved (Thom and Seidl, 2016).

Multiple factors influence the impact of natural disturbances on biodiversity. Among key components are disturbance severity and extent (Viljur et al., 2022). Severity is measured by the degree of damage to pre-disturbance vegetation, while extent is linked to the affected area. Both moderate disturbance extent and severity often support the highest levels of biodiversity, although these results are still debated (Moi et al., 2020; Viljur et al., 2022). The history of past disturbances also shapes ecosystem structure and has lasting effects on biodiversity (Kozák et al., 2021; Zemlerová et al., 2023). Similarly, historical land use affects an ecosystem's vulnerability to natural disturbances and influences biodiversity outcomes (Cerioni et al., 2024; Foster et al., 1998). Management decisions also play a crucial role, particularly in forests, where active interventions – such as logging, soil tilling, tree planting, fencing, or thinning – are commonly implemented in disturbed areas both to secure the production value of regenerating stands and to harvest damaged timber (Sanginés de Cárcer et al., 2021). These management practices often result in substantial changes to ecosystem structure and the associated biotic communities (Thorn et al., 2018). Altogether, the complex interplay of these factors underscores the need for comprehensive studies to understand context-specific effects of natural disturbances on biodiversity.

Lastly, the impact of natural disturbances on biodiversity is not consistent over time (Krebs, 2008). Due to their sudden nature, disturbance events often cause the most significant changes to biotic communities immediately after they occur (Jentsch and White, 2019). As succession unfolds, these changes may gradually diminish as the ecosystem returns toward its pre-disturbance state (Fig. 3A; Krebs, 2008). The time required for this recovery depends on the type of ecosystem, among other influencing factors. For instance, in open habitats, the effects of disturbances may disappear relatively quickly due to the rapid regeneration of vegetation and thus restoration of the ecosystem structure (Heim et al., 2019; Mérő et al., 2015). In contrast, disturbances in forest ecosystems can have long-lasting impacts, and reaching the pre-disturbance state may take decades or even centuries (Hilmers et al., 2018). In some cases (e.g., when several disturbances strike the ecosystem at the same time), disturbances can cause irreversible transformation of the ecosystem (Fig. 3B; Krebs, 2008). For example, this can occur in peatland ecosystems during smoldering fires, which release carbon stored in the peat back into the carbon cycle, thereby completely altering ecosystem dynamics (Kettridge et al., 2015; Rein, 2011). Due to the potential long-lasting and irreversible impact of natural disturbances on ecosystems, long-term studies are crucial to develop strong foundations for management strategies after disturbance events.

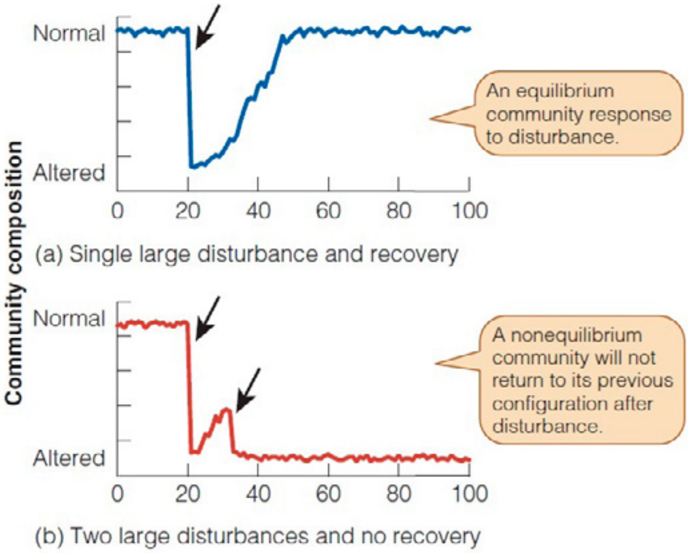


Figure 3. Schematic illustration of the two effects of disturbance events (marked with arrows) on ecological communities. The first graph (A) shows the ecosystem returning to the pre-disturbance state several decades after the disturbance. The second graph (B) depicts a situation where two consecutive disturbance events result in an irreversibly altered community composition. The x-axis represents years. Adapted from: Krebs, 2008.

1.3. Birds as model organisms in disturbance studies

Among many groups of species affected by natural disturbances, birds are excellent model organisms for studying the ecological effects of disturbance and post-disturbance management. Due to their high mobility, they quickly respond to changes in forest structure caused by disturbance, and multiple bird species represent a variety of life histories (different food, breeding sites, wintering strategies, etc.) so species-specific responses to habitat change can usually be attributed to certain habitat changes and resource availability. From a practical point of view, it is important that birds can be surveyed reliably at relatively low cost without the use of lethal methods and they have a long history of worldwide monitoring (Begehold et al., 2015; Moning and Müller, 2009; Schmeller et al., 2012). In addition, birds often serve as focal species in conservation efforts, acting as "umbrella species" that help protect a wide range of other taxa (Roberge and Angelstam, 2004). They are also frequently used as indicators of biodiversity (Fraixedas et al., 2020). Therefore, detailed knowledge of changes in the composition and density of bird assemblages after disturbance can help us understand ecological mechanisms and impacts associated with windstorms, fire, or insect outbreaks. This knowledge may then form strong foundations for management strategies after disturbance events.

1.4. Existing knowledge gaps in natural disturbance impact on birds

Although birds are among the best-studied taxa in relation to the impacts of natural disturbances on biodiversity in temperate ecosystems, many aspects of this impact remain relatively unknown. This is largely due to the low predictability of natural disturbances in both time and space, which hinders the use of experimental approaches and introduces potential biases (Driscoll et al., 2010). For example, the great majority of studies lack any information about pre-disturbance community states and this information is essential to disentangle the effect of disturbance from natural spatial and temporal variation in biotic communities (Smith, 2002). Additionally, the unpredictability of disturbances often results in hypotheses being tested within single, spatially limited ecosystems, making it difficult to generalize findings to other contexts (Turner, 2010). For example, many long-term studies come from North America (e.g., Duguid et al., 2016; Hutto and Young, 2002; Schieck and Song, 2006), where bird species composition is different and the scale of natural disturbances often does not correspond to that of temperate European ecosystems. The 1988 Yellowstone fires in the United States illustrate this mismatch well – the total burned area reached 250,000 hectares, which exceeds the total size of Białowieża Forest, the largest remaining patch of primeval temperate lowland forest in Europe (Jaroszewicz et al., 2019; Turner et al., 2003).

The majority of studies on the effects of natural disturbances on biodiversity focus on a single point in time – typically within the first few years following a disturbance event (Thorn et al., 2018). However, this period represents only a small fraction of the time required for many ecosystems to return to their pre-disturbance state (Hilmers et al., 2018; Krebs, 2008). Research on the impact of post-disturbance management similarly tends to lack long-term evaluation (Thorn et al., 2018). Where long-term assessments do exist, they are often based on space-for-time substitution, which can lead to misleading conclusions about the true effects of disturbance events (Kreyling, 2024). As a result, management recommendations are often made without the support of robust long-term data, which can lead to a mismatch with long-term biodiversity conservation goals.

Certain ecosystems are also better represented in disturbance studies than others. For example, ecosystems with a high level of naturalness (e.g., primeval forests) are often underrepresented in European disturbance research, primarily due to their limited extent and, more broadly, the inherent unpredictability of disturbance events (Sabatini et al., 2018). However, studies conducted under natural conditions are crucial, as they provide valuable baselines for nature restoration and rewilding efforts across Europe (Mutillod et al., 2024; Wesołowski, 2007). Other underrepresented ecosystems include those that were historically resilient to natural disturbances, where such events occurred only rarely. In recent years, climate change has led to a rapid increase in fire frequency within some of these ecosystems, for example in peatlands (Kettridge et al., 2015; Okruszko et al., 2011). Although this represents a significant conservation challenge, data remain scarce due to the historically low incidence of disturbances in peatland ecosystems.

Addressing how bird diversity responds to natural disturbances is particularly important in the face of climate change, which is increasing the frequency and severity of disturbances across European ecosystems, and amid the global decline of many bird species (Grehan, 1993; Lees et al., 2022; Seidl et al., 2017). Understanding both species-specific and community-level responses of birds to different disturbance events is crucial for guiding conservation efforts aimed at halting these declines. To develop effective conservation strategies, it is essential to empirically evaluate bird responses to natural disturbances across diverse ecosystems and temporal scales.

2. Aims of the thesis

The aim of the thesis was to improve our understanding of the complex disturbance impact on biodiversity. To do this, I analyzed the response of birds, as a model taxon, to the three separate disturbance events, representing the most significant natural disturbance agents in temperate Europe: wind, wildfire, and bark beetle outbreak. Each disturbance occurred in a different ecosystem – managed forest, open wetland, and natural forest, respectively – and each is addressed in a separate chapter of the thesis. In these chapters, I tested hypotheses concerning the effects of disturbances and/or post-disturbance management strategies, with the overarching goal of developing a broad understanding of disturbance impact on bird communities. I examined post-disturbance biodiversity responses across a range of temporal scales, from one year to two decades after the event, and, whenever possible, incorporated pre-disturbance data on bird diversity and nearby undisturbed sites as controls. Based on my findings, I aimed to provide insights that would strengthen the foundation for conservation and management strategies following natural disturbances.

More specifically, the questions I addressed in each individual chapter were:

Chapter I: What is the short-term impact (i.e., the first three months after the disturbance) of a large wetland wildfire on breeding bird diversity and community composition? Which species and ecological groups are most affected by the fire? Does wildfire reduce bird species diversity in wetlands? From a conservation perspective, how can the short-term effects of fire on bird communities be evaluated?

Chapter II: What are the effects of windthrow on two decades of bird community succession in a production forest? How do succession patterns change under active post-disturbance management? Are two decades sufficient for bird communities in windthrow sites to converge with those in unaffected forest? From a conservation perspective, is there a rationale for leaving windthrow areas unmanaged in production forests?

Chapter III: What are the effects of bark beetle outbreak on bird community composition in a highly natural forest? How do these effects change due to the post-disturbance management? Do natural disturbances shift bird communities toward those typical of open-habitat ecosystems? Which has a greater impact on forest bird communities: the natural disturbance or the subsequent management intervention?

Chapter I

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ORIGINAL PAPER

Large fire initially reduces bird diversity in Poland's largest wetland biodiversity hotspot

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Abstract

Freshwater wetlands are widely recognized as biodiversity hotspots for many organisms, including birds. Climate change and the projected increased risk of wetland fires may pose a major threat to wetland biodiversity in the future. There is urgent need to assess short- and long-term effect of fires on avian biodiversity and to establish relevant management implications. We analysed the short-term (first 3 months after fire) effect of a large (5 500 ha) spring wildfire on the community of breeding marshland birds in the best-preserved Polish local wetland biodiversity hotspot: Biebrza Valley. We compared the avian community structure and abundance of certain species before and after the fire on the 18 permanent transects located in both burned and unburned habitats. Within first breeding season post fire, fire significantly reduced pooled abundance and species richness of the whole bird community. Three bird species of special conservation concern (including aquatic warbler) temporarily disappeared from burned areas, and the numbers of 11 other species declined. In contrast, only 3 species benefited from the fire, none of which depended on marshes as their primary habitat. Although the reported strong initial fire effect is likely to fade away in subsequent years, its immediate detrimental effects on marshland birds should not be underestimated. We conclude that it is essential to temporarily provide the unburned adjacent refuge areas with additional protection and bird-friendly management and to focus on preventing further degradation of marshes to increase their resilience to fire.

Keywords Wildfire · Marshlands · Avian biodiversity · Biebrza Valley · Disturbance · Aquatic warbler

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Introduction

Freshwater ecosystems, including wetlands, are widely recognized as biodiversity hotspots for both plants and animals (Dertien et al. 2020; Reid et al. 2019). Although they cover only 0.8% of the world's land area, they host nearly 6% of all described animal species, including 33% of all vertebrates (Dudgeon et al. 2006). However, their area continues to shrink at an alarming rate; since the beginning of the twentieth century, the global area of freshwater wetlands has declined by 64–71% (Davidson 2014). In Europe, between 1970 and 2008 alone, the total area of natural wetlands declined by 50% (Dixon et al. 2016). The condition of the remaining wetlands is deteriorating mainly due to further anthropogenic water level regulation, habitat degradation, water pollution and invasive species (Dudgeon et al. 2006). As a result, wetland-associated biodiversity is declining faster than ever worldwide (Reid et al. 2019). For example, 40% of European freshwater fishes are threatened according to the IUCN (Reid et al. 2019) and over 50% of wetland bird species in Europe are declining (BirdLife International 2017). Huge efforts are now being made to restore lost wetlands or create new ones to support threatened wetland biodiversity (Kačergytė et al. 2021; Szalkiewicz et al. 2018).

Recent predictive models show that wetland-associated biodiversity may face further changes and degradation under pressure of climate change (Reid et al. 2019). In temperate zones of Northern Hemisphere, predicted warming across all seasons is expected, among other factors, to increase the annual evapotranspiration to precipitation ratio (Čížková et al. 2013), frequency of soil moisture droughts (Grillakis 2019) and reduce snow cover depth (Brown and Mote 2009), leading to increased vulnerability of wetlands to fire (Čížková et al. 2013; Kettridge et al. 2015; Turetsky et al. 2015). This impact is expected to strike central European wetlands with particular severity (Okruszko et al. 2011). Although fire regularly occurs in some wetland ecosystems, and may help to promote wetland-associated biodiversity (Kotze 2013; Martin and Kirkman 2009), the development of a new disturbance regime with higher fire frequency or severity may pose a threat on sensitive species or habitats, thus creating new challenges in wetland conservation.

With the expected increased impact of fires on freshwater wetland ecosystems, there is an urgent need to assess both short-term and long-term consequences on wetland birds. This topic is understudied in Europe (but see Mérő et al. 2015) partly due to the low predictability of wildfires at local scales, so many studies lack reliable assessments of bird diversity prior to the fire event, making it difficult to disentangle fire effects from random environmental variability. This may lead to biased conclusions on the true fire effects (Smith 2002). Accuracy in assessing fire effects is crucial for building knowledge base for further wetland management, although temporal aspects need to be taken into account to clearly separate short-term effects, occurring early after fire event, from long-term consequences.

Birds, often being focal species in wetland conservation (e.g., Ramsar Convention), may be affected by fires in various, species-depending ways. Short-term fire effects are often attributed to fire-induced iterations of vegetation cover; For example, species preferring tall vegetation, like reedbeds, tussocks, shrubs or tall grass may lose their habitats due to fire (Curnutt et al. 1998; Isacch et al. 2004). In contrast, short-term reduction of vegetation biomass may provide suitable foraging grounds for species preferring short vegetation, like waders or geese (Mitchell et al. 2006; Vogl 1973). The effect of fire on birds of prey seems complex: short-term reduction of plant biomass and height due to fire may facilitate prey detection and availability (Barnard 1987) but also reduce prey densities (Sharp Bowman et al. 2017). In a longer term, fire may effectively slow down succession in wetlands, helping to maintain suitable habitat for wetland specialists (Conway et al. 2010), while for some species, long-term effects may even contradict short-term effects (Grzywaczewski et al. 2014). As a consequence, impact of fire on wetland birds often remains unclear and depends on time scale considered. Unfortunately, for many regions large-scale empirical evaluations of fire consequences for wetland birds are not available.

Biebrza Valley is recognized as largest, best-preserved Polish wetland and one of the largest wetlands in central and western Europe. It is an important breeding and migratory site for birds (ca. 270 species observed within its borders, Biebrza National Park 2021) and hosts 75% of the EU population (20% of the global population) of the aquatic warbler *Acrocephalus paludicola*, the rarest migratory bird in Europe (Świętochowski et al. 2010). It is recognized as most important breeding site in central and western Europe for several other wetland birds (e.g. great snipe *Gallinago media*, corn crake *Crex crex* and spotted crake *Porzana porzana*) (Birdlife International 2017).

Here we evaluate the initial impact (i.e. observed within 3 months since the fire event) of large wildfire of spring 2020 (5500 ha; largest open landscape fire in Poland after World War II) on bird community in Biebrza Valley. We hypothesize that: (1) As fire immediately reduces vegetation structure and kills the shrubs (Conway et al. 2010), shortly after fire bird species preferring tall vegetation for nesting, foraging and as shelters will be negatively impacted. Importantly, we expect that many marshland species of high conservation concern may fall into this group. (2) Several bird species preferring short vegetation and open landscape structure for which shrubs encroachment and expansion of tall vegetation is a threat, will increase in number at burned sites immediately after the fire. 3) Bearing in mind the possible species-specific responses to fire, the composition of the whole marsh-dependent bird community will be markedly altered by the fire, but with little change, if any, in overall bird abundance and species richness.

Materials and methods

Study site

The Biebrza Valley located in NE Poland (53°28′48.3"N 22°38′19.3"E) (Fig. 1a) is recognized as best preserved large complex of fen marshes in western and central Europe (Żurek 2005). The valley covers 136 900 ha, extending along the entire length (164 km) of Biebrza River. Roughly half of the area (66 800 ha) is protected as Biebrza National Park, the largest national park in Poland. It is recognized as a wetland of International Importance (Ramsar Convention Secretariat 2013) and Important Bird and Biodiversity Area (IBA, Birdlife International 2021).

Biebrza Valley was formed due to complex accumulation-erosion interactions during the last two Pleistocene glaciations and interglacials. Intensity and direction of those processes differed within the area, and three major units can be divided as a result: Upper Basin, Middle Basin and Lower Basin (Żurek 2005). Upper Basin is the most narrow part of Biebrza Valley (1.5 km wide) with total area of 12 000 ha. Its bottom is covered with thick layer of peat (3–6 m) and gyttja (mud formed by partial peat decay) (Żurek 2005). Middle Basin is much wider (20 × 40 km) and nearly rectangular in shape. Peat layer cover 45 000 ha and reaches up to 3 m in depth (Dembek et al. 2005). Lower Basin is 12–15 km wide and it’s formed mainly by one large fen with peat layer depth

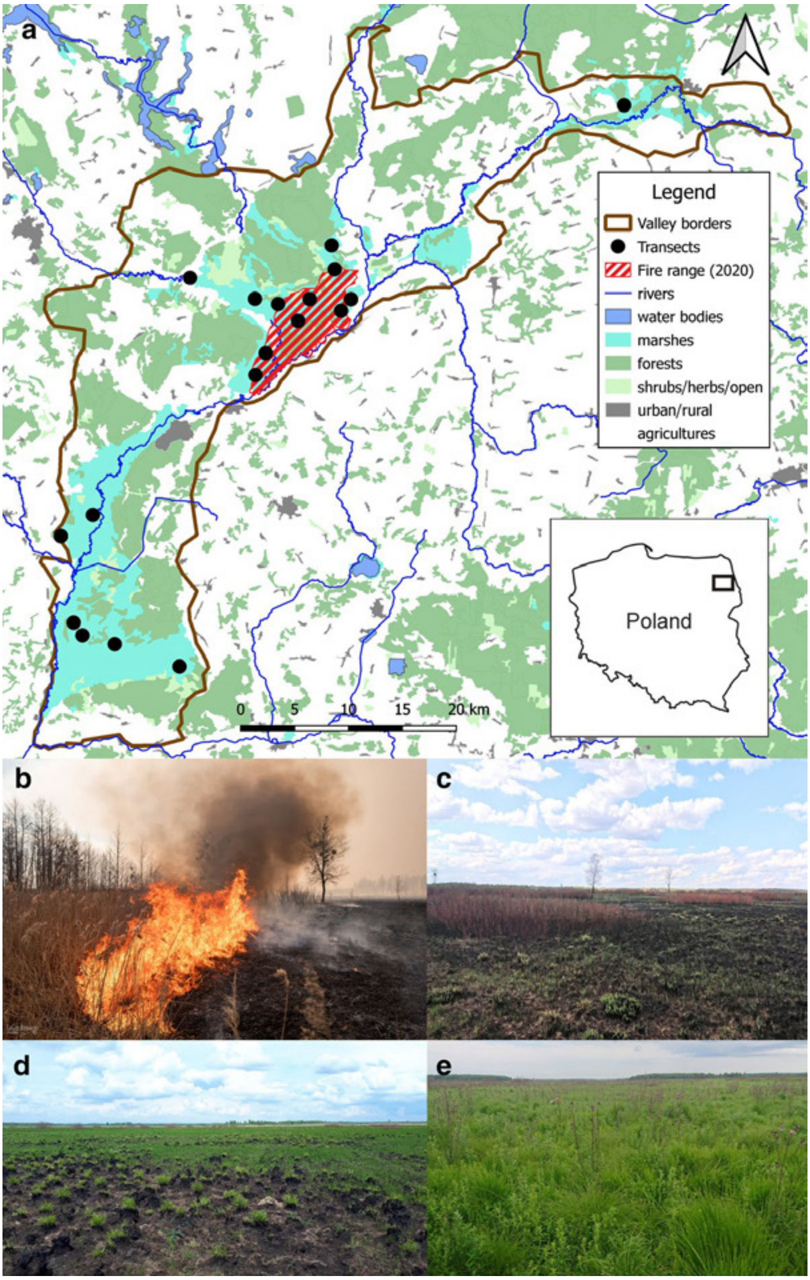


Fig. 1 Study site; **a** Location of fire and 18 bird count transects **b** Fire front (19th April) **c** Post-fire marsh landscape after 2 weeks (4th May) **d** Post-fire marsh landscape after 5 weeks (28th May) **e** Post-fire marsh landscape after 11 weeks (3rd July)

rarely exceeding 2 m (Dembek et al. 2005; Żurek 2005). Sand and gravel layer of average depth 5–15 m (20–30 m in Lower Basin) spans underneath the peat (Żurek 2005). Upper and Middle basins were subject to partial drainage due to human activity in the past, while Lower Basin was left largely undisturbed (Birdlife International 2021).

The valley covers a mosaic of landscapes, with marshes and non-agricultural open areas occupying ca. 30% of the area (Świętochowski et al. 2010). Large parts of Biebrza Valley consist of regularly flooded bogs and wet meadows dominated by sedge (*Carex* spp.) and oxbow lakes covered with reed (*Phragmites australis*). Unflooded areas consist mainly of pine (*Pinus sylvestris*), alder (*Alnus* spp.), willow (*Salix* spp.), and mixed forests, as well as sedge beds, bogs, pastures and meadows (Birdlife International 2021). Sedge, sedge moss, and reed peat soils cover majority of the valley, with numerous elevated moraine islands of loamy sand and gravel spread throughout the area. The valley is sparsely populated and agriculture (mostly extensive in character) has been largely abandoned in recent decades, resulting in scrub encroachment in many parts of the valley (Dembek et al. 2005). Some habitat management (mowing) has been introduced as conservation measures (Lachmann et al. 2010).

Natural fires were present in Biebrza Valley prior to human settlement, helping to shape vegetation of the valley's peatlands. However, in recent decades fires started to be perceived as one of the major threats to Biebrza Valley's ecosystems, because of their increasing frequency and area covered (Dembek et al. 2005). Recent yearly number of fires in the valley vary greatly depending on seasonal weather conditions: Between 2015 and 2019 there were 55 fires in total, which covered total area of 765 ha (Rutkowski et al. 2021). Prior to 2020, largest single fire occurred in 2002 and covered ca. 1 200 ha (Kania et al. 2006). Majority of the fires in the region are human-caused and occur during winter-spring period due to illegal burning (Szczygieł et al. 2021). Valley is constantly monitored for the presence of fires with the use of terrestrial patrols and video cameras. Wherever possible, fires are extinguished as soon as detected by State & Voluntary Fire Services, State Forests and Biebrza National Park (Rutkowski et al. 2021). Among other local threats to biodiversity, the most important is decline in groundwater levels (due to dredging, channelization, and water management), followed by the succession of expansive plant species (Ramsar Convention Secretariat 2013; Świętochowski et al. 2010).

Fire of 2020

During April 19–26, 2020, a large human-caused wildfire occurred over an area of 5500 ha (4% of the total area) in the central part of Biebrza Valley (Fig. 1a). It was the largest open landscape fire in Poland after World War II (Szczygieł et al. 2021). Before the fire, the water level in the valley was extremely low, marking the lowest April water level in the Biebrza River in last 20 years (Institute of Meteorology and Water Management, Poland). Majority of the burned area consisted of marshlands. As a result of the fire, more than 90% of the surface vegetation (mainly dead biomass of reeds, tussocks and grasses from the previous year, but also shrubs and small trees) was burned and the area became significantly less covered with tall vegetation (Fig. 1b). Soon after the fire, surface vegetation began to re-sprout; At the beginning of May (ca. two weeks after the fire – Fig. 1c) vegetation was still scarce and there was observable difference between burned and control areas (mean NDVI values 0.25 ± 0.05 SD vs. 0.46 ± 0.17 SD, respectively) (Durka 2020). The green cover fully recovered within two months (Fig. 1d-e); Observed NDVI differences virtually disappeared by 8th June (burned vs. control 0.59 ± 0.11 vs. 0.60 ± 0.13) (Durka 2020).

Breeding bird counts

Systematic bird counts took place in the area in 2015–2016 (i.e. 5 years before the fire) and 18 line transects were established throughout the Biebrza Valley's marshlands to cover the most important breeding sites of birds (Fig. 1a). Each transect consisted of two parallel lines (each 1 km long) divided into five sections (200 m long, 10 sections per transect). The minimum distance between transect centers was 1.4 km (4.2 km on average), while the distance between sections of the nearest adjacent transects was always greater than 600 m. The 2020 fire affected the area containing six full transects, and one half of an additional transect (Fig. 1a). All other transects remained intact, providing controls for the fire effect.

Bird abundance data were collected during slow walks at a constant pace along transects (hereafter each such walk is referred to as a "survey"), following Gregory et al. (2004). Surveys were conducted nine times in each transect: three times per breeding season (1–15 May, 20–31 May, 5–21 June), in three years (2015, 2016, 2020). Each survey lasted approximately 1.5 h between 4 and 9 am, on days with good visibility and no or light rain. During each survey, birds were counted within hearing/seeing distance. Surveys were conducted by the same team of experienced ornithologists for all survey periods. The three surveys for each transect in given year were often done by two or more ornithologists. The final abundance of each species in a given transect section and year was considered, for this study, to be maximum abundance from the three surveys, and this value was used in all further statistical analyses.

In this study, we focused on marshland birds defined as species that typically inhabit wet meadows, pastures, tussock-covered marshes, reedbeds and shrubs (according to Kuczyński and Chylarecki 2012; Sikora et al. 2007). This group was chosen for analysis as it is of highest conservation concern and the target of most conservation efforts aimed at bird protection in the area. Species typical for other habitats, such as woodlands (woodpeckers, tits, treecreepers), urban areas (martins, swallows, swifts) and open water (ducks, swans, geese, grebes, terns and gulls) were excluded from the analysis. We also excluded some raptors that have very large territories or mainly hunting in flight (white-tailed eagle *Haliaeetus albicilla*, hobby *Falco subbuteo*), but left harriers (*Circus* spp.), common buzzard *Buteo buteo* and eurasian kestrel *Falco tinnunculus*. Bird flocks larger than 50 individuals (Eurasian Starling *Sturnus vulgaris*, Northern Lapwing *Vanellus vanellus*) were also excluded as largely migrating. A total of 63 species were included (hereafter called "marshland birds”), while 62 were excluded from further analysis (see Appendix Tables 1–2 for details).

Using data on 63 marshland bird species, six indices of bird diversity were calculated for each transect section and year: abundance and richness of all species, abundance and richness of “Species of European Conservation Concern” (SPECs; Birdlife International 2017), and abundance and richness of species included in Polish Red List of Birds, listing rare or quickly declining species in Poland (red-listed; Wilk et al. 2020).

BACI study design

Each data record (i.e., abundance of each species in a single transect section in a given year) was attributed to one of two time periods (before vs after the fire) and one of two treatments (fire vs no fire). Such approach, known as before-after control-impact study design (BACI), allowed us to disentangle the fire effect from a natural temporal and spatial variation of a biological response driven by factors other than the treatment of interest

(Smith 2002). Following the design, our records were therefore divided into four groups: before-control (BC), before-impact (BI), after-control (AC), after-impact (AI), hereafter referred to as the “BACI groups”.

Statistical analysis: GAMMs, logistic regression and indicator species analysis

For all bird species with abundance ≥ 15 individuals (i.e. 47 species; in case of remaining 16 species generated models exceeded maximum number of iterations), generalized additive mixed models (GAMM) in “mgcv” package (Wood 2017) in R (version 4.1.0, R. Core Team 2013) were fitted. GAMMs were chosen as they allow to fit random effects as penalized regression terms, which are faster to compute and more reliable than conventional random effects in general mixed models (Wood 2017). In each GAMM, species abundance was a response variable and three explanatory variables were considered: period (before vs after fire), treatment (fire vs no fire) and interaction of these two, the latter being a formal test of the fire effect. Also, random effects of year, transect and section were included to account for spatial and temporal dependency of the data, and were fitted with ridge penalty splines (Wood 2017). All 47 GAMMs were fitted using negative binomial distribution and logarithmic link with theta dispersion parameter estimated directly from data. This approach was preferred over Poisson distribution, because of overdispersion observed in most species (variance to mean ratio, White and Bennetts 1996). We reported “positive short-term fire effect” on a species if period/treatment interaction coefficient had value above 0 with associated $p < 0.05$ and “negative short-term fire effect” for coefficients below 0 ($p < 0.05$).

Seven species were absent in one of four BACI groups (specifically: after-impact, see Appendix Table 3 for details), resulting in a problem of perfect data separation. As a result, confidence intervals of model coefficients were impossible to estimate using standard maximum likelihood methods (GAMM) (Heinze 2006). Hence, to obtain interpretable results for those seven species, logistic regression models were performed instead of GAMMs (Firth; see Appendix Table 4 for details). Species occurrence (i.e. abundance transformed to presence/absence binomial values) was used as a response variable, while period, treatment, their interaction and transect as explanatory variables. The coefficient was obtained using penalized maximum likelihood method (Firth 1993) in “logisft” package (Heinze et al. 2020) in R.

Another six GAMMs were performed to analyse how six diversity indices (i.e., abundance and species richness of all marshland bird species, SPEC species and red-listed species) changed in response to fire. Here we followed the procedure described above for species-specific GAMMs.

Spatial autocorrelation of residuals of the models was checked with spline correlograms using “ncf” package (Bjornstad 2020) in R. As in no case we did record significant spatial autocorrelation of the residuals and in all cases correlation never exceeded 0.1 we assume the models meet the criteria of spatial independency of data. Predicted values and confidence intervals from the models were plotted using ggplot2, ggeffects (GAMMs) and DAMisc (logistic regressions) packages (Armstrong 2021; Lüdecke 2018; Wickham 2016) in R.

In addition to GAMM and logistic regression models, we performed two Indicator Species Analyses using “indicspecies” package in R (9999 permutations, De Cáceres and Legendre 2009). We compared separately after-impact group with before-impact group (AI vs BI; same area before and after the fire) and after-control with after-impact group (AC vs

Fig. 2 Short-term impact of fire on bird community in Biebrza Valley, NE Poland; Effect size, meant as model coefficient of interaction between period (before vs after) and impact of wildfire (fire vs control) as found by GAMM/Firth's logistic regression models, was presented for: **a** 47 marshland bird species (abundance ≥ 15), **b** diversity indices for all 63 marshland bird species. Additional diversity indices were calculated for those belonging to Species of Special European Conservation Concern according to Birdlife International 2017 (SPEC, n = 31) and species present on Polish Red List of Birds according to Wilk et al. 2020 (red-listed, n = 18). Horizontal bars represent 95% confidence intervals. Significance level of fire effect was presented for each species (**p < 0.01; *p < 0.05). Trophic guilds were attributed following Pigot et al. (2020). Further details provided in Appendix Tables 3, 4. ▶

AI; same period of time, control and burned areas). We used threshold of $p < 0.05$ to determine indicator species for both categories in each of the two analyses.

Statistical analysis: MANOVA, PCA

To analyse differences in bird communities between BACI groups, Permutational Analysis of Variance (PERMANOVA) was performed. Differences in bird abundances were transformed into Bray–Curtis dissimilarity matrix in "vegan" R package. To make the number of records the same for before and after time periods, data records from 2015 to 2016 (i.e., both years before the fire) were averaged. Bird community compositions of four BACI groups were compared using PERMANOVA on two levels: transect and section. Prior to transect level analysis, section abundances were averaged in each transect separately for before and after time periods.

Next, multivariate homogeneity of groups dispersions (PERMDISP2) test was performed to check for homogeneity of variances between treatment groups (Anderson 2006; Oksanen et al. 2020). Permutational MANOVA (9999 permutations) and Pairwise Permutational MANOVA with Bonferroni p-value correction (9999 permutations) were used on each dissimilarity matrices to statistically test differences in species composition among BACI groups (Anderson 2001; Martinez Arbizu 2020).

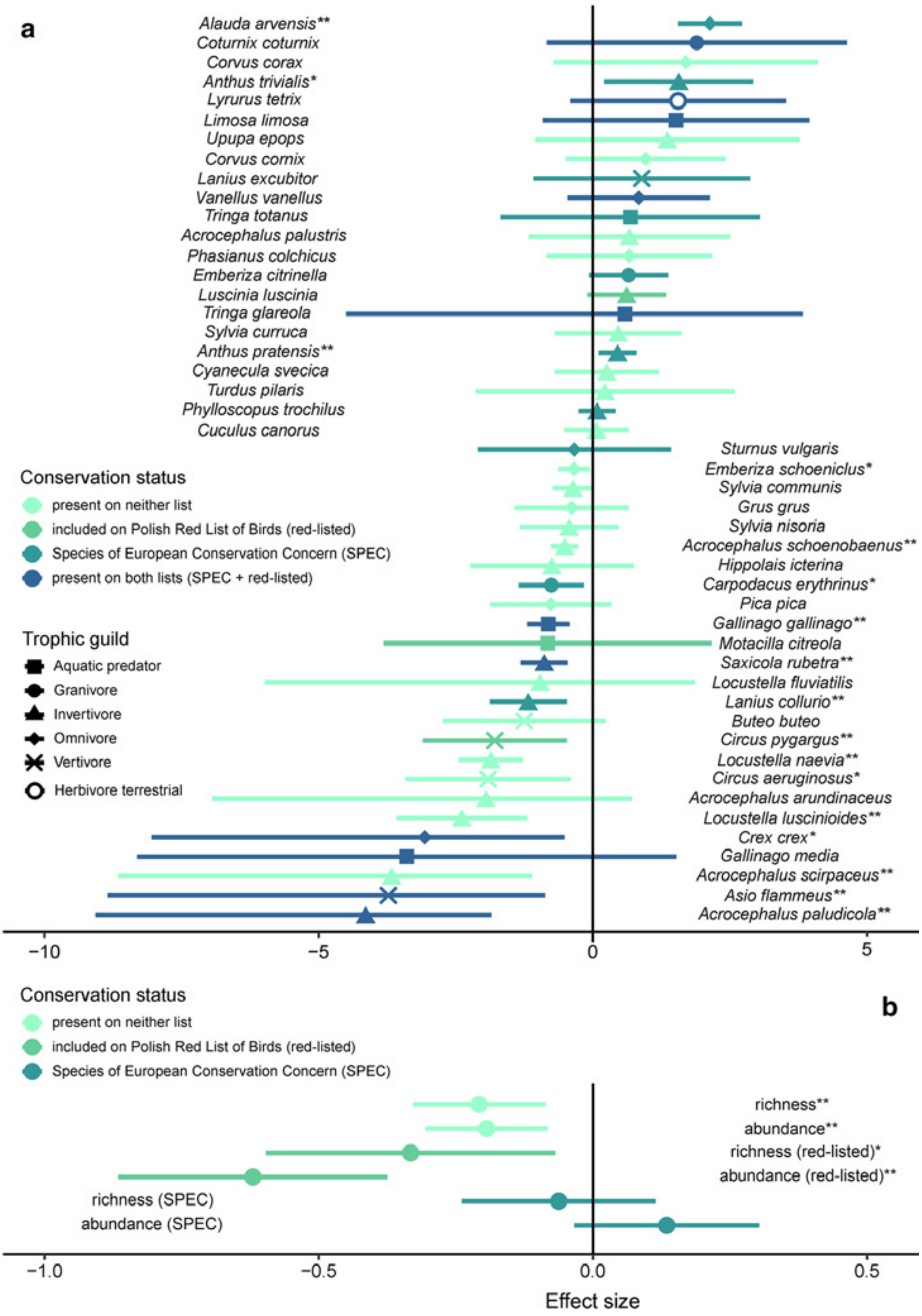
To visualize differences in bird communities detected with PERMANOVA, principal component analysis (PCA) was performed based on scaled, Hellinger-transformed species data (Oksanen et al. 2020).

Results

A total of 9786 marshland bird observations were recorded. The five most common species were as follows: sedge warbler *Acrocephalus schoenobaenus* (n = 1234), common reed bunting *Emberiza schoeniclus* (1072), common snipe *Gallinago gallinago* (821), meadow pipit (791) and willow warbler *Phylloscopus trochilus* (572). Mean bird abundance on a section was 18.1 (SD = 6.85) and mean species richness was 9.46 (SD = 3.03). 31 out of 63 marshland birds were included in list of European Birds of Conservation Concern SPEC (six of which are globally threatened) and 18 species in Polish Red List of Birds (four with "Critically Endangered" status).

Species-level short-term response to fire

Fire turned out to be important (statistically significant interaction between period and treatment was recorded) for abundance of 17 species among 47 tested, having short-term



positive effect on three species and negative on 14 (Figs. 2a, 3). All three species positively affected by the fire were species of European conservation concern (included on SPEC list), while among 14 negatively affected species, five were included on both lists (SPEC and Polish Red List of Birds), one only on Polish Red List of Birds and two only on SPEC.

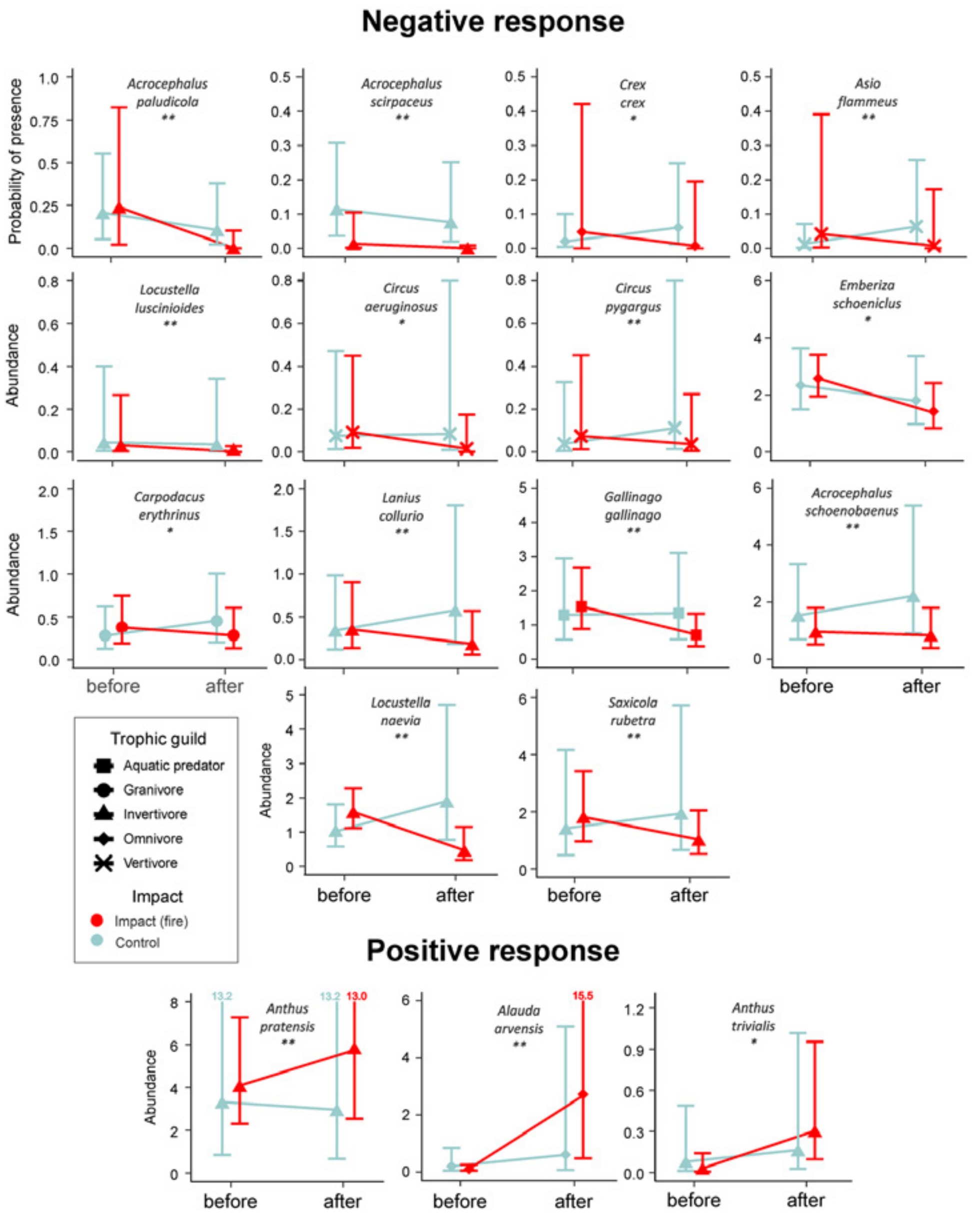


Fig. 3 Short-term impact of fire on bird community in Biebrza Valley, NE Poland; Abundance (GAMM models) and probability of presence (Firth logistic regression models), of marshland birds significantly ($p < 0.05$) impacted by fire in relation to time (before vs after fire) and impact (fire vs control), as predicted by models described in Fig. 2 and Appendix Table 4. Vertical bars represent 95% confidence intervals. In cases, where upper confidence intervals exceeded scale, they were shown on the graphs as numbers. Significance level of fire effect was presented for each species (**$p < 0.01$; *$p < 0.05$). Trophic guilds were attributed following Pigot et al. (2020)

Four of the negatively affected species temporarily disappeared from burned areas after the fire (aquatic warbler, short-eared owl *Asio flammeus*, corn crake and reed warbler *Acrocephalus scirpaceus*; see Appendix Table 3 for details).

We identified 12 indicator species for fire treatment, with five species common for both performed analysis (BI vs. AI & AC vs. AI) (Table 1a, b). In both cases, Eurasian skylark (*Alauda arvensis*) was best indicator species for fire (Indicator value > 0.75). We identified 10 species being indicators of control areas (i.e. no fire), with six species common for both analysis. Indicator species detected for control areas slightly differed between two performed analysis, with common snipe and common grasshopper warbler (*Locustella naevia*) among best indicator species for both.

Community-level short-term response to fire

Fire immediately altered the abundance and richness of studied bird assemblage (Fig. 2b, Fig. 4). The total abundance of all 63 marshland species remained constant after the fire on impact areas (difference = 0.03), but at the same time increased by 4.43 individuals on control sites (Fig. 4). Fire caused decline of species richness by 0.3 species/section, while

Table 1 Significant ($p < 0.05$) indicator species for fire and control areas compared within same space, but different time period (a. before/impact vs. after/impact) and different space, but same time period (b. after/control vs after/impact)

Before/fire vs after/fire					
Treatment = Before/fire			Treatment = After/fire		
Species	Indicator value	p value	Species	Indicator value	p value
Emberiza schoeniclus	0.78	0.000	*Alauda arvensis*	0.90	0.000
Gallinago gallinago	0.74	0.000	*Phylloscopus trochilus*	0.61	0.047
Locustella naevia	0.71	0.000	*Anthus pratensis*	0.60	0.013
Locustella luscinioides	0.61	0.000	*Luscinia luscinia*	0.51	0.000
Saxicola rubetra	0.60	0.021	*Anthus trivialis*	0.43	0.000
Acrocephalus paludicola	0.56	0.000	*Emberiza citrinella*	0.42	0.006
Acrocephalus scirpaceus	0.38	0.003	*Phasianus colchicus*	0.38	0.009
Circus aeruginosus	0.37	0.013	*Coturnix coturnix*	0.36	0.000
			Corvus cornix	0.34	0.003
			Lanius excubitor	0.33	0.003
			Lyrurus tetrix	0.29	0.048
After/no fire vs after/fire					
Treatment = After/no fire			Treatment = After/fire		
Species	Indicator value	p value	Species	Indicator value	p value
Locustella naevia	0.71	0.000	*Alauda arvensis*	0.79	0.000
Gallinago gallinago	0.67	0.001	*Anthus pratensis*	0.62	0.012
Saxicola rubetra	0.60	0.013	*Phasianus colchicus*	0.41	0.000
Locustella luscinioides	0.53	0.000	*Cyanecula svecica*	0.37	0.048
Lanius collurio	0.52	0.007	*Coturnix coturnix*	0.34	0.004
Acrocephalus paludicola	0.44	0.001	*Lyrurus tetrix*	0.30	0.003
Circus aeruginosus	0.40	0.006			
Circus pygargus	0.38	0.041			

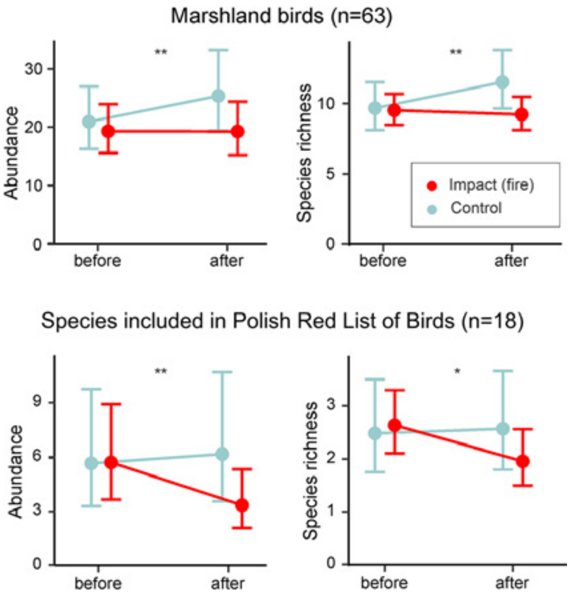


Fig. 4 Short-term impact of fire on bird community in Biebrza Valley, NE Poland; Diversity indices of all 63 marshland birds in relation to time (before vs after) and impact (fire vs control) as predicted by models described in Fig. 2b and Appendix Table 4. Only diversity indices, which were significantly affected by fire ($p < 0.05$), are shown. Significance level of fire effect was presented for each index (**$p < 0.01$; *$p < 0.05$). Vertical bars represent 95% confidence intervals

on control areas richness increased by 1.86 species/section. Similar trend was observed for red-listed species, in which abundance and richness increased in control areas (by 0.51 and 0.09 respectively) and decreased in impact areas (by 2.37 and 0.68 respectively). Abundance and richness of SPEC species did not change due to fire (Fig. 2b).

Permutational MANOVA showed a separation of bird community recorded at burned sites shortly after fire as compared to remaining BACI groups. However, as homogeneity of variance test among BACI groups confirmed violation at the level of sections ($F = 17.5$, $p < 0.001$), we restricted PERMANOVA analysis to data at the level of transects (homogeneity test results, $F = 1.57$, $p = 0.21$). Bird assemblages of BACI groups significantly differed from each other (PERMANOVA, $F = 1.75$, $p < 0.05$; Fig. 5a). This difference, however, resulted solely from the difference between BI and AI (pairwise PERMANOVA, $F = 2.98$, $p < 0.05$) and there was no significant difference between any other pair of BACI groups. We show visual separation of those two significantly different BACI groups (before-fire and after-fire) using PCA (Fig. 5a-b).

Discussion

Our study clearly demonstrated that – partly contradicting our hypothesis – large wildfire substantially reduced diversity of marshland birds in burned area of Biebrza Valley in first weeks after the fire event. This effect was observed both in the overall abundance and species richness of marshland birds and at the species level, including abundances of species of high conservation concern. Only a few species benefited from the fire, but none of them inhabits marshlands as its primary habitat (Kuczyński and Chylarecki 2012). These results are in general consistent with the observed short-term impact of wildfires (Heim et al. 2019) and prescribed fires (Hanowski et al. 1999; Mérő et al. 2015) in temperate wetlands (but see Conway et al. 2010). Below, we discuss fire-induced mechanisms potentially leading to a short-term decline of marshland birds and their implications for wetland biodiversity conservation and management, as well as possible long-term effects.

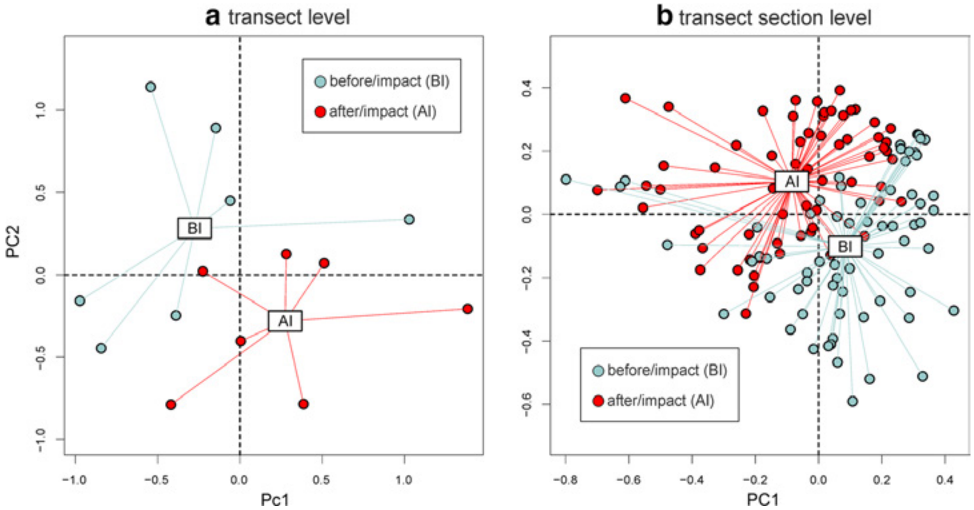


Fig. 5 Principal component analysis (PCA) performed on Hellinger-transformed marshland bird community matrix in two time periods: before and immediately after the fire. using transects (**a**) and single sections of transects (each transect = 10 sections) (**b**). Fire-induced short-term alteration of the two bird communities (before-impact and after-impact) for which significant differences were confirmed (PERMANOVA $p < 0.05$) were visualized. Presented PC1 and PC2 axes explain in total 37% of variance on the transect level (**a**) and 18% on the section level (**b**)

Bird community—short-term response to fire

As predicted, fire immediately benefited some bird species of open habitats that avoid tall vegetation. Two out of three positively affected species are generalists of open habitats and inhabit primarily cropland, including arable land (Eurasian skylark) and grassland (meadow pipit), while none relies on marshlands as their main habitat (Kuczyński and Chylarecki 2012). Several marshland species preferring short vegetation were observed on the study area, e.g. northern lapwing and godwit *Limosa limosa* (Żmihorski et al. 2018), but contrary to our hypothesis, they did not respond positively to fire. Also, none of typical marshland species were identified among indicator species for burned area.

In contrast, the numbers of several marshland bird specialists inhabiting tall vegetation, reeds and tussocks immediately declined, confirming our predictions. Temporary loss of suitable habitat structures negatively impacted reed passerines (sedge warbler, common reed bunting, common grasshopper warbler), open marshland passerines (aquatic warbler), and open marshland non-passerine birds (common snipe). Several marsh raptors also showed a negative response to fire (Montagu's harrier *Circus pygargus*, marsh harrier *Circus aeruginosus*, short-eared owl). Most of the above mentioned species were also identified as indicator species for control areas. Similar short-term patterns, although from slightly different ecosystems, were identified in wetlands of Argentina (Isacch et al. 2004) and eastern Russia (Heim et al. 2019), where the vast majority of wetland specialists declined after fire.

Short-term vegetation removal seems to be the main driver of observed initial decline of marshland birds, since most of the negatively impacted species rely on tall vegetation for foraging and breeding and short sward does not provide them with suitable habitats. In addition, gleaning arboreal species (dependent on tall vegetation for foraging; see

Appendix Table 4 for details) were identified among roughly half of indicator species of control areas (e.g., common grasshopper warbler, Savi's warbler *Locustella luscinioides*).

As fire influences short-term food availability in variety of habitats (Panzer 2002; Sileshi and Mafongoya 2006; Vieira and Briani 2013), food base alteration could be another important driver of observed fire effect. In case of our study, insects started to occur at burned sites just a few days after the fire, and some groups (e.g., beetles Coleoptera) even increased in diversity in burned areas (Jaworski et al. in preparation), so the food base likely remained available for at least some insectivorous species. However, as invertebrates react to the fire in different species-dependent ways (García-Domínguez et al. 2010; Panzer 2002), the food availability for some insectivorous specialists could be temporarily reduced. The aquatic warbler, for example, is an insectivorous species that forages in low vegetation directly adjacent to higher vegetation and apparently benefits from the varied structure of its foraging habitat (Tanneberger et al. 2013). Fire may have temporarily simplified habitat structure to the point that it became incompatible for the species, contributing to the loss of this important species from burned areas.

At the same time, fire provided better access to bare soil as a foraging layer, as most of the dead biomass disappeared, thus improving invertebrate availability for some birds (Hoste-Danyłow et al. 2010). All three species that showed a positive response to fire in our analysis were mainly ground foragers (Appendix Table 4). In addition, ground foraging species formed majority of indicator species for burned areas, despite no confirmed positive fire effect on some of them (e.g., black grouse *Lyrurus tetrix*, common quail *Coturnix coturnix,* yellowhammer *Emberiza citrinella,* thrush nightingale *Luscinia luscinia*).

Contrary to invertebrates, fire caused an immediate decline in the density of small mammals, especially the disappearance of the most common rodent species in the valley—the root vole *Microtus oeconomus* (Borowski et al. in preparation). Rodents are a basic food item for all three birds of prey negatively affected by the fire—short-eared owl (Lesiński et al. 2016), montagu's harrier (Kitowski et al. 2021) and marsh harrier (Brzeziński and Żmihorski 2009). Since the availability of prey is one of the main factors influencing population densities and habitat use in birds of prey (Korpimäki and Norrdahl 1991; Newton 2007), the temporal absence of rodents could largely contribute to the observed short-term decline of these species on burned areas.

Implications for conservation

The impact of fire on wetland species of conservation concern is ambiguous and there is an ongoing debate if it should be recommended as a management tool (Conway et al. 2010; Hochkirch and Adorf 2007). In short term, fire may positively affect some species of high conservation concern, while causing declines in others (Conway et al. 2010; Heim et al. 2019; Isacch et al. 2004). In our study, fire negatively affected marshland bird specialists and led to temporary disappearance of four species (aquatic warbler, short-eared owl, corn crake and reed warbler). Some studies show similar short-term effects of fire on specialist species of high conservation concern in wetlands (Curnutt et al. 1998; Heim et al. 2019) and highlight the importance of unburned adjacent areas as refugia that allow survival and recolonization of burned areas by rare species (Grzywaczewski et al. 2014; Heim et al. 2019; Shaw et al. 2021). We therefore suggest that when fires occur, adjacent areas that have not burned could be temporarily covered with additional protection and bird-friendly management (e.g., delayed or reduced mowing).

In contrast, several rare and/or currently declining species actually benefitted from the fire in short term (Eurasian skylark, meadow pipit, and largely similar trends observed for yellowhammer, thrush nightingale, common quail, northern lapwing, godwit and black grouse) (Chylarecki et al. 2018). It suggests that burned marshland patches may become important local habitats for these declining species. Therefore, we encourage to temporarily introduce bird-friendly protection measures (e.g. limited access for people) in burned marshes as well.

However, to establish general management implications it is crucial to take into consideration both short-term and long-lasting fire effects. In numerous studies, strong initial response of bird community was recorded during first year after fire, to virtually disappear after 3–4 years (Heim et al. 2019; Mérő et al. 2015; Newman et al. 2018). In addition, wetland species of highest conservation concern, negatively affected by fire during first year, often returned to pre-fire abundances (Yellow-breasted bunting *Emberiza aureola* in Heim et al. 2019) or even reported increase (Aquatic warbler in Grzywaczewski et al. 2014) already one year after the fire. In longer term, fire can help keep marshes open by stopping the encroachment of scrub and trees, benefiting wetland herbaceous vegetation and associated biodiversity (Kotze 2013; Martin and Kirkman 2009; O'Connor et al. 2020). Overgrowth of shrubs and trees in marshes is one of the greatest threats to marsh biodiversity (Čížková et al. 2013; Kotowski and Piórkowski 2005), also in Biebrza Valley (Dembek et al. 2005). For these reasons, introduction of fire as management tool is recommended in some wetland environments to protect marshland birds (Conway et al. 2010), even despite negative short-term effects on target species (Grzywaczewski et al. 2014). Therefore, the consequences of fires, even if initially negative, can be different and diverse in the long term and need to be monitored.

Predicted increased fire frequency due to climate change may shorten intervals between fires (change of fire regime) which permanently alters vegetation structure and thus pose a serious threat to related biodiversity, including birds (Chalmandrier et al. 2013; Gosper et al. 2019). Increased fire frequencies affect vegetation structure also in temperate wetlands (Heim et al. 2019) and are hypothesized to affect bird community in a longer scale. In addition, expected changes in fire regime may increase risk of peat layer ignition. In contrary to surface fires, peat fires permanently damage peat layers, causing permanent ecosystem changes (Filkov et al. 2015; Kettridge et al. 2015). They may facilitate scrub expansion on wetlands, posing major threat to wetland-specific biodiversity (Kettridge et al. 2015; Sulwiński et al. 2020).

Many marshland species of conservation concern may exist in the form of metapopulations, as suitable habitat patches are usually heavily fragmented and scattered over large areas, while individuals disperse among them (Żmihorski et al. 2016). Theory predicts that while large patches may serve as population sources, small ones are also important as "stepping stones" that enhance network connectivity and thus increase population survival (Hanski 1999). In such systems, species might find refuge in adjacent unburned patches and then recolonize the burned patches the next year when the fire effect subsides. However, climate change, along with water management, often leads to further drying of water-dependent ecosystems and can cause severe droughts and synchronized fires over large areas. The simultaneous burning of large areas can wipe out large metapopulation fragments and significantly reduce connectivity between patches, with dramatic consequences for rare marsh species. It is therefore critical to prevent further drainage of marshes, while restoring previous water levels and dynamics to increase their resilience to fire.

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Data availability The datasets generated during and/or analysed during the current study are not publicly available due to their possible future use in another article, but are available from the corresponding author on reasonable request.

Code availability The code generated during and/or analysed during the current study is not yet publicly available, but will be published in case the manuscript is accepted for publication.

Declarations

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Appendix Table 1

List of marshland birds

Species classification		Species name		
Order	*Family*	*Latin*	*English*	*Polish*
Accipitriformes	Accipitridae	*Buteo buteo*	common buzzard	myszołów
Accipitriformes	Accipitridae	*Circus aeruginosus*	western marsh harrier	błotniak stawowy
Accipitriformes	Accipitridae	*Circus cyaneus*	hen harrier	błotniak zbożowy
Accipitriformes	Accipitridae	*Circus pygargus*	montagu's harrier	błotniak łąkowy
Bucerotiformes	Upupidae	*Upupa epops*	eurasian hoopoe	dudek
Charadriiformes	Charadriidae	*Vanellus vanellus*	northern lapwing	czajka
Charadriiformes	Scolopacidae	*Actitis hypoleucos*	common sandpiper	brodziec piskliwy
Charadriiformes	Scolopacidae	*Calidris pugnax*	ruff	batalion
Charadriiformes	Scolopacidae	*Gallinago gallinago*	common snipe	kszyk
Charadriiformes	Scolopacidae	*Gallinago media*	great snipe	dubelt
Charadriiformes	Scolopacidae	*Limosa limosa*	black-tailed godwit	rycyk
Charadriiformes	Scolopacidae	*Numenius arquata*	eurasian curlew	kulik wielki
Charadriiformes	Scolopacidae	*Tringa glareola*	wood sandpiper	łęczak
Charadriiformes	Scolopacidae	*Tringa totanus*	common redshank	krwawodziób
Ciconiiformes	Ciconiidae	*Ciconia ciconia*	white stork	bocian biały
Ciconiiformes	Ciconiidae	*Ciconia nigra*	black stork	bocian czarny
Cuculiformes	Cuculidae	*Cuculus canorus*	common cuckoo	kukułka
Falconiformes	Falconidae	*Falco tinnunculus*	common kestrel	pustułka
Galliformes	Phasianidae	*Coturnix coturnix*	common quail	przepiórka
Galliformes	Phasianidae	*Lyrurus tetrix*	black grouse	cietrzew
Galliformes	Phasianidae	*Phasianus colchicus*	common pheasant	bażant
Gruiformes	Gruidae	*Grus grus*	common crane	żuraw
Gruiformes	Rallidae	*Crex crex*	corn crake	derkacz
Gruiformes	Rallidae	*Porzana porzana*	spotted crake	kropiatka
Gruiformes	Rallidae	*Rallus aquaticus*	water rail	wodnik
Passeriformes	Acrocephalidae	*Acrocephalus arundinaceus*	great reed warbler	trzciniak
Passeriformes	Acrocephalidae	*Acrocephalus paludicola*	aquatic warbler	wodniczka
Passeriformes	Acrocephalidae	*Acrocephalus palustris*	marsh warbler	łozówka
Passeriformes	Acrocephalidae	*Acrocephalus schoenobaenus*	sedge warbler	rokitniczka
Passeriformes	Acrocephalidae	*Acrocephalus scirpaceus*	eurasian reed warbler	trzcinniczek

Passeriformes	Acrocephalidae	*Hippolais icterina*	icterine warbler	zaganiacz
Passeriformes	Alaudidae	*Alauda arvensis*	eurasian skylark	skowronek
Passeriformes	Corvidae	*Corvus corax*	common raven	kruk
Passeriformes	Corvidae	*Corvus cornix*	hooded crow	wrona siwa
Passeriformes	Corvidae	*Pica pica*	eurasian magpie	sroka
Passeriformes	Emberizidae	*Emberiza citrinella*	yellowhammer	trznadel
Passeriformes	Emberizidae	*Emberiza schoeniclus*	common reed bunting	potrzos
Passeriformes	Fringillidae	*Carpodacus erythrinus*	common rosefinch	dziwonia
Passeriformes	Fringillidae	*Linaria cannabina*	common linnet	makolągwa
Passeriformes	Laniidae	*Lanius collurio*	red-backed shrike	gąsiorek
Passeriformes	Laniidae	*Lanius excubitor*	great grey shrike	srokosz
Passeriformes	Locustellidae	*Locustella fluviatilis*	river warbler	strumieniówka
Passeriformes	Locustellidae	*Locustella luscinioides*	savi's warbler	brzęczka
Passeriformes	Locustellidae	*Locustella naevia*	common grasshopper warbler	świerszczak
Passeriformes	Motacillidae	*Anthus pratensis*	meadow pipit	świergotek łąkowy
Passeriformes	Motacillidae	*Anthus trivialis*	tree pipit	świergotek drzewny
Passeriformes	Motacillidae	*Motacilla citreola*	citrine wagtail	pliszka cytrynowa
Passeriformes	Motacillidae	*Motacilla flava*	western yellow wagtail	pliszka żółta
Passeriformes	Muscicapidae	*Cyanecula svecica*	bluethroat	podróżniczek
Passeriformes	Muscicapidae	*Luscinia luscinia*	thrush nightingale	słowik szary
Passeriformes	Muscicapidae	*Oenanthe oenanthe*	northern wheatear	białorzytka
Passeriformes	Muscicapidae	*Saxicola rubetra*	whinchat	pokląskwa
Passeriformes	Panuridae	*Panurus biarmicus*	bearded reedling	wąsatka
Passeriformes	Phylloscopidae	*Phylloscopus trochilus*	willow warbler	piecuszek
Passeriformes	Remizidae	*Remiz pendulinus*	eurasian penduline tit	remiz
Passeriformes	Sturnidae	*Sturnus vulgaris*	common starling	szpak
Passeriformes	Sylviidae	*Sylvia communis*	common whitethroat	cierniówka
Passeriformes	Sylviidae	*Sylvia curruca*	lesser whitethroat	piegża
Passeriformes	Sylviidae	*Sylvia nisoria*	barred warbler	jarzębatka
Passeriformes	Turdidae	*Turdus pilaris*	fieldfare	kwiczoł
Pelecaniformes	Ardeidae	*Botaurus stellaris*	eurasian bittern	bąk
Piciformes	Picidae	*Jynx torquilla*	eurasian wryneck	krętogłów
Strigiformes	Strigidae	*Asio flammeus*	short-eared owl	uszatka błotna

Appendix Table 2

List of species excluded from "marshland birds"

Species classification		Species name			Reason of exclusion from "marshland birds"
Order	*Family*	*Latin*	*English*	*Polish*	
Accipitriformes	Accipitridae	*Accipiter gentilis*	northern goshawk	jastrząb	Large territories
Accipitriformes	Accipitridae	*Accipiter nisus*	eurasian sparrowhawk	krogulec	Large territories
Accipitriformes	Accipitridae	*Clanga clanga*	greater spotted eagle	orlik grubodzioby	Large territories
Accipitriformes	Accipitridae	*Clanga pomarina*	lesser spotted eagle	orlik krzykliwy	Large territories
Accipitriformes	Accipitridae	*Haliaeetus albicilla*	white-tailed eagle	bielik	Large territories
Accipitriformes	Accipitridae	*Pernis apivorus*	european honey buzzard	trzmielojad	Large territories
Accipitriformes	Pandionidae	*Pandion haliaetus*	osprey	rybołów	Large territories
Anseriformes	Anatidae	*Anas platyrhynchos*	mallard	krzyżówka	Typical for other habitats
Anseriformes	Anatidae	*Anser anser*	greylag goose	gęgawa	Typical for other habitats
Anseriformes	Anatidae	*Cygnus olor*	mute swan	łabędź niemy	Typical for other habitats
Anseriformes	Anatidae	*Mareca strepera*	gadwall	krakwa	Typical for other habitats
Anseriformes	Anatidae	*Spatula clypeata*	northern shoveller	płaskonos	Typical for other habitats
Anseriformes	Anatidae	*Spatula querquedula*	garganey	cyranka zwyczajna	Typical for other habitats
Apodiformes	Apodidae	*Apus apus*	common swift	jerzyk	Large territories
Charadriiformes	Laridae	*Chlidonias hybrida*	whiskered tern	rybitwa białowąsa	Typical for other habitats
Charadriiformes	Laridae	*Chlidonias leucopterus*	white-winged tern	rybitwa białoskrzydła	Typical for other habitats
Charadriiformes	Laridae	*Chlidonias niger*	black tern	rybitwa czarna	Typical for other habitats
Charadriiformes	Laridae	*Larus ridibundus*	black-headed gull	śmieszka	Typical for other habitats
Charadriiformes	Laridae	*Sterna hirundo*	common tern	rybitwa rzeczna	Typical for other habitats
Charadriiformes	Scolopacidae	*Tringa ochropus*	green sandpiper	samotnik	Typical for other habitats
Columbiformes	Columbidae	*Columba oenas*	stock dove	siniak	Typical for other habitats
Columbiformes	Columbidae	*Columba palumbus*	common wood pigeon	grzywacz	Typical for other habitats
Columbiformes	Columbidae	*Streptopelia turtur*	european turtle dove	turkawka	Typical for other habitats

Falconiformes	Falconidae	*Falco subbuteo*	hobby	kobuz	Large territories/hunting in flight
Gruiformes	Rallidae	*Gallinula chloropus*	common moorhen	kokoszka	Typical for other habitats
Passeriformes	Aegithalidae	*Aegithalos caudatus*	long-tailed tit	raniuszek	Typical for other habitats
Passeriformes	Alaudidae	*Lullula arborea*	woodlark	lerka	Typical for other habitats
Passeriformes	Corvidae	*Garrulus glandarius*	eurasian jay	sójka	Typical for other habitats
Passeriformes	Fringillidae	*Carduelis carduelis*	european goldfinch	szczygieł	Typical for other habitats
Passeriformes	Fringillidae	*Chloris chloris*	european greenfinch	dzwoniec	Typical for other habitats
Passeriformes	Fringillidae	*Coccothraustes coccothraustes*	hawfinch	grubodziób	Typical for other habitats
Passeriformes	Fringillidae	*Fringilla coelebs*	common chaffinch	zięba	Typical for other habitats
Passeriformes	Fringillidae	*Pyrrhula pyrrhula*	eurasian bullfinch	gil	Typical for other habitats
Passeriformes	Fringillidae	*Serinus serinus*	european serin	kulczyk	Typical for other habitats
Passeriformes	Fringillidae	*Spinus spinus*	eurasian siskin	czyż	Typical for other habitats
Passeriformes	Hirundinidae	*Delichon urbicum*	common house martin	oknówka	Typical for other habitats
Passeriformes	Hirundinidae	*Hirundo rustica*	barn swallow	dymówka	Typical for other habitats
Passeriformes	Hirundinidae	*Riparia riparia*	sand martin	brzegówka	Typical for other habitats
Passeriformes	Muscicapidae	*Erithacus rubecula*	european robin	rudzik	Typical for other habitats
Passeriformes	Muscicapidae	*Ficedula hypoleuca*	european pied flycatcher	muchołówka żałobna	Typical for other habitats
Passeriformes	Oriolidae	*Oriolus oriolus*	eurasian golden oriole	wilga	Typical for other habitats
Passeriformes	Paridae	*Cyanistes caeruleus*	blue tit	modraszka	Typical for other habitats
Passeriformes	Paridae	*Parus major*	great tit	bogatka	Typical for other habitats
Passeriformes	Paridae	*Poecile montanus*	willow tit	czarnogłówka	Typical for other habitats
Passeriformes	Paridae	*Poecile palustris*	marsh tit	sikora uboga	Typical for other habitats
Passeriformes	Phylloscopidae	*Phylloscopus collybita*	common chiffchaff	pierwiosnek	Typical for other habitats
Passeriformes	Phylloscopidae	*Phylloscopus sibilatrix*	wood warbler	świstunka leśna	Typical for other habitats
Passeriformes	Prunellidae	*Prunella modularis*	dunnock	pokrzywnica	Typical for other habitats
Passeriformes	Sylviidae	*Sylvia atricapilla*	eurasian blackcap	kapturka	Typical for other habitats

Passeriformes	Sylviidae	*Sylvia borin*	garden warbler	gajówka	Typical for other habitats
Passeriformes	Troglodytidae	*Troglodytes troglodytes*	eurasian wren	strzyżyk	Typical for other habitats
Passeriformes	Turdidae	*Turdus merula*	common blackbird	kos	Typical for other habitats
Passeriformes	Turdidae	*Turdus philomelos*	song thrush	śpiewak	Typical for other habitats
Passeriformes	Turdidae	*Turdus viscivorus*	mistle thrush	paszkot	Typical for other habitats
Pelecaniformes	Ardeidae	*Ardea alba*	great egret	czapla biała	Typical for other habitats
Pelecaniformes	Ardeidae	*Ardea cinerea*	grey heron	czapla siwa	Typical for other habitats
Piciformes	Picidae	*Dendrocopos leucotos*	white-backed woodpecker	dzięcioł białogrzbiety	Typical for other habitats
Piciformes	Picidae	*Dendrocopos major*	great spotted woodpecker	dzięcioł duży	Typical for other habitats
Piciformes	Picidae	*Dryobates minor*	lesser spotted woodpecker	dzięciołek	Typical for other habitats
Piciformes	Picidae	*Dryocopus martius*	black woodpecker	dzięcioł czarny	Typical for other habitats
Piciformes	Picidae	*Picus canus*	grey-headed woodpecker	dzięcioł zielonosiwy	Typical for other habitats
Podicipediformes	Podicipedidae	*Tachybaptus ruficollis*	little grebe	perkozek	Typical for other habitats

Appendix Table 3

Species abundances and conservation status

Species name	Conservation status	Species abundance				
		before/ control	after/ control	before/ fire	after/ fire	Total
Acrocephalus schoenobaenus	present on neither list	469	338	298	129	1234
Emberiza schoeniclus	present on neither list	462	178	339	93	1072
Gallinago gallinago	SPEC, red-listed	385	202	190	44	821
Anthus pratensis	SPEC	332	142	191	126	791
Phylloscopus trochilus	SPEC	200	155	118	99	572
Sylvia communis	present on neither list	171	138	124	70	503
Saxicola rubetra	SPEC, red-listed	190	130	131	37	488
Alauda arvensis	SPEC	85	116	16	185	402
Locustella naevia	present on neither list	119	109	112	16	356
Grus grus	present on neither list	153	103	44	23	323
Sturnus vulgaris	SPEC	183	94	13	24	314
Locustella luscinioides	present on neither list	140	55	83	3	281
Acrocephalus paludicola	SPEC, red-listed	117	39	74	0	230
Carpodacus erythrinus	SPEC	71	57	61	23	212
Cuculus canorus	present on neither list	82	57	39	29	207
Lanius collurio	SPEC	70	59	50	13	192
Luscinia luscinia	red-listed	69	58	16	25	168
Emberiza citrinella	SPEC	74	47	18	22	161
Vanellus vanellus	SPEC, red-listed	72	28	20	20	140
Sylvia nisoria	present on neither list	39	16	58	15	128
Circus aeruginosus	present on neither list	54	28	26	2	110
Circus pygargus	red-listed	19	31	22	4	76
Cyanecula svecica	present on neither list	21	13	20	16	70
Anthus trivialis	SPEC	24	25	3	15	67

Corvus cornix	present on neither list	27	26	4	10	67
Sylvia curruca	present on neither list	27	17	8	8	60
Acrocephalus scirpaceus	present on neither list	22	6	28	0	56
Pica pica	present on neither list	13	17	15	9	54
Limosa limosa	SPEC, red-listed	42	7	3	2	54
Hippolais icterina	present on neither list	19	15	8	3	45
Turdus pilaris	present on neither list	30	4	6	1	41
Lanius excubitor	SPEC	10	12	4	12	38
Tringa totanus	SPEC	23	9	3	2	37
Buteo buteo	present on neither list	8	14	8	4	34
Phasianus colchicus	present on neither list	6	4	10	13	33
Acrocephalus palustris	present on neither list	18	6	5	3	32
Motacilla citreola	red-listed	8	1	21	1	31
Gallinago media	SPEC, red-listed	1	2	23	1	27
Tringa glareola	SPEC, red-listed	22	1	4	0	27
Upupa epops	present on neither list	13	10	1	3	27
Corvus corax	present on neither list	17	3	2	2	24
Lyrurus tetrix	SPEC, red-listed	8	3	5	8	24
Locustella fluviatilis	present on neither list	10	2	5	0	17
Coturnix coturnix	SPEC, red-listed	2	3	1	10	16
Crex crex	SPEC, red-listed	4	6	6	0	16
Acrocephalus arundinaceus	present on neither list	7	6	3	0	16
Asio flammeus	SPEC, red-listed	1	5	9	0	15
Rallus aquaticus	present on neither list	10	1	2	0	13
Numenius arquata	SPEC, red-listed	4	6	0	0	10
Botaurus stellaris	SPEC, red-listed	4	0	3	0	7

Ciconia ciconia	present on neither list	6	0	1	0	7
Calidris pugnax	SPEC, red-listed	6	0	0	0	6
Oenanthe oenanthe	SPEC	4	0	0	1	5
Panurus biarmicus	present on neither list	3	0	2	0	5
Jynx torquilla	SPEC	0	1	1	2	4
Linaria cannabina	SPEC	0	3	0	0	3
Falco tinnunculus	SPEC	1	2	0	0	3
Motacilla flava	SPEC	3	0	0	1	4
Remiz pendulinus	present on neither list	2	1	0	0	3
Ciconia nigra	present on neither list	1	0	1	0	2
Circus cyaneus	SPEC, red-listed	0	0	2	0	2
Actitis hypoleucos	SPEC	2	0	0	0	2
Porzana porzana	present on neither list	1	0	0	0	1

SPEC -Species of European Conservation Concern
red-listed - Present on Polish Red List of Birds

Appendix Table 4
Model summaries

Species/diversity index	*Trophic guild*	*Foraging guild*	*Model used*	*Coefficient value (interaction of period and impact)*	*Lower 95% CI*	*Upper 95% CI*	*Adj.R2 (GAMM) / pseudo-R2 (logistic)*	*p value*
Acrocephalus arundinaceus	Invertivore	Glean arboreal	Firth	-1.95	-6.94	0.71	0.27	0.166
Acrocephalus paludicola	Invertivore	Glean arboreal	Firth	-4.14	-9.07	-1.85	0.44	0
Acrocephalus palustris	Invertivore	Glean arboreal	GAMM	0.67	-1.17	2.51	0.04	0.475
Acrocephalus schoenobaenus	Invertivore	Glean arboreal	GAMM	-0.51	-0.76	-0.26	0.63	0
Acrocephalus scirpaceus	Invertivore	Glean arboreal	Firth	-3.67	-8.65	-1.11	0.47	0.003
Alauda arvensis	Omnivore	NA	GAMM	2.14	1.55	2.72	0.81	0
Anthus pratensis	Invertivore	Ground	GAMM	0.45	0.11	0.8	0.69	0.01
Anthus trivialis	Invertivore	Ground	GAMM	1.57	0.21	2.93	0.32	0.024
Asio flammeus	Vertivore	Air to surface	Firth	-3.73	-8.85	-0.87	0.13	0.008
Buteo buteo	Vertivore	Perch	GAMM	-1.25	-2.74	0.24	0.06	0.1
Carpodacus erythrinus	Granivore	Generalist	GAMM	-0.76	-1.35	-0.16	0.11	0.012
Circus aeruginosus	Vertivore	Air to surface	GAMM	-1.91	-3.42	-0.4	0.3	0.013
Circus pygargus	Vertivore	Air to surface	GAMM	-1.79	-3.1	-0.47	0.31	0.008
Corvus corax	Omnivore	NA	GAMM	1.7	-0.71	4.11	0.06	0.168
Corvus cornix	Omnivore	NA	GAMM	0.97	-0.49	2.42	0.13	0.194
Coturnix coturnix	Granivore	Ground	GAMM	1.9	-0.84	4.63	0.06	0.174
Crex crex	Omnivore	NA	Firth	-3.06	-8.04	-0.51	0.17	0.015
Cuculus canorus	Invertivore	Glean arboreal	GAMM	0.07	-0.52	0.65	0.1	0.822
Cyanecula svecica	Invertivore	Ground	GAMM	0.26	-0.7	1.21	0.18	0.598
Emberiza citrinella	Granivore	Ground	GAMM	0.65	-0.07	1.38	0.56	0.076
Emberiza schoeniclus	Omnivore	NA	GAMM	-0.34	-0.63	-0.05	0.32	0.021
Gallinago gallinago	Aquatic predator	Ground	GAMM	-0.81	-1.2	-0.42	0.37	0
Gallinago media	Aquatic predator	Ground	GAMM	-3.39	-8.31	1.52	0.03	0.176
Grus grus	Omnivore	NA	GAMM	-0.39	-1.43	0.66	0.09	0.468
Hippolais icterina	Invertivore	Glean arboreal	GAMM	-0.74	-2.23	0.75	0.32	0.327

Species/diversity index	*Trophic guild*	*Foraging guild*	*Model used*	*Coefficient value (interaction of period and impact)*	*Lower 95% CI*	*Upper 95% CI*	*Adj.R2 (GAMM) / pseudo-R2 (logistic)*	*p value*
Lanius collurio	Invertivore	Sally ground	GAMM	-1.18	-1.88	-0.47	0.18	0.001
Lanius excubitor	Vertivore	Perch	GAMM	0.89	-1.08	2.87	0.06	0.375
Limosa limosa	Aquatic predator	Ground	GAMM	1.52	-0.91	3.95	0.18	0.221
Locustella fluviatilis	Invertivore	Glean arboreal	Firth	-0.96	-5.99	1.86	0.24	0.537
Locustella luscinioides	Invertivore	Glean arboreal	GAMM	-2.39	-3.58	-1.19	0.53	0
Locustella naevia	Invertivore	Glean arboreal	GAMM	-1.86	-2.44	-1.27	0.27	0
Luscinia luscinia	Invertivore	Ground	GAMM	0.62	-0.1	1.34	0.37	0.091
Lyrurus tetrix	Herbivore terrestrial	Generalist	GAMM	1.56	-0.41	3.52	0.18	0.121
Motacilla citreola	Aquatic predator	Ground	GAMM	-0.82	-3.81	2.17	0.14	0.59
Phasianus colchicus	Omnivore	NA	GAMM	0.67	-0.84	2.18	0.12	0.386
Phylloscopus trochilus	Invertivore	Glean arboreal	GAMM	0.08	-0.26	0.42	0.57	0.647
Pica pica	Omnivore	NA	GAMM	-0.77	-1.87	0.34	0.38	0.175
Saxicola rubetra	Invertivore	Sally ground	GAMM	-0.88	-1.31	-0.46	0.41	0
Sturnus vulgaris	Omnivore	NA	GAMM	-0.34	-2.1	1.43	0.06	0.709
Sylvia communis	Invertivore	Glean arboreal	GAMM	-0.36	-0.73	0.01	0.41	0.058
Sylvia curruca	Invertivore	Glean arboreal	GAMM	0.46	-0.69	1.62	0.12	0.431
Sylvia nisoria	Invertivore	Glean arboreal	GAMM	-0.43	-1.33	0.47	0.33	0.351
Tringa glareola	Aquatic predator	Ground	Firth	0.59	-4.5	3.83	0.14	0.748
Tringa totanus	Aquatic predator	Ground	GAMM	0.69	-1.68	3.05	0.02	0.57
Turdus pilaris	Invertivore	Ground	GAMM	0.22	-2.14	2.58	0.67	0.853
Upupa epops	Invertivore	Ground	GAMM	1.36	-1.05	3.77	0.09	0.268
Vanellus vanellus	Omnivore	NA	GAMM	0.84	-0.46	2.14	0.05	0.205
Abundance (all marshland birds)	-	-	GAMM	-0.19	-0.3	-0.08	0.32	0.001
Abundance (Polish Red-list of birds)	-	-	GAMM	-0.62	-0.87	-0.37	0.36	0
Abundance (SPEC)	-	-	GAMM	0.13	-0.03	0.3	0.37	0.118
Richness (all marshland birds)	-	-	GAMM	-0.21	-0.33	-0.09	0.31	0.001
Richness (Polish Red-list of birds)	-	-	GAMM	-0.33	-0.6	-0.07	0.27	0.013
Richness (SPEC)	-	-	GAMM	-0.06	-0.24	0.11	0.35	0.489

Chapter II

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RESEARCH ARTICLE

Salvage logging and subsequent post-windthrow management diminish forest bird communities for two decades

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Abstract

1. Post-disturbance forest management is known to impair biodiversity, including bird communities, but most studies focus on short-term effects of salvage logging, without recognition of the cumulative, lasting impact of collective post-disturbance silvicultural practices.
2. We tracked bird community succession in a temperate pine forest from 5 to 19 years after wind disturbance in managed and unmanaged windthrow areas, covering the period from gap creation to early canopy regeneration and comparing it to nearby production forest unaffected by wind disturbance.
3. Bird communities of unmanaged windthrow were consistently the richest in terms of bird abundance and richness. They hosted comparable forest bird diversity to unaffected production stands throughout the study period, as well as a substantial diversity of farmland birds.
4. Managed and unmanaged windthrows followed two distinct successional pathways and did not converge. Despite the bird communities in both windthrows gradually resembling those found in undisturbed forests as the canopy regenerated, each type of windthrow and the unaffected production forest maintained distinct communities until the end of the study.
5. *Synthesis and applications*. Restraining from any active post-windthrow management sets bird succession on a distinct pathway, leading to unique and diverse bird communities. We advocate viewing natural disturbances as cost-effective ecosystem restoration tools, provided no active management is implemented. Furthermore, we advise against using the term 'salvage logging' to refer to collective post-disturbance silvicultural practices, as its varying interpretation may lead to growing confusion as the number of long-term studies increase.

KEYWORDS
active management, biodiversity, disturbance, forest regeneration, secondary succession, silvicultural practices, spontaneous development, wind

1 | INTRODUCTION

Wind disturbance is a key factor shaping the dynamics of temperate European forests, affecting approximately 0.12% of their standing volume annually (Schuck & Schelhaas, 2013). In managed forests, wind disturbance is typically followed by extraction of the fallen and damaged trees (i.e. salvage logging), and later tilling, replanting and other management actions focusing on high future production value of regenerating tree stands (Diaci et al., 2017). However, such intensive forest management impairs several other ecosystem services of the forest, including biodiversity (Leverkus et al., 2020) and thus leaving windthrow areas untouched is often advocated, especially in protected areas (Müller et al., 2018; Sanginés de Cárcer et al., 2021). In this option, salvage logging, tilling and tree replanting are not performed and natural tree regeneration is promoted instead. As wind damage in European forests rises with the progression of climate change and has almost doubled over the period of 1951–2010 (Gregow et al., 2017; Seidl et al., 2011), understanding the impact of these two different management options on biodiversity is increasingly important for developing sustainable policies for European forests (Schuck & Schelhaas, 2013).

The decision to actively manage the windthrow has an immediate impact on biodiversity. On managed windthrows, salvage logging impairs species reliant on decaying wood and early forest growth stages, otherwise thriving after forest disturbances (Viljur et al., 2022). Tilling, performed soon after salvage logging, disrupts the forest floor structure and vegetation, impacting ground-dwelling arthropods (Košulič et al., 2021). On the other hand, increased canopy openness enhances ground-related floral resources available for pollinators, such as butterflies (Cours et al., 2023). Although active post-windthrow management benefits specific open-canopy taxa, the immediate effects of post-disturbance management on forest biodiversity are considered detrimental (Thorn et al., 2018).

However, as succession unfolds, disturbed forests gradually transition from open and semi-open areas to closed forest habitats (Hilmers et al., 2018). During that process, some initial effects of salvage logging may disappear (e.g. increased density of flowers and insolation), while others (e.g. removal of snags and surviving trees) continue to shape biodiversity for decades (Courbaud et al., 2022; Cours et al., 2023; Gärtner et al., 2023; Thorn et al., 2020). Tilling, fencing and, notably, tree replanting impact the forest structure by shaping the emerging canopy layer (Hotta et al., 2021; Lindenmayer et al., 2012; Ramirez et al., 2019), which is later modified during thinning (Dieler et al., 2017). While the resulting changes have a documented impact on biodiversity (Klein et al., 2022; Latterini et al., 2023), many of them only become apparent after the regeneration of the canopy layer.

The majority of studies comparing the effects of post-disturbance management on biodiversity focus on the first 5 years after a disturbance event (Thorn et al., 2018). During this period, early-successional biota thrive, often becoming a focal point of management discussions (e.g. Rost et al., 2012). However, this period of increased canopy openness constitutes only a small portion of the overall temperate forest succession cycle (Hilmers et al., 2018). The long-term conservation value of forest disturbances relies also on intermediate- and late-successional forest species, gradually increasing in numbers over the course of canopy regeneration (Wesołowski et al., 2018). Since the populations of these species may decline in the initial stages of forest succession (Fuller, 2000), management policies based solely on early post-disturbance assessments may deviate from long-term biodiversity conservation goals. This highlights the importance of long-term studies to inform management policies (Georgiev et al., 2020).

In this study, we compared the effects of two post-windthrow management strategies—managed windthrow (salvage logged, and then subsequently tilled, replanted, fenced and thinned) versus unmanaged windthrow (no intervention) on succession patterns of bird communities from gap formation through early stages of canopy regeneration after a large wind disturbance event (5–19 years after the disturbance; Hilmers et al., 2018). In parallel, as a control, we monitored bird communities in an adjacent, unaffected forest. We used birds as model organisms because of their sensitivity to changes in the forest structure and age caused by natural and human-caused disturbances (Wesołowski et al., 2018). We hypothesized that the initial negative impact of salvage logging on bird diversity (Żmihorski, 2010) would be reinforced and sustained by the subsequent set of silvicultural treatments, thus contributing to a lasting impact persisting for two decades. We also expected that bird communities in both managed and unmanaged windthrows would become more similar to those in unaffected production forests as tree cover regenerated and early-succession species could be replaced by forest-dwelling species. Finally, we anticipated that over time, the bird communities in both managed and unmanaged windthrow areas would converge, as initially distinct early-successional communities could be replaced by similar intermediate- and late-successional species during the process of forest regrowth.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study was conducted in Pisz Forest, a 100,000 ha forest complex used for wood production located in NE Poland (53°38′18.1″ N, 21°29′52.1″ E). The dominant tree species in the forest is Scots pine (*Pinus silvestris*), accounting for 84% of all trees. Additionally, silver birch (*Betula pendula*) and Norway spruce (*Picea abies*) are also present. The majority of forest stands are between 30 and 70 years old (Dobrowolska, 2015). Despite being managed for wood production, Pisz Forest remains an Important Bird and Biodiversity Area (IBA), with a total of 202 bird species recorded (Ryś, 2010).

In July 2002, a powerful windstorm damaged trees across a 12,000 ha area, affecting 2.5 million m^3 of timber (Figure 1). In the next 2 years, most of the timber was removed through salvage logging. The soil was then tilled to facilitate replanting. The replanting took 6 years, aiming to restore the tree species composition to

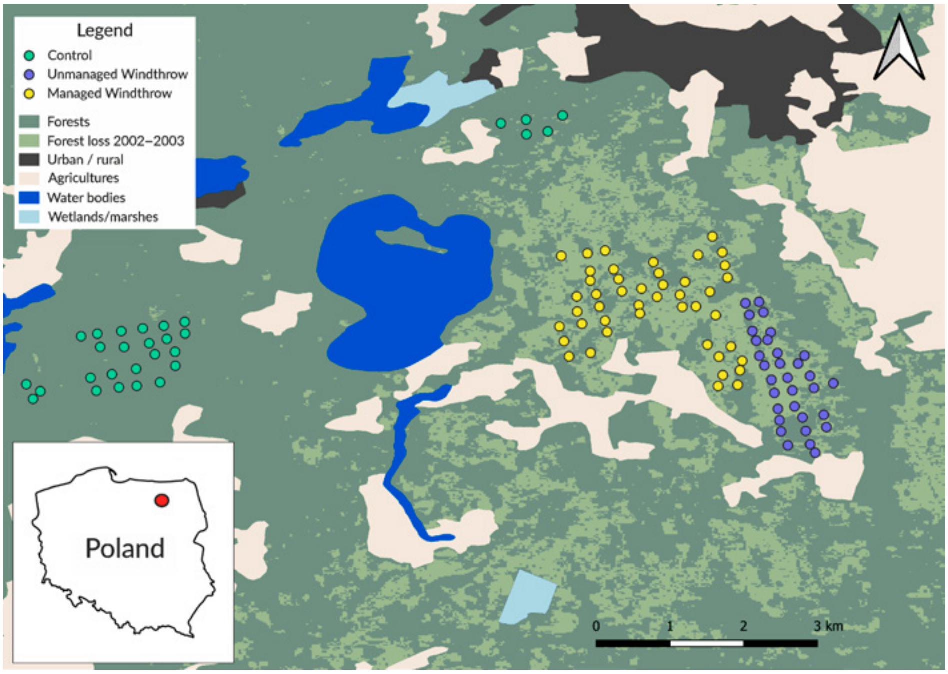

FIGURE 1 Study area: 106 point-count sites belonging to 3 forest habitats: Managed windthrow ($n=45$), unmanaged windthrow ($n=32$), control forest ($n=29$) in the context of forest loss (2002–2003) reflecting the wind damage (Hansen et al., 2013).

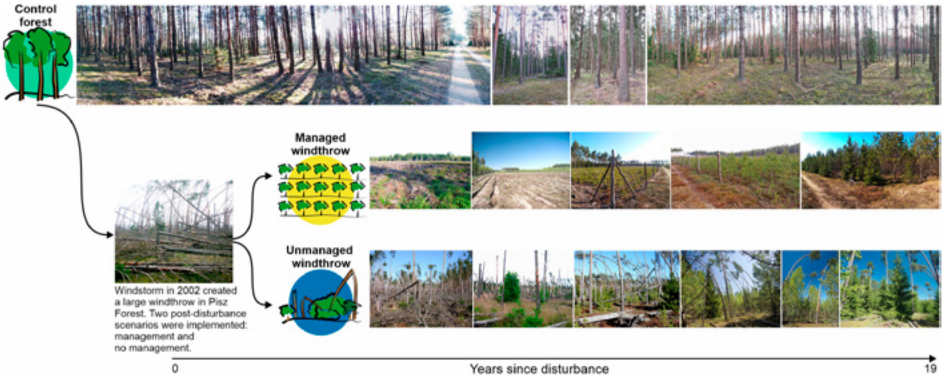

FIGURE 2 The three forest habitats: After the windthrow of 2002 managed part was salvage logged, tilled, replanted, fenced and thinned while unmanaged windthrow was left without any intervention. Unaffected production forest (control) experienced no visible management during our study.

its approximate pre-disturbance state. Most replanted areas were fenced to protect them from ungulates (Maszkiewicz, 2018), and thinning has recently begun (see Figure S1 for details). However, a single large patch (476 ha) of wind-disturbed forest was left without any intervention (i.e. no salvaging nor replanting was performed; see Figure 2). In this patch, 44% of the area saw almost all trees killed, 4% remained undisturbed, and damage on the rest varied between 10% and 90% (G. Zajączkowski & B. Dzierża, unpublished data). In consequence, Pisz Forest could be divided into three types of forest habitats: managed windthrow (disturbed and then managed through salvage logging, tilling, replanting, fencing and thinning), unmanaged windthrow (disturbed but left unmanaged), and control forest (pine plantations aged 30–90 years, undisturbed by the wind; Figures 1 and 2). The management approach for each habitat type remained consistent throughout the study period.

2.2 | Bird surveys

We established 106 point-count sites in three different forest habitats: managed windthrow ($n=45$), unmanaged windthrow ($n=32$) and control forest ($n=29$), located at the intersections of 300 × 300 m grid imposed over the study area (Figure 1). Control sites were established within 1–6 km of the windthrow, which is close enough to minimize the effects of biogeographical gradients in species distributions. We conducted first bird counts in 2007 (i.e. 5 years after wind disturbance) and performed them in total seven times between 2007 and 2021 (i.e. in 2007, 2011, 2013, 2015, 2019, 2020 and 2021), covering period between 5 and 19 years after the disturbance event. To encompass both sedentary and migrating breeding species, two visits were made to each point-count site annually, one in April and one in June. The survey order for point-count sites was interleaved, alternating between the three forest habitats. During each visit, all birds observed and heard (excluding those flying over the canopy) were recorded for a 10-minute duration. Bird counts were conducted in the early morning, before 10:00 am, on days with good visibility and no heavy rain nor wind. Throughout the entire study period, a consistent team of three ornithologists conducted the counts. For each species, the highest abundance from the two visits to a specific point-count site in a given year was utilized for subsequent analysis. Since we did not account for imperfect bird detection, recorded bird abundances are not corrected for undetected individuals and should be treated as an index. We did not need any licence or permit to carry out our field work and our study did not require any ethical approval.

2.3 | Statistical analysis

To monitor changes in bird community over time, we employed Generalized Additive Mixed Models (GAMMs) with the 'mgcv' package in R (R Core Team, 2021; Wood, 2017). For each of the 106 point-count sites and across seven study years, we calculated species richness (sum of species with at least one individual at site), rarefied richness (expected number of species for 20 random individuals, based on rarefaction implemented in 'iNEXT' R package; Hsieh et al., 2016) and abundance for all bird species, as well as separately for forest (intermediate- to late-succession species) and farmland (early-succession) birds based on the habitat classification from the PanEuropean Common Bird Monitoring Scheme (2022). We employed nine GAMMs to examine the relationships between bird richness and abundance (comprising all, forest and farmland species) and the forest habitat (managed windthrow, unmanaged windthrow and control), time elapsed since disturbance and their interaction. To address the spatial and temporal dependencies in the data, we included random year and site effects using ridge penalty splines (Wood, 2017). To test whether the distance between the three habitats could interfere with our results, we divided our control sites into two groups (north and west of the disturbed area) and checked for visible separation of their bird communities using NMDS ('vegan' R package; Oksanen et al., 2022). The spatial distance between the two control groups was about the same as the maximum distance between any two habitat types in our study area. We assessed spatial autocorrelation of each models' residuals with spline correlograms using 'ncf' R package (Bjornstad, 2020), summarized in Figure S2. In models where significant autocorrelation was detected, we fitted site coordinates using thin plate regression splines, manually adjusting the number of knots (k-value) to eliminate autocorrelation while maintaining the models' simplicity. To minimize the correlation between coordinates and habitats, we scaled coordinates within each habitat (mean = 0, SD = 1). We then compared AIC scores between GAMMs with and without time and habitat interaction, selecting the more parsimonious model. For models that included interaction, we computed marginal means for each year within the study period (5–19 years post-disturbance) and compared them among the forest habitats to identify periods of significant differences, using pairwise comparisons with Tukey p-value adjustment in the 'emmeans' R package (Lenth, 2023). All nine GAMMs were fitted using the Maximum Likelihood method with a Poisson or Negative Binomial (rarefied richness) distribution and log-link. To facilitate visual comparisons, our results were presented in relation to the abundance/richness values of control forest, serving as baseline values (0).

We fitted species-specific GAMMs to compare the responses of individual species to post-windthrow management over time, as described earlier for bird communities. To ensure model convergence, we excluded species with a cumulative abundance below 50 individuals throughout the entire study period. We visualized only the species that showed differences in abundance between managed and unmanaged windthrows for the entire study period (i.e. models without interaction favoured and significant habitat differences), while models for all species are presented in Figures S3 and S4.

To test if bird communities differed between the three habitats in each study year we used Permutational Multivariate Analysis of Variance (PERMANOVA): we calculated Bray–Curtis dissimilarity matrix for all point-count sites separately for each study year (seven dissimilarity matrices; Ricotta & Podani, 2017) and compared bird communities pairwise between all three forest habitats (with Bonferroni's correction). We used pseudo-F value to quantify effect size of PERMANOVA. We fitted linear models with the obtained F-value as the response variable and time since disturbance as the explanatory variable to assess habitat dissimilarity changes for each pair. Because of unequal number of point-count sites within each forest habitat (45 vs

29 vs 32), we repeated PERMANOVA on 20 randomly generated balanced subsets of 29 points per forest habitat to confirm robustness of our results (Anderson & Walsh, 2013). PERMANOVA were calculated using 'vegan' and 'pairwiseAdonis' R packages (Martinez Arbizu, 2017).

Finally, to test the convergence/divergence trends of bird communities among each forest habitat, we performed Community Trajectory Analysis using 'ecotraj' R package (De Cáceres et al., 2019). We averaged bird community data over each habitat and year, calculated Bray–Curtis dissimilarity matrix and created one trajectory per forest habitat as a vector linking averaged bird community states of consecutive study years. Next, we conducted Mann–Kendall trend test to assess convergence/divergence trends for each pair of bird community trajectories. We used PcoA to represent the trajectories in two dimensions.

3 | RESULTS

Throughout the whole study period, a total of 13,140 bird observations belonging to 93 species were recorded (Table S1). Mean bird abundance per point was 17.71 (4.85 SD), mean species richness per point was 13.12 (3.54 SD). The three most common species recorded were common chaffinch *Fringilla coelebs* ($n = 1915$), willow warbler *Phylloscopus trochilus* ($n = 936$) and great spotted woodpecker *Dendrocopos major* ($n = 686$). The distance between the habitats did not interfere significantly with our results (Figure S5).

Unmanaged windthrow hosted the highest richness and abundance of all bird species, followed by managed windthrow and control forest, over the whole study period (Figure 3; Figure S6). Trends of total abundance and richness were similar across the three forest habitats. In contrast, forest bird abundance and richness increased over time for both windthrows as compared to control: Control forest maintained higher diversity of forest birds as compared to managed windthrow for 12 years (abundance) and 15 years (richness) following disturbance, while the diversity of forest birds was similar to unmanaged windthrow for most of the study period (Table S2). However, towards the end of the study, unmanaged windthrow sites began to host more forest birds compared to control forest. When compared to managed windthrow, unmanaged windthrow sites hosted a higher diversity of forest birds for 16 (abundance) and 17 (richness) years after the disturbance. Patterns for rarefied richness were largely similar to those reported for richness, albeit with reduced contrast between the two windthrows, likely due to a shared species pool (Figures S3, S4 and S6).

Farmland bird richness and abundance, initially high on both windthrows, consistently declined over time, but remained higher as compared to control until the end of the study (Table S2). The richness and abundance of farmland birds declined faster on unmanaged windthrow, and 9 years after the disturbance, managed windthrow started to host the most diverse farmland bird community among the three forest habitats.

Nine species were more abundant in unmanaged windthrow compared to managed windthrow throughout the entire study period: two woodpeckers (black—*Dryocopus martius* and great spotted woodpecker), two thrushes (song—*Turdus philomelos* and mistle—*Turdus viscivorus*), two tits (great—*Parus major* and willow—*Poecile montanus*), common cuckoo *Cuculus canorus*, Eurasian wren *Troglodytes troglodytes* and common chaffinch (Figure 4). They comprised five forest species, three cavity excavators (woodpeckers and willow tit) with no representation from farmland birds. Conversely, all three species more abundant in managed windthrow were open-habitat birds linked to farmland (Eurasian skylark *Alauda arvensis* and hooded crow *Corvus cornix*) or forest gaps (woodlark *Lullula arborea*).

Bird communities in the three forest habitats were distinct in each study year (PERMANOVA, $p < 0.01$; Figure 5; Table S3). Initially, both windthrows differed more from the control forest than from each other. Over time, windthrows became less distinct from the control forest, while the managed and unmanaged windthrows maintained consistent differences. By the study's end, all three forest habitats were almost equally dissimilar from each other. With the exception of 13th year post-disturbance (2015), the bird communities in the control forest resembled those in unmanaged windthrow more than in managed windthrow. The balanced design PERMANOVA confirmed result reliability, although in two instances, the differences between managed and unmanaged windthrows were nearly significant (5 and 17 years post-disturbance; Figure S7).

We observed directional changes in bird communities in all three forest habitats (Figure 6). Bird communities tended to converge between managed windthrow and control forests as well as unmanaged windthrow and control forests (Kendall trend test, $p < 0.05$). However, no converging or diverging trends were detected between managed and unmanaged windthrows, confirming the consistent distinction of their bird communities over time. Importantly, this distinction was not due to a time lag, where communities might follow each other's trajectories but represent earlier successional stages. Instead, the communities followed parallel trajectories without overlapping. Year-to-year changes exhibited parallel trends across forest habitats, likely influenced by fluctuations in regional bird abundances.

4 | DISCUSSION

Our study revealed the enduring effect of two distinct management strategies applied after a major wind disturbance on bird communities in a temperate pine forest. By encompassing not only salvage logging but also subsequent silvicultural measures, our research provided unique insights into the overall impact of active windthrow management on bird populations. Consistent implementation of these distinct strategies enabled us to monitor and compare the succession of bird communities over the period from gap creation

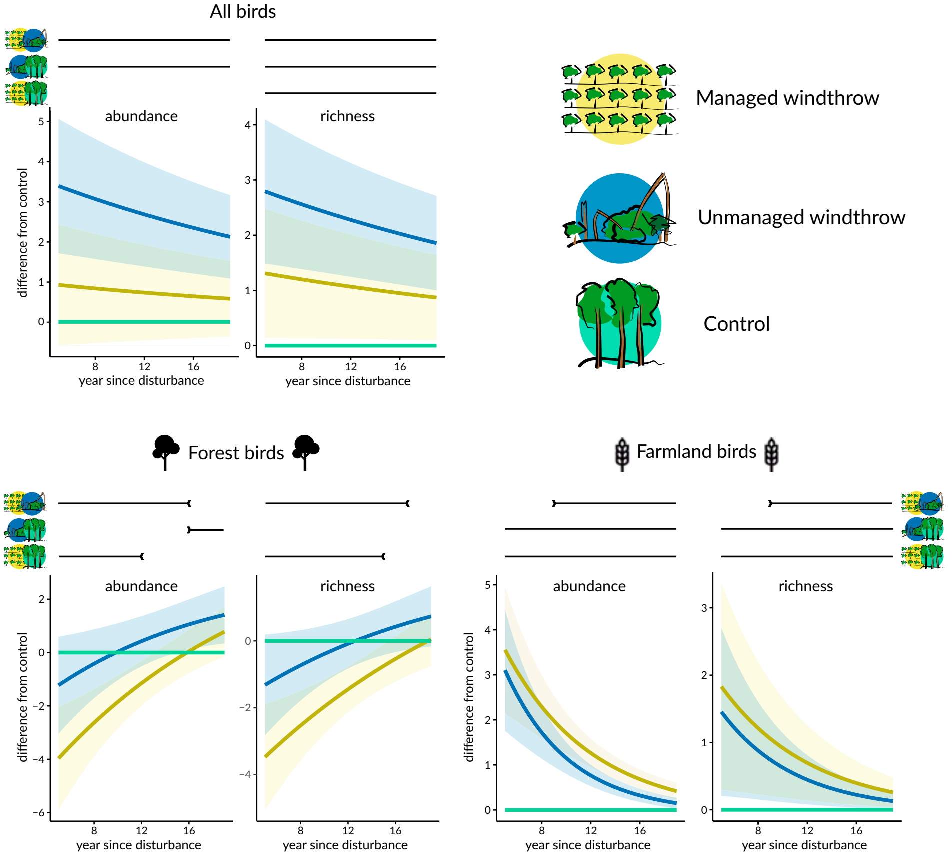

FIGURE 3 Abundance and richness of bird communities on managed and unmanaged windthrows as compared to control forests. Contrasts between marginal means for both windthrows and control (i.e. unmanaged windthrow—control and managed windthrow—control; shown as response values) are presented with associated 95% CIs and control (baseline value of 0). Above each graph, periods of time of significant difference ($p < 0.05$) are indicated, based on pairwise comparisons of marginal means with Tukey p-value adjustment (Table S2). In cases of models with no interaction included, significant difference was assumed for the whole study period based on model parameters (Figure S6). For rarefied richness, see Figures S3 and S4.

to early stage of canopy regeneration (Hilmers et al., 2018), which is particularly rare in the context of post-disturbance studies (Thorn et al., 2018).

We demonstrated that post-windthrow forest management, in contrast to leaving a windthrow unmanaged, had a lasting adverse effect on forest birds, persisting even after the emergence of new canopy layer, thereby confirming our first hypothesis. Furthermore, we observed a turnover of bird communities from early-successional to intermediate- and late-successional species on both managed and unmanaged windthrows, leading to an increasing resemblance to control forests, thus confirming our second hypothesis. However, despite this similar species turnover pattern, bird communities in managed and unmanaged windthrows remained distinct throughout the entire study period, with their dissimilarity remaining consistent over time, contrary to our third hypothesis. Therefore, we proved that restraining from any post-windthrow management have set succession of bird communities on a unique pathway, supporting higher avian diversity than both disturbed and unaffected managed stands. These findings have significant management implications, as discussed below.

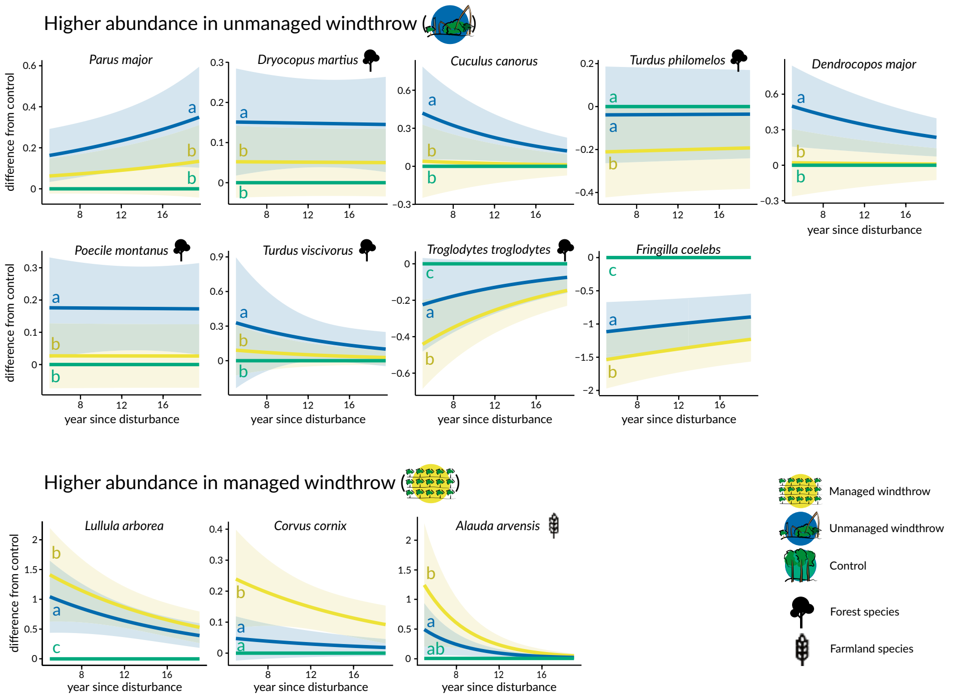

FIGURE 4 Abundances of individual bird species which maintained significant differences between two windthrow habitats throughout the entire study period. Contrasts between marginal means for both windthrows and control (i.e. unmanaged windthrow—control and managed windthrow—control; shown as response values) are presented with associated 95% CIs and control (baseline value of 0). Significant differences ($p < 0.05$) between habitats are indicated with symbols, based on model outputs (Figure S6; see also Figures S3 and S4 for remaining species).

4.1 | Restraining from post-windthrow management positively affects bird succession

The initial distinctiveness of unmanaged windthrow bird communities can be attributed to disturbance legacies like damaged trees, snags and downed dead wood, providing refuge for forest species (Basile et al., 2022; Żmihorski, 2010). However, despite the recolonization of both managed and unmanaged windthrows by forest birds, their community distinctions remained consistent. Thus, it is the difference in the regenerating canopy layer properties (tree density, species richness and structural complexity) between managed and unmanaged windthrows that appears to play a key role in maintaining bird community distinctions (Skłodowski, 2020; Szwagrzyk et al., 2018). As these properties are expected to remain different in a long run (Cerioni et al., 2024; Lindenmayer et al., 2012), and with bird communities showing no sign of convergence, the succession paths for managed and unmanaged windthrows are likely to remain distinct for decades (see also Georgiev et al., 2020). While succession pathway of bird communities in managed windthrow is likely to mimic that of forest clear-cuts in production stands, due to comparable management activities, we predict that unmanaged windthrow will follow a different path typical of natural forests, characterized by varied age structures, abundant tree-related microhabitats and dead wood.

4.2 | Value of unmanaged windthrow for bird diversity as compared to undisturbed forest stands

We showed that unmanaged windthrow consistently hosted more diverse bird communities over two decades compared to control forests. Some forest species were continuously more abundant on undisturbed windthrows, including ecosystem engineers (the excavators). Prior to the disturbance, our study site lacked the variety of coarse dead wood forms crucial for forest birds, a characteristic often observed in temperate forests managed for timber production (Kirby et al., 1998). Therefore, windthrow-induced increase of those resources could benefit some species,

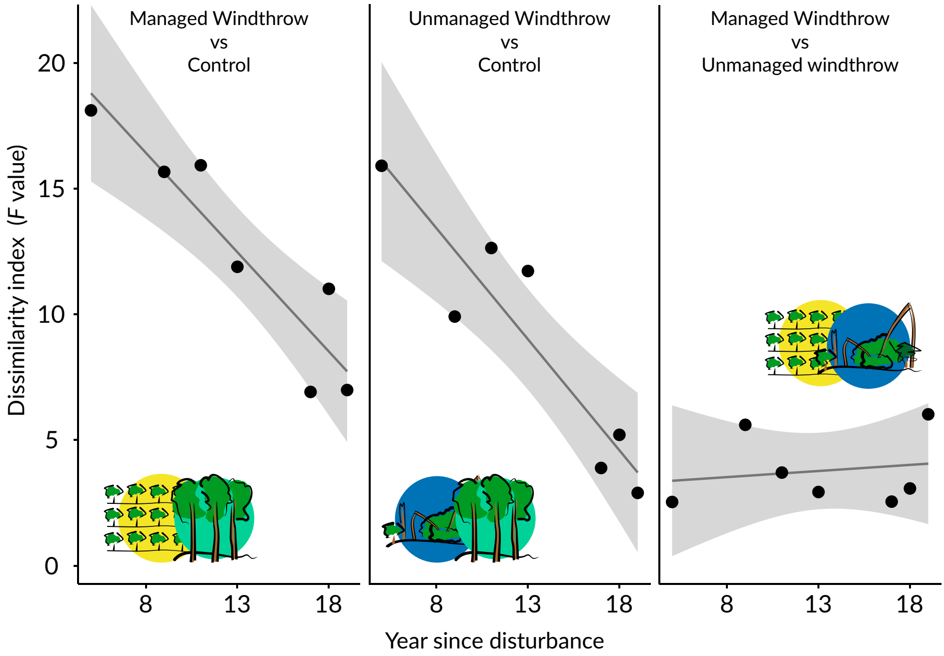

FIGURE 5 Pairwise dissimilarities for all three forest habitats in seven study years and associated trend lines with 95% CIs, calculated from linear models. Bird communities in managed and unmanaged windthrows, as well as the control, were distinct in each study year (PERMANOVA, $p < 0.01$). Dissimilarity gradually decreased with time for control versus managed and control versus unmanaged windthrow pairs but not for unmanaged versus managed windthrow pair.

such as woodpeckers (Basile et al., 2022), which support the diversity of other cavity nesters (Trzcinski et al., 2022), counterbalancing the decline of some closed-canopy species (Fuller, 2000; Żmihorski, 2010). Increased dead wood amount may affect forest biodiversity for decades, as it gradually decays, benefitting an array of saproxylic invertebrates (Cours et al., 2023; Thorn et al., 2020), an important food source for birds. In addition, the spatial structure of unmanaged windthrow becomes increasingly complex over time as the canopy layer regenerates; windthrow survivors loom over the regenerating trees, being highly variable both in species and height (Skłodowski, 2020; Szwagrzyk et al., 2018). In contrary, canopy of control forest in our study is formed by trees of uniform age and height, and the sub-canopy tree layer is generally sparse, resulting in a simple spatial structure being maintained over time. Moreover, the age of control forests (30–90 years) is too young to develop various old-growth characteristics (Bauhus et al., 2009). Therefore, we predict that unmanaged windthrows' relative importance for forest birds will remain consistently high as the forest succession unfolds, underlining their value for conservation of forest biodiversity.

4.3 | Role of combined management activities in shaping biodiversity over a long term

In the literature, 'salvage logging' is commonly understood in two ways: first, as the removal of dead and damaged trees—an initial step in active post-disturbance management; second, as a collective term for active post-disturbance management (which may include tilling, fencing, replanting or thinning). In short-term studies, using 'salvage logging' to refer to overall post-disturbance management seems justifiable, given its pivotal role in shaping habitat differences until canopy regeneration occurs. Yet the impact of salvage logging operation seem to fade away with time as it affects the emerging canopy layer only to a limited extent (Cours et al., 2023; Leverkus et al., 2021), in contrast to subsequent management actions, such as replanting and tilling. For instance, Hotta et al. (2021) observed that salvage logging alone had minimal effects on tree species composition and biomass recovery in Japanese hemiboreal forests, whereas combining it with soil scarification led to a long-term transition from coniferous to birch-dominated forests. Tree replanting programs significantly impact

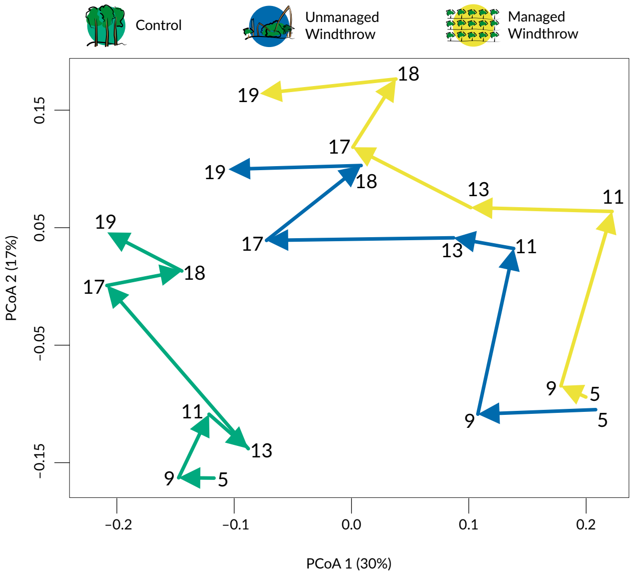

FIGURE 6 Succession of bird communities, presented as vectors linking average bird community states of consecutive study years along two PCoA axes. Community trajectories of both windthrows tended to converge with the control (i.e. distance between their respective community states decreased with time; Kendall trend test, $p < 0.05$), while no such trend was detected between managed and unmanaged windthrows.

forest structure, potentially lowering structural diversity and introducing invasive species (Lindenmayer et al., 2012). While other activities such as thinning also influence forest dynamics (Dieler et al., 2017), they are not implemented until several years after the disturbance. Therefore, in practice, the reported long term effects of 'salvage logging' on biodiversity may highly vary depending on the authors' understanding and use of this term. Based on that, we recommend authors to: (i) discontinue the use of 'salvage logging' as a comprehensive term for collective management activities following disturbances. While we recognize the need for a unified term for simplicity amid diverse post-management approaches, we suggest adopting a distinct collective term for these activities (e.g. 'intense/active forest management'; see in Cerioni et al., 2024). This will facilitate distinguishing the effects of single management activities (i.e. salvage logging) from the collective silvicultural practices; (ii) outline the management actions undertaken at their study sites as clearly as possible to facilitate future comparisons of separate effects of post-disturbance silvicultural practices and (iii) exercise caution when extrapolating findings from studies involving vastly different post-management scenarios, especially in long-term studies or meta-analyses.

4.4 | Management implications

During recent centuries, natural European forests have been largely replaced with silvicultural plantations to enhance timber production, putting forest biodiversity at risk (Halme et al., 2013). To halt this trend, EU recently agreed that ≥30% of poor-condition ecosystems should be placed under recovery measures by 2030 (Council of the European Union, 2023), which is now hotly debated (Rabesandratana, 2023). Despite of increasing need for restoration of European forests (Sabatini et al., 2020), management schemes in disturbed forests still follow centuries-old procedures based on salvage logging, even in protected areas (Lindenmayer et al., 2012; Müller et al., 2018). Our results prove that even heavily damaged forest plantation, when left unmanaged, serves as refuge for forest biodiversity post-disturbance (Cours et al., 2023) and as surrogate habitats for farmland species (Rost et al., 2012; Żmihorski et al., 2016), leading to increased biodiversity, maintained at least until early canopy regeneration. Thus, in the short term, unmanaged windthrows support the restoration of underrepresented early-successional forests in Europe, and, in the long-term, the development of rare late-successional forests with old-growth characteristics (Bauhus et al., 2009; Hilmers et al., 2018; Thorn et al., 2020). For these reasons, we call for increased recognition of unmanaged disturbed forests when establishing protected areas as for example Swedish Hälleskogsbrännan reserve (6420 ha of burnt forest left unmanaged after Västmanland wildfire in 2014; Gustafsson et al., 2019) or Polish Szast reference forest (covering 476 ha of unmanaged windthrow created after 2002 windstorm in Pisz Forest, our study area).

Instead of perceiving forest disturbances exclusively as economic catastrophes, we encourage to treat them also as a low-cost ecosystem restoration tools (Hobbs et al., 2007), capable of resetting forest succession and guiding it onto a novel path rich in biodiversity (Thorn et al., 2020). This pathway may possibly meet the criteria for a successful long-term forest restoration without generating any additional costs (as opposed to some expensive forest restoration programs—Swezy et al., 2021). In addition, refraining from management after a disturbance leads to structurally complex, species-diverse forests (Szwagrzyk et al., 2018), which may become more resilient to future disturbances compared to single-species monocultures (Jactel et al., 2017). As forest damage due to disturbances increases due to climate change (Seidl et al., 2011), the inclusion of disturbed forests into restoration policies may become increasingly important and economically rational.

Our current understanding of forest ecosystem succession following disturbance events remains incomplete, and there is substantial uncertainty regarding the outcomes of post-disturbance management. While our study is among the lengthiest, it still covers only a fraction of the time needed for the full regeneration of a temperate forest (Hilmers et al., 2018; Thorn et al., 2018). Single long-term studies often do not encompass the diversity of European forests and frequently overlook the broader landscape context (Leverkus et al., 2018). Moreover, the impact of post-disturbance management on biodiversity vary depending on what silvicultural treatments have been applied (Hotta et al., 2021). In our case, salvage logging was followed by tilling, replanting, fencing and thinning, typical of intensive silviculture in Central Europe. However, a range of intermediate management scenarios available after forest disturbances, such as partial logging and salvage logging without replanting, deserve recognition (Cours et al., 2023). As a result, we advocate for the establishment of more long-term research projects based on permanent plots in various disturbed forest habitats under diverse management scenarios to provide strong foundations for protection of forest biodiversity in Europe.

AUTHOR CONTRIBUTIONS

Michał Walesiak—data analysis, writing leader; Michał Żmihorski—initiated and conceptualized the study. Rosanne Michielsen, Grzegorz Mikusiński—critical contribution to the data analysis, interpretation and revisions. Authors and field assistants are from or work in the study country.

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CONFLICT OF INTEREST STATEMENT

None of the authors declare any conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via Open Forest Data https://doi.org/10.48370/OFD/JVPBC5 (Walesiak et al., 2024). R code data available from Zenodo https://doi.org/10.5281/zenodo.12675108 (Walesiak & Żmihorski, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Silvicultural treatments applied to the managed windthrow area in Pisz Forest, NE Poland, after the windstorm in 2002.

Figure S2: Results of spatial autocorrelation analyses.

Figure S3: GAMM marginal means plots (absolute response on *y*-axes).

Figure S4: GAMM marginal means plots (contrasts on *y*-axes).

Figure S5: Comparison of bird communities between the two groups of control points (NMDS).

Figure S6: GAMM model outputs.

Figure S7: Results of PERMANOVA analysis (balanced design).

Table S1: Summary of abundances.

Table S2: Marginal means pairwise comparison results.

Table S3: PERMANOVA results.

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Figure S1 - Silvicultural treatments applied to the managed windthrow area in Pisz Forest, NE Poland, after the windstorm in 2002

Salvage-logging
Damaged trees were removed within first three years after the storm (2002-2005; Maszkiewicz, 2018). Trees that survived the windstorm but were visibly damaged (partly broken or curved) were also logged and removed from the windthrow area. At most sites, tree stumps were also removed, and large branches were either removed or mulched (chopped into smaller pieces).

Effect of salvage-logging

Tilling
After removing the wood biomass, the soil surface was prepared for tree replanting by tilling. The entire salvaged area was tilled with a tractor-powered plow, overturning the soil to expose the layer beneath the topsoil.


Effect of soil tilling

Replanting

Seedlings of trees, primarily one-year-old pines (*Pinus sylvestris*) approximately 10 cm tall, were planted between 2002-2008 along lines created by tilling (Maszkiewicz, 2018). These lines were spaced about 1 meter apart, with seedlings planted every 50 to 100 cm within each line. In Poland, planting density for pines typically ranges between 8,000 to 10,000 seedlings per hectare (Silvicultural Guidelines, 2012). Replanting approximated the tree species composition from before the disturbance, albeit with a slightly increased share of deciduous species (e.g., pedunculate oak Quercus robur increased from 0.4% to 2.3%, and silver birch Betula pendula from 6% to 9.5%; Maszkiewicz, 2018).

Effect of tree planting

Fencing

After planting, most areas were fenced with 2.2-meter-tall steel mesh attached to vertical wood poles placed approximately every 5-10 meters, to protect the seedlings from ungulates.

Fenced tree plantations

Thinning

As the planted trees grow, the stand density becomes too high. Therefore, some trees were removed (i.e., cut) in a process called thinning to reduce tree density as they mature.

Thinned, ca. 10-year old pine stand with cut trees left on the ground

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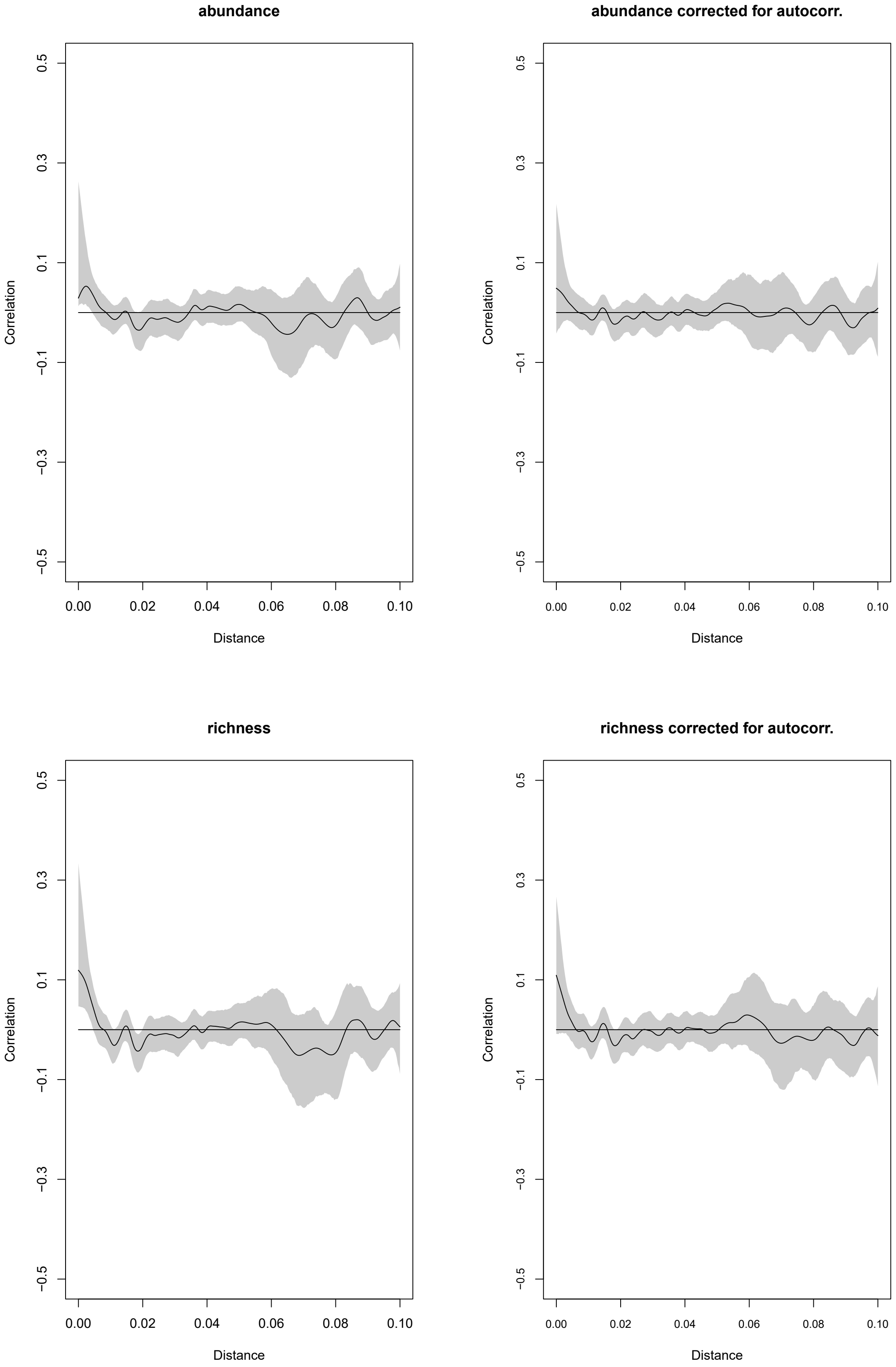
Figure S2 – Results of spatial autocorrelation analyses


abundance
abundance corrected for autocorr.
richness
richness corrected for autocorr.
Correlation
0.5
0.3
0.1
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−0.3
−0.5
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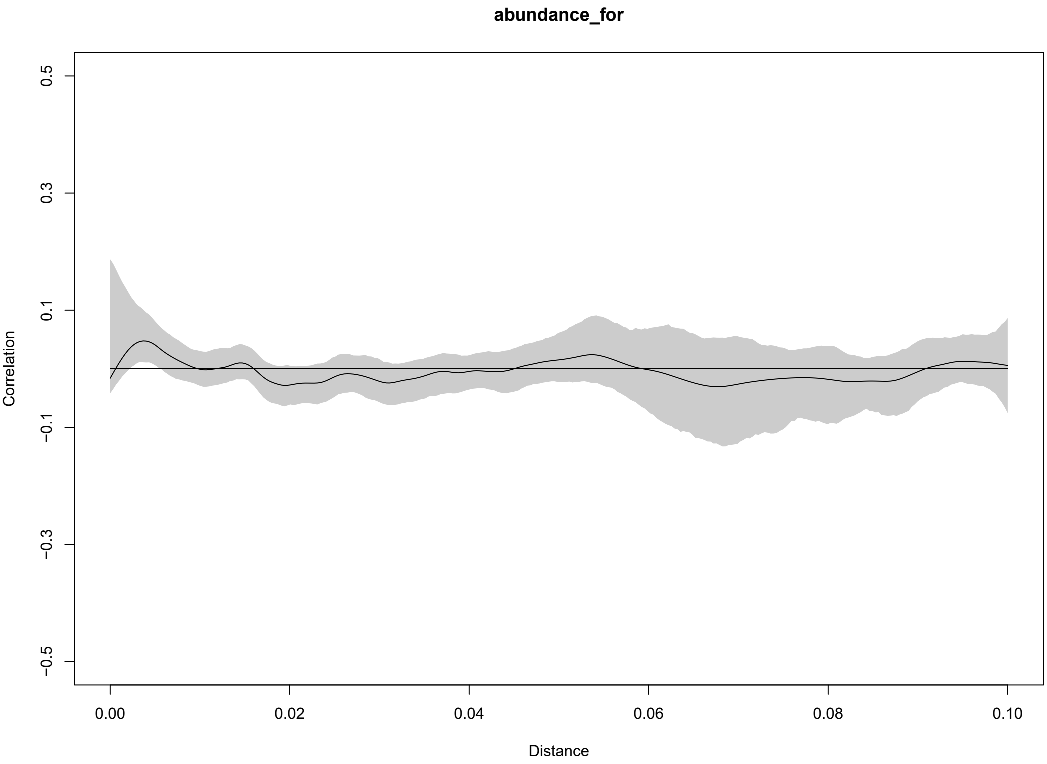
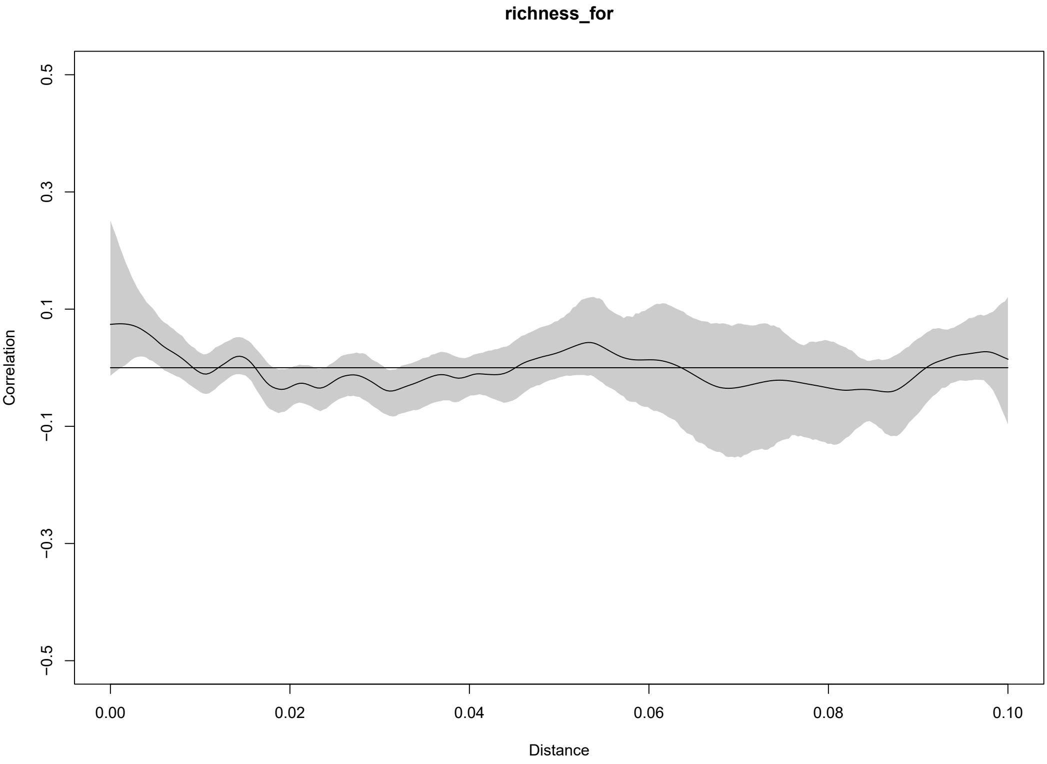
0.02
0.04
0.06
0.08
0.10
Distance


abundance_for
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


richness_for
Correlation
0.5
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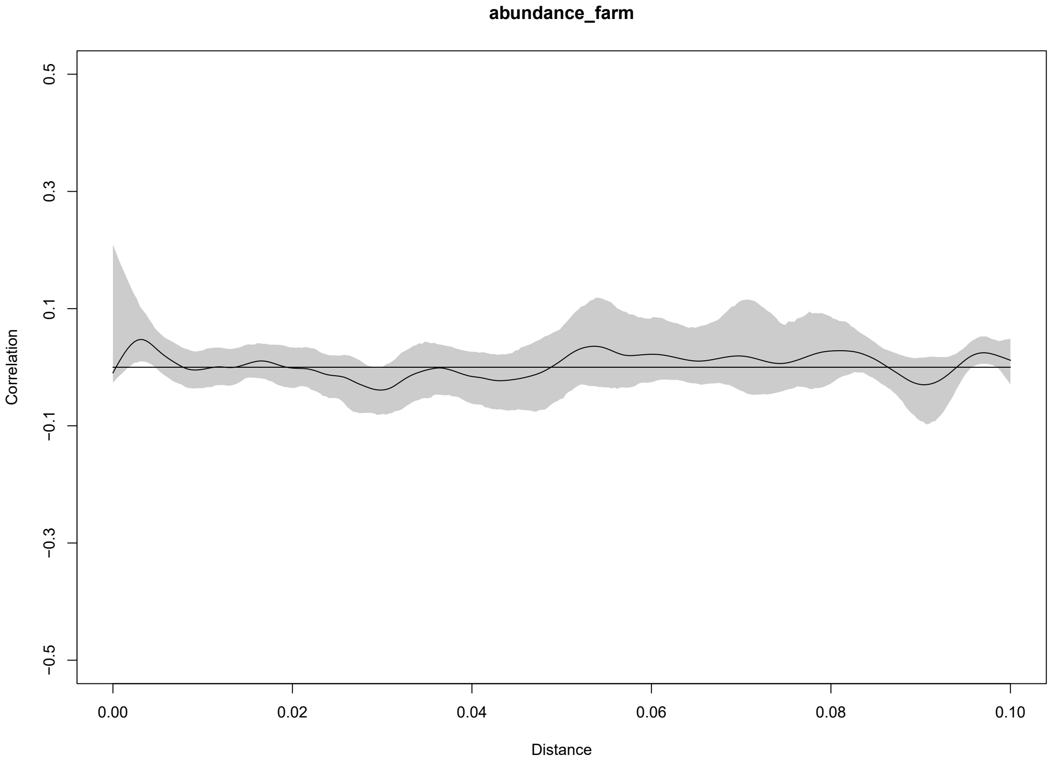
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


abundance_farm
Correlation
0.5
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0.1
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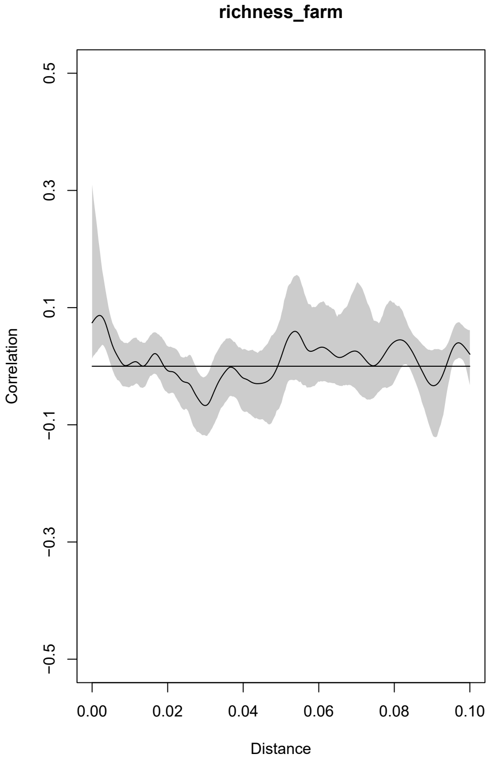
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


richness_farm
Correlation
0.5
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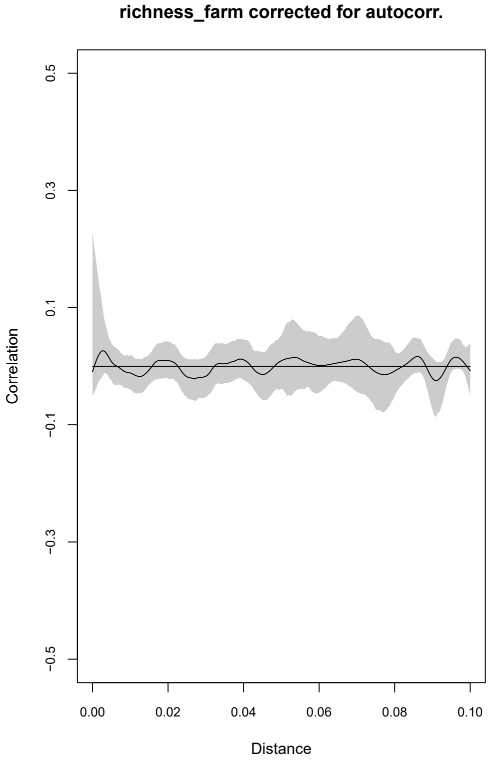
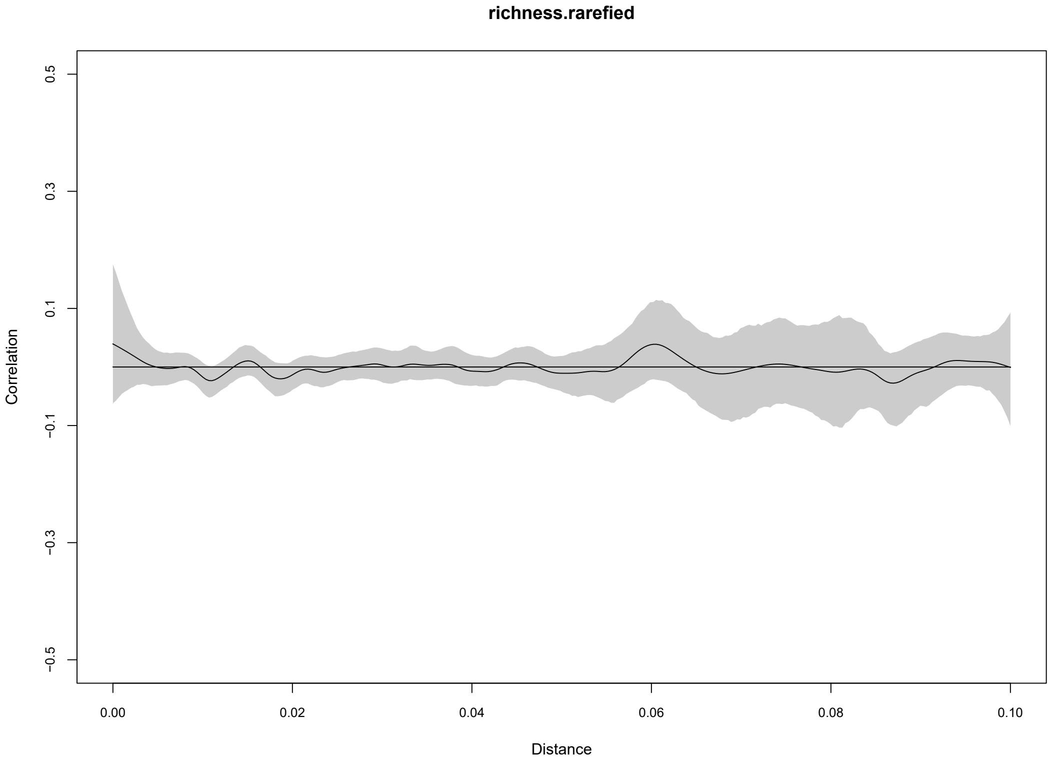
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


richness_farm corrected for autocorr.
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


richness.rarefied
Correlation
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0.1
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−0.3
−0.5
0.00
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0.04
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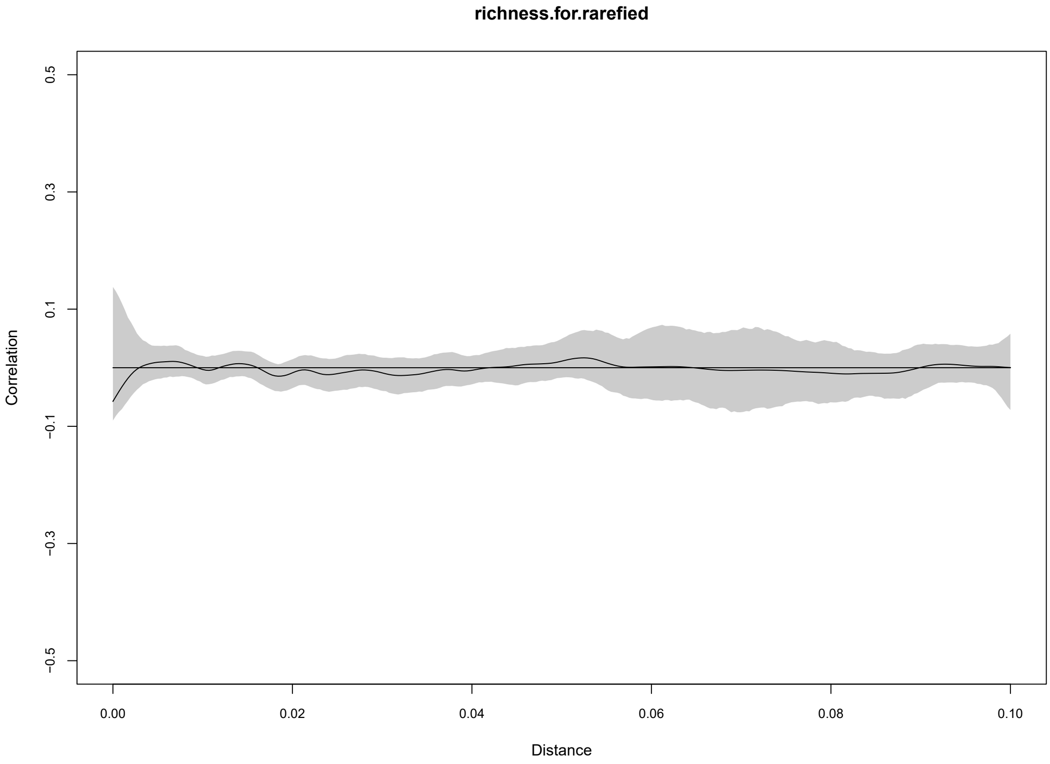
Distance


richness.for.rarefied
Correlation
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0.1
−0.1
−0.3
−0.5
0.00
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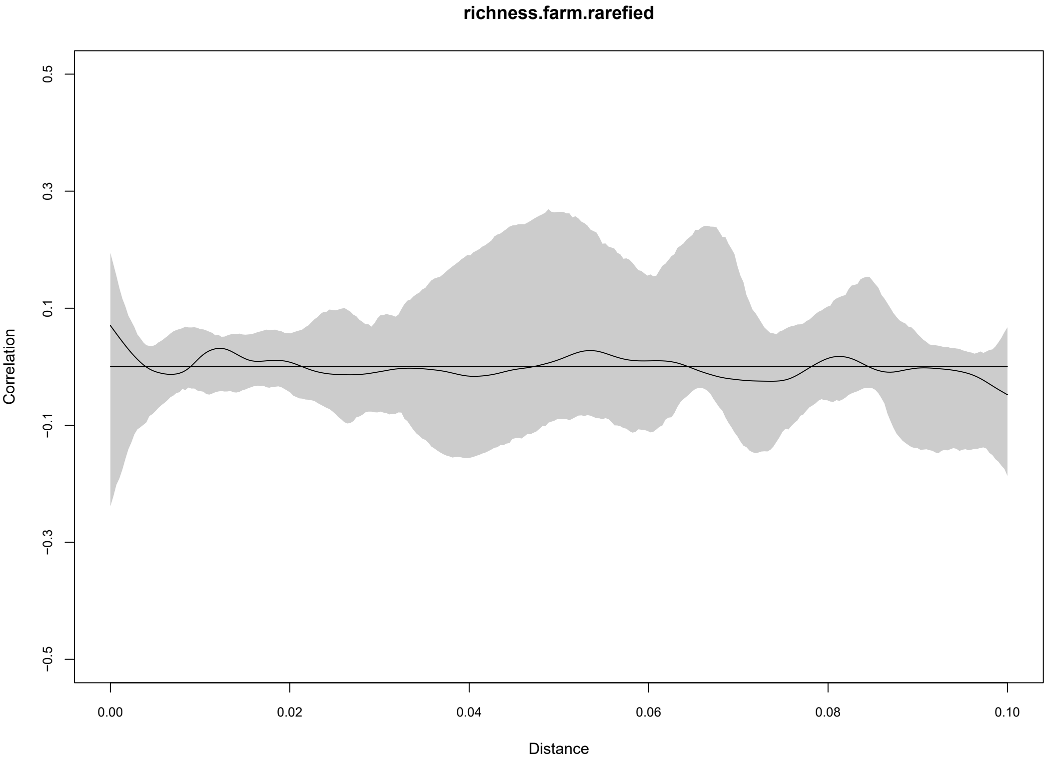
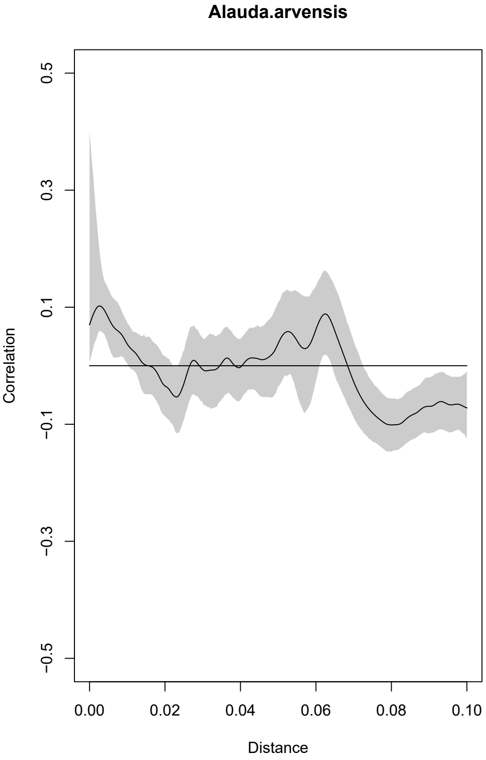
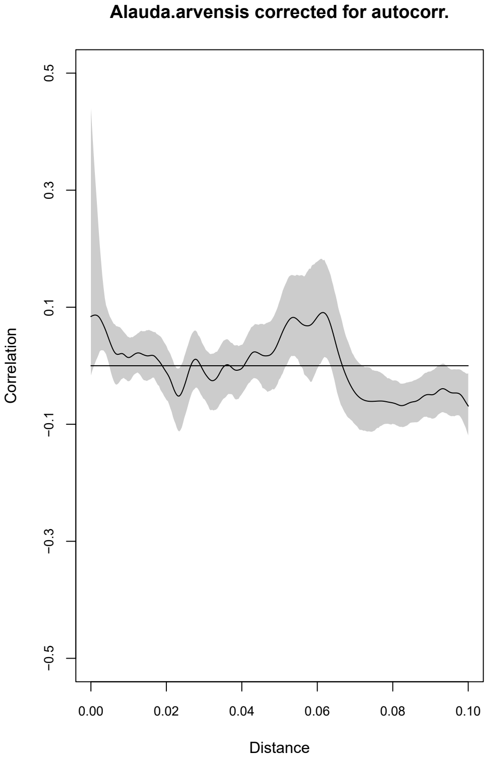
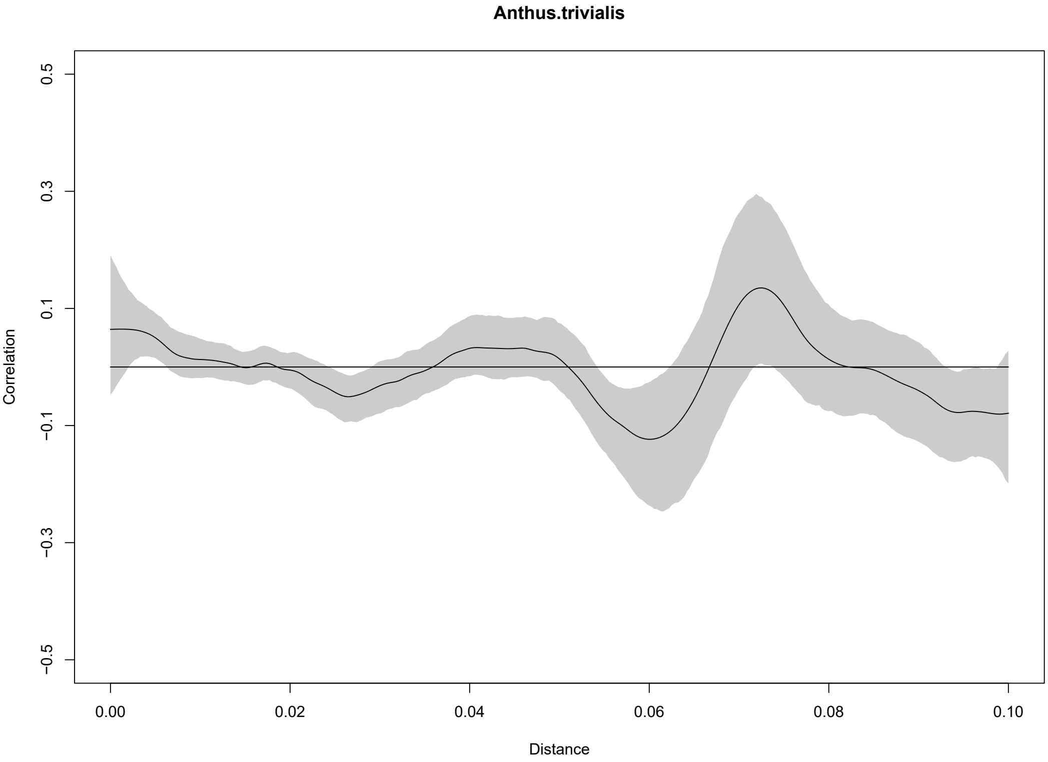
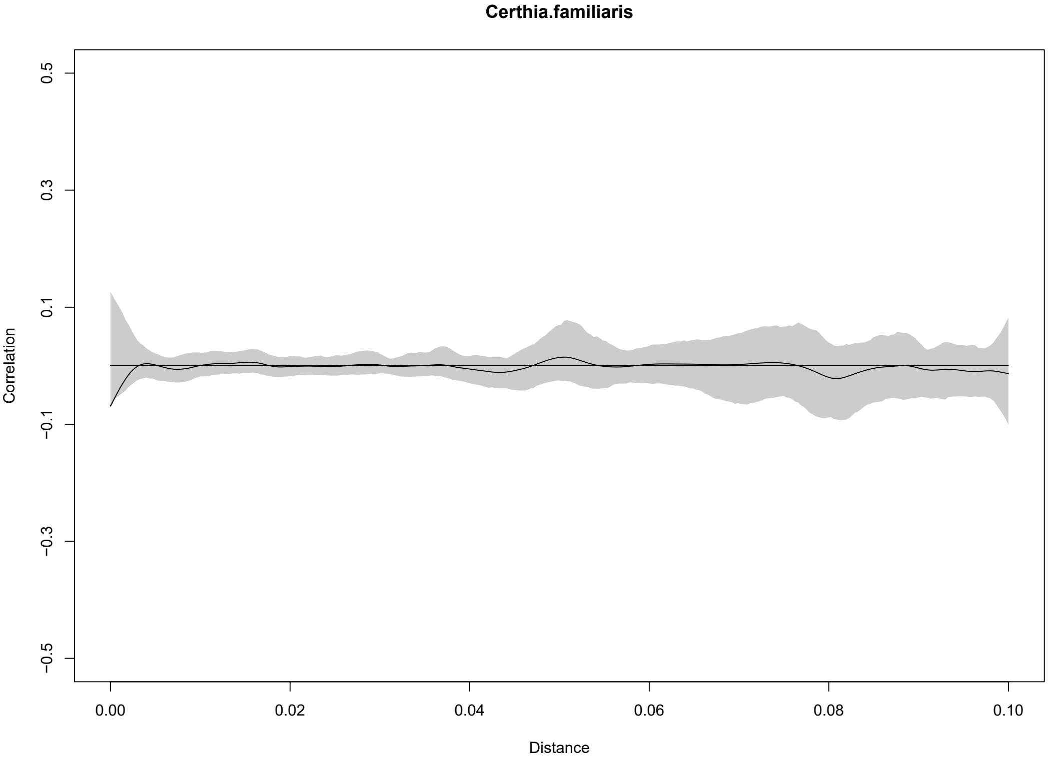
0.04
0.06
0.08
0.10
Distance

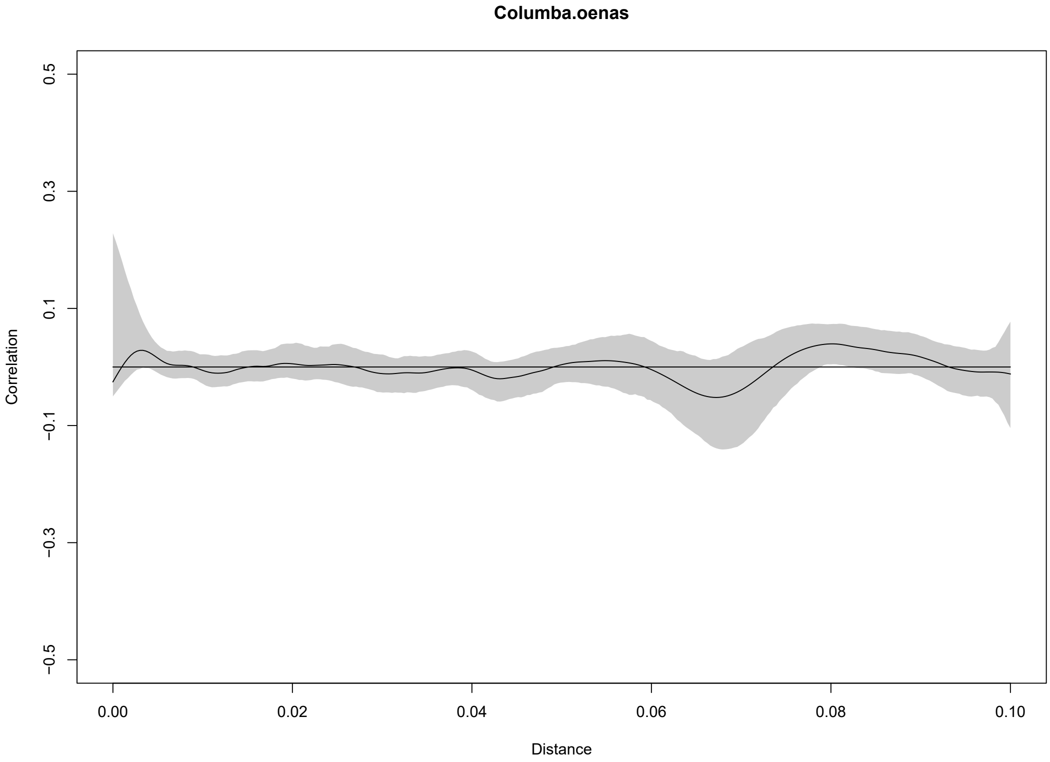

richness.farm.rarefied
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Alauda.arvensis
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance

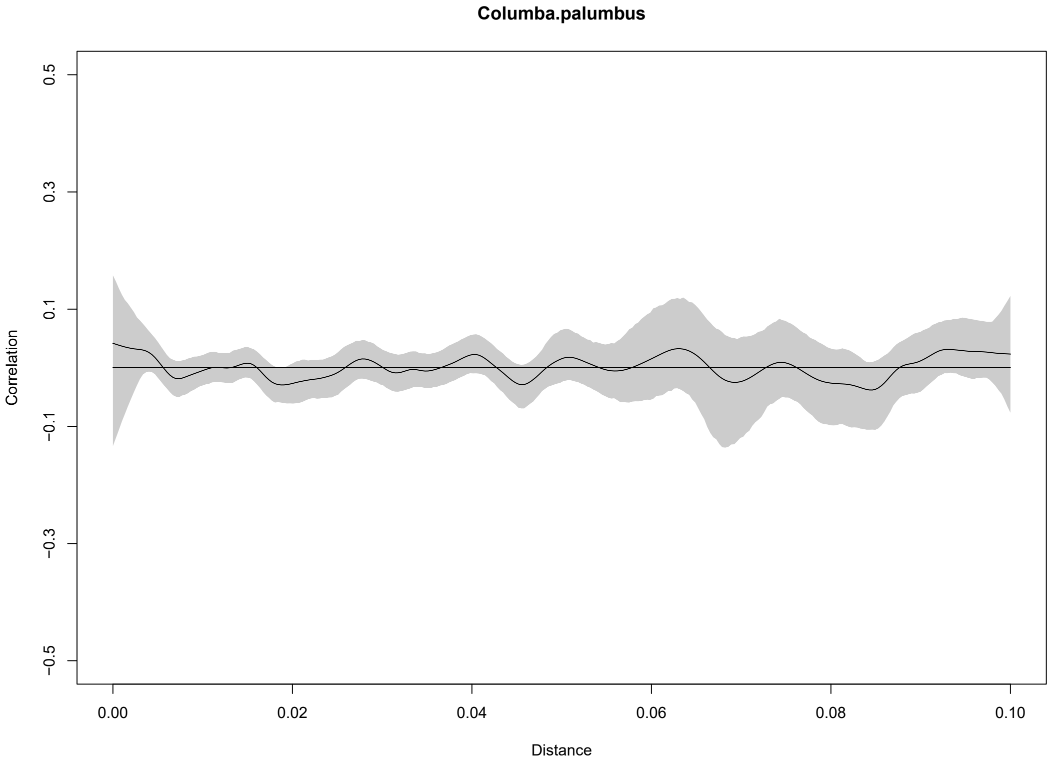

Alauda.arvensis corrected for autocorr.
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Anthus.trivialis
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance

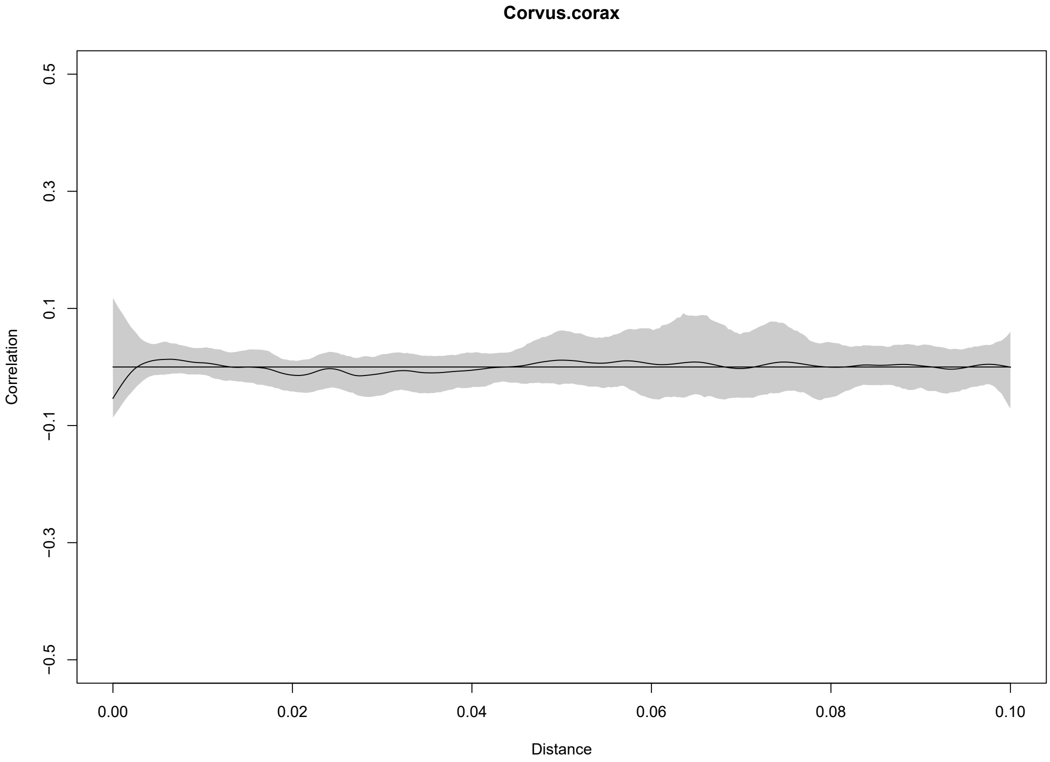

Certhia.familiaris
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance

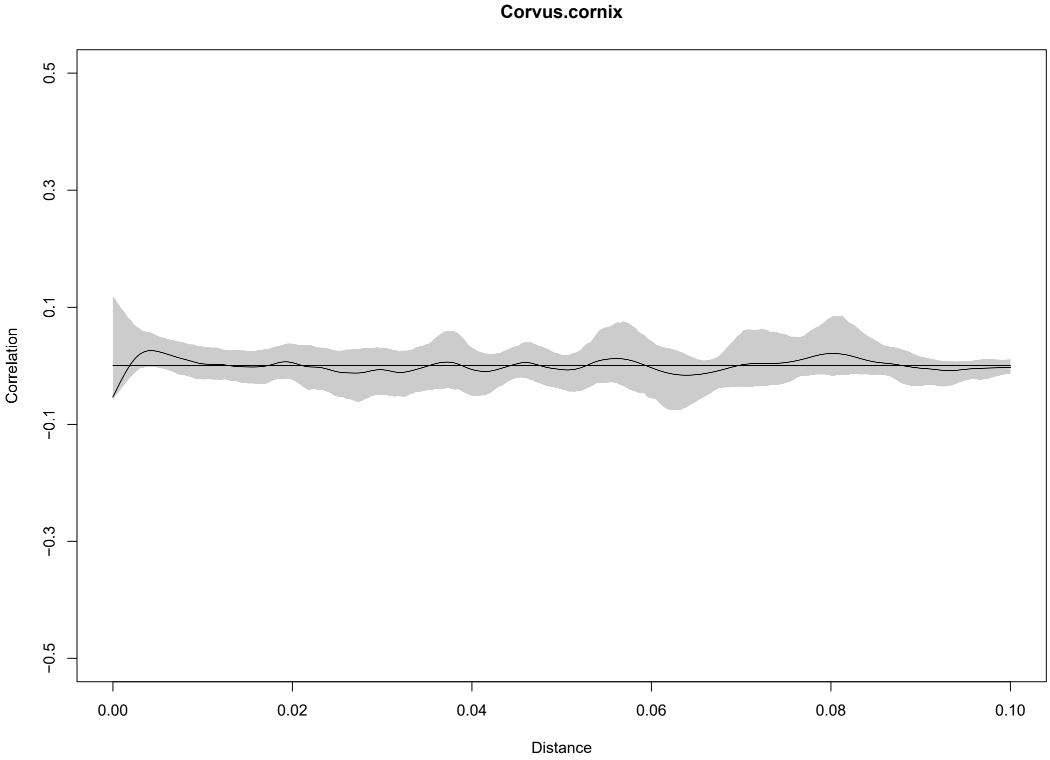


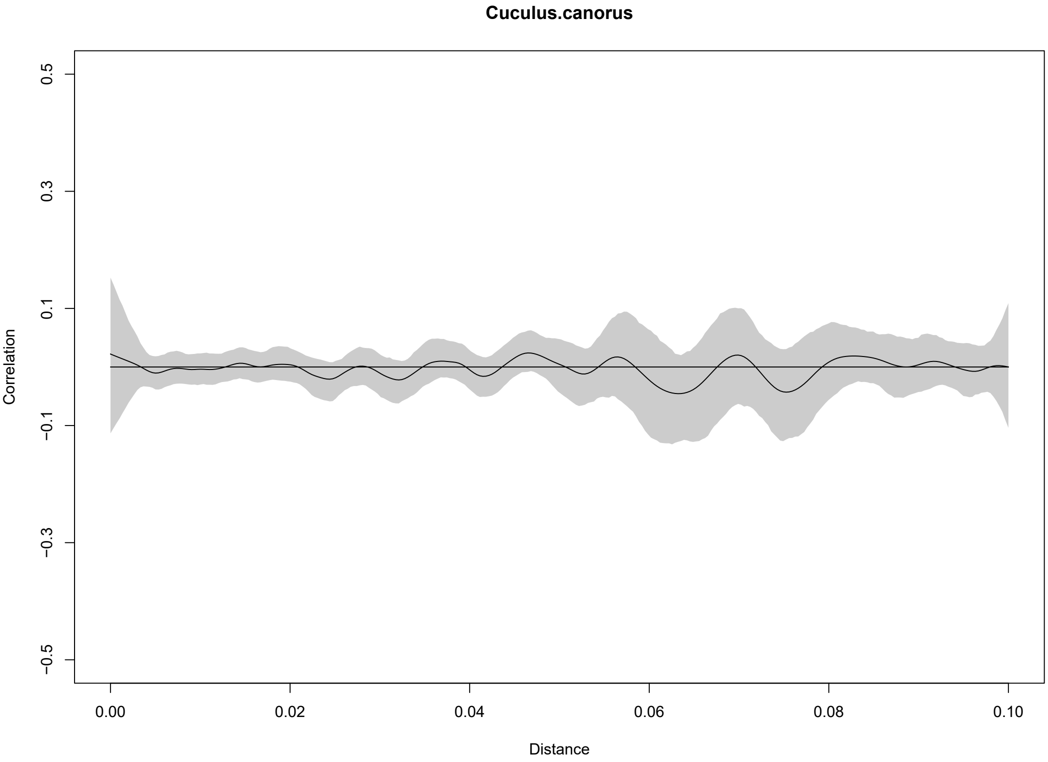
Columba.oenas

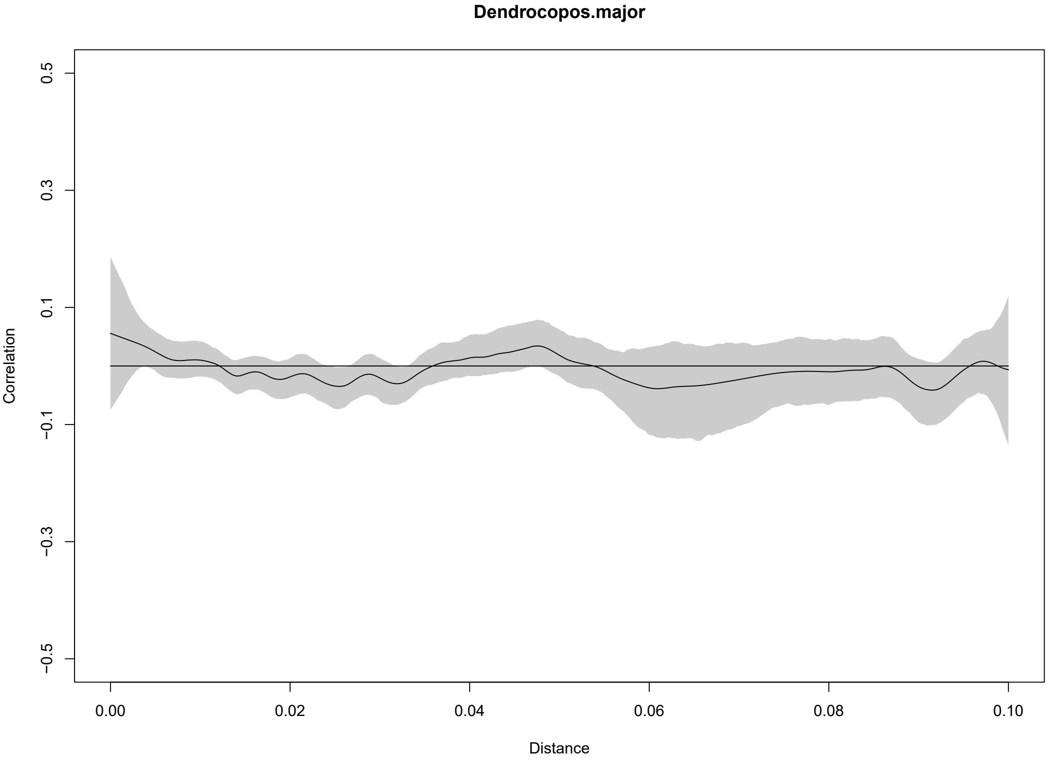


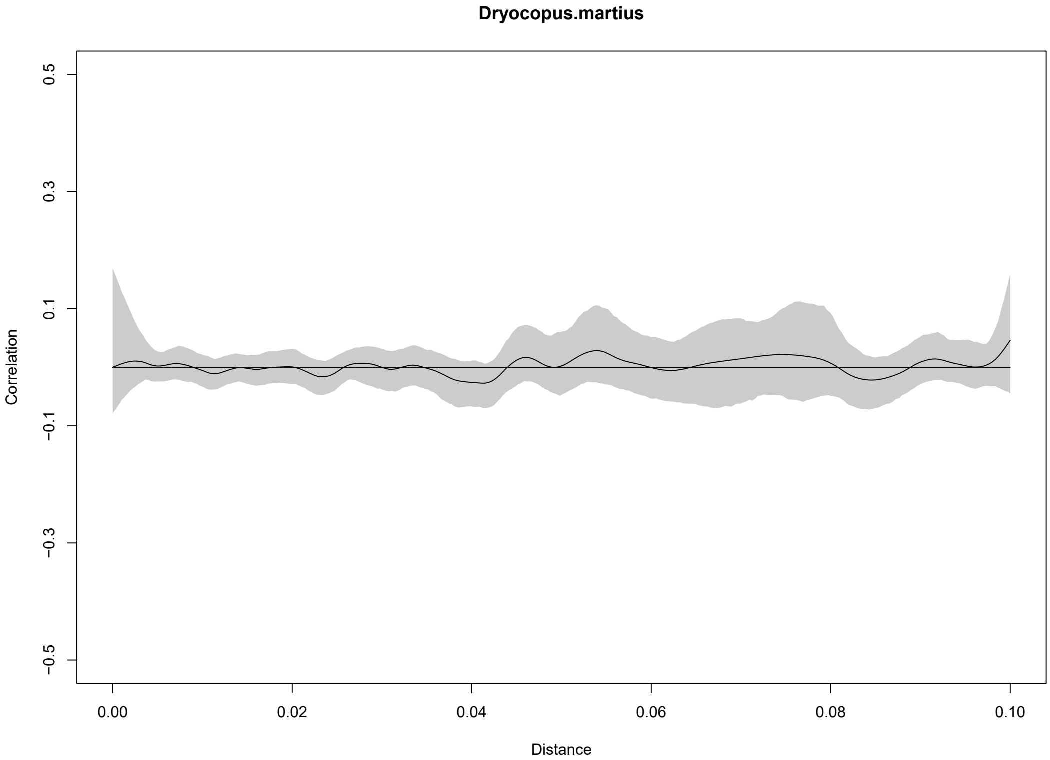
Columba.palumbus


Corvus.corax
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance

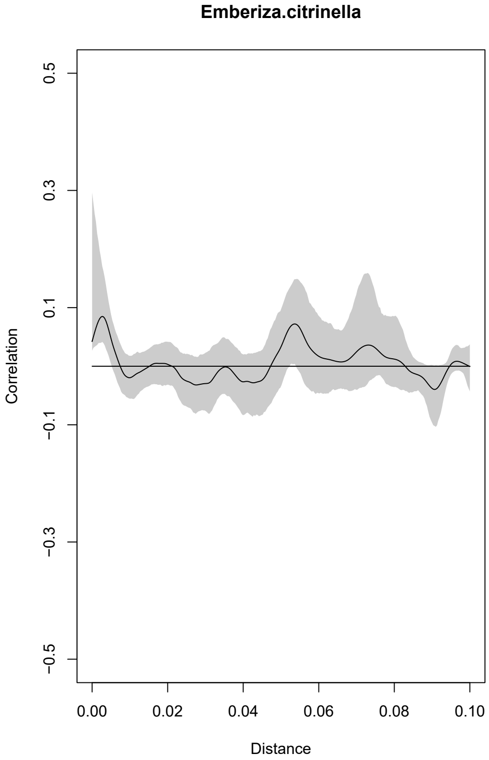

Corvus.cornix
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Cuculus.canorus
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance

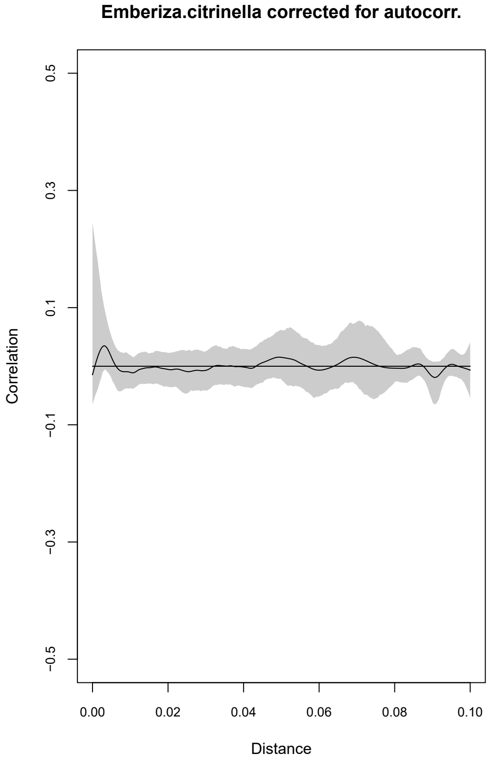

Dendrocopos.major
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance



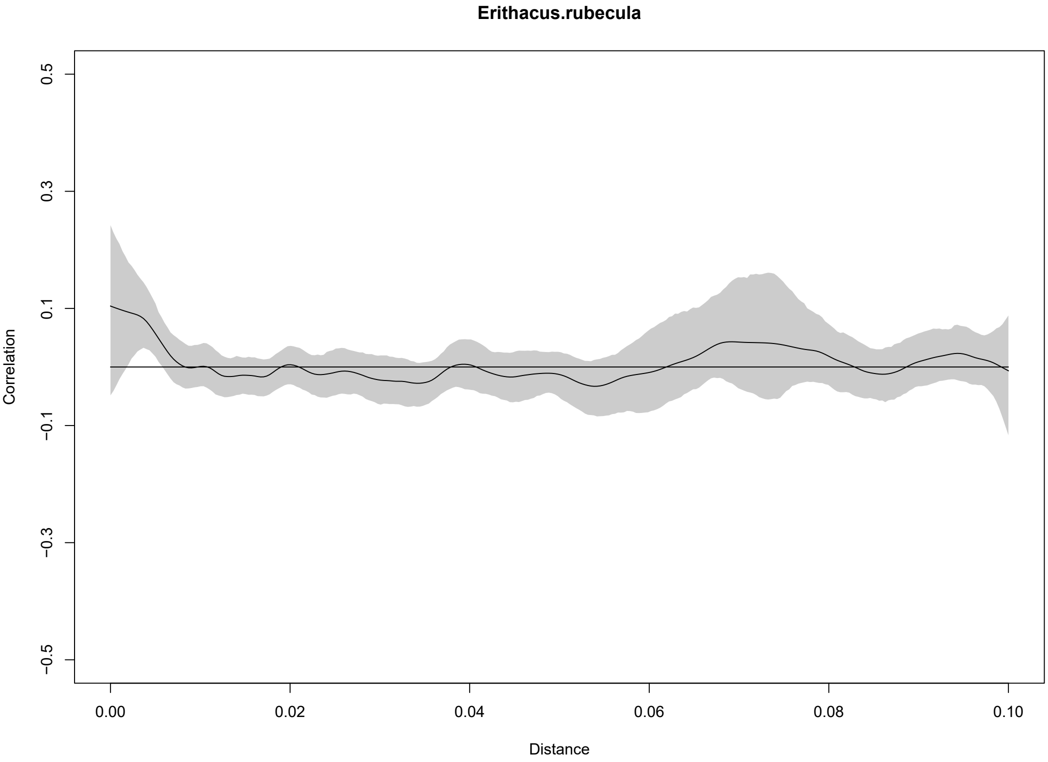
Dryocopus.martius

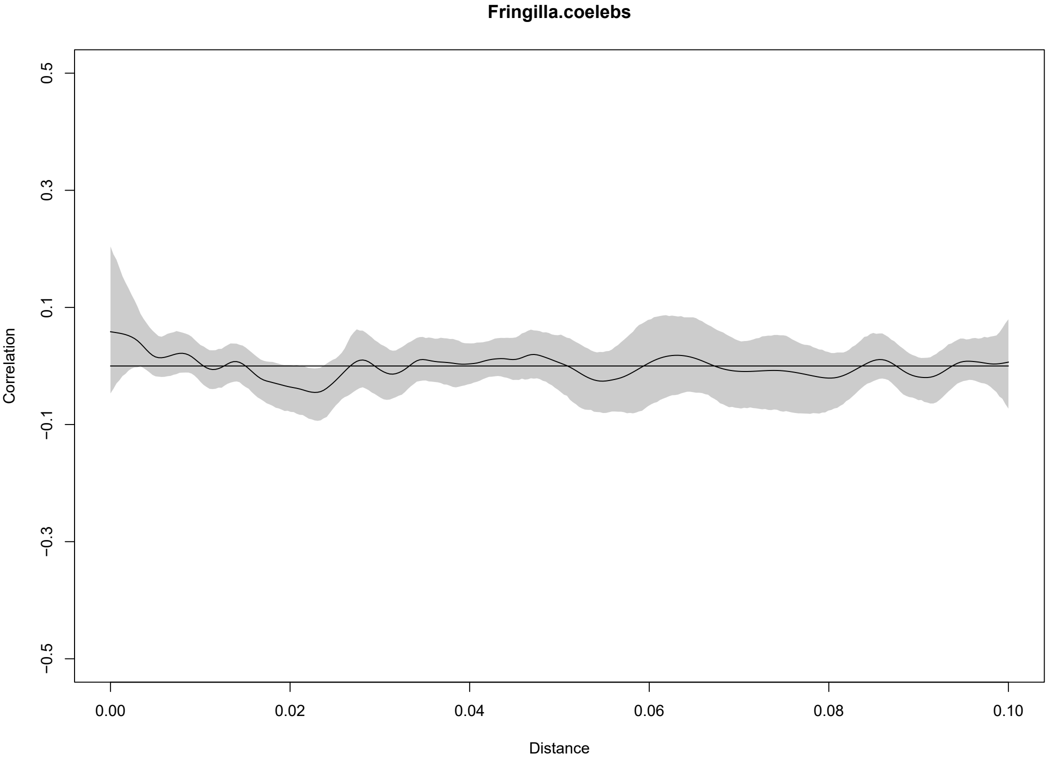


Emberiza.citrinella

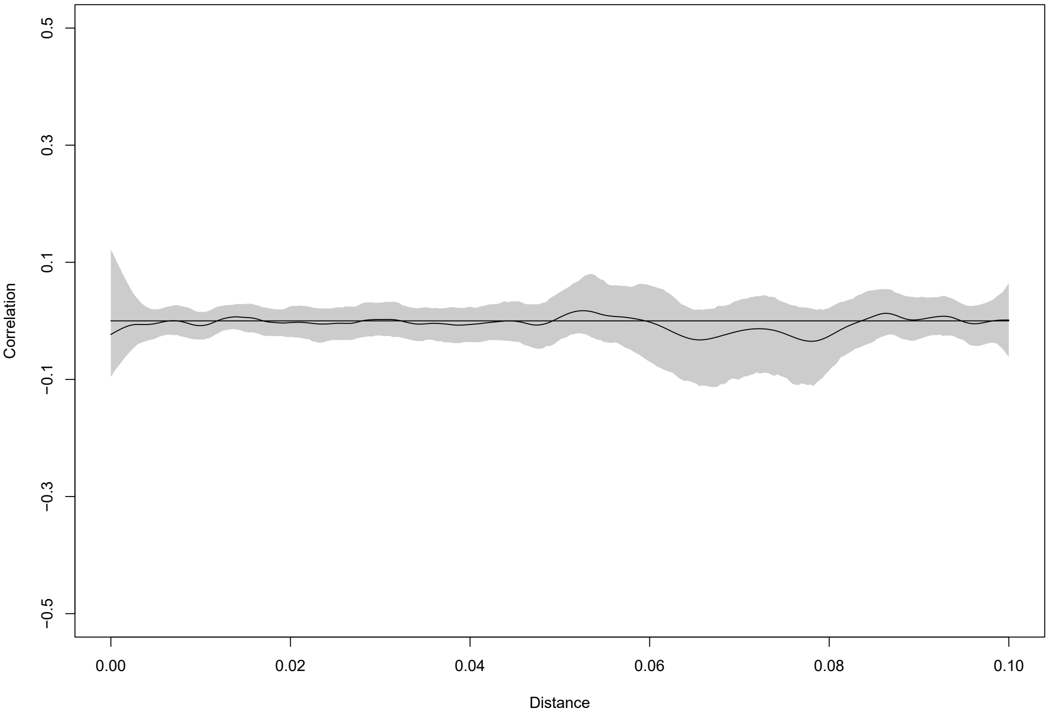


Emberiza.citrinella corrected for autocorr.

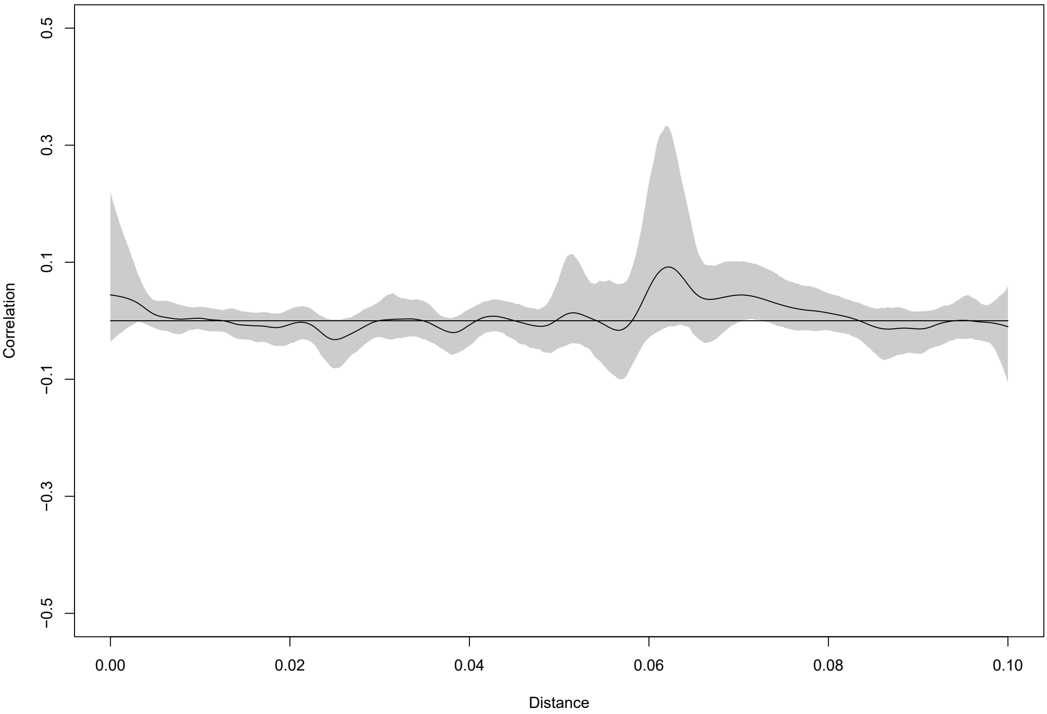

Erithacus.rubecula
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance

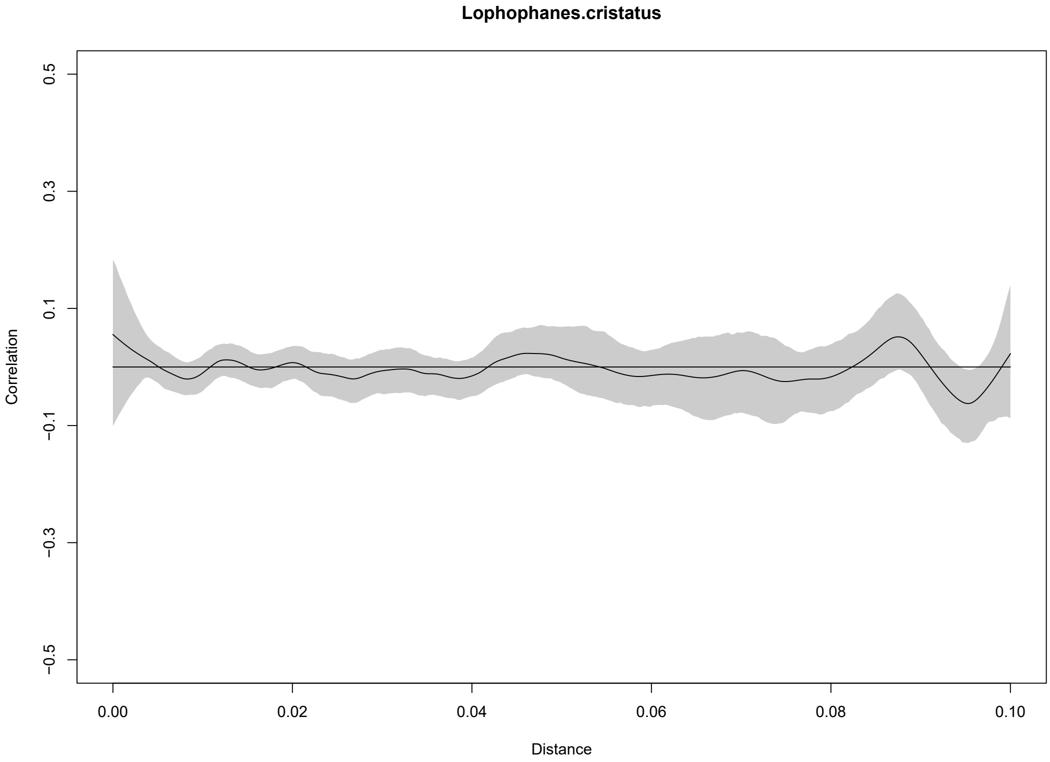

Fringilla.coelebs
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance

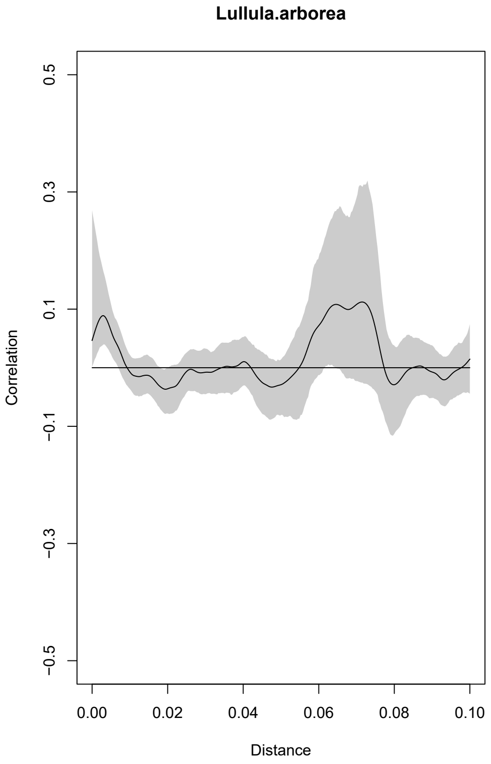
Garrulus.glandarius

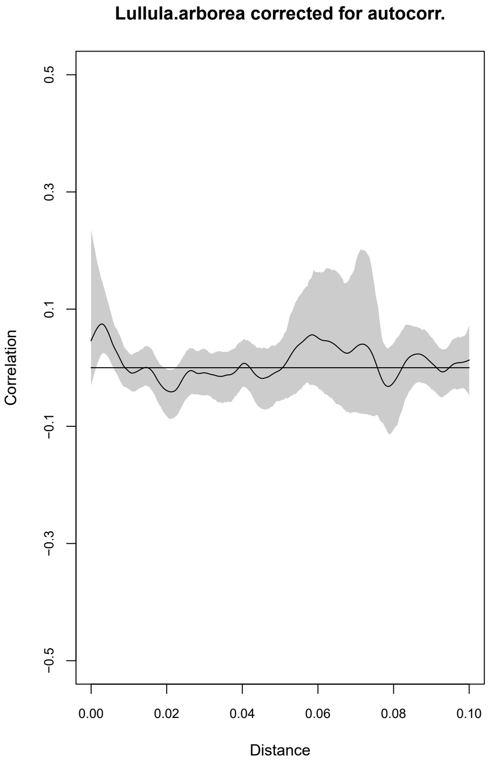


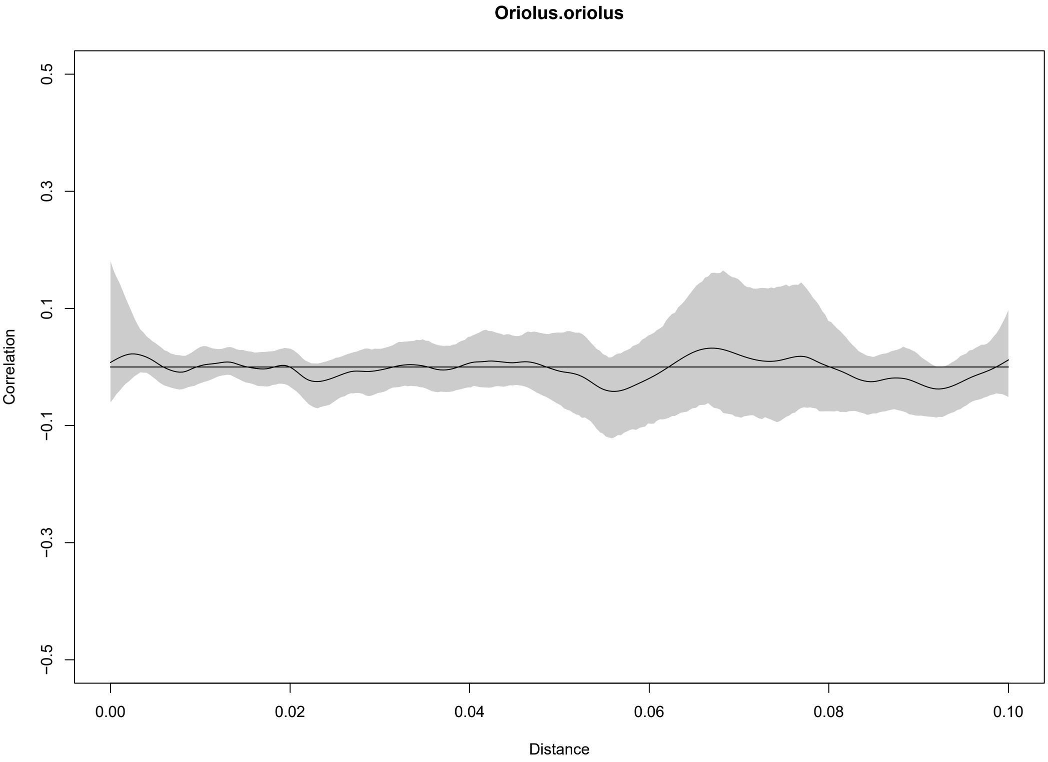
Grus.grus

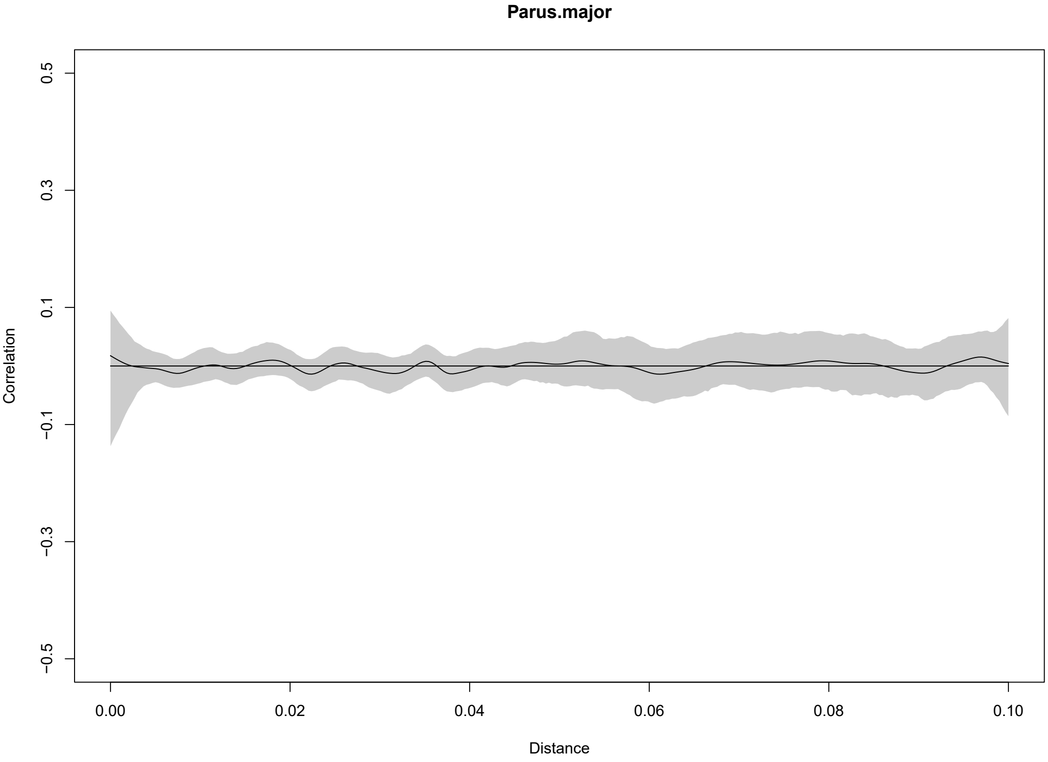


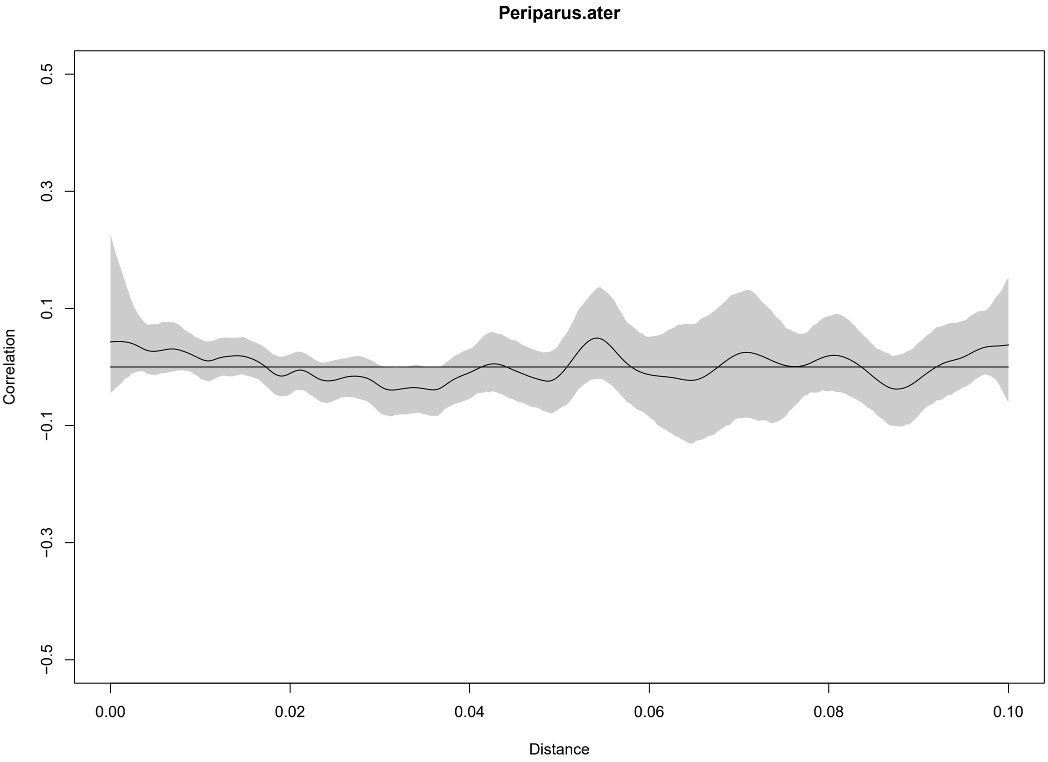

Lophophanes.cristatus


Lullula.arborea


Lullula.arborea corrected for autocorr.


Oriolus.oriolus
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Parus.major
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Periparus.ater
Correlation
0.5
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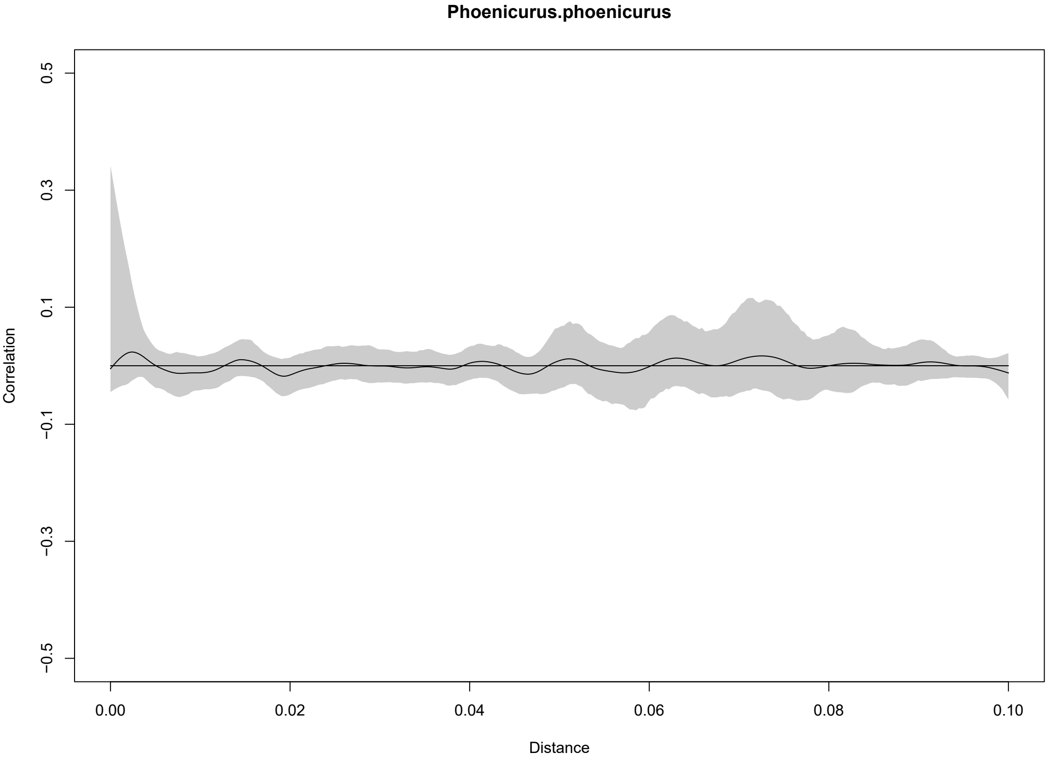
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Phoenicurus.phoenicurus
Correlation
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−0.3
−0.5
0.00
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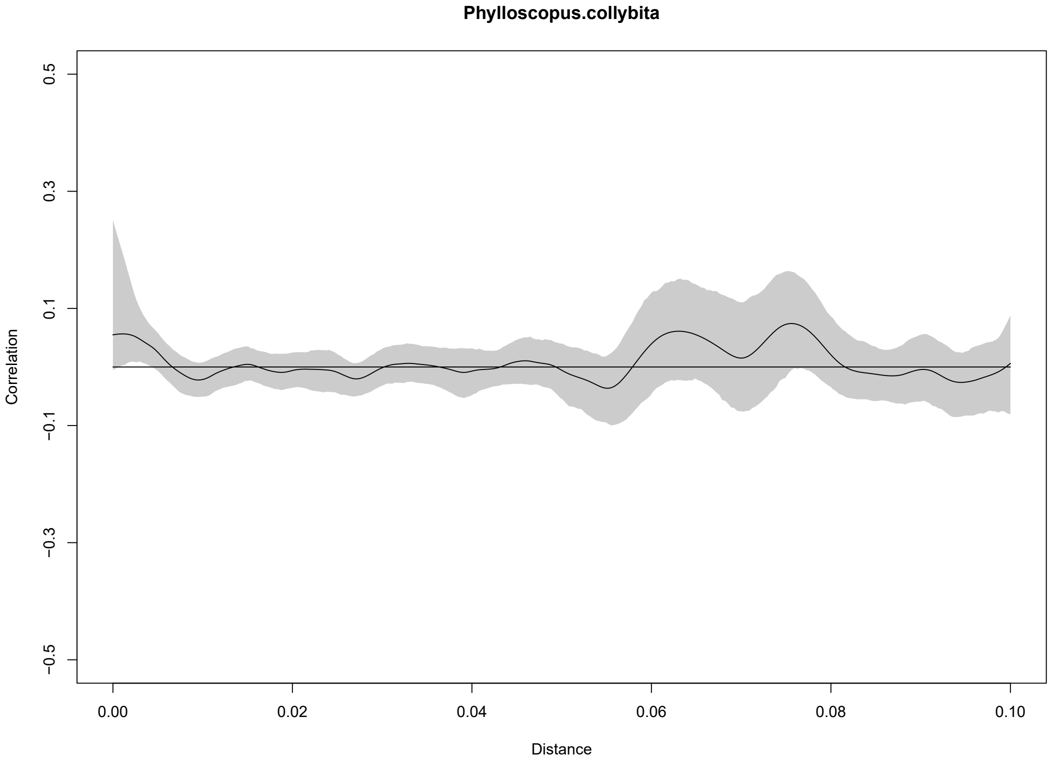
0.04
0.06
0.08
0.10
Distance


Phylloscopus.collybita
Correlation
0.5
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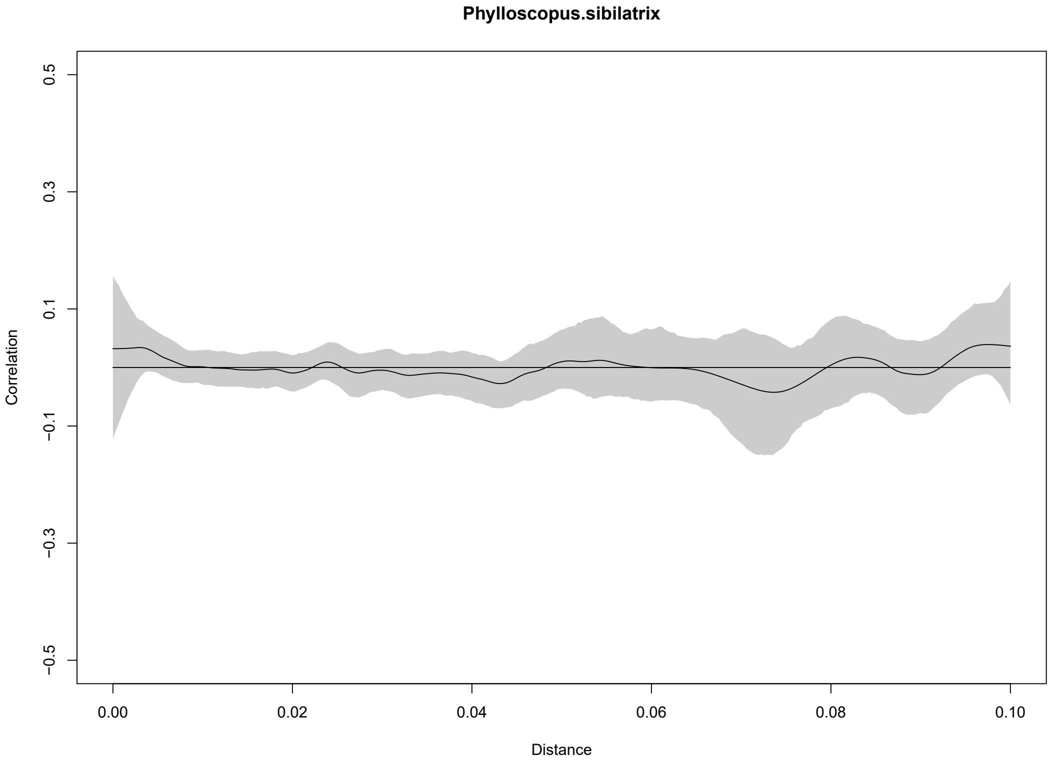
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Phylloscopus.sibilatrix
Correlation
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0.1
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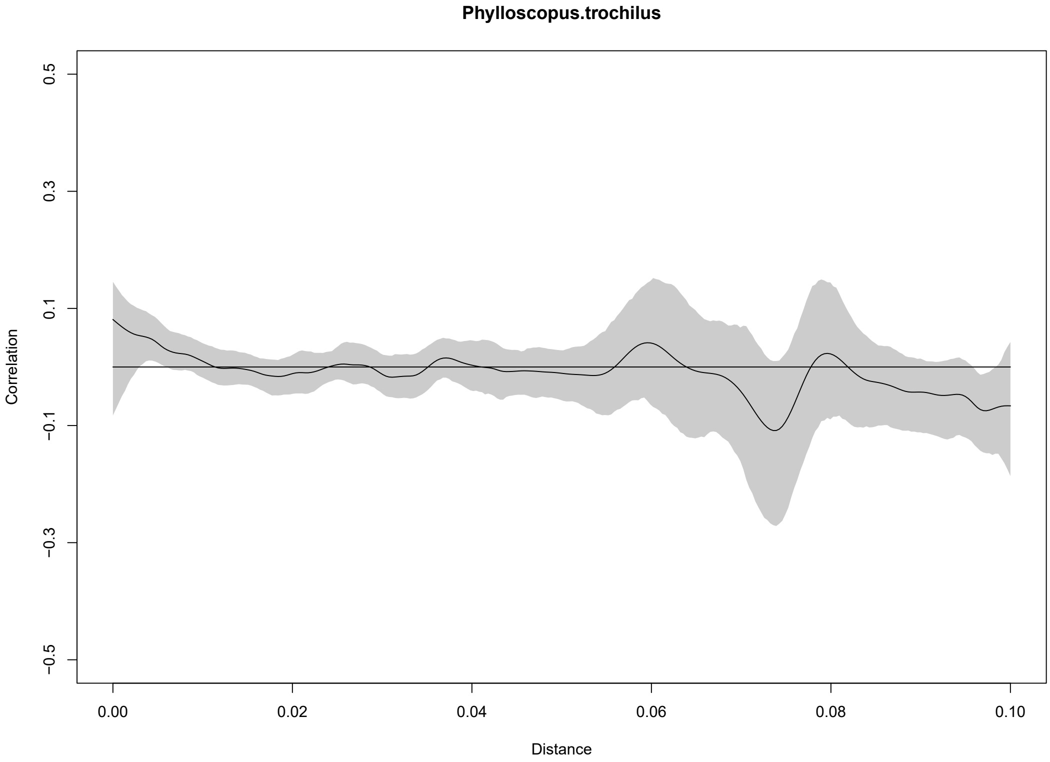
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Phylloscopus.trochilus
Correlation
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0.1
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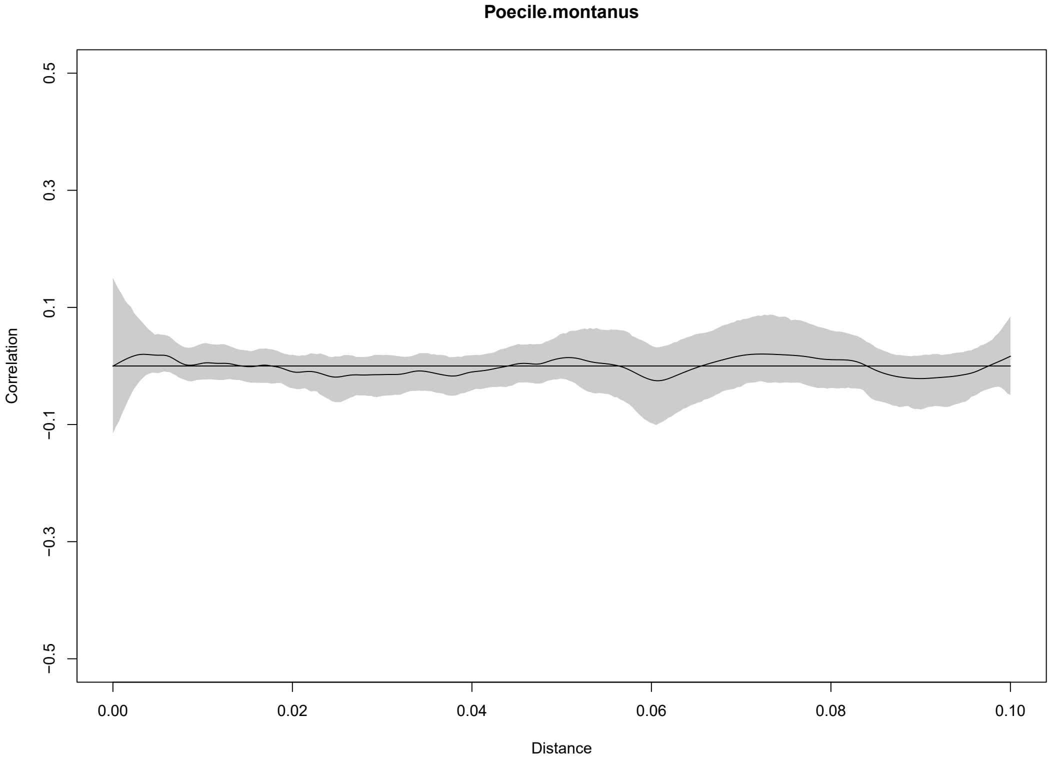
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Poecile.montanus
Correlation
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−0.3
−0.5
0.00
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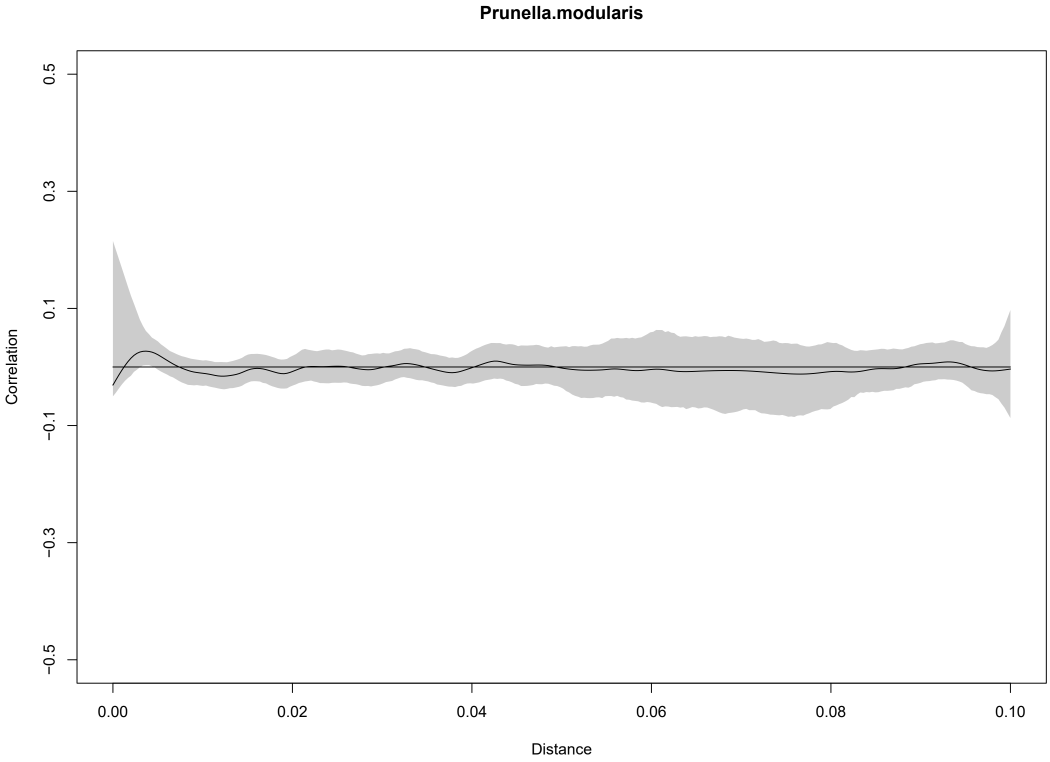
0.04
0.06
0.08
0.10
Distance


Prunella.modularis
Correlation
0.5
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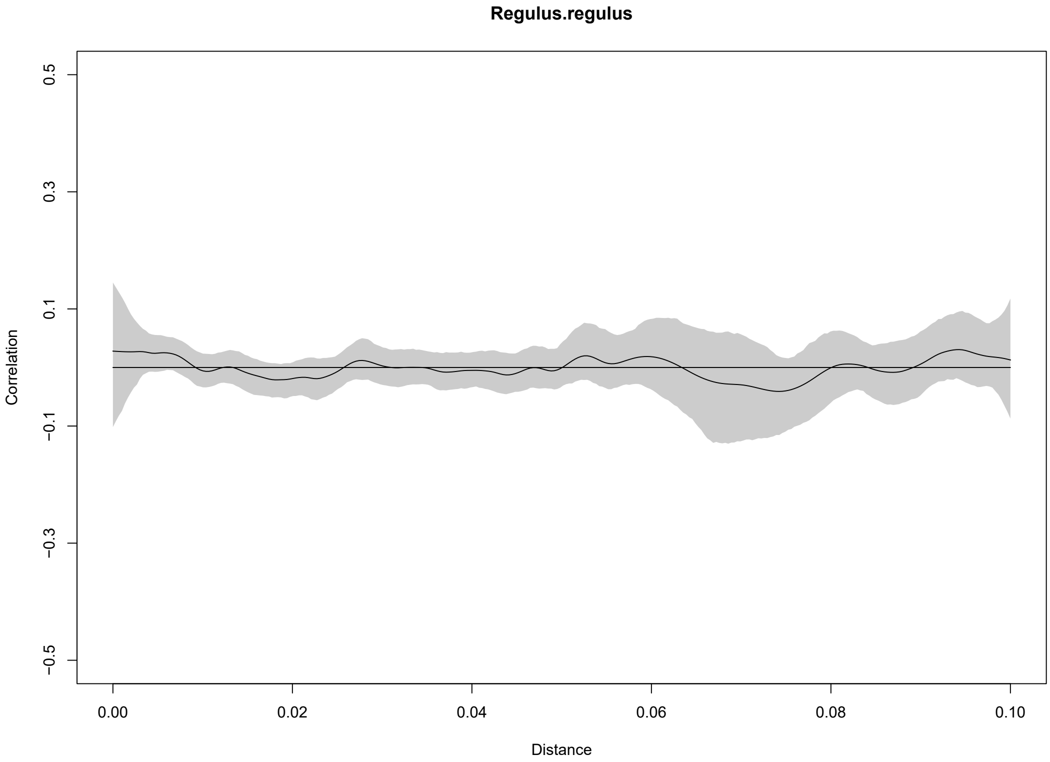
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Regulus.regulus
Correlation
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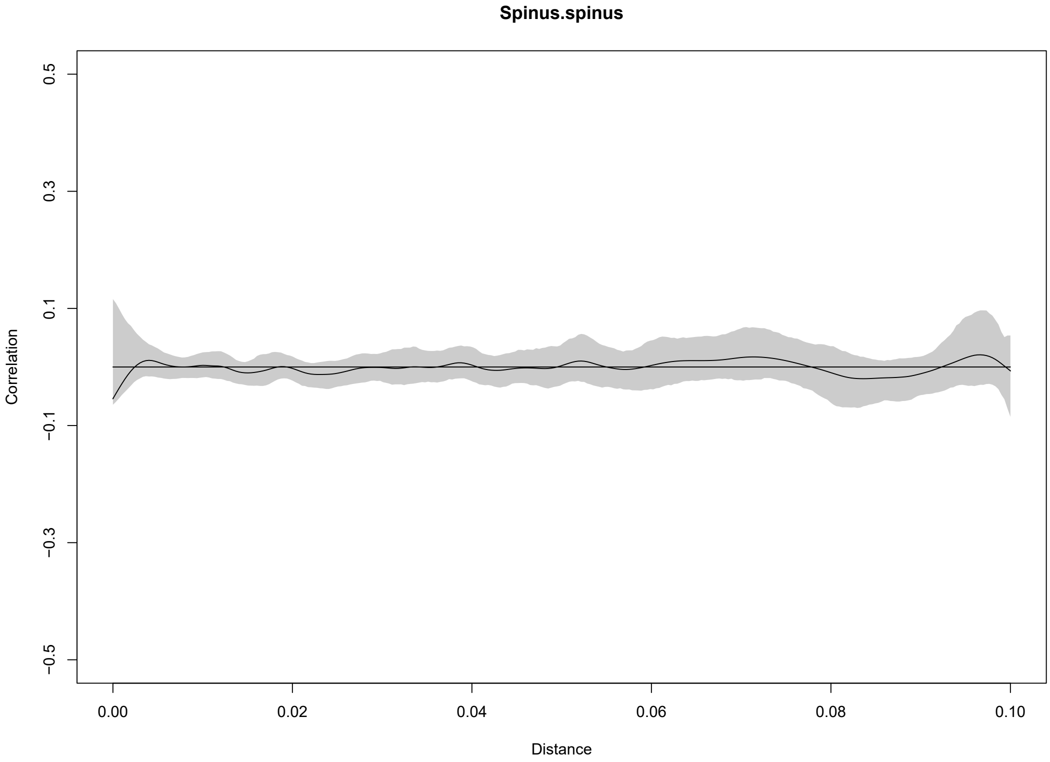
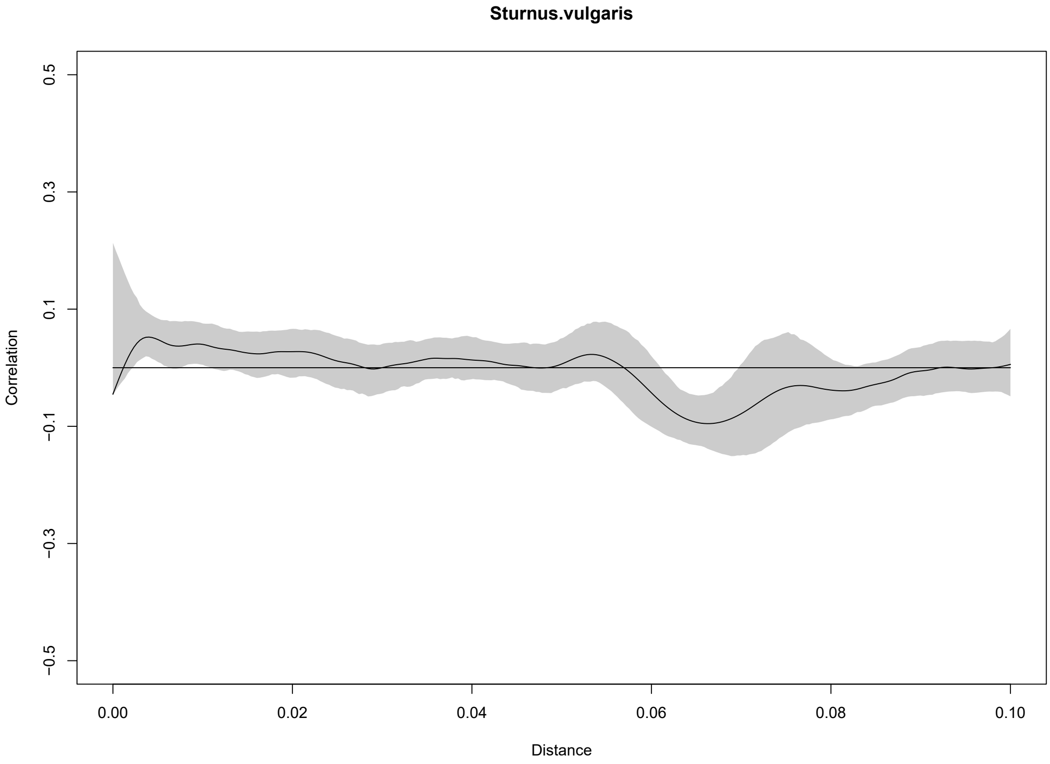
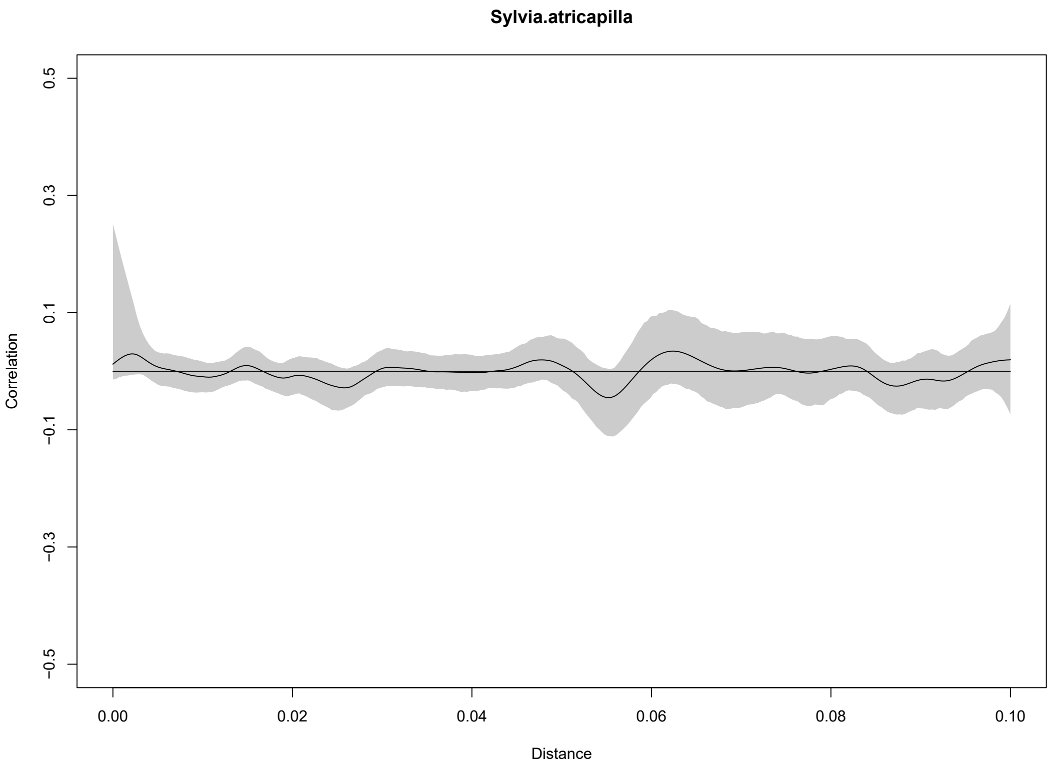
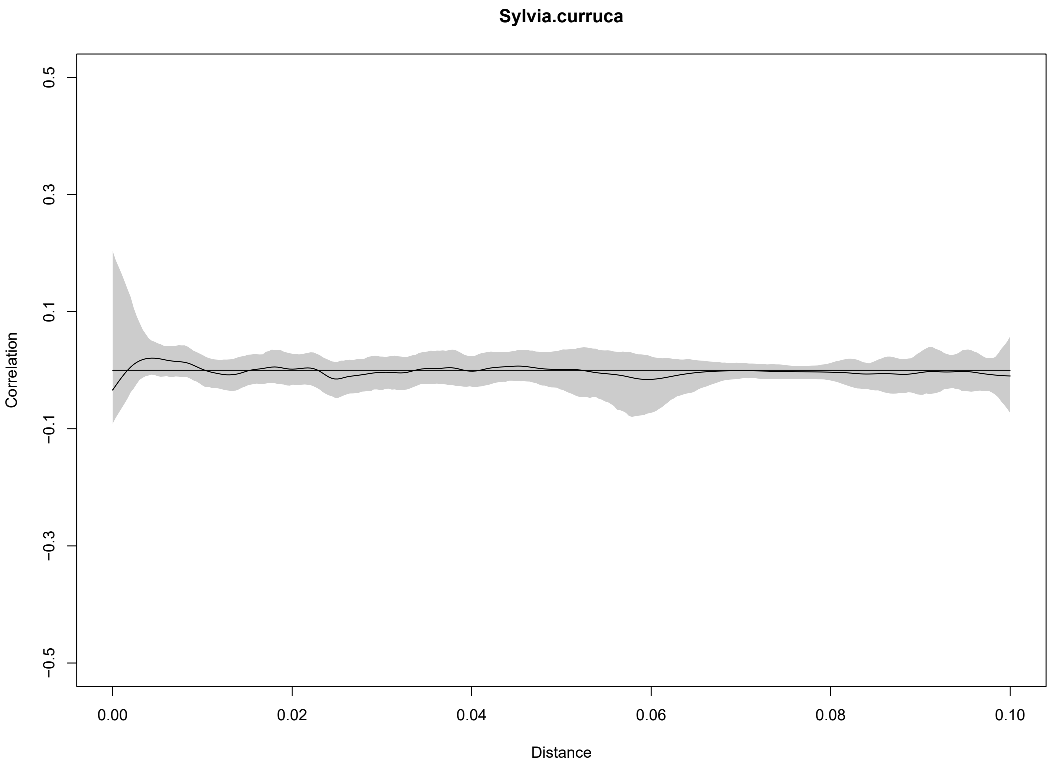
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Spinus.spinus


Sturnus.vulgaris


Sylvia.atricapilla
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Sylvia.curruca
Correlation
0.5
0.3
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−0.3
−0.5
0.00
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0.04
0.06
0.08
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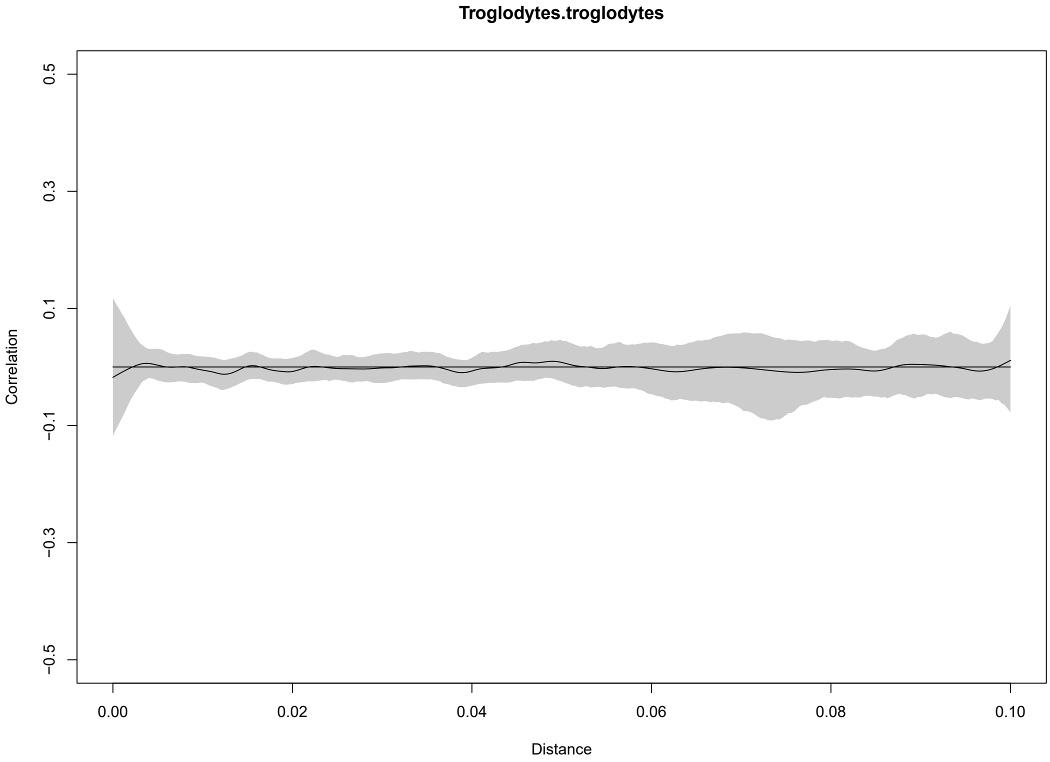
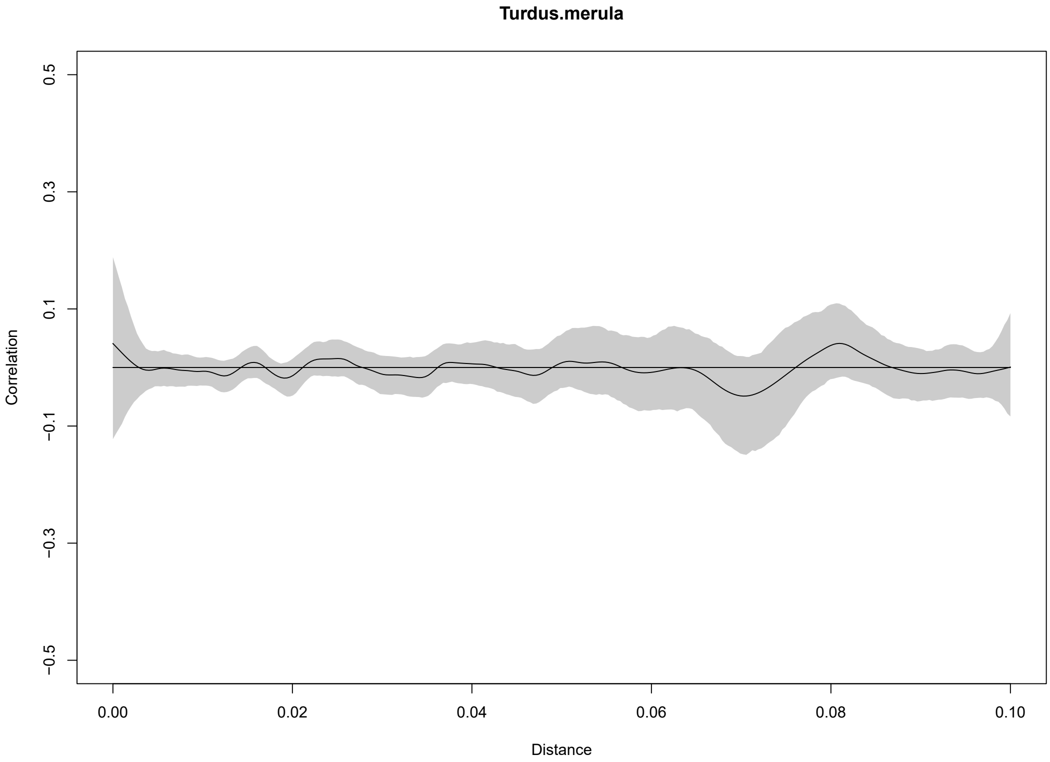
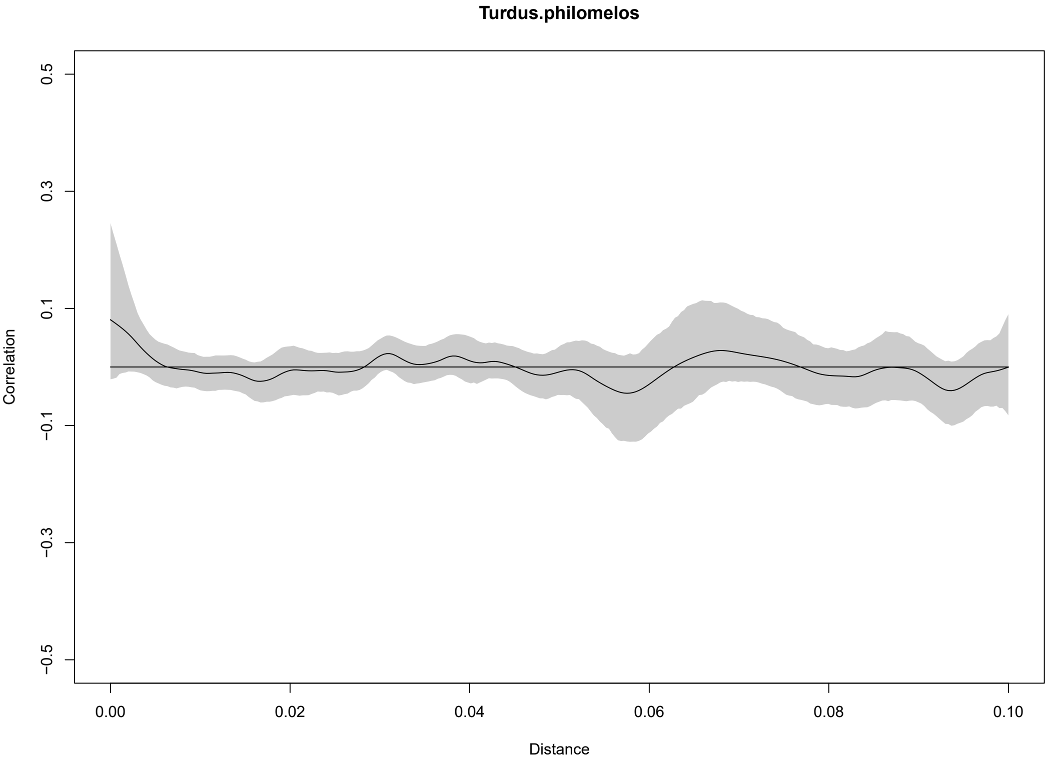
Distance


Troglodytes.troglodytes
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Turdus.merula
Correlation
0.5
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Turdus.philomelos
Correlation
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0.1
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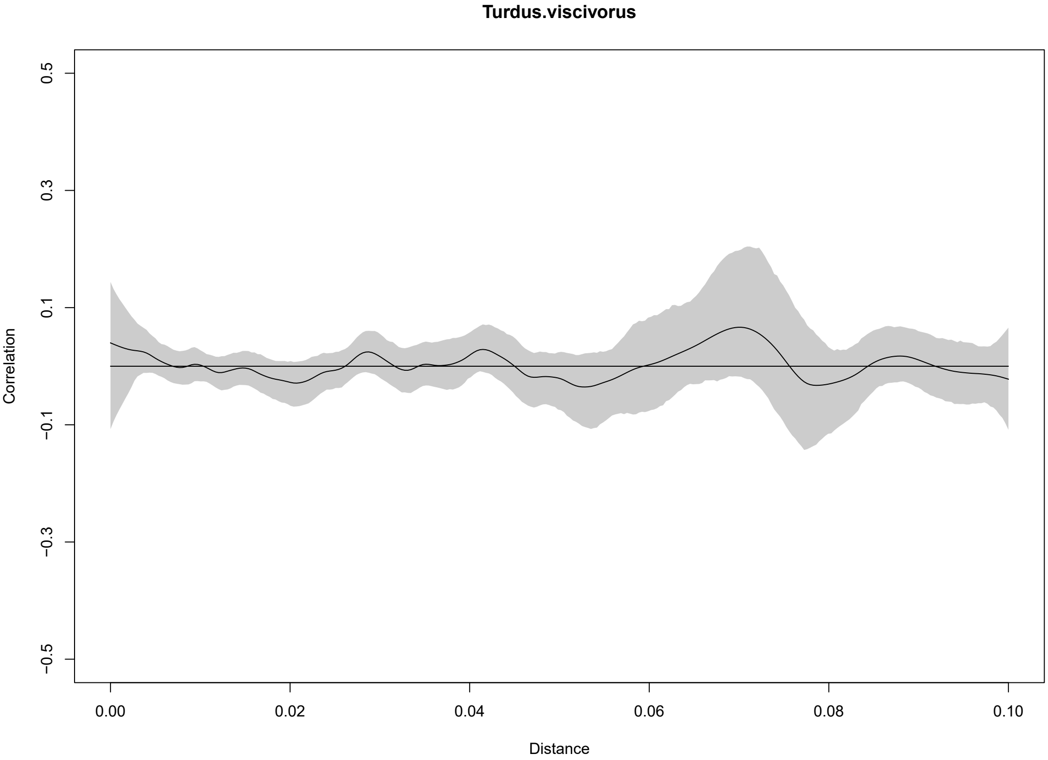
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance


Turdus.viscivorus
Correlation
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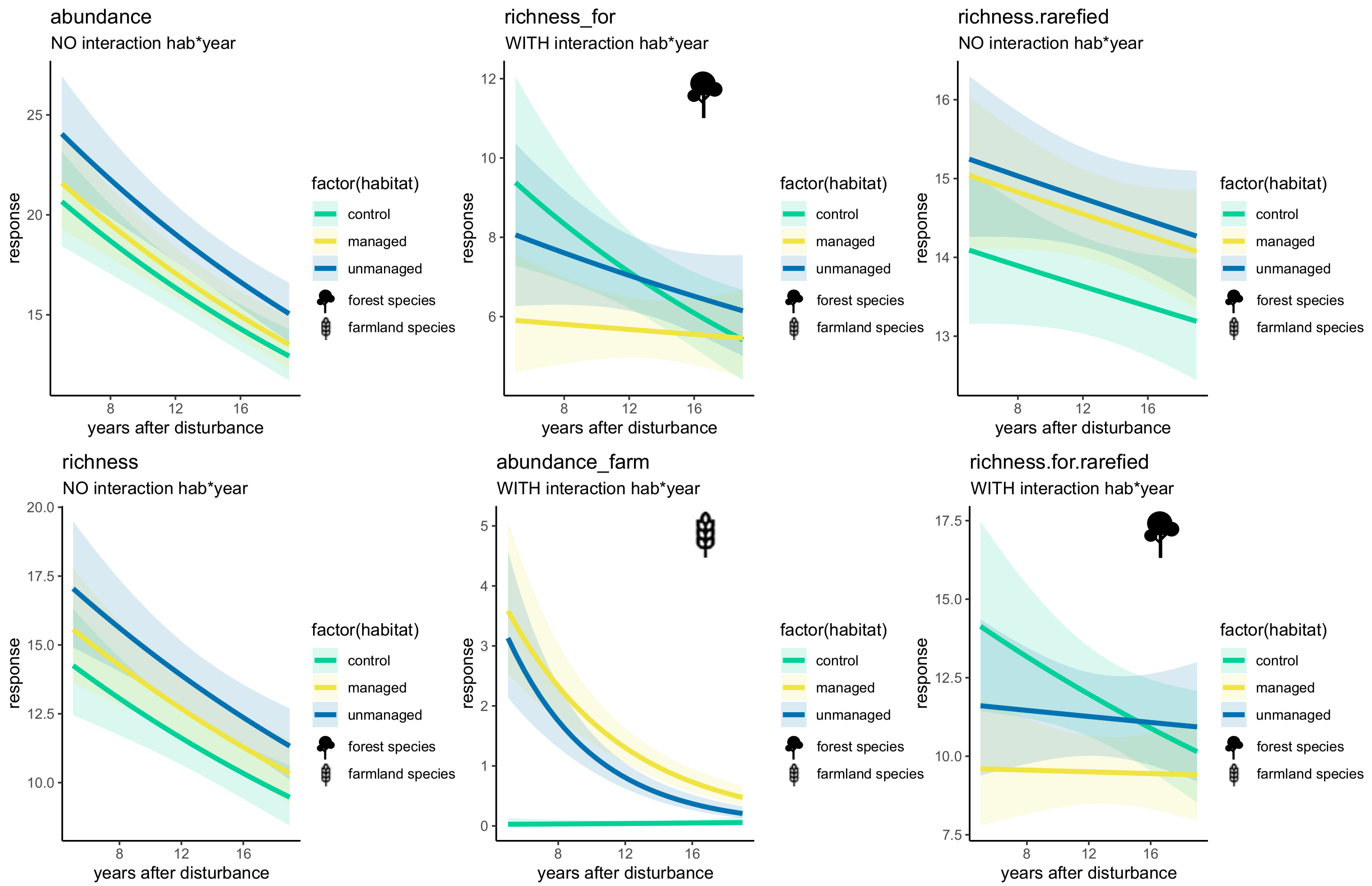
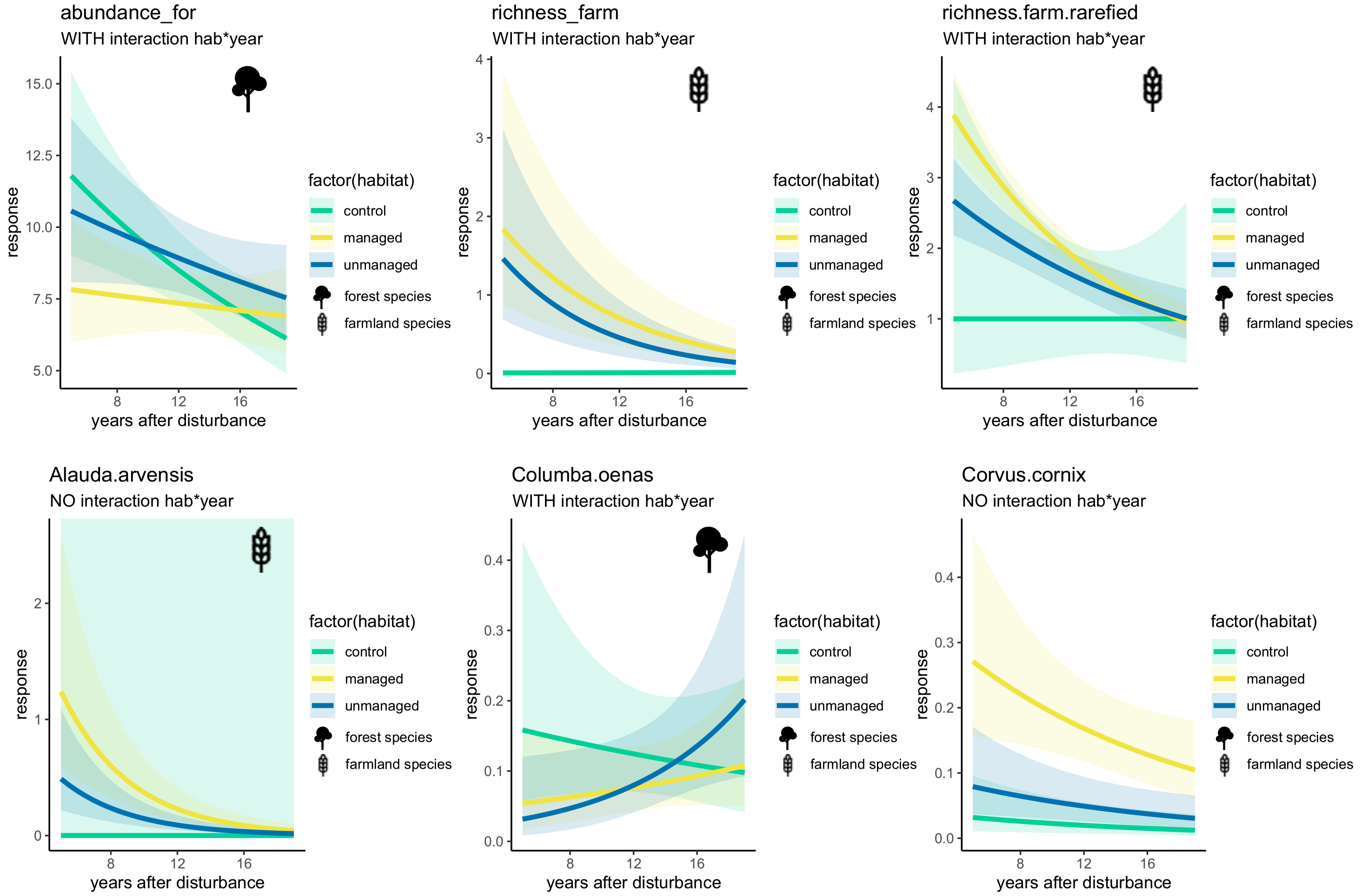
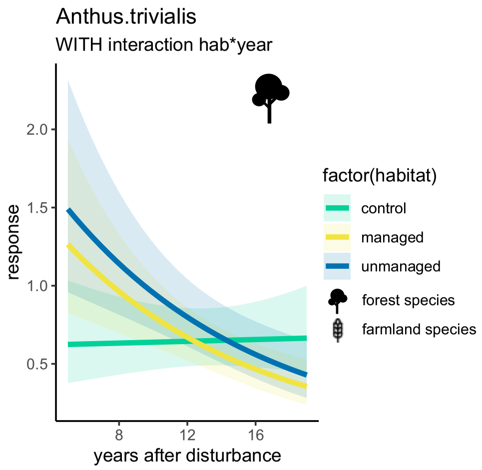
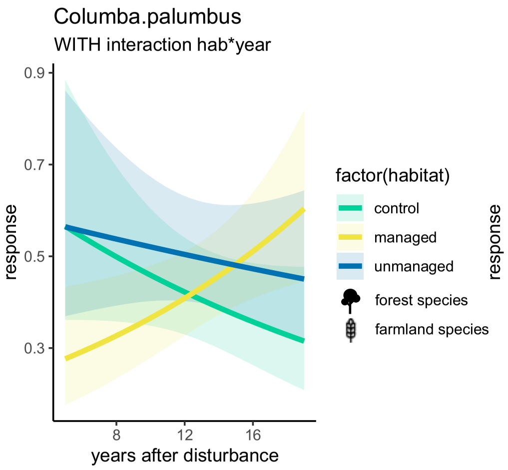
0.3
0.1
−0.1
−0.3
−0.5
0.00
0.02
0.04
0.06
0.08
0.10
Distance

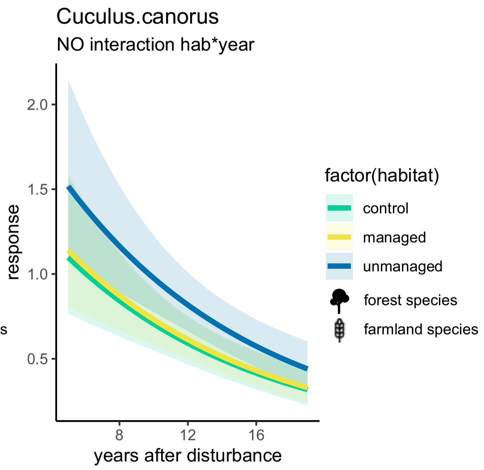
Figure S3 – GAMM marginal means plots (absolute response on y-axes)

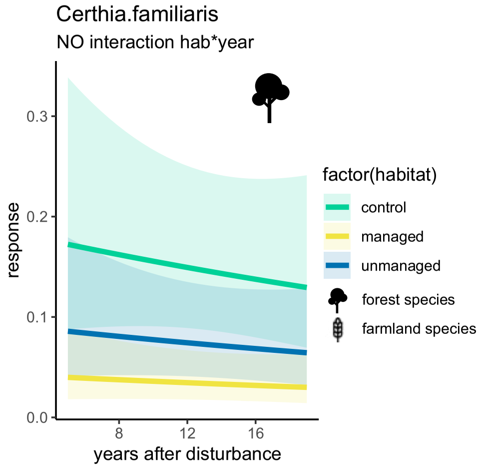

abundance
NO interaction hab*year
response
25
20
15
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness_for
WITH interaction hab*year
response
12
10
8
6
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness.rarefied
NO interaction hab*year
response
16
15
14
13
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness
NO interaction hab*year
response
20.0
17.5
15.0
12.5
10.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
abundance_farm
WITH interaction hab*year
response
5
4
3
2
1
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness.for.rarefied
WITH interaction hab*year
response
17.5
15.0
12.5
10.0
7.5
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

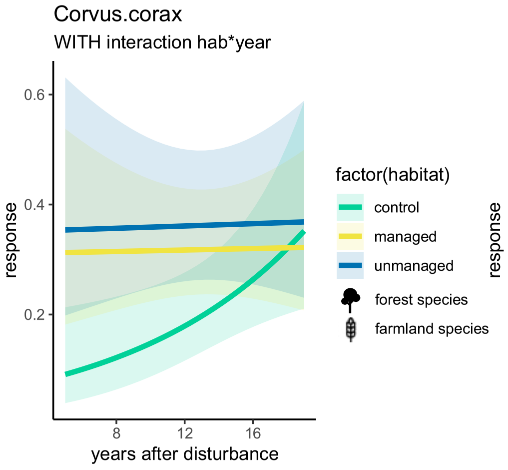

abundance_for
WITH interaction hab*year
response
15.0
12.5
10.0
7.5
5.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness_farm
WITH interaction hab*year
response
4
3
2
1
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness.farm.rarefied
WITH interaction hab*year
response
4
3
2
1
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
Alauda.arvensis
NO interaction hab*year
response
2
1
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
Columba.oenas
WITH interaction hab*year
response
0.4
0.3
0.2
0.1
0.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
Corvus.cornix
NO interaction hab*year
response
0.4
0.3
0.2
0.1
0.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

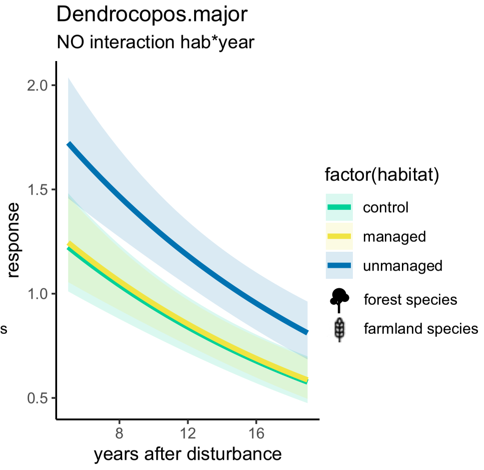

Anthus.trivialis
WITH interaction hab*year
response
2.0
1.5
1.0
0.5
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

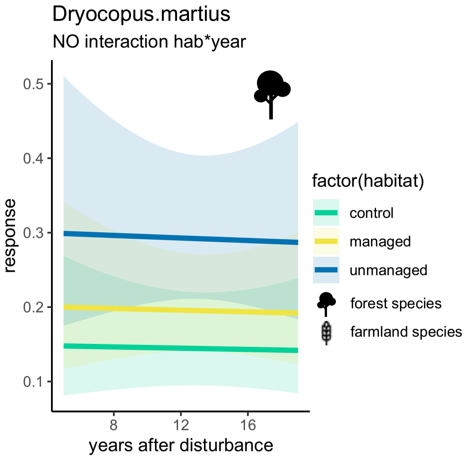

Columba.palumbus
WITH interaction hab*year
response
0.9
0.7
0.5
0.3
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

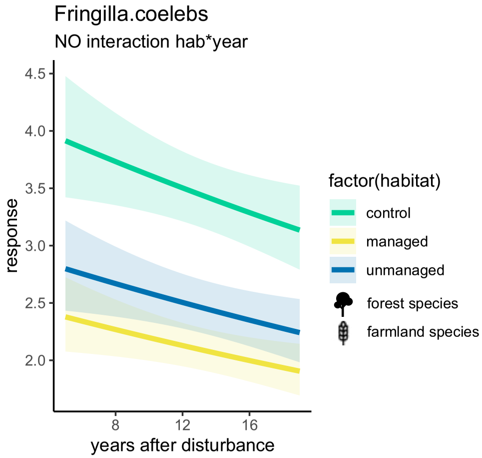

Cuculus.canorus
NO interaction hab*year
response
2.0
1.5
1.0
0.5
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

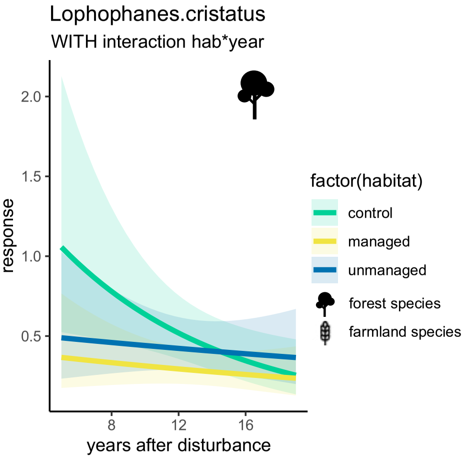

Certhia.familiaris
NO interaction hab*year
response
0.3
0.2
0.1
0.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

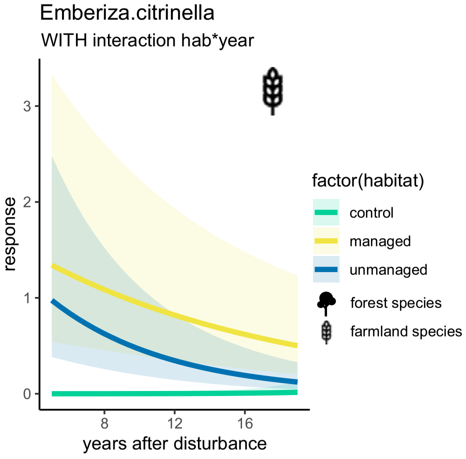

Corvus.corax
WITH interaction hab*year
response
0.6
0.4
0.2
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

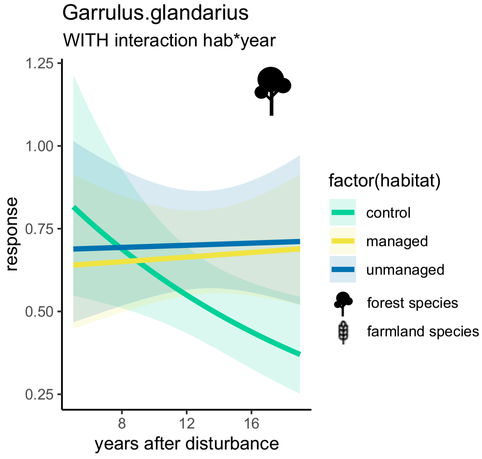

Dendrocopos.major
NO interaction hab*year
response
2.0
1.5
1.0
0.5
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

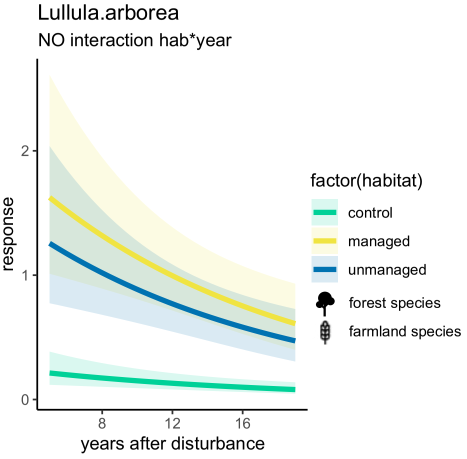

Dryocopus.martius
NO interaction hab*year
response
0.5
0.4
0.3
0.2
0.1
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

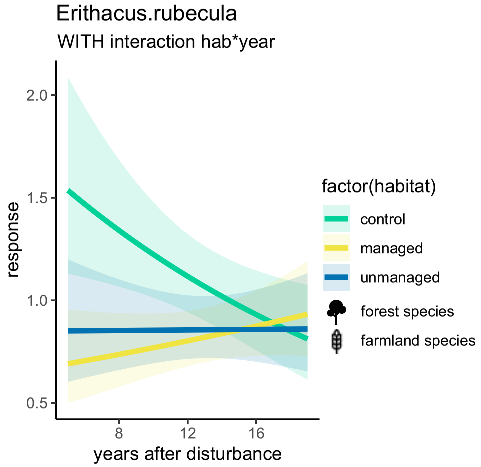

Fringilla.coelebs
NO interaction hab*year
response
4.5
4.0
3.5
3.0
2.5
2.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species


Lophophanes.cristatus
WITH interaction hab*year
response
2.0
1.5
1.0
0.5
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species


Emberiza.citrinella
WITH interaction hab*year
response
3
2
1
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

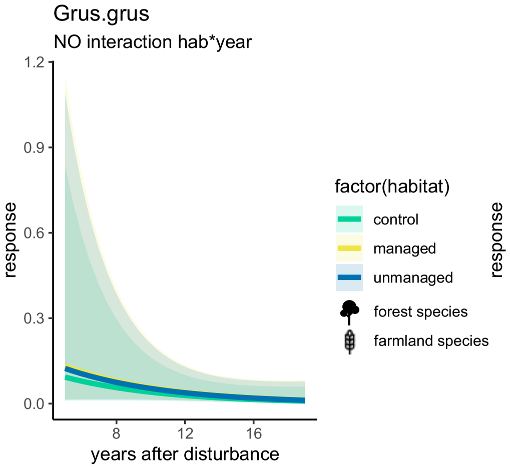

Garrulus.glandarius
WITH interaction hab*year
response
1.25
1.00
0.75
0.50
0.25
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species


Lullula.arborea
NO interaction hab*year
response
2
1
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species



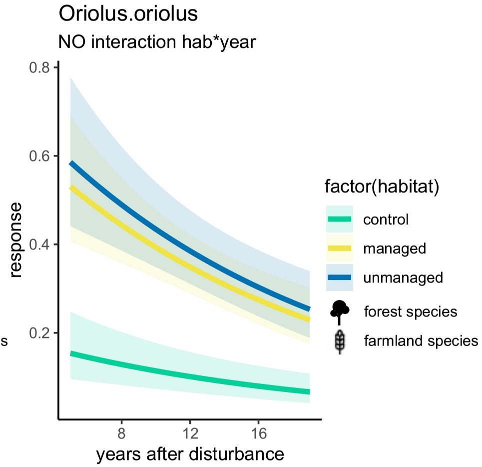
Erithacus.rubecula

WITH interaction hab*year



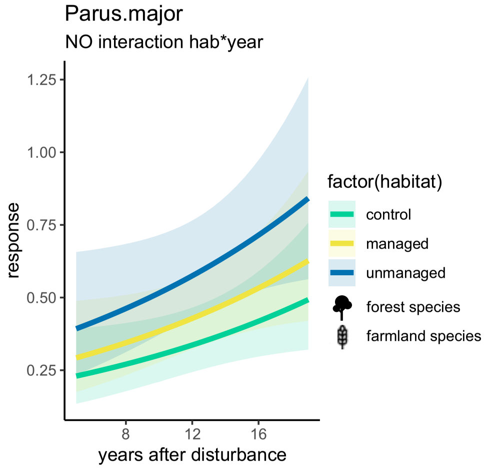
Grus.grus

NO interaction hab*year



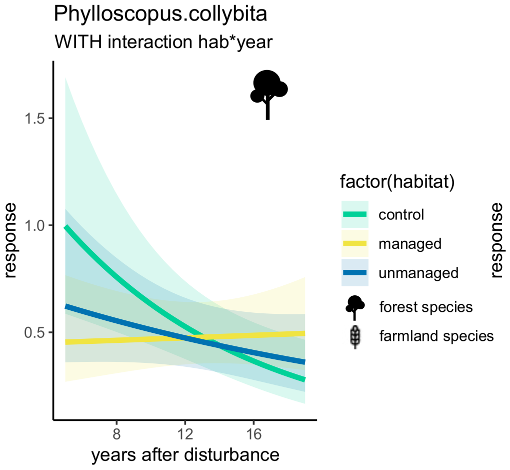
Oriolus.oriolus

NO interaction hab*year



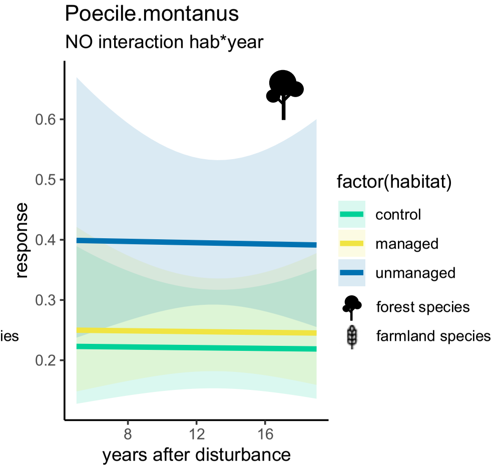
Parus.major

NO interaction hab*year



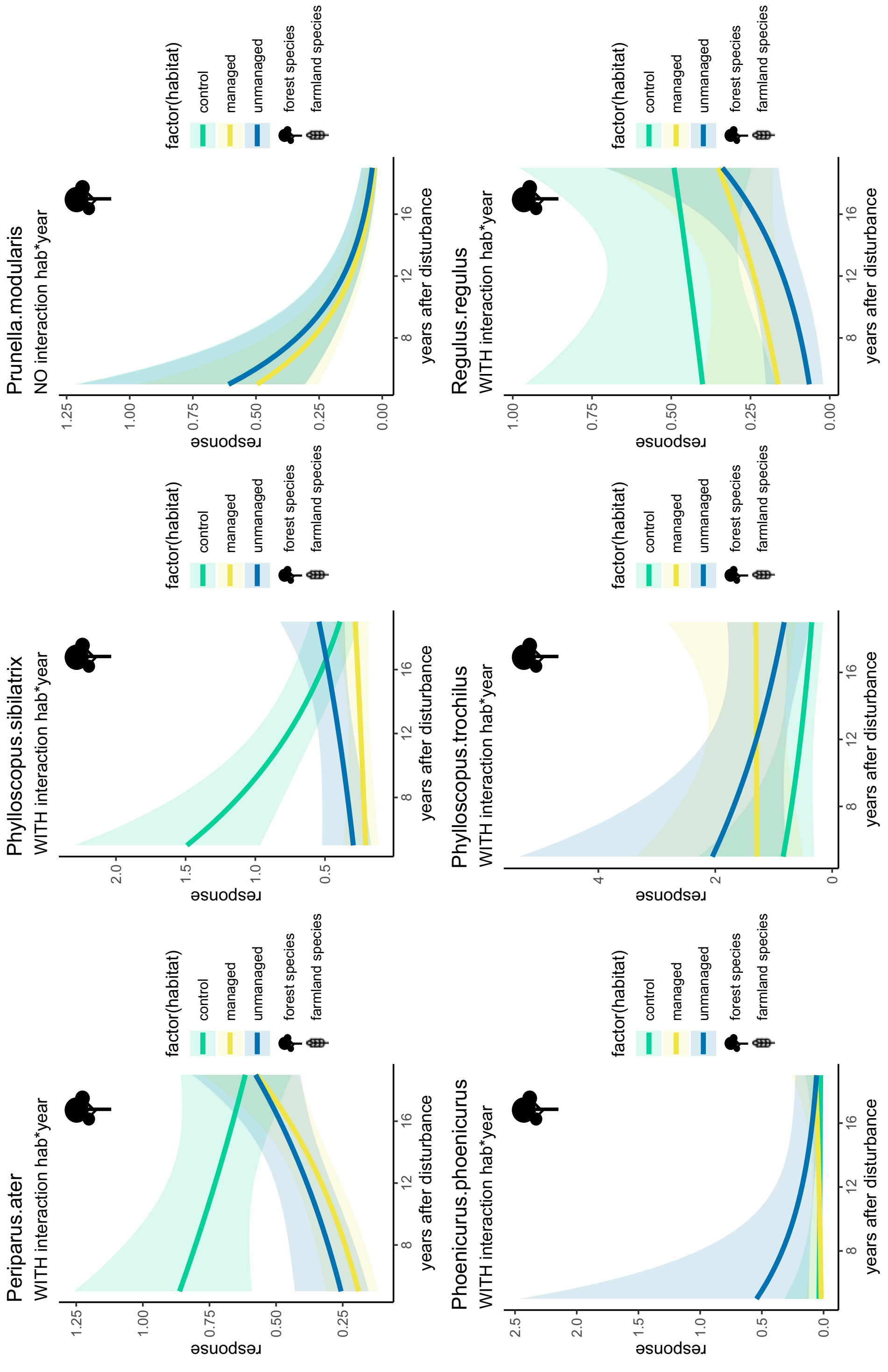
Phylloscopus.collybita

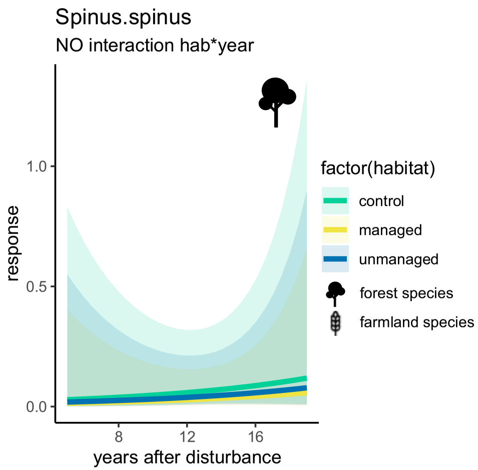
WITH interaction hab*year

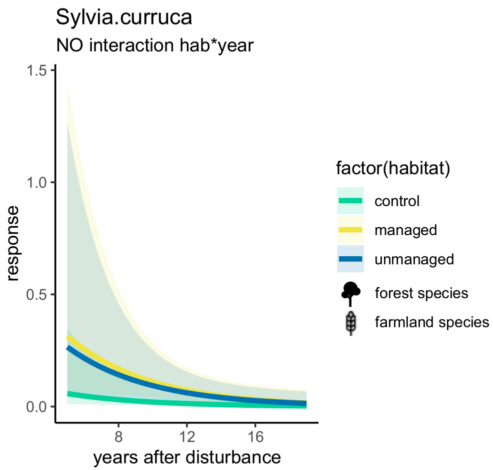


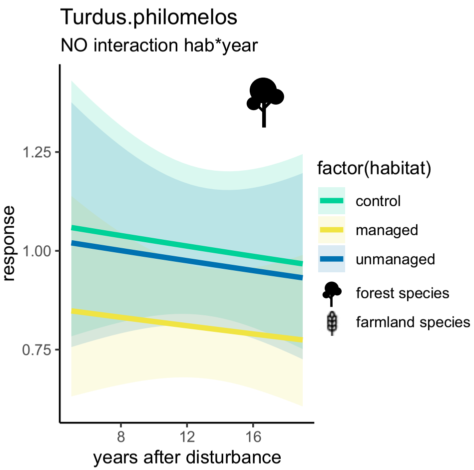
Poecile.montanus

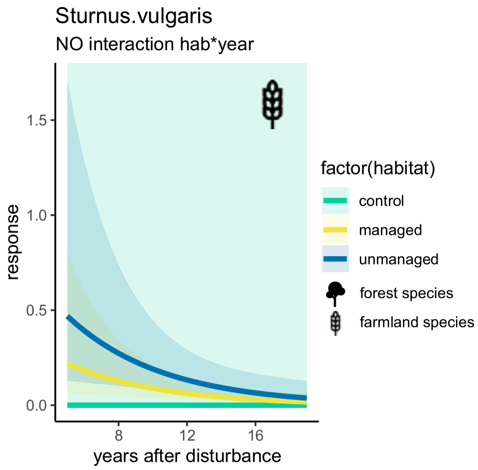
NO interaction hab*year

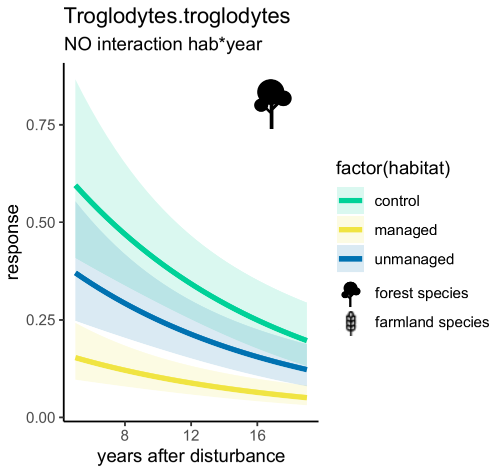

Periparus.ater
WITH interaction hab*year
response
1.25
1.00
0.75
0.50
0.25
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
Phylloscopus.sibilatrix
WITH interaction hab*year
response
2.0
1.5
1.0
0.5
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
Prunella.modularis
NO interaction hab*year
response
1.25
1.00
0.75
0.50
0.25
0.00
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
Phoenicurus.phoenicurus
WITH interaction hab*year
response
2.5
2.0
1.5
1.0
0.5
0.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
Phylloscopus.trochilus
WITH interaction hab*year
response
4
2
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
Regulus.regulus
WITH interaction hab*year
response
1.00
0.75
0.50
0.25
0.00
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

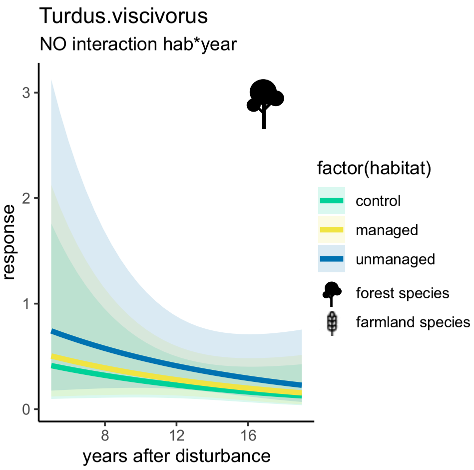

Spinus.spinus
NO interaction hab*year
response
1.0
0.5
0.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

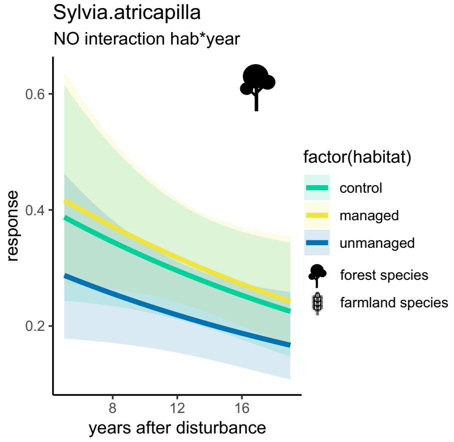

Sylvia.curruca
NO interaction hab*year
response
1.5
1.0
0.5
0.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species


Turdus.philomelos
NO interaction hab*year
response
1.25
1.00
0.75
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species


Sturnus.vulgaris
NO interaction hab*year
response
1.5
1.0
0.5
0.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species


Troglodytes.troglodytes
NO interaction hab*year
response
0.75
0.50
0.25
0.00
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species


Turdus.viscivorus
NO interaction hab*year
response
3
2
1
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species


Sylvia.atricapilla
NO interaction hab*year
response
0.6
0.4
0.2
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

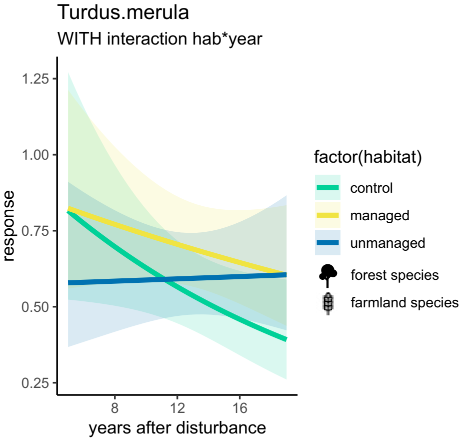
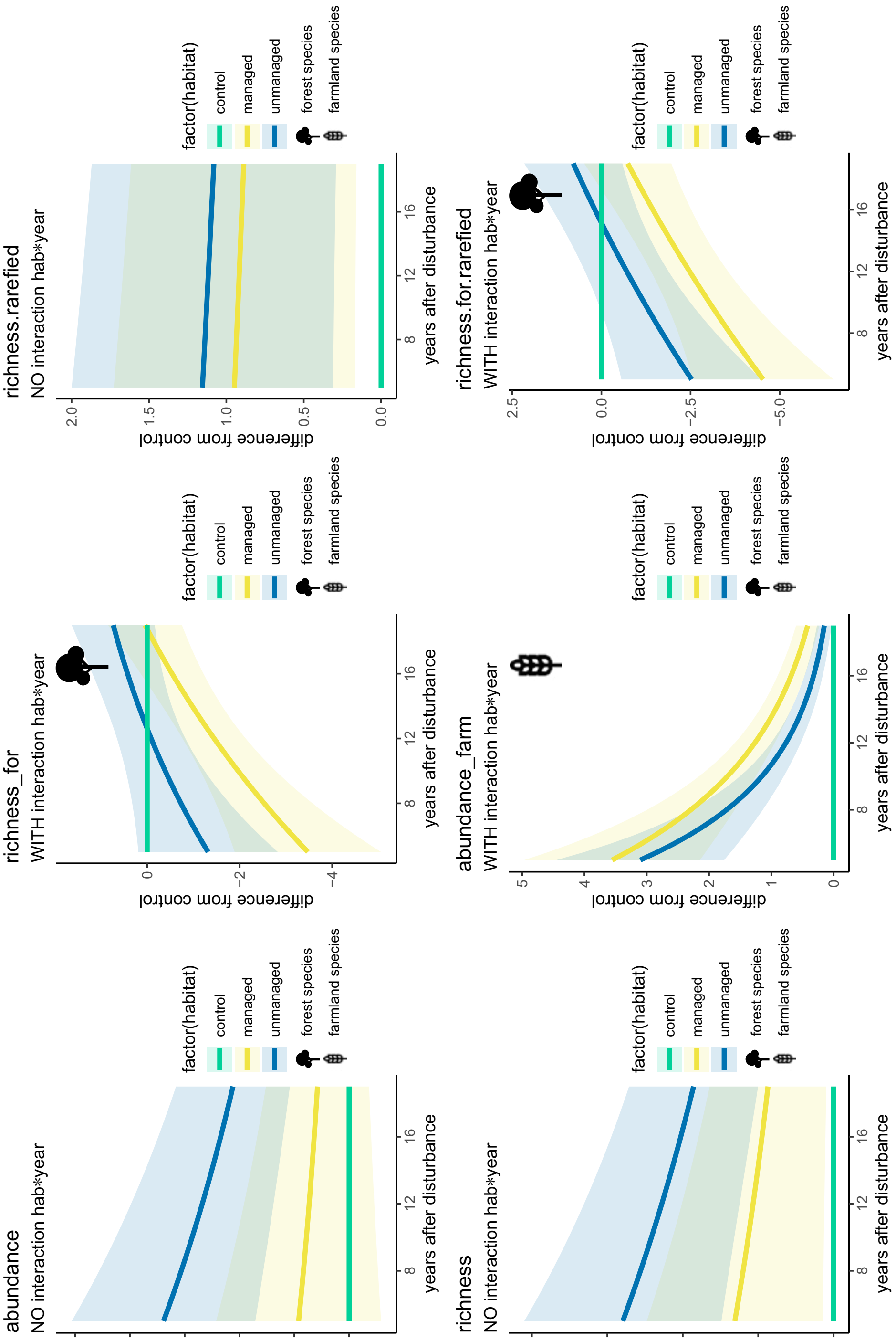
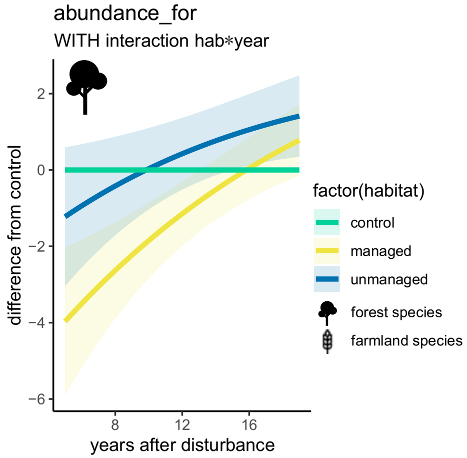
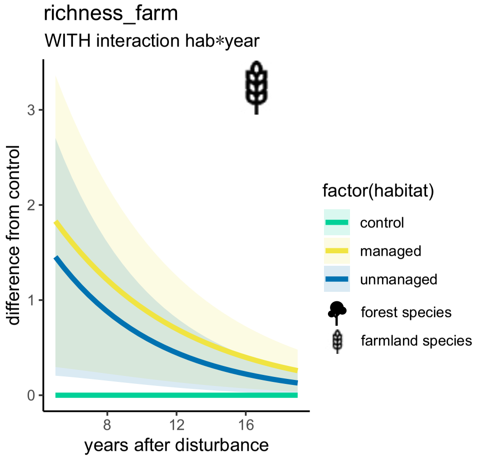

Turdus.merula
WITH interaction hab*year
response
1.25
1.00
0.75
0.50
0.25
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

Figure S4 – GAMM marginal means plots (contrasts on y-axes)

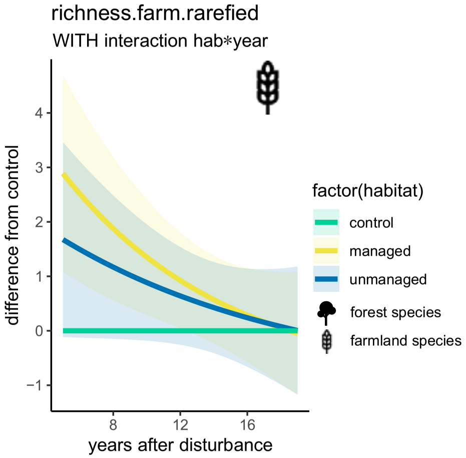

abundance
NO interaction hab*year
difference from control
5
4
3
2
1
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness_for
WITH interaction hab*year
difference from control
0
−2
−4
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness.rarefied
NO interaction hab*year
difference from control
2.0
1.5
1.0
0.5
0.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness
NO interaction hab*year
difference from control
4
3
2
1
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
abundance_farm
WITH interaction hab*year
difference from control
5
4
3
2
1
0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species
richness.for.rarefied
WITH interaction hab*year
difference from control
2.5
0.0
−2.5
−5.0
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species


abundance_for

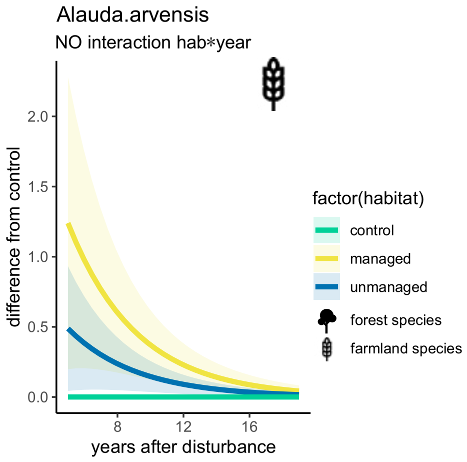
WITH interaction hab*year


richness_farm

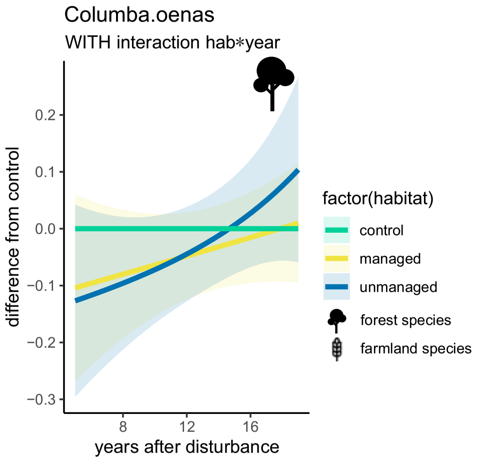
WITH interaction hab*year


richness.farm.rarefied

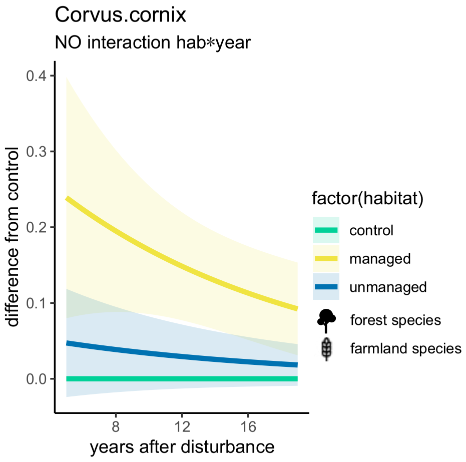
WITH interaction hab*year


Alauda.arvensis

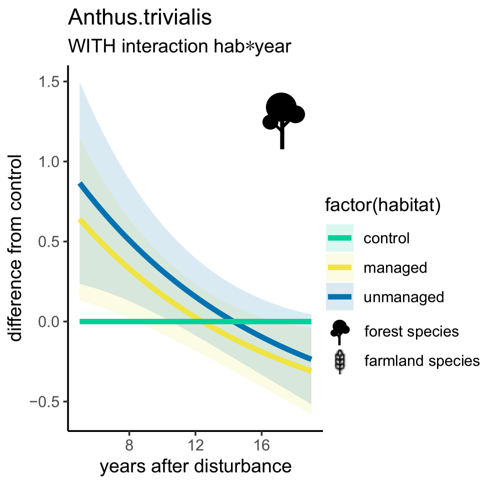
NO interaction hab*year

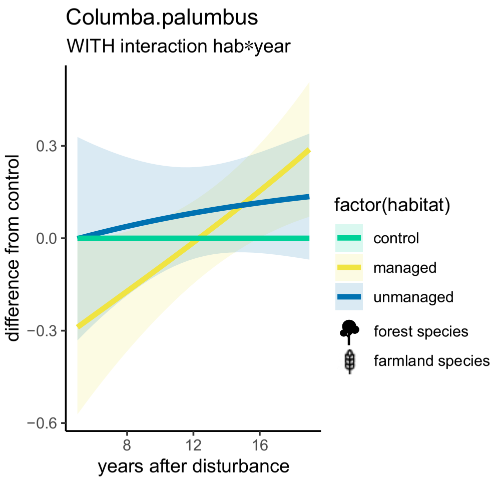

Columba.oenas

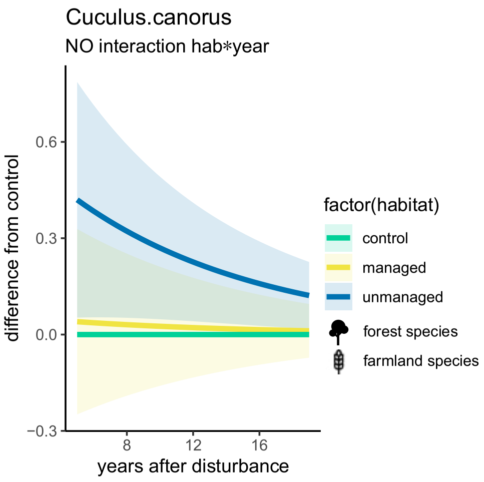
WITH interaction hab*year

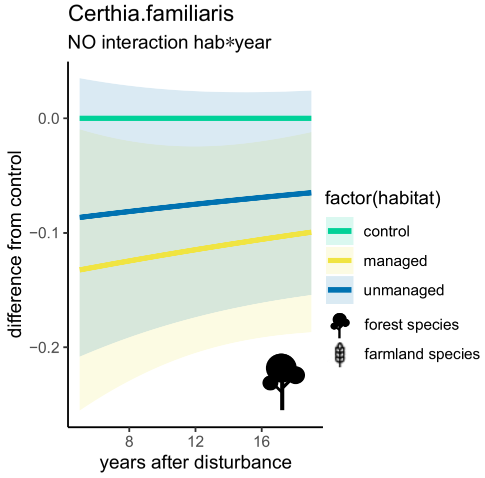

Corvus.cornix

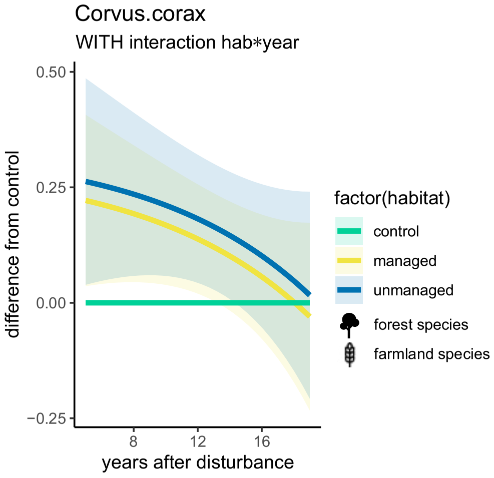
NO interaction hab*year

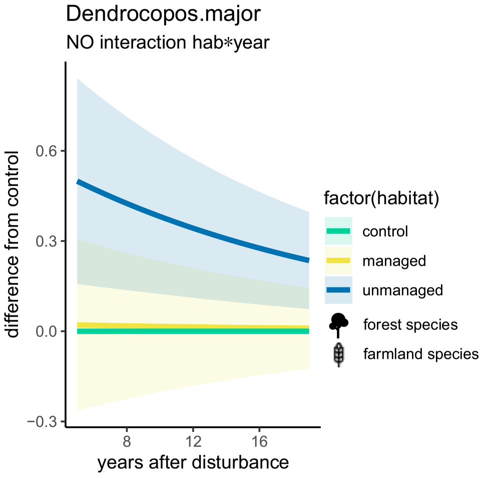

Anthus.trivialis
WITH interaction hab*year
difference from control
1.5
1.0
0.5
0.0
−0.5
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

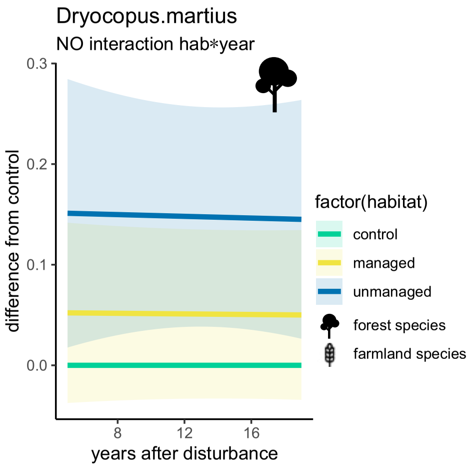

Columba.palumbus
WITH interaction hab*year
difference from control
0.3
0.0
−0.3
−0.6
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

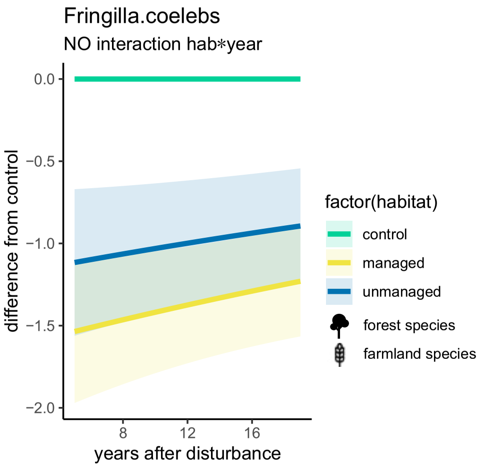

Cuculus.canorus
NO interaction hab*year
difference from control
0.6
0.3
0.0
−0.3
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

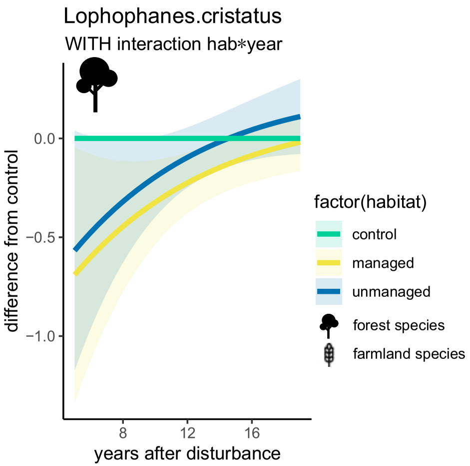

Certhia.familiaris
NO interaction hab*year
difference from control
0.0
−0.1
−0.2
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

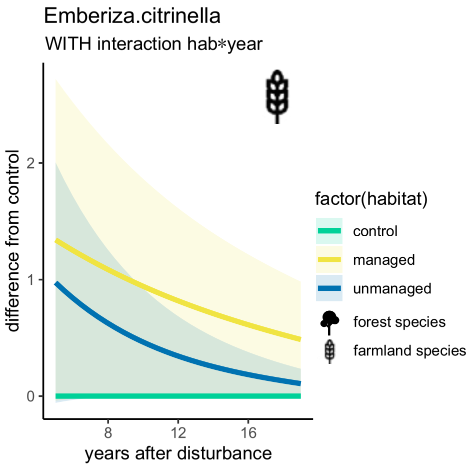

Corvus.corax
WITH interaction hab*year
difference from control
0.50
0.25
0.00
−0.25
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

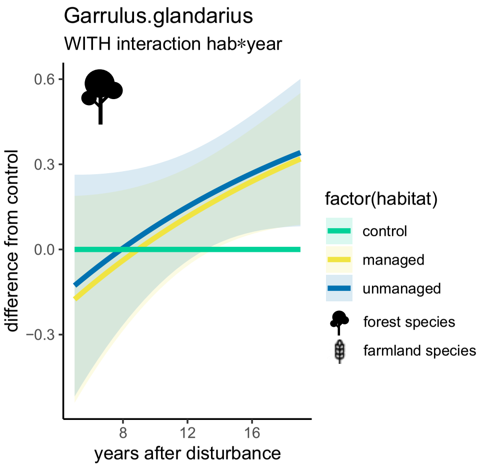

Dendrocopos.major
NO interaction hab*year
difference from control
0.6
0.3
0.0
−0.3
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

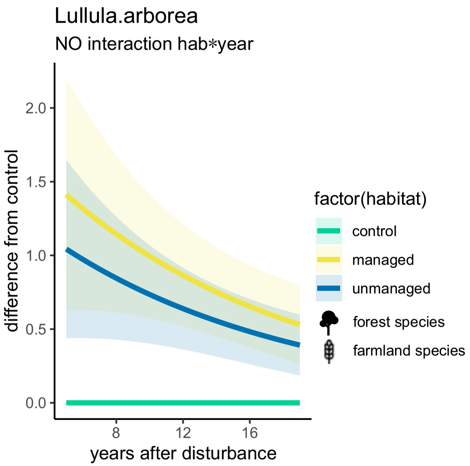

Dryocopus.martius
NO interaction hab*year

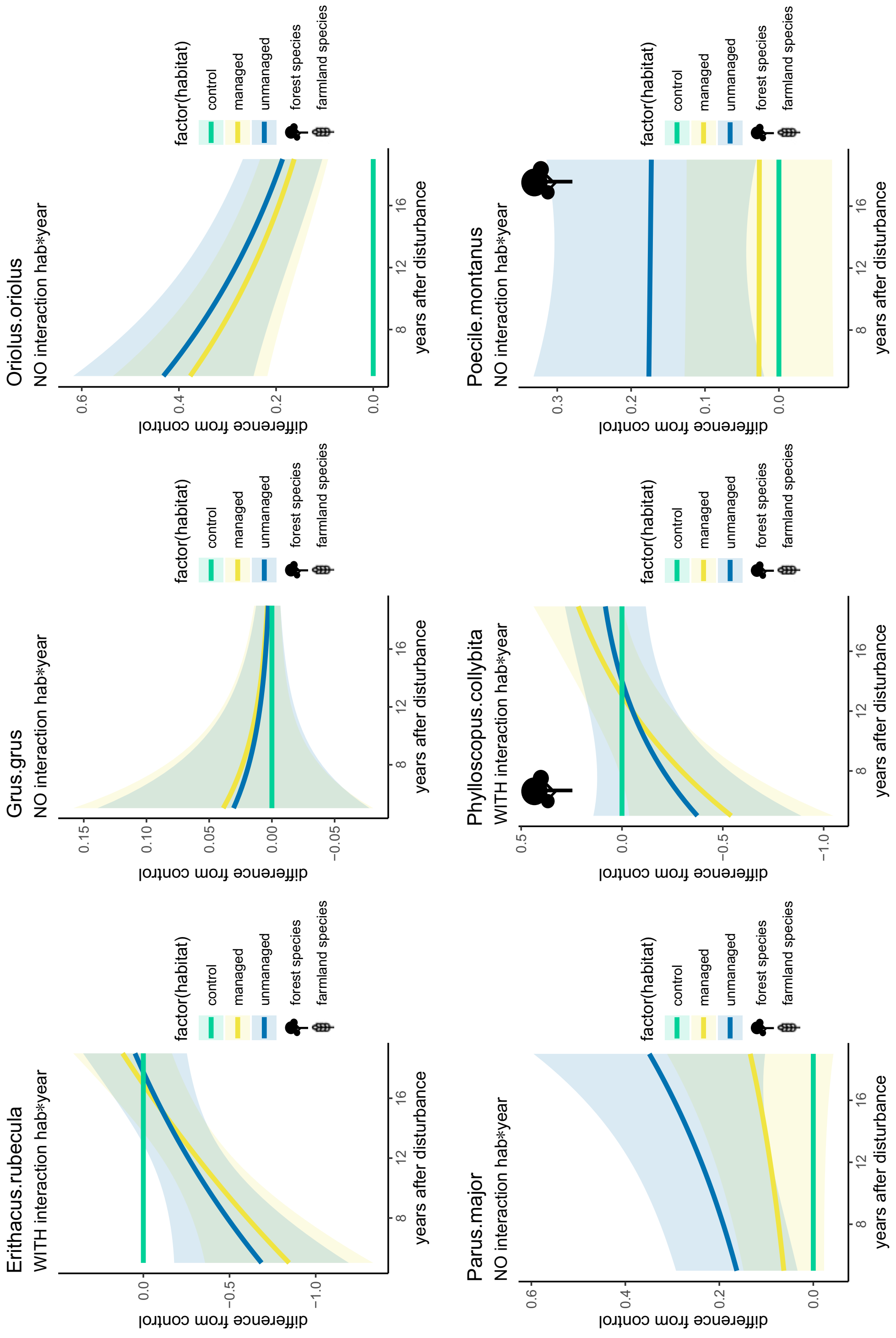

Fringilla.coelebs
NO interaction hab*year


Lophophanes.cristatus
WITH interaction hab*year


Emberiza.citrinella
WITH interaction hab*year

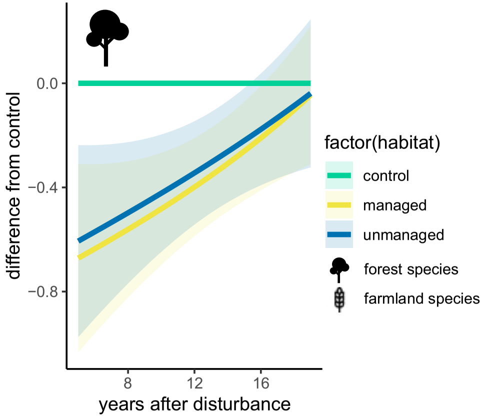

Garrulus.glandarius
WITH interaction hab*year


Lullula.arborea
NO interaction hab*year


Erithacus.rubecula
WITH interaction hab*year
Grus.grus
NO interaction hab*year
Oriolus.oriolus
NO interaction hab*year
Parus.major
NO interaction hab*year
Phylloscopus.collybita
WITH interaction hab*year
Poecile.montanus
NO interaction hab*year
difference from control
years after disturbance
8
12
16
factor(habitat)
control
managed
unmanaged
forest species
farmland species
0.0
−0.5
−1.0
0.15
0.10
0.05
0.00
−0.05
0.6
0.4
0.2
0.5
0.3
0.1

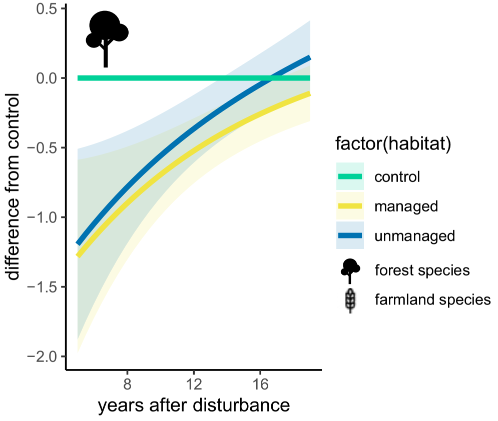
Periparus.ater

WITH interaction hab*year



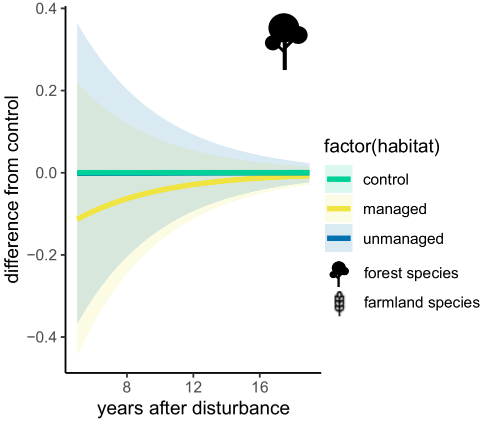
Phylloscopus.sibilatrix

WITH interaction hab*year



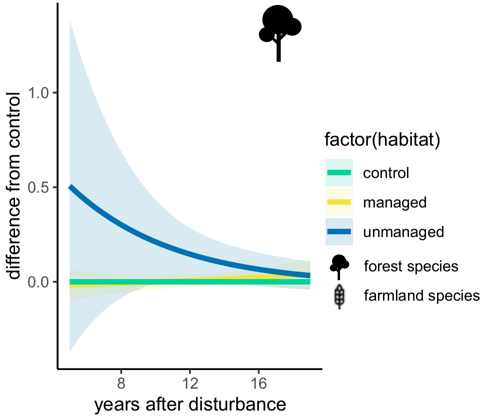
Prunella.modularis

NO interaction hab*year



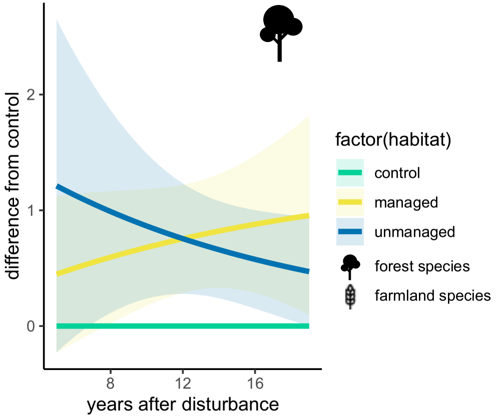
Phoenicurus.phoenicurus

WITH interaction hab*year



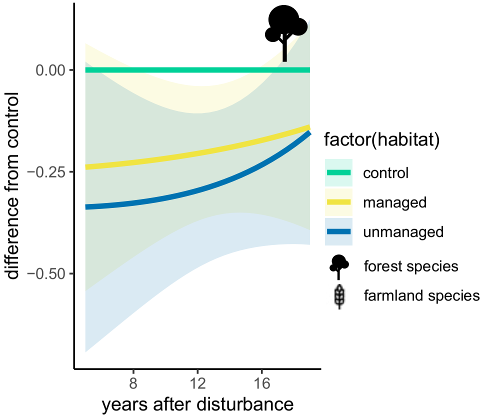
Phylloscopus.trochilus

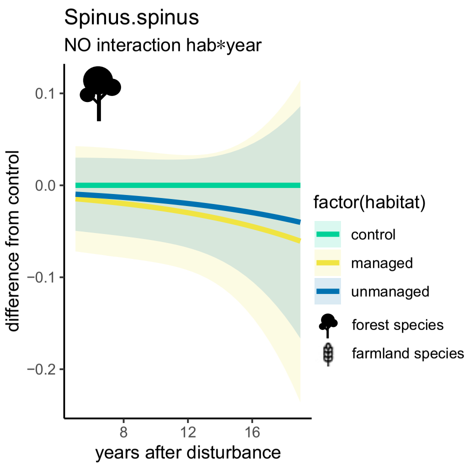
WITH interaction hab*year



Regulus.regulus

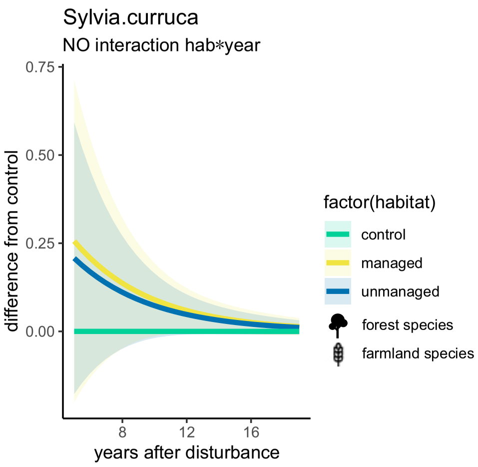
WITH interaction hab*year





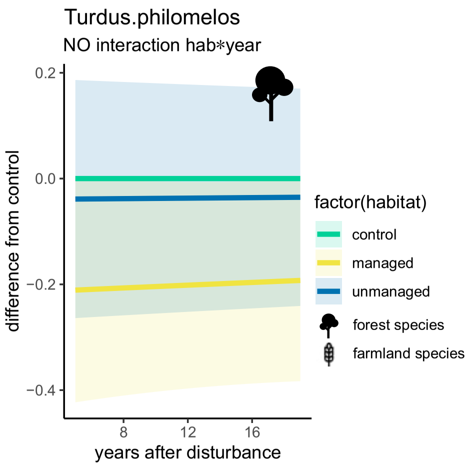
Spinus.spinus

NO interaction hab*year



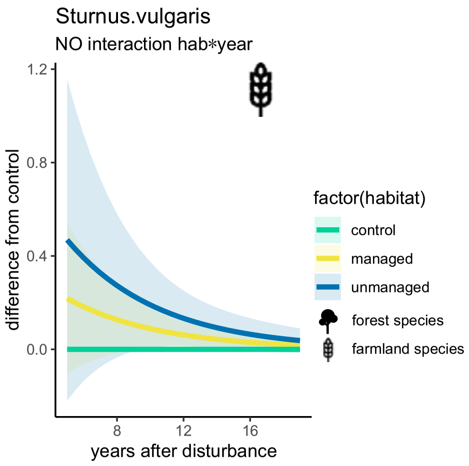
Sylvia.curruca

NO interaction hab*year



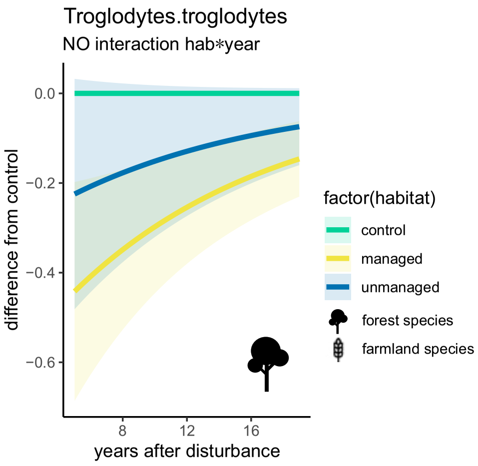
Turdus.philomelos

NO interaction hab*year



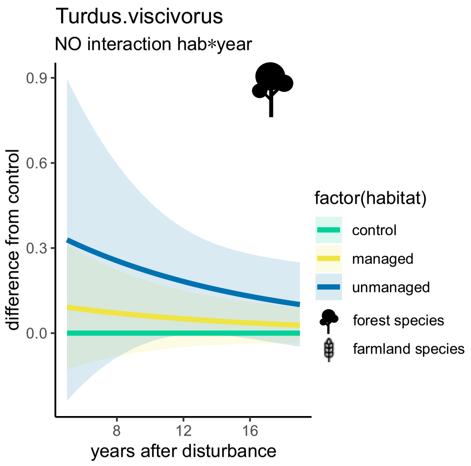
Sturnus.vulgaris

NO interaction hab*year



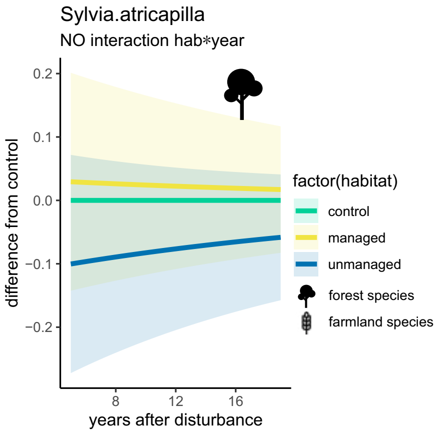
Troglodytes.troglodytes

NO interaction hab*year



Turdus.viscivorus

NO interaction hab*year


Sylvia.atricapilla
NO interaction hab*year
0.2
0.1
0.0
−0.1
−0.2
difference from control
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

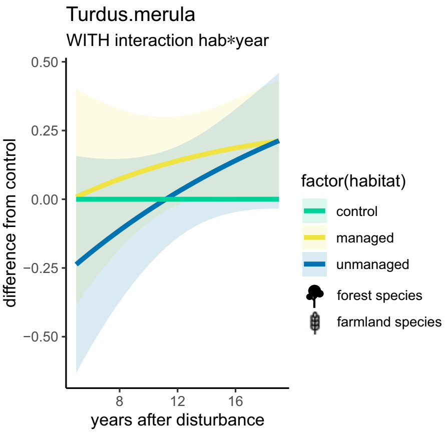
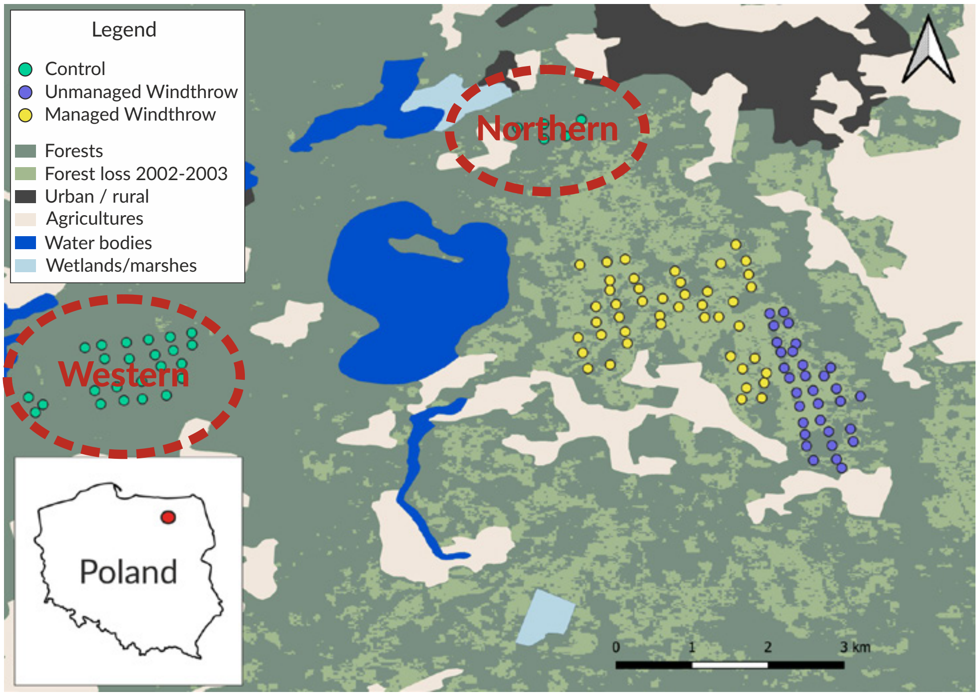

Turdus.merula
WITH interaction hab*year
0.50
0.25
0.00
−0.25
−0.50
difference from control
8
12
16
years after disturbance
factor(habitat)
control
managed
unmanaged
forest species
farmland species

Figure S5 – Comparison of bird communities between the two groups of control points (NMDS)


Legend
Control
Unmanaged Windthrow
Managed Windthrow
Forests
Forest loss 2002-2003
Urban / rural
Agricultures
Water bodies
Wetlands/marshes
Northern
Western
Poland
0
1
2
3 km

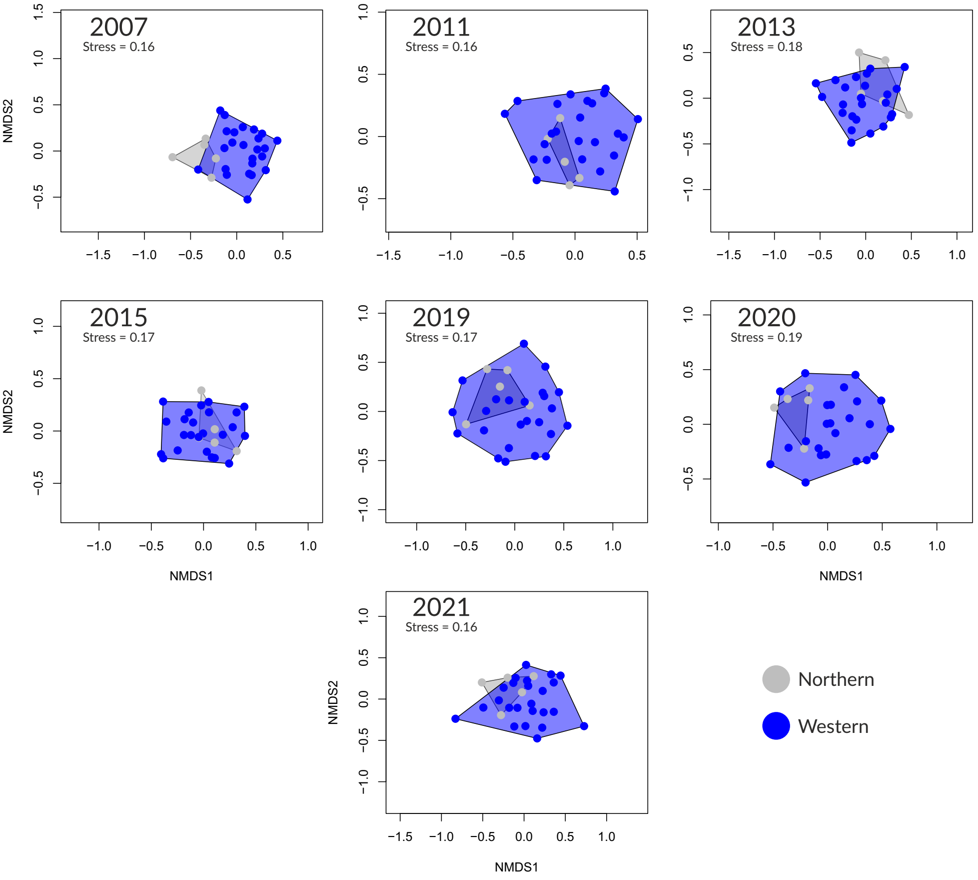
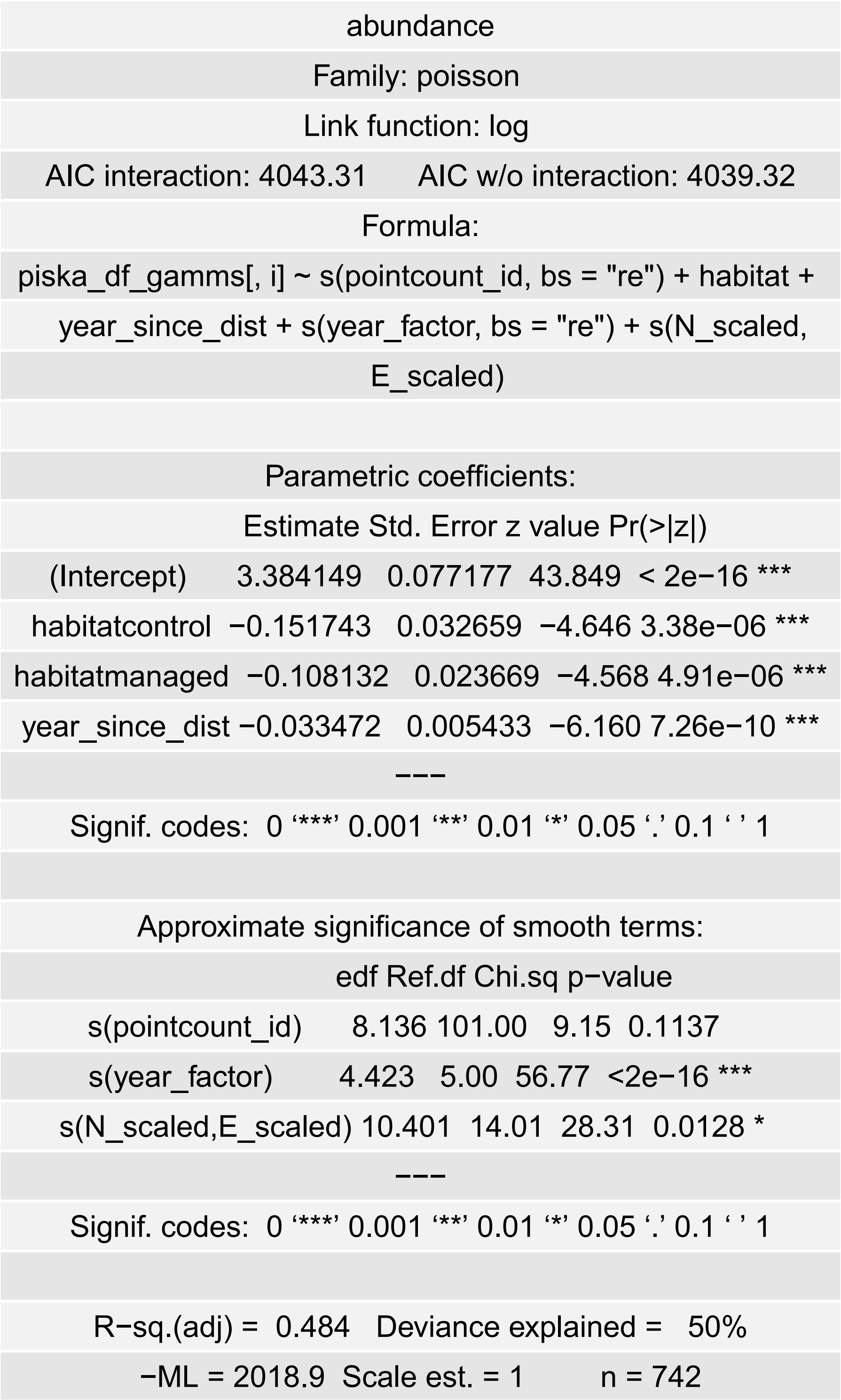
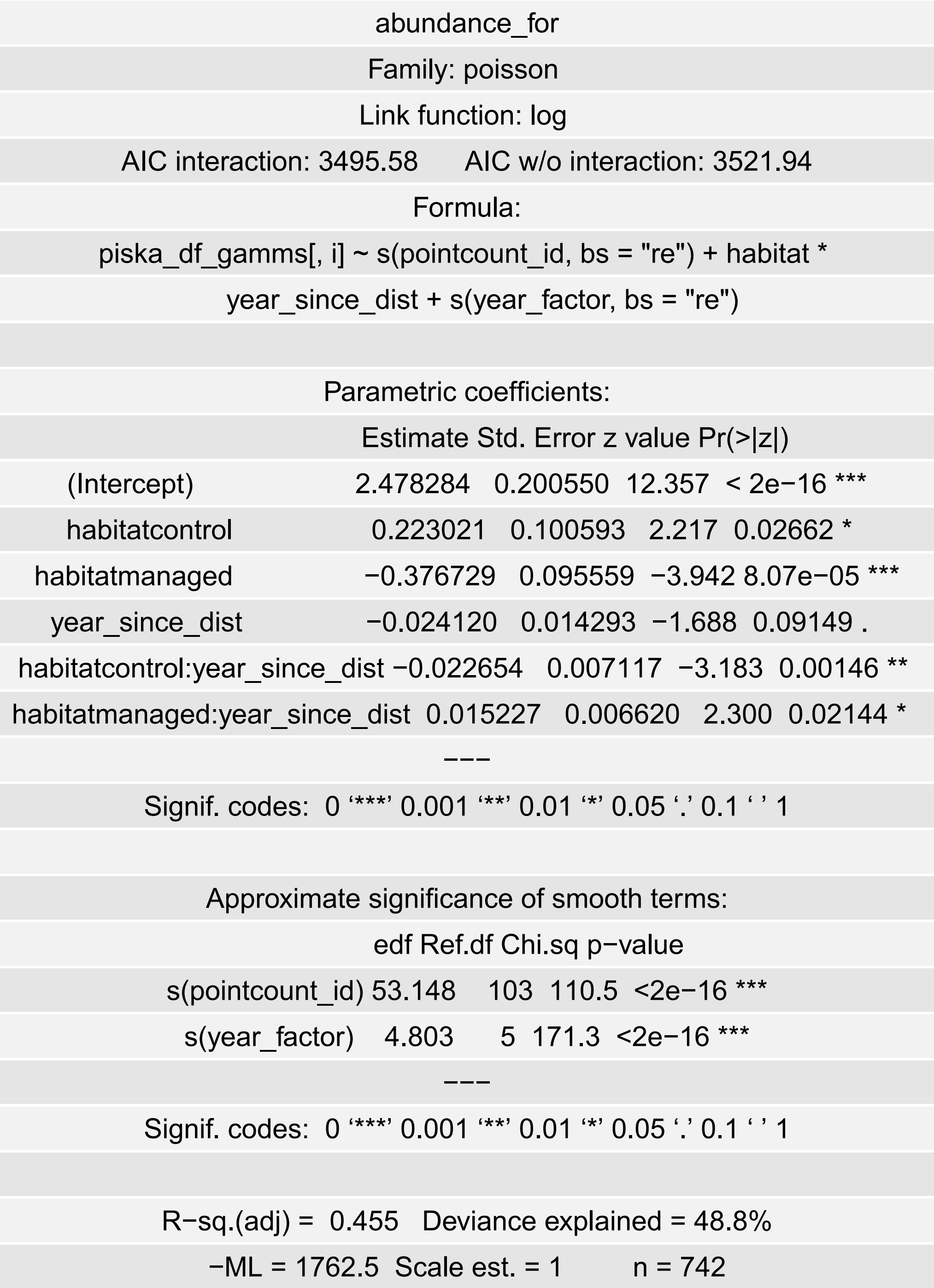

2007
Stress = 0.16
2011
Stress = 0.16
2013
Stress = 0.18
2015
Stress = 0.17
2019
Stress = 0.17
2020
Stress = 0.19
2021
Stress = 0.16
NMDS1
NMDS2
Northern
Western

Figure S6 – GAMM model outputs



```
abundance
Family: poisson
Link function: log
AIC interaction: 4043.31      AIC w/o interaction: 4039.32
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
    year_since_dist + s(year_factor, bs = "re") + s(N_scaled,
    E_scaled)

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      3.384149   0.077177  43.849  < 2e−16 ***
habitatcontrol  −0.151743   0.032659  −4.646 3.38e−06 ***
habitatmanaged  −0.108132   0.023669  −4.568 4.91e−06 ***
year_since_dist −0.033472   0.005433  −6.160 7.26e−10 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                      edf Ref.df Chi.sq p−value
s(pointcount_id)      8.136 101.00   9.15  0.1137
s(year_factor)        4.423   5.00  56.77  <2e−16 ***
s(N_scaled,E_scaled) 10.401  14.01  28.31  0.0128 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.484   Deviance explained =   50%
−ML = 2018.9  Scale est. = 1         n = 742
```

```
richness
Family: poisson
Link function: log
AIC interaction: 3689.49      AIC w/o interaction: 3685.62
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
    year_since_dist + s(year_factor, bs = "re") + s(N_scaled,
    E_scaled)

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      3.030291   0.093102  32.548  < 2e−16 ***
habitatcontrol  −0.179033   0.035773  −5.005 5.60e−07 ***
habitatmanaged  −0.091119   0.025923  −3.515  0.00044 ***
year_since_dist −0.029196   0.006576  −4.440 9.01e−06 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                         edf Ref.df Chi.sq p−value
s(pointcount_id)     0.01632 101.00  0.016  0.5036
s(year_factor)       4.47100   5.00 63.663  <2e−16 ***
s(N_scaled,E_scaled) 9.59531  13.33 21.254  0.0794 .
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.449   Deviance explained = 45.6%
−ML = 1846.9  Scale est. = 1         n = 742
```

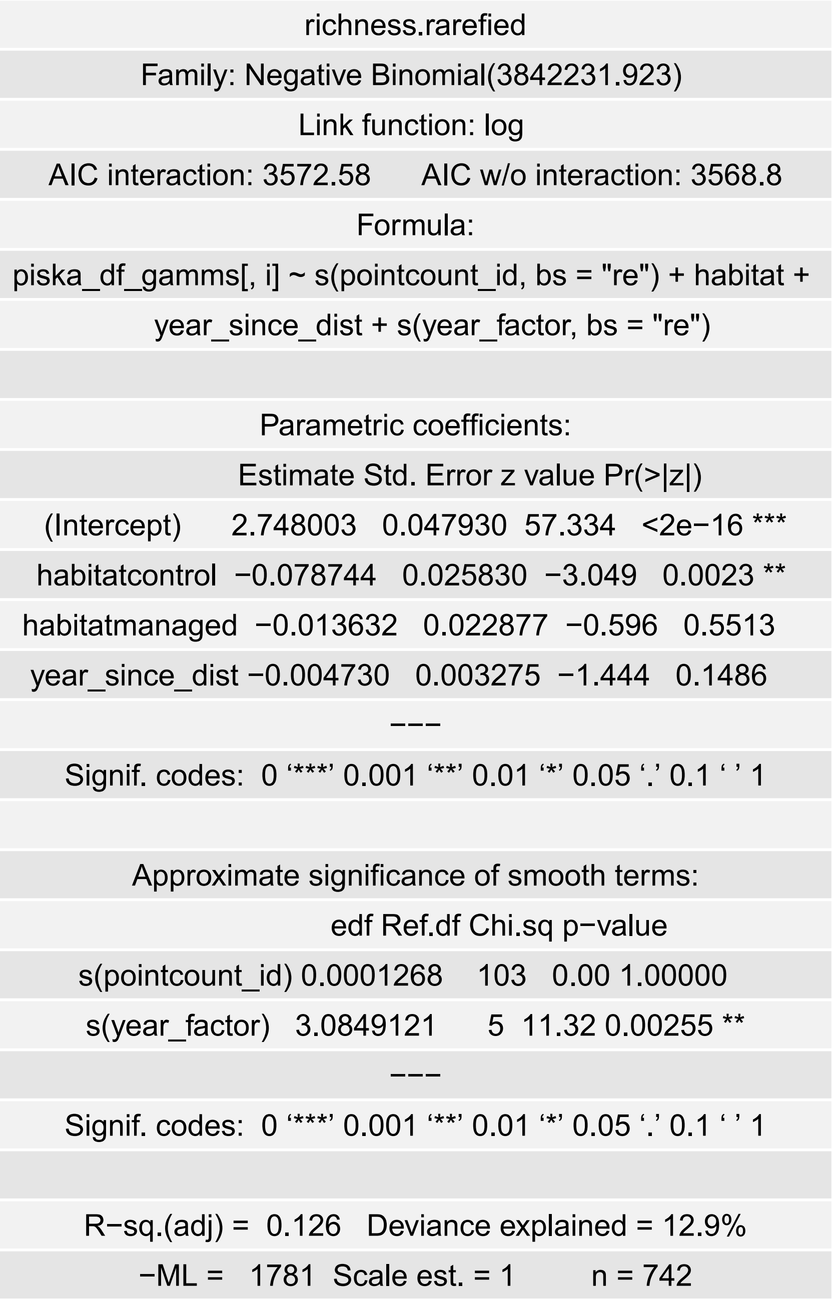


```
abundance_for
Family: poisson
Link function: log
AIC interaction: 3495.58      AIC w/o interaction: 3521.94
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                 Estimate Std. Error z value Pr(>|z|)
(Intercept)                      2.478284   0.200550  12.357  < 2e−16 ***
habitatcontrol                   0.223021   0.100593   2.217  0.02662 *
habitatmanaged                  −0.376729   0.095559  −3.942 8.07e−05 ***
year_since_dist                 −0.024120   0.014293  −1.688  0.09149 .
habitatcontrol:year_since_dist −0.022654   0.007117  −3.183  0.00146 **
habitatmanaged:year_since_dist  0.015227   0.006620   2.300  0.02144 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq p−value
s(pointcount_id) 53.148    103  110.5  <2e−16 ***
s(year_factor)    4.803      5  171.3  <2e−16 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.455   Deviance explained = 48.8%
−ML = 1762.5  Scale est. = 1         n = 742
```

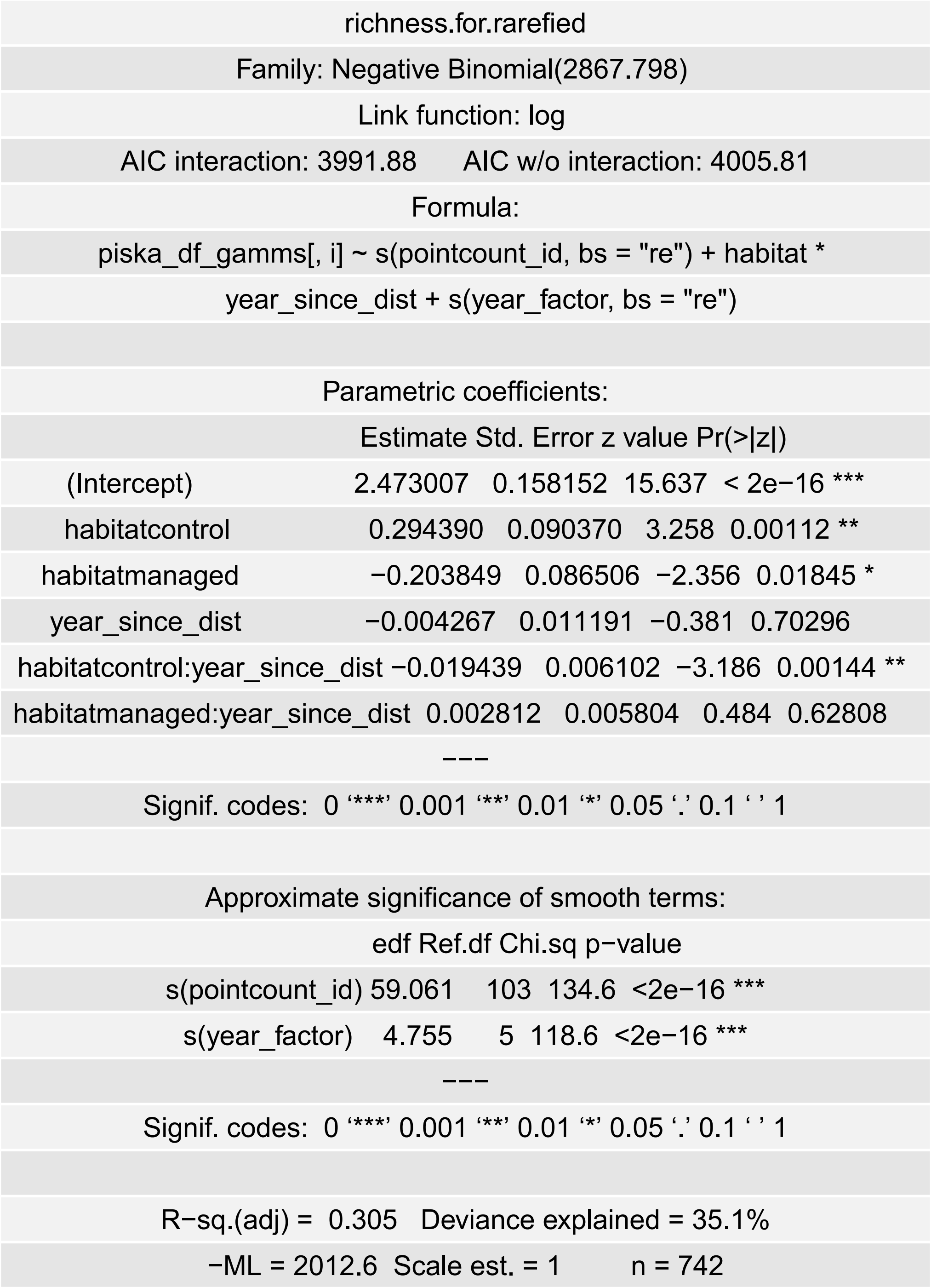
```
richness_for
Family: poisson
Link function: log
AIC interaction: 3179.07      AIC w/o interaction: 3194.64
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                              Estimate Std. Error z value Pr(>|z|)
(Intercept)                    2.18399    0.18892  11.560  < 2e−16 ***
habitatcontrol                 0.25083    0.10898   2.302 0.021350 *
habitatmanaged                −0.38044    0.10559  −3.603 0.000315 ***
year_since_dist               −0.01939    0.01350  −1.436 0.150930
habitatcontrol:year_since_dist −0.01988    0.00786  −2.530 0.011407 *
habitatmanaged:year_since_dist  0.01379    0.00747   1.845 0.064977 .
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq  p−value
s(pointcount_id) 37.545    103  59.87 0.000126 ***
s(year_factor)    4.714      5 112.41  < 2e−16 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.438   Deviance explained = 46.4%
−ML = 1595.6  Scale est. = 1         n = 742
```

```
abundance_farm
Family: poisson
Link function: log
AIC interaction: 1427.58      AIC w/o interaction: 1438.5
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                      2.11117    0.29141   7.245 4.34e−13 ***
habitatcontrol                  −5.94125    1.16353  −5.106 3.29e−07 ***
habitatmanaged                  −0.11245    0.22612  −0.497  0.61898
year_since_dist                 −0.19395    0.02348  −8.260  < 2e−16 ***
habitatcontrol:year_since_dist  0.24498    0.07960   3.078  0.00209 **
habitatmanaged:year_since_dist  0.04948    0.01965   2.517  0.01183 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq  p−value
s(pointcount_id) 44.288    103 107.41  < 2e−16 ***
s(year_factor)    3.597      5  22.85 1.21e−05 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.645   Deviance explained = 64.5%
−ML = 721.75  Scale est. = 1         n = 742
```

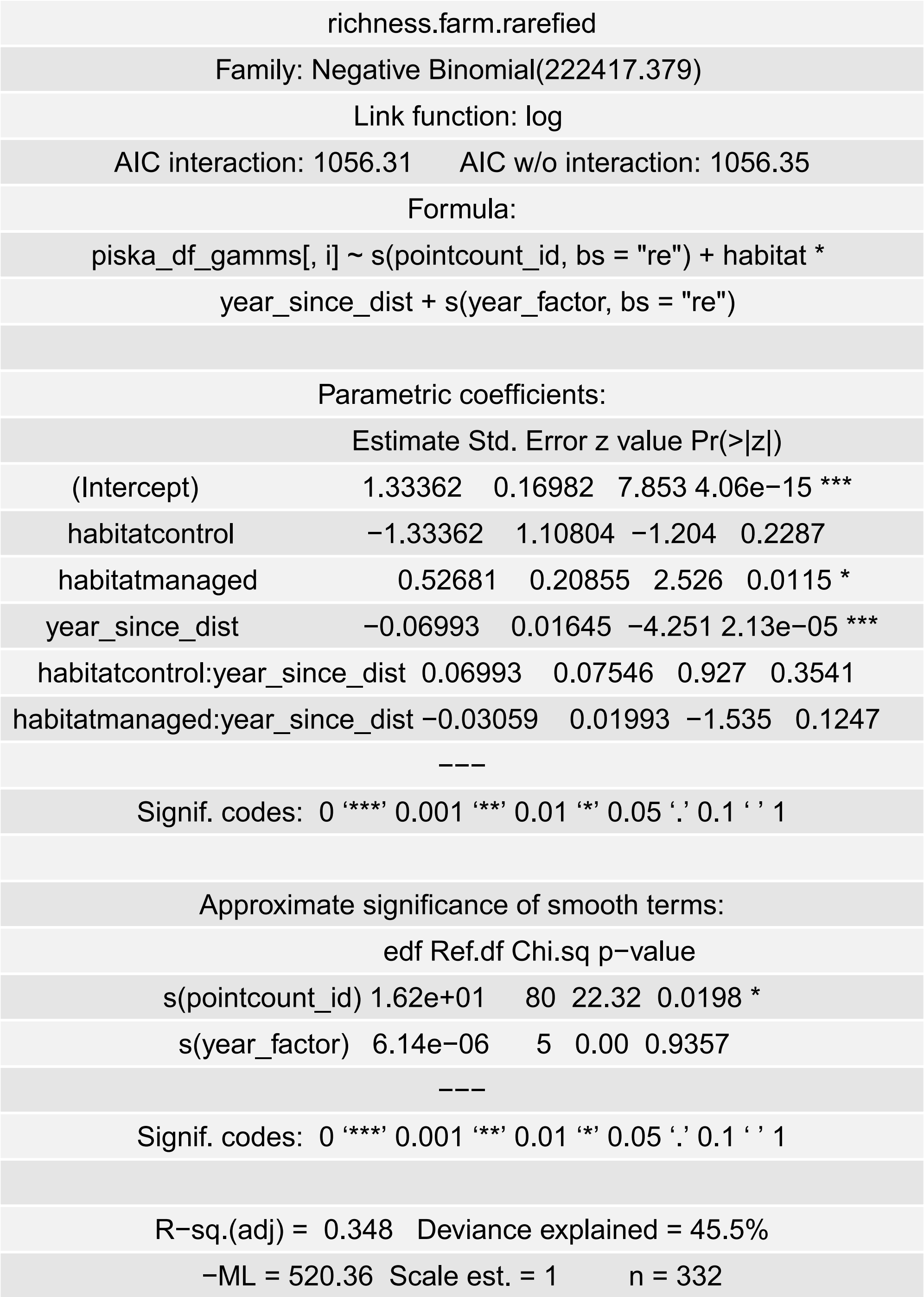
```
richness_farm
Family: poisson
Link function: log
AIC interaction: 1316.55      AIC w/o interaction: 1322.24
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
    year_since_dist + s(year_factor, bs = "re") + s(N_scaled,
    E_scaled, k = 60, fx = TRUE)

Parametric coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                     1.55236    0.32062   4.842 1.29e−06 ***
habitatcontrol                 −6.43405    1.25688  −5.119 3.07e−07 ***
habitatmanaged                  0.07830    0.24992   0.313  0.75404
year_since_dist                −0.16654    0.02090  −7.967 1.62e−15 ***
habitatcontrol:year_since_dist  0.21473    0.07789   2.757  0.00584 **
habitatmanaged:year_since_dist  0.03003    0.02077   1.446  0.14829
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                         edf Ref.df Chi.sq p−value
s(pointcount_id)    1.456e−04     44   0.00 0.13153
s(year_factor)      2.677e+00      5  10.25 0.00268 **
s(N_scaled,E_scaled) 5.900e+01     59  77.29 0.05531 .
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =   0.61   Deviance explained = 61.5%
−ML = 594.64  Scale est. = 1         n = 742
```



```
richness.rarefied
Family: Negative Binomial(3842231.923)
Link function: log
AIC interaction: 3572.58      AIC w/o interaction: 3568.8
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      2.748003   0.047930  57.334   <2e−16 ***
habitatcontrol  −0.078744   0.025830  −3.049   0.0023 **
habitatmanaged  −0.013632   0.022877  −0.596   0.5513
year_since_dist −0.004730   0.003275  −1.444   0.1486
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                      edf Ref.df Chi.sq p−value
s(pointcount_id) 0.0001268    103   0.00 1.00000
s(year_factor)   3.0849121      5  11.32 0.00255 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.126   Deviance explained = 12.9%
−ML =   1781  Scale est. = 1         n = 742
```



```
richness.for.rarefied
Family: Negative Binomial(2867.798)
Link function: log
AIC interaction: 3991.88      AIC w/o interaction: 4005.81
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                  Estimate Std. Error z value Pr(>|z|)
(Intercept)                       2.473007   0.158152  15.637  < 2e−16 ***
habitatcontrol                    0.294390   0.090370   3.258  0.00112 **
habitatmanaged                   −0.203849   0.086506  −2.356  0.01845 *
year_since_dist                  −0.004267   0.011191  −0.381  0.70296
habitatcontrol:year_since_dist −0.019439   0.006102  −3.186  0.00144 **
habitatmanaged:year_since_dist  0.002812   0.005804   0.484  0.62808
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq p−value
s(pointcount_id) 59.061    103  134.6  <2e−16 ***
s(year_factor)    4.755      5  118.6  <2e−16 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.305   Deviance explained = 35.1%
−ML = 2012.6  Scale est. = 1         n = 742
```

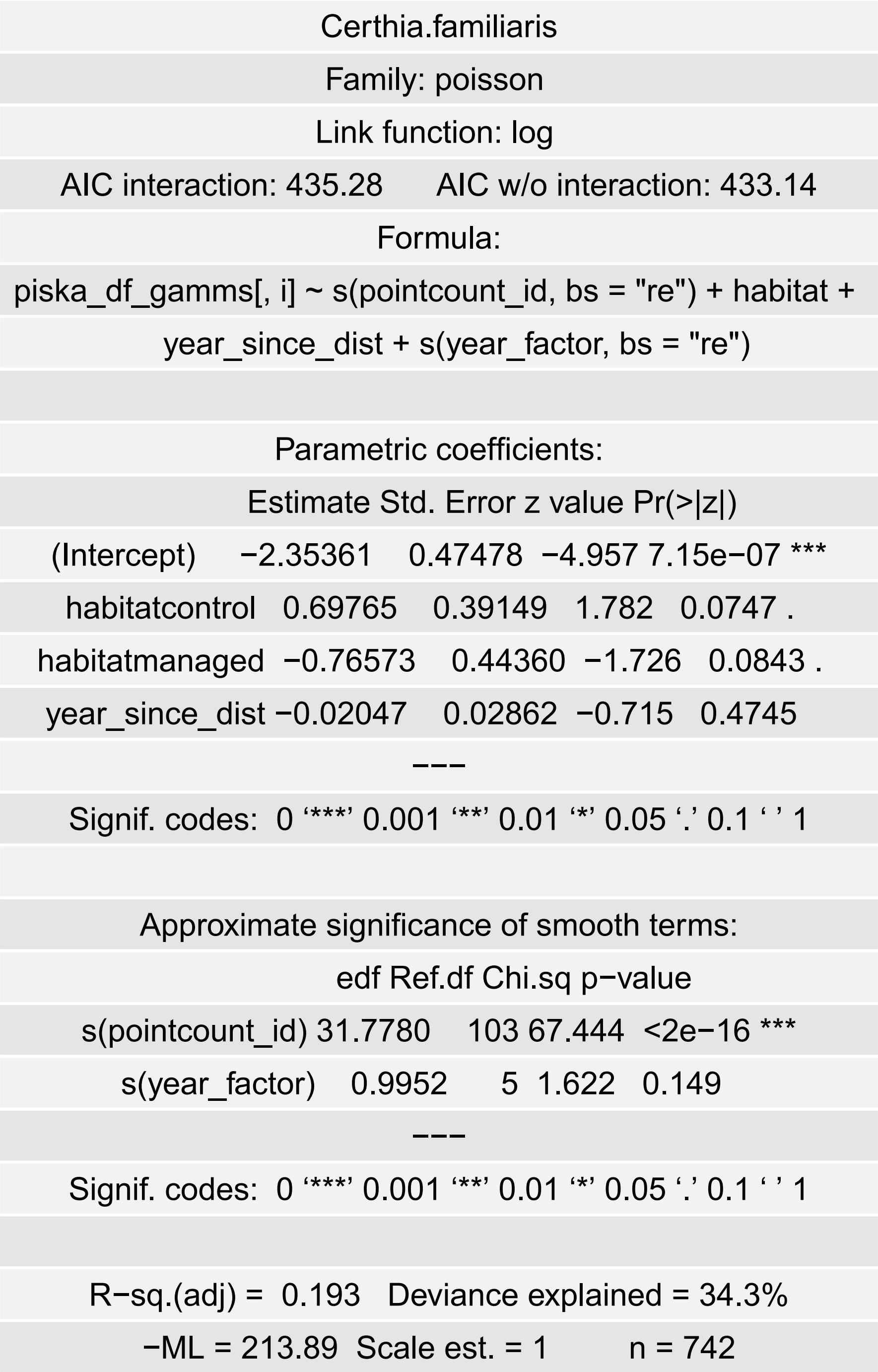


```
richness.farm.rarefied
Family: Negative Binomial(222417.379)
Link function: log
AIC interaction: 1056.31      AIC w/o interaction: 1056.35
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                  Estimate Std. Error z value Pr(>|z|)
(Intercept)                        1.33362    0.16982   7.853 4.06e−15 ***
habitatcontrol                    −1.33362    1.10804  −1.204   0.2287
habitatmanaged                     0.52681    0.20855   2.526   0.0115 *
year_since_dist                   −0.06993    0.01645  −4.251 2.13e−05 ***
habitatcontrol:year_since_dist     0.06993    0.07546   0.927   0.3541
habitatmanaged:year_since_dist    −0.03059    0.01993  −1.535   0.1247
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df Chi.sq p−value
s(pointcount_id) 1.62e+01     80  22.32  0.0198 *
s(year_factor)   6.14e−06      5   0.00  0.9357
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.348   Deviance explained = 45.5%
−ML = 520.36  Scale est. = 1         n = 332
```

```
Alauda.arvensis
Family: poisson
Link function: log
AIC interaction: 521.36      AIC w/o interaction: 517.98
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
    year_since_dist + s(year_factor, bs = "re") + s(N_scaled,
    E_scaled)

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      2.838e−01  4.949e−01   0.574    0.566
habitatcontrol  −5.738e+01  4.710e+06   0.000    1.000
habitatmanaged   9.326e−01  2.110e−01   4.420 9.87e−06 ***
year_since_dist −2.415e−01  3.892e−02  −6.205 5.48e−10 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                         edf Ref.df Chi.sq p−value
s(pointcount_id)      0.001336     73  0.001 0.55380
s(year_factor)        2.578385      5 11.740 0.00126 **
s(N_scaled,E_scaled) 10.250104     14 35.870 0.00109 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.473   Deviance explained = 56.4%
−ML = 259.55  Scale est. = 1         n = 742
NA
```

CAUTION: estimates for control unreliable: inflated standard errors (due to 0 observations in control)

```
Anthus.trivialis
Family: poisson
Link function: log
AIC interaction: 1505.22      AIC w/o interaction: 1521.81
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                 Estimate Std. Error z value Pr(>|z|)
(Intercept)                      0.844129   0.331449   2.547 0.010872 *
habitatcontrol                  −1.337298   0.335950  −3.981 6.87e−05 ***
habitatmanaged                  −0.155724   0.272058  −0.572 0.567055
year_since_dist                 −0.089047   0.024581  −3.623 0.000292 ***
habitatcontrol:year_since_dist   0.093504   0.024314   3.846 0.000120 ***
habitatmanaged:year_since_dist −0.001722   0.021309  −0.081 0.935578
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq  p−value
s(pointcount_id) 41.37    103  70.91 1.17e−05 ***
s(year_factor)    3.96      5  25.91 5.27e−06 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.324   Deviance explained = 30.1%
−ML = 755.58  Scale est. = 1         n = 742
```

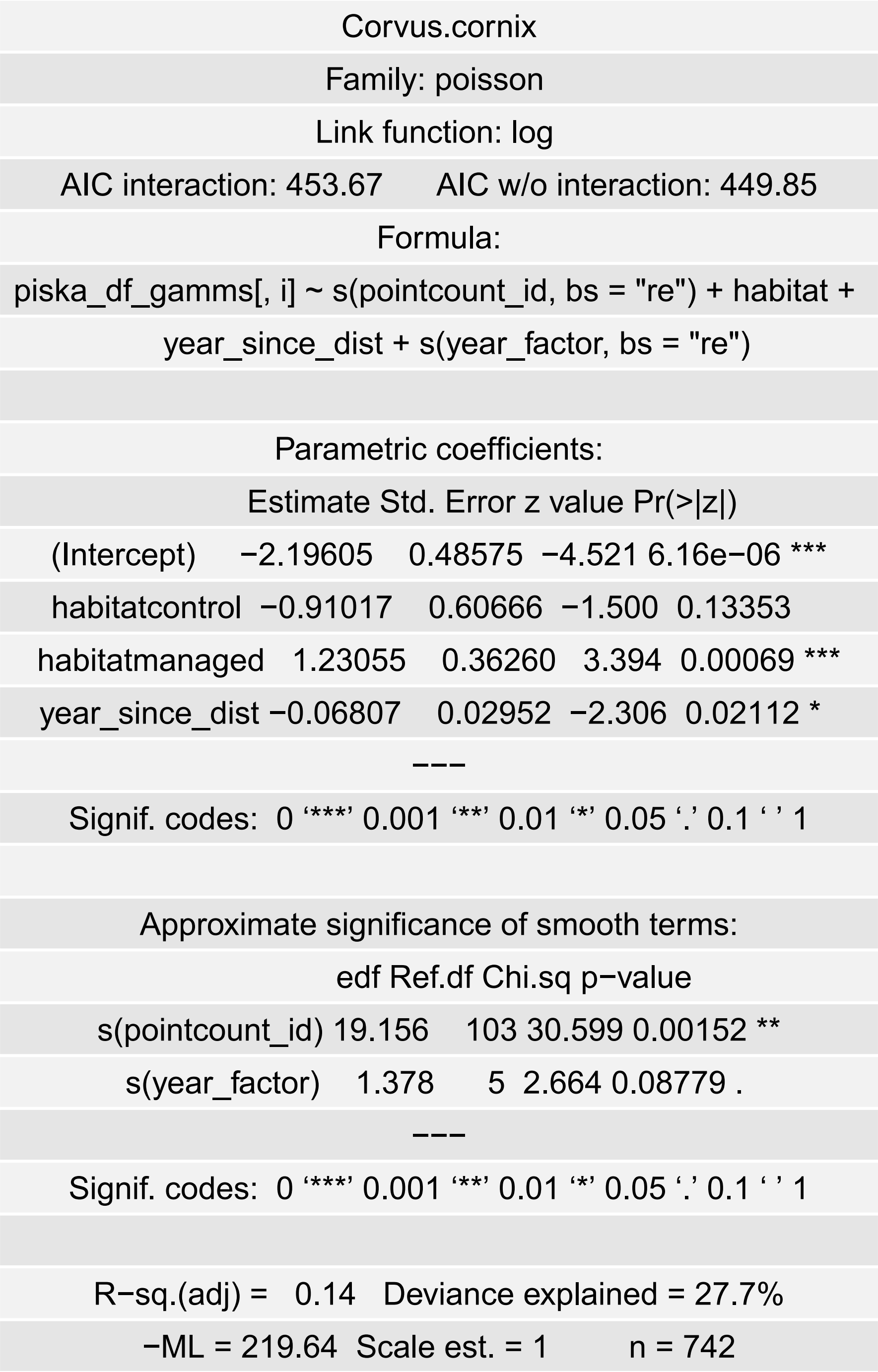


```
Certhia.familiaris
Family: poisson
Link function: log
AIC interaction: 435.28      AIC w/o interaction: 433.14
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)     −2.35361    0.47478  −4.957 7.15e−07 ***
habitatcontrol   0.69765    0.39149   1.782   0.0747 .
habitatmanaged  −0.76573    0.44360  −1.726   0.0843 .
year_since_dist −0.02047    0.02862  −0.715   0.4745
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq p−value
s(pointcount_id) 31.7780    103 67.444  <2e−16 ***
s(year_factor)    0.9952      5  1.622   0.149
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.193   Deviance explained = 34.3%
−ML = 213.89  Scale est. = 1         n = 742
```

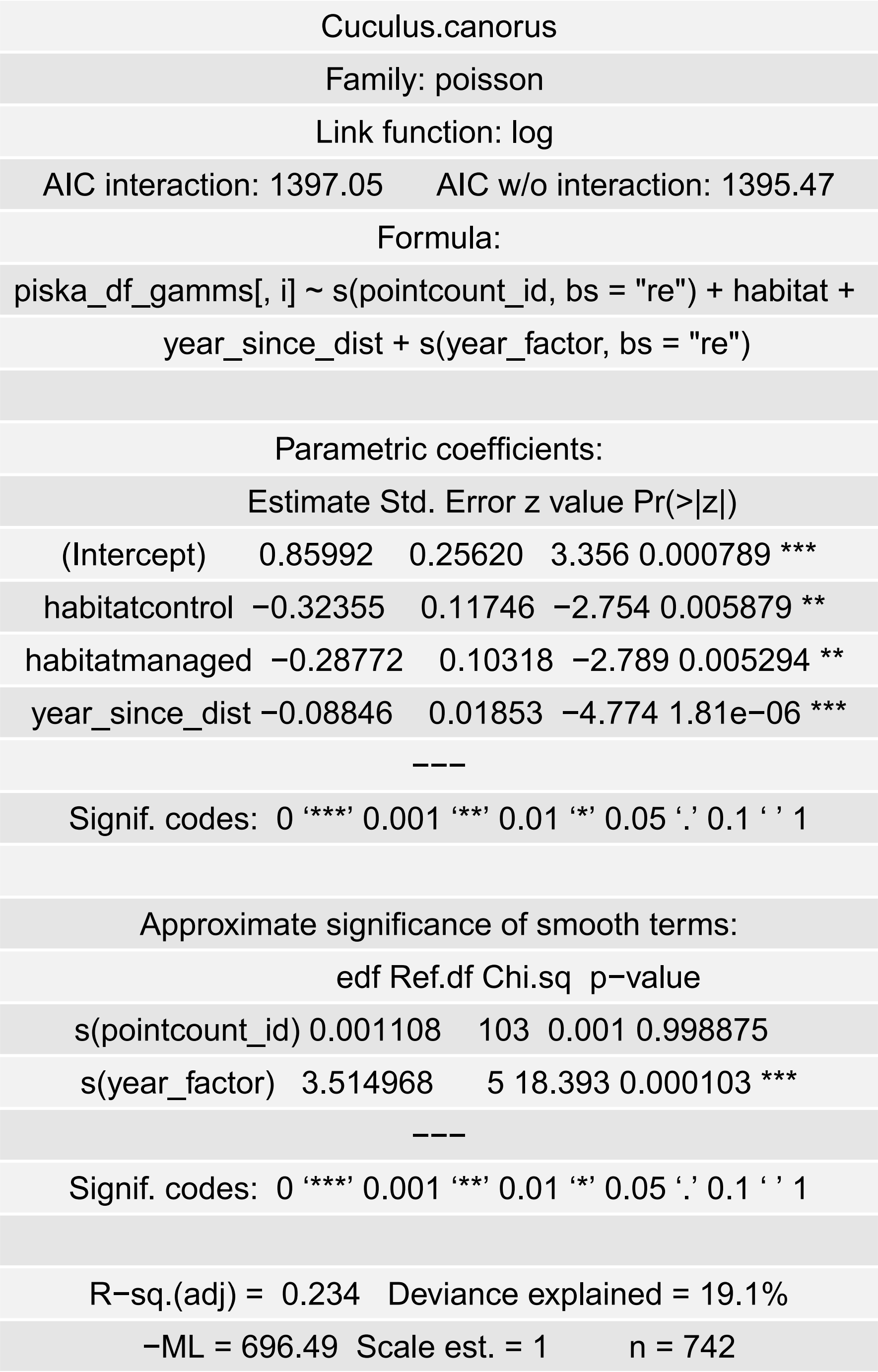
```
Columba.oenas
Family: poisson
Link function: log
AIC interaction: 527.06      AIC w/o interaction: 530.4
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                 Estimate Std. Error z value Pr(>|z|)
(Intercept)                      −4.11684    0.97780  −4.210 2.55e−05 ***
habitatcontrol                    2.44678    1.01083   2.421   0.0155 *
habitatmanaged                    0.95966    1.04875   0.915   0.3602
year_since_dist                   0.13239    0.06324   2.094   0.0363 *
habitatcontrol:year_since_dist   −0.16685    0.06652  −2.508   0.0121 *
habitatmanaged:year_since_dist   −0.08351    0.06689  −1.248   0.2119
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq  p−value
s(pointcount_id) 24.417    103  37.56 0.000669 ***
s(year_factor)    3.412      5  14.01 0.001076 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.153   Deviance explained =   24%
−ML = 259.84  Scale est. = 1         n = 742
```

```
Columba.palumbus
Family: poisson
Link function: log
AIC interaction: 1239.18      AIC w/o interaction: 1248.38
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                              Estimate Std. Error z value Pr(>|z|)
(Intercept)                   −0.49211    0.32083  −1.534  0.12506
habitatcontrol                 0.13093    0.39465   0.332  0.74006
habitatmanaged                −1.07256    0.38900  −2.757  0.00583 **
year_since_dist               −0.01608    0.02332  −0.689  0.49057
habitatcontrol:year_since_dist −0.02569    0.02956  −0.869  0.38482
habitatmanaged:year_since_dist  0.07188    0.02716   2.647  0.00813 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                     edf Ref.df Chi.sq p−value
s(pointcount_id) 0.001906    103  0.002 0.88517
s(year_factor)   2.773225      5  8.726 0.00772 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.0419   Deviance explained = 4.59%
−ML = 614.55  Scale est. = 1         n = 742
```

```
Corvus.corax
Family: poisson
Link function: log
AIC interaction: 1078.94      AIC w/o interaction: 1081.58
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                     −1.0537414  0.4287612  −2.458  0.01399 *
habitatcontrol                  −1.8249964  0.6385574  −2.858  0.00426 **
habitatmanaged                  −0.1194530  0.4316555  −0.277  0.78199
year_since_dist                  0.0028973  0.0301172   0.096  0.92336
habitatcontrol:year_since_dist   0.0936546  0.0412899   2.268  0.02332 *
habitatmanaged:year_since_dist −0.0007988  0.0299789  −0.027  0.97874
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq p−value
s(pointcount_id) 26.468    103  38.35 0.00245 **
s(year_factor)    3.379      5  13.85 0.00105 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.0703   Deviance explained = 14.2%
−ML = 536.07  Scale est. = 1         n = 742
```



```
Corvus.cornix
Family: poisson
Link function: log
AIC interaction: 453.67      AIC w/o interaction: 449.85
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)     −2.19605    0.48575  −4.521 6.16e−06 ***
habitatcontrol  −0.91017    0.60666  −1.500  0.13353
habitatmanaged   1.23055    0.36260   3.394  0.00069 ***
year_since_dist −0.06807    0.02952  −2.306  0.02112 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq p−value
s(pointcount_id) 19.156    103 30.599 0.00152 **
s(year_factor)    1.378      5  2.664 0.08779 .
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =   0.14   Deviance explained = 27.7%
−ML = 219.64  Scale est. = 1         n = 742
```

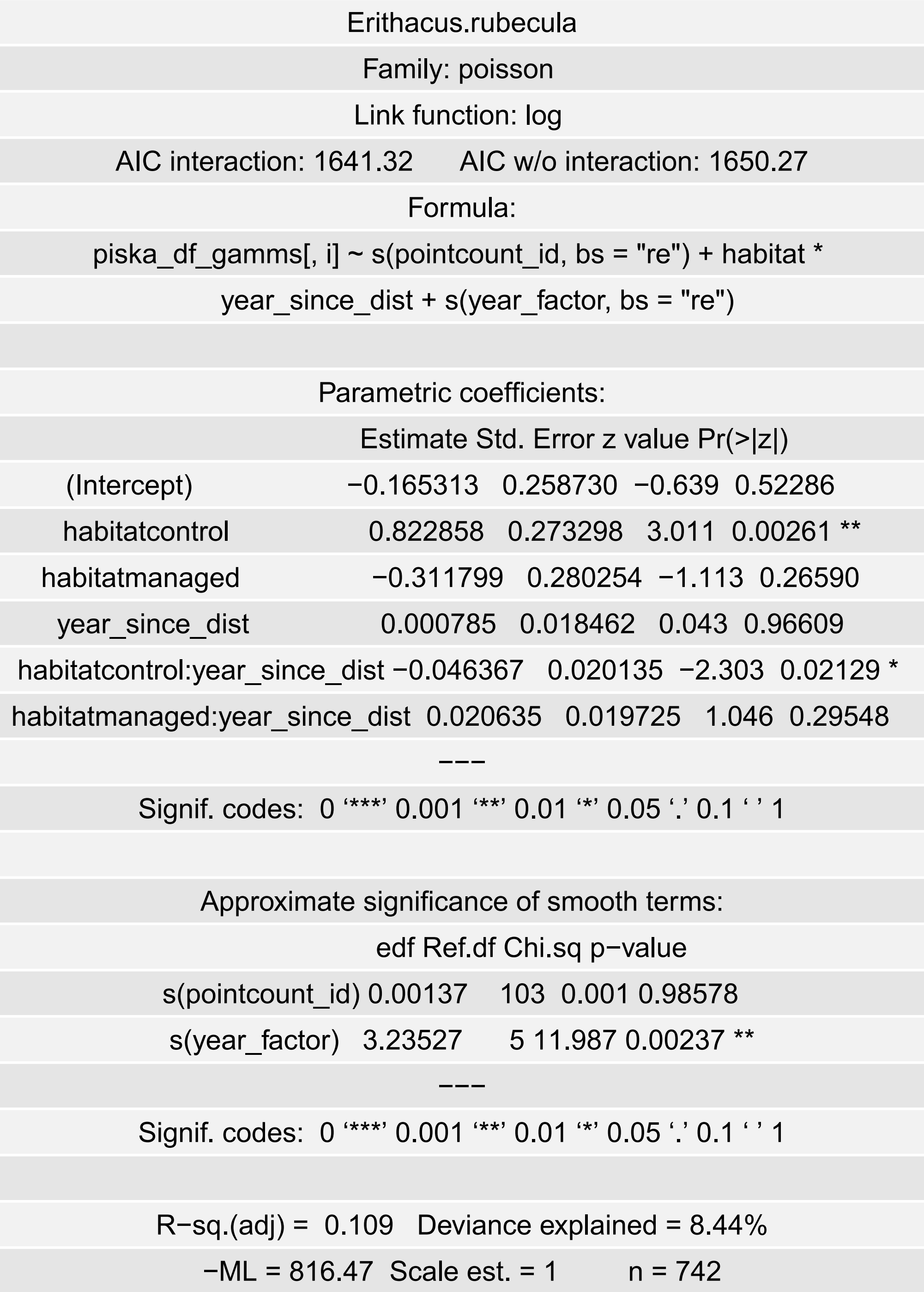


```
Cuculus.canorus
Family: poisson
Link function: log
AIC interaction: 1397.05      AIC w/o interaction: 1395.47
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)      0.85992    0.25620   3.356 0.000789 ***
habitatcontrol  −0.32355    0.11746  −2.754 0.005879 **
habitatmanaged  −0.28772    0.10318  −2.789 0.005294 **
year_since_dist −0.08846    0.01853  −4.774 1.81e−06 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                     edf Ref.df Chi.sq  p−value
s(pointcount_id) 0.001108    103  0.001 0.998875
s(year_factor)   3.514968      5 18.393 0.000103 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.234   Deviance explained = 19.1%
−ML = 696.49  Scale est. = 1         n = 742
```

```
Dendrocopos.major
Family: poisson
Link function: log
AIC interaction: 1732.95      AIC w/o interaction: 1732.22
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      0.813212   0.114015   7.132 9.86e−13 ***
habitatcontrol  −0.342109   0.104831  −3.263 0.001101 **
habitatmanaged  −0.325116   0.092623  −3.510 0.000448 ***
year_since_dist −0.053788   0.007813  −6.885 5.79e−12 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                      edf Ref.df Chi.sq p−value
s(pointcount_id) 9.936424    103 11.408   0.147
s(year_factor)   0.001028      5  0.001   0.496

R−sq.(adj) =  0.148   Deviance explained = 12.7%
−ML = 857.82  Scale est. = 1         n = 742
```

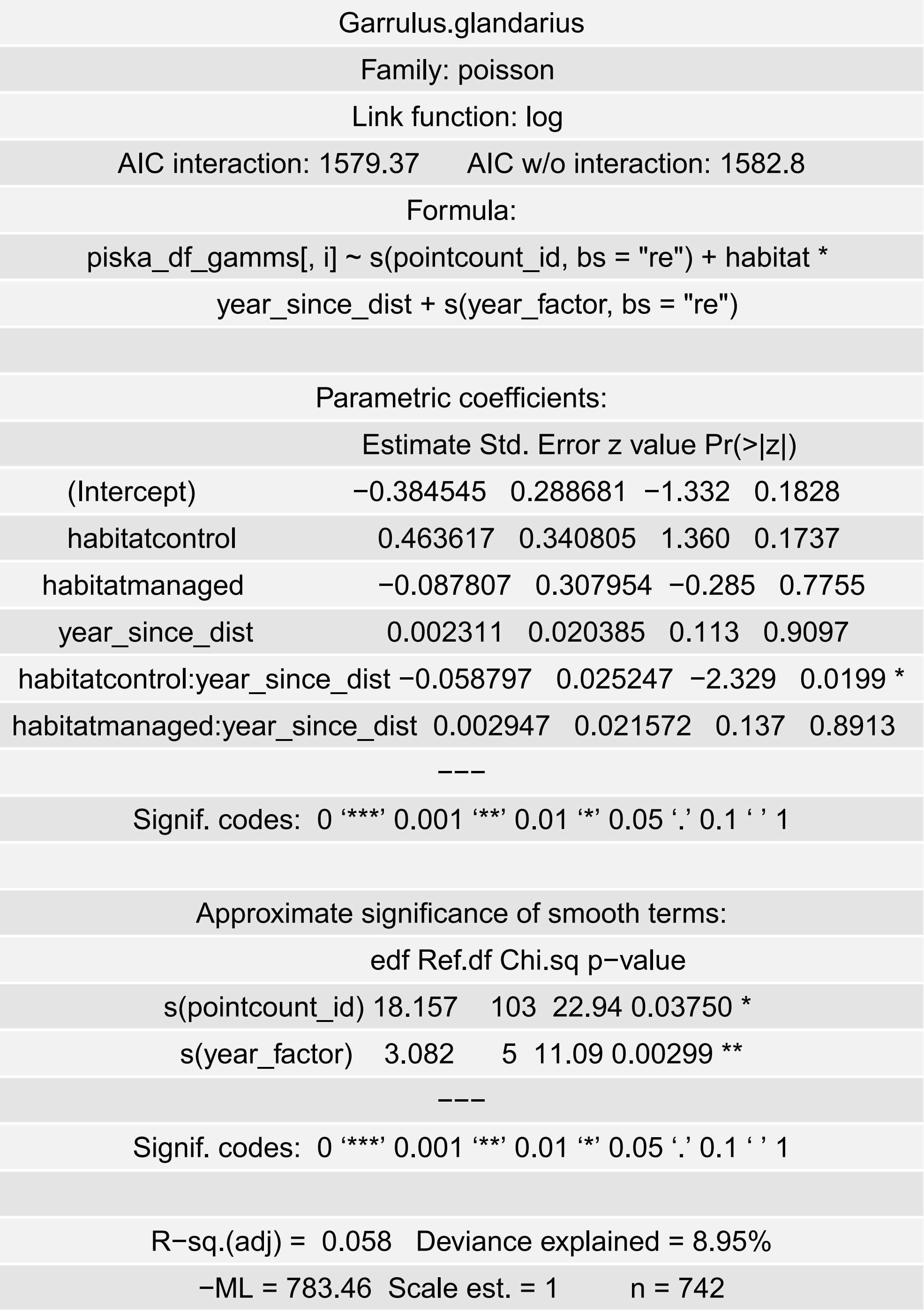
```
Dryocopus.martius
Family: poisson
Link function: log
AIC interaction: 833.28      AIC w/o interaction: 829.68
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)     −1.193133   0.387411  −3.080  0.00207 **
habitatcontrol  −0.704426   0.228744  −3.080  0.00207 **
habitatmanaged  −0.402219   0.184680  −2.178  0.02941 *
year_since_dist −0.002915   0.026719  −0.109  0.91312
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq p−value
s(pointcount_id) 8.700    103  9.799 0.18601
s(year_factor)   3.058      5 10.813 0.00345 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.0453   Deviance explained = 8.59%
−ML = 407.38  Scale est. = 1         n = 742
```

```
Emberiza.citrinella
Family: poisson
Link function: log
AIC interaction: 1062.6      AIC w/o interaction: 1078.58
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re") + s(N_scaled,
E_scaled, k = 60, fx = TRUE)

Parametric coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                      0.31041    0.48200   0.644  0.51957
habitatcontrol                 −10.17168    2.78480  −3.653  0.00026 ***
habitatmanaged                  −0.06938    0.36001  −0.193  0.84718
year_since_dist                 −0.14806    0.02827  −5.237 1.63e−07 ***
habitatcontrol:year_since_dist   0.42601    0.15597   2.731  0.00631 **
habitatmanaged:year_since_dist   0.07772    0.02753   2.823  0.00476 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                         edf Ref.df Chi.sq p−value
s(pointcount_id)      0.000101     44  0.000 0.02022 *
s(year_factor)        2.961049      5  9.877 0.00568 **
s(N_scaled,E_scaled) 59.000000     59 86.315 0.01174 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.439   Deviance explained = 50.9%
−ML = 467.63  Scale est. = 1         n = 742
```



```
Erithacus.rubecula
Family: poisson
Link function: log
AIC interaction: 1641.32      AIC w/o interaction: 1650.27
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                  Estimate Std. Error z value Pr(>|z|)
(Intercept)                      −0.165313   0.258730  −0.639  0.52286
habitatcontrol                    0.822858   0.273298   3.011  0.00261 **
habitatmanaged                   −0.311799   0.280254  −1.113  0.26590
year_since_dist                   0.000785   0.018462   0.043  0.96609
habitatcontrol:year_since_dist −0.046367   0.020135  −2.303  0.02129 *
habitatmanaged:year_since_dist  0.020635   0.019725   1.046  0.29548
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                      edf Ref.df Chi.sq p−value
s(pointcount_id) 0.00137    103  0.001 0.98578
s(year_factor)   3.23527      5 11.987 0.00237 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.109   Deviance explained = 8.44%
−ML = 816.47  Scale est. = 1         n = 742
```

```
Fringilla.coelebs
Family: poisson
Link function: log
AIC interaction: 2337.55      AIC w/o interaction: 2337.41
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      1.108349   0.098379  11.266  < 2e−16 ***
habitatcontrol   0.335590   0.056877   5.900 3.63e−09 ***
habitatmanaged  −0.162531   0.057630  −2.820   0.0048 **
year_since_dist −0.015853   0.006628  −2.392   0.0168 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                      edf Ref.df Chi.sq p−value
s(pointcount_id) 0.002431    103  0.001  1.0000
s(year_factor)   2.420726      5  6.538  0.0192 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.288   Deviance explained =   27%
−ML = 1165.1  Scale est. = 1         n = 742
```

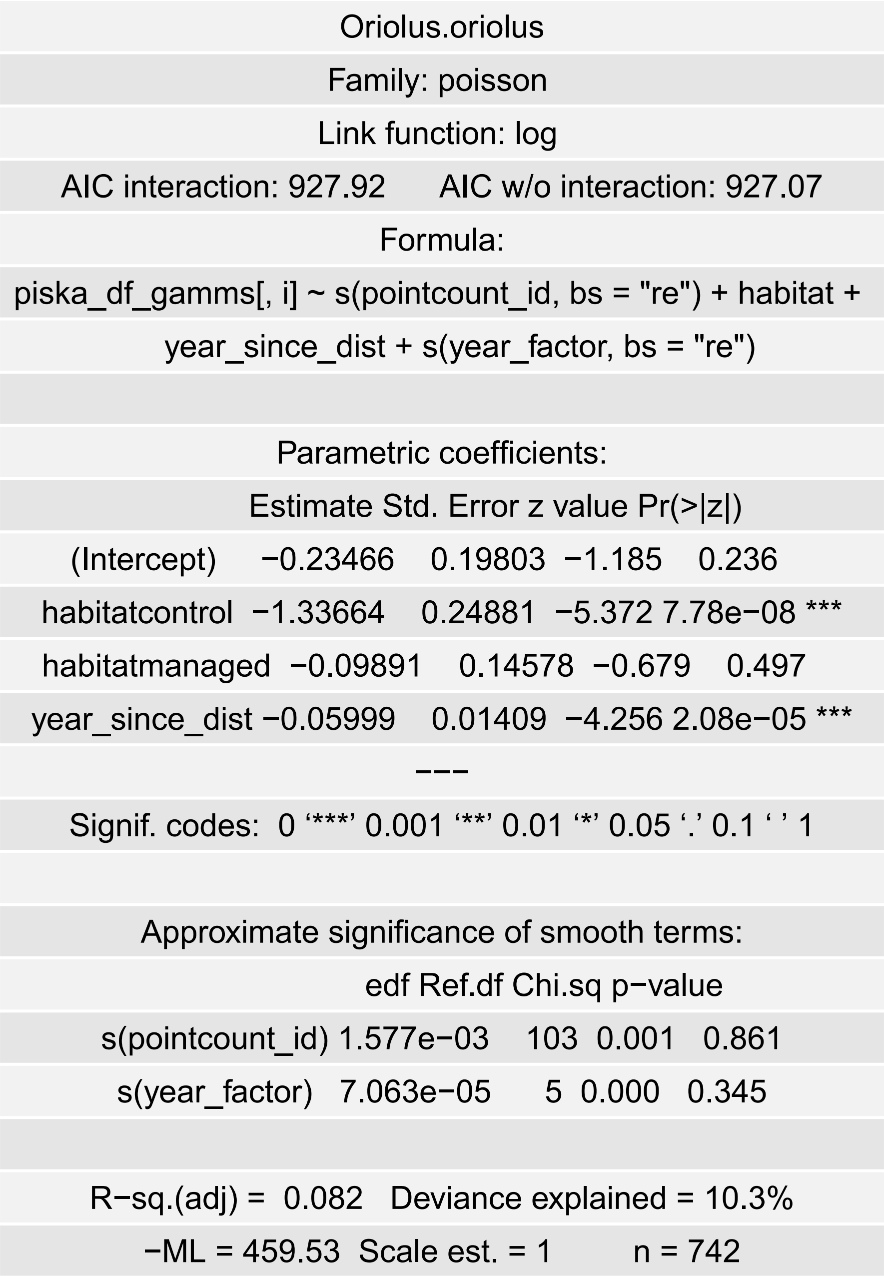


```
Garrulus.glandarius
Family: poisson
Link function: log
AIC interaction: 1579.37      AIC w/o interaction: 1582.8
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                              Estimate Std. Error z value Pr(>|z|)
(Intercept)                  −0.384545   0.288681  −1.332   0.1828
habitatcontrol                0.463617   0.340805   1.360   0.1737
habitatmanaged               −0.087807   0.307954  −0.285   0.7755
year_since_dist               0.002311   0.020385   0.113   0.9097
habitatcontrol:year_since_dist −0.058797   0.025247  −2.329   0.0199 *
habitatmanaged:year_since_dist  0.002947   0.021572   0.137   0.8913
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq p−value
s(pointcount_id) 18.157    103  22.94 0.03750 *
s(year_factor)    3.082      5  11.09 0.00299 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.058   Deviance explained = 8.95%
−ML = 783.46  Scale est. = 1         n = 742
```

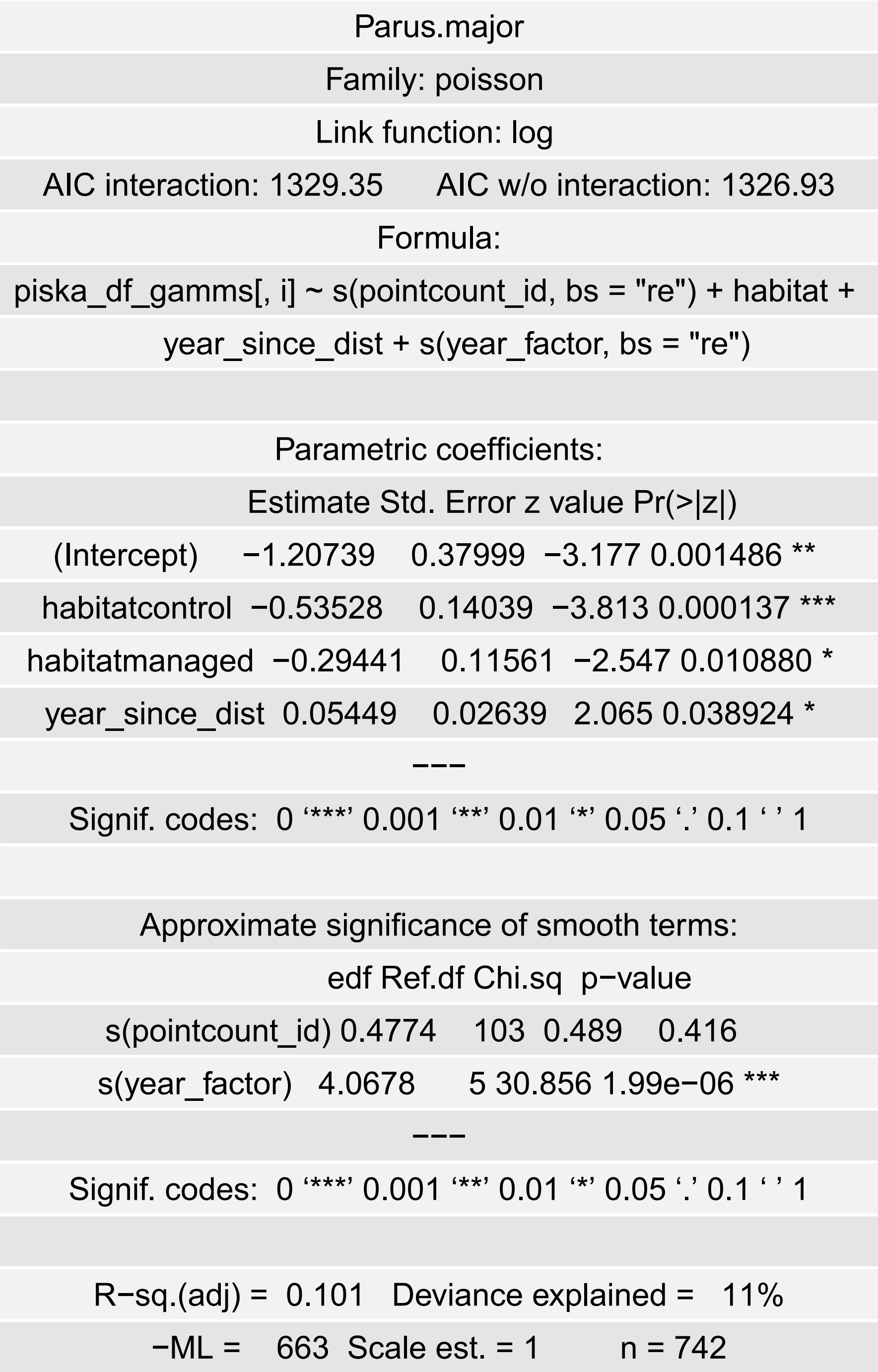
```
Grus.grus
Family: poisson
Link function: log
AIC interaction: 344.19      AIC w/o interaction: 341.22
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)     −1.25112    1.63793  −0.764    0.445
habitatcontrol  −0.28455    0.33485  −0.850    0.395
habitatmanaged   0.06454    0.27524   0.234    0.815
year_since_dist −0.16814    0.11900  −1.413    0.158

Approximate significance of smooth terms:
                     edf Ref.df Chi.sq  p−value
s(pointcount_id) 0.002258    103  0.002    0.529
s(year_factor)   3.853198      5 29.098 9.71e−07 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.282   Deviance explained = 44.6%
−ML = 171.81  Scale est. = 1         n = 742
```

```
Lophophanes.cristatus
Family: poisson
Link function: log
AIC interaction: 1136.24      AIC w/o interaction: 1140.35
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                     Estimate Std. Error z value Pr(>|z|)
(Intercept)                          −0.61097    0.56254  −1.086  0.27744
habitatcontrol                        1.17440    0.41482   2.831  0.00464 **
habitatmanaged                       −0.23607    0.44463  −0.531  0.59546
year_since_dist                      −0.02081    0.04072  −0.511  0.60934
habitatcontrol:year_since_dist −0.08082    0.03207  −2.520  0.01173 *
habitatmanaged:year_since_dist −0.01060    0.03289  −0.322  0.74730
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                      edf Ref.df Chi.sq  p−value
s(pointcount_id) 0.003069    103  0.003    0.648
s(year_factor)   4.340379      5 32.022 9.15e−07 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.105   Deviance explained = 12.2%
−ML = 567.59  Scale est. = 1         n = 742
```

```
Lullula.arborea
Family: poisson
Link function: log
AIC interaction: 1351.7      AIC w/o interaction: 1350.62
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
    year_since_dist + s(year_factor, bs = "re") + s(N_scaled,
    E_scaled)

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)       0.51407    0.31673   1.623  0.10458
habitatcontrol   −1.77355    0.23220  −7.638 2.21e−14 ***
habitatmanaged    0.25747    0.12210   2.109  0.03497 *
year_since_dist  −0.07003    0.02220  −3.154  0.00161 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df Chi.sq  p−value
s(pointcount_id)    12.998 101.00  16.04   0.0403 *
s(year_factor)       3.911   5.00  25.04 6.71e−06 ***
s(N_scaled,E_scaled) 8.944  11.87  21.04   0.0469 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =   0.36   Deviance explained = 35.6%
−ML = 674.61  Scale est. = 1         n = 742
```



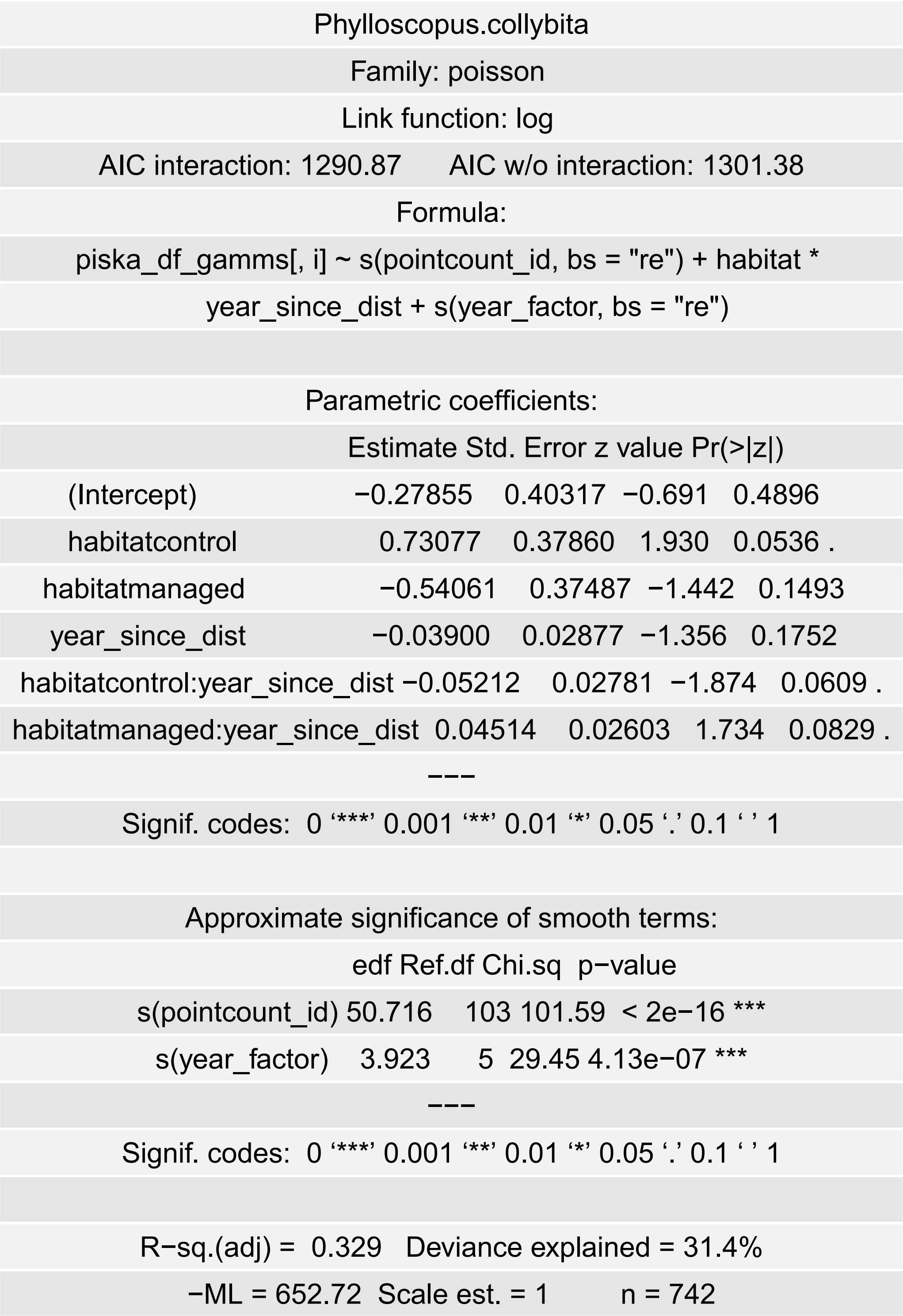
```
Oriolus.oriolus
Family: poisson
Link function: log
AIC interaction: 927.92      AIC w/o interaction: 927.07
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
    year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      −0.23466    0.19803  −1.185    0.236
habitatcontrol   −1.33664    0.24881  −5.372 7.78e−08 ***
habitatmanaged   −0.09891    0.14578  −0.679    0.497
year_since_dist  −0.05999    0.01409  −4.256 2.08e−05 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                      edf Ref.df Chi.sq p−value
s(pointcount_id) 1.577e−03    103  0.001   0.861
s(year_factor)   7.063e−05      5  0.000   0.345

R−sq.(adj) =  0.082   Deviance explained = 10.3%
−ML = 459.53  Scale est. = 1         n = 742
```



```
Parus.major
Family: poisson
Link function: log
AIC interaction: 1329.35      AIC w/o interaction: 1326.93
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)     −1.20739    0.37999  −3.177 0.001486 **
habitatcontrol  −0.53528    0.14039  −3.813 0.000137 ***
habitatmanaged  −0.29441    0.11561  −2.547 0.010880 *
year_since_dist  0.05449    0.02639   2.065 0.038924 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq  p−value
s(pointcount_id) 0.4774    103  0.489    0.416
s(year_factor)   4.0678      5 30.856 1.99e−06 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.101   Deviance explained =   11%
−ML =    663  Scale est. = 1        n = 742
```

```
Periparus.ater
Family: poisson
Link function: log
AIC interaction: 1297.99      AIC w/o interaction: 1311.16
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                     −1.65192    0.37946  −4.353 1.34e−05 ***
habitatcontrol                   1.62429    0.42094   3.859 0.000114 ***
habitatmanaged                  −0.39651    0.47554  −0.834 0.404393
year_since_dist                  0.05800    0.02529   2.294 0.021802 *
habitatcontrol:year_since_dist −0.08208    0.02855  −2.875 0.004045 **
habitatmanaged:year_since_dist  0.02034    0.03094   0.657 0.510935
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq p−value
s(pointcount_id) 23.123    103 30.918  0.0150 *
s(year_factor)    2.468      5  6.318  0.0257 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.145   Deviance explained = 16.7%
−ML = 642.58  Scale est. = 1         n = 742
```

```
Phoenicurus.phoenicurus
Family: poisson
Link function: log
AIC interaction: 433.86      AIC w/o interaction: 441.66
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                      0.19772    1.16568   0.170  0.86531
habitatcontrol                  −3.34774    1.36390  −2.455  0.01411 *
habitatmanaged                  −4.52140    1.11689  −4.048 5.16e−05 ***
year_since_dist                 −0.16146    0.08778  −1.839  0.06586 .
habitatcontrol:year_since_dist  0.13095    0.10485   1.249  0.21172
habitatmanaged:year_since_dist  0.24504    0.08103   3.024  0.00249 **
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                      edf Ref.df Chi.sq  p−value
s(pointcount_id) 0.0008373    103  0.001    0.929
s(year_factor)   4.2234391      5 33.036 2.12e−06 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.169   Deviance explained = 28.8%
−ML = 216.58  Scale est. = 1         n = 742
```

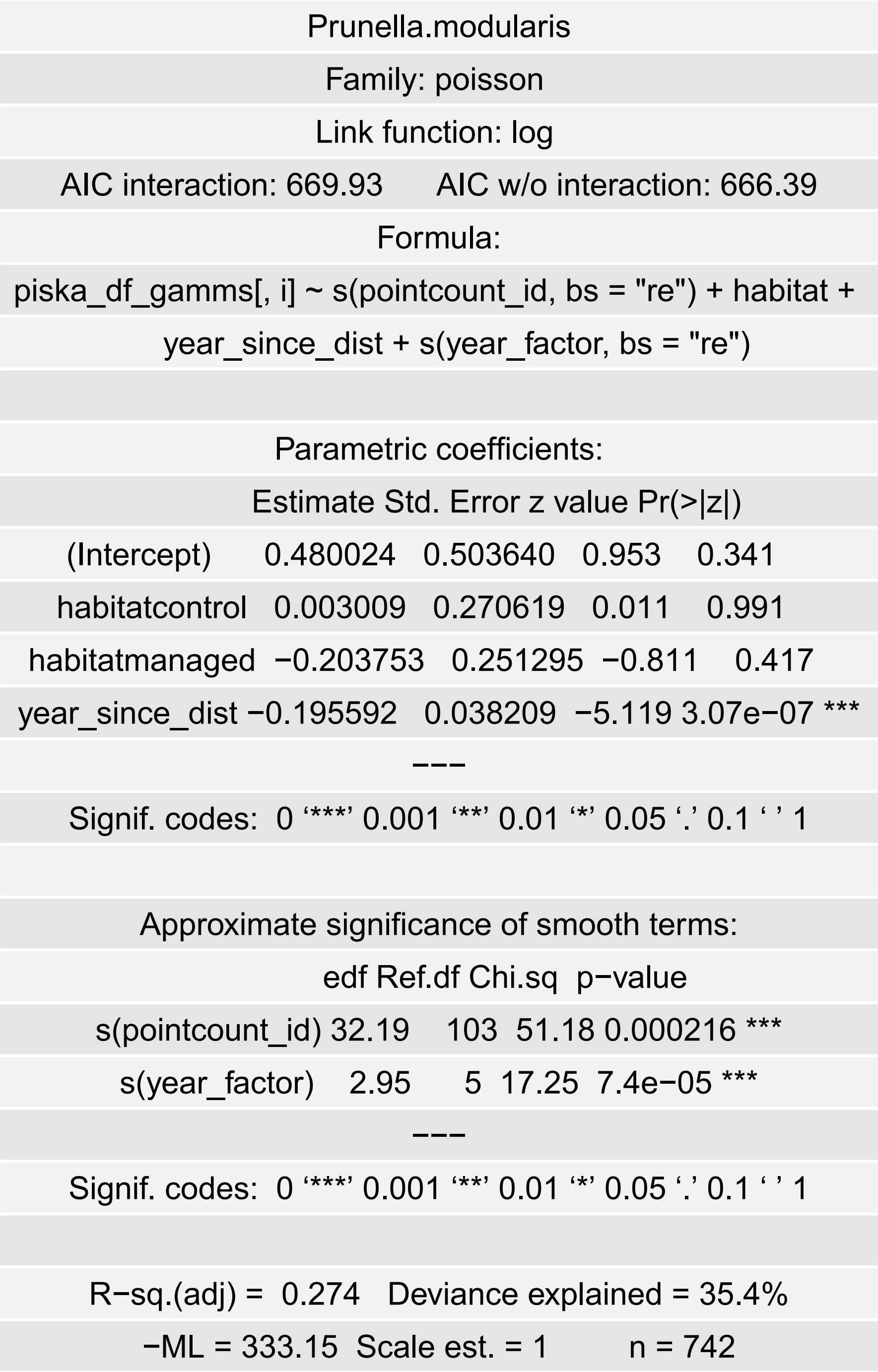


```
Phylloscopus.collybita
Family: poisson
Link function: log
AIC interaction: 1290.87      AIC w/o interaction: 1301.38
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                              Estimate Std. Error z value Pr(>|z|)
(Intercept)                   −0.27855    0.40317  −0.691   0.4896
habitatcontrol                 0.73077    0.37860   1.930   0.0536 .
habitatmanaged                −0.54061    0.37487  −1.442   0.1493
year_since_dist               −0.03900    0.02877  −1.356   0.1752
habitatcontrol:year_since_dist −0.05212    0.02781  −1.874   0.0609 .
habitatmanaged:year_since_dist  0.04514    0.02603   1.734   0.0829 .
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq  p−value
s(pointcount_id) 50.716    103 101.59  < 2e−16 ***
s(year_factor)    3.923      5  29.45 4.13e−07 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.329   Deviance explained = 31.4%
−ML = 652.72  Scale est. = 1         n = 742
```

```
Phylloscopus.sibilatrix
Family: poisson
Link function: log
AIC interaction: 1181.28      AIC w/o interaction: 1208.64
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                 Estimate Std. Error z value Pr(>|z|)
(Intercept)                      −1.43122    0.41144  −3.479 0.000504 ***
habitatcontrol                    2.30702    0.41274   5.589 2.28e−08 ***
habitatmanaged                   −0.24714    0.49201  −0.502 0.615454
year_since_dist                   0.04319    0.02789   1.548 0.121503
habitatcontrol:year_since_dist   −0.13845    0.02882  −4.803 1.56e−06 ***
habitatmanaged:year_since_dist   −0.02121    0.03315  −0.640 0.522229
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq  p−value
s(pointcount_id) 38.897    103  66.98 2.47e−05 ***
s(year_factor)    3.359      5  14.40 0.000692 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.361   Deviance explained = 32.8%
−ML = 591.69  Scale est. = 1         n = 742
```

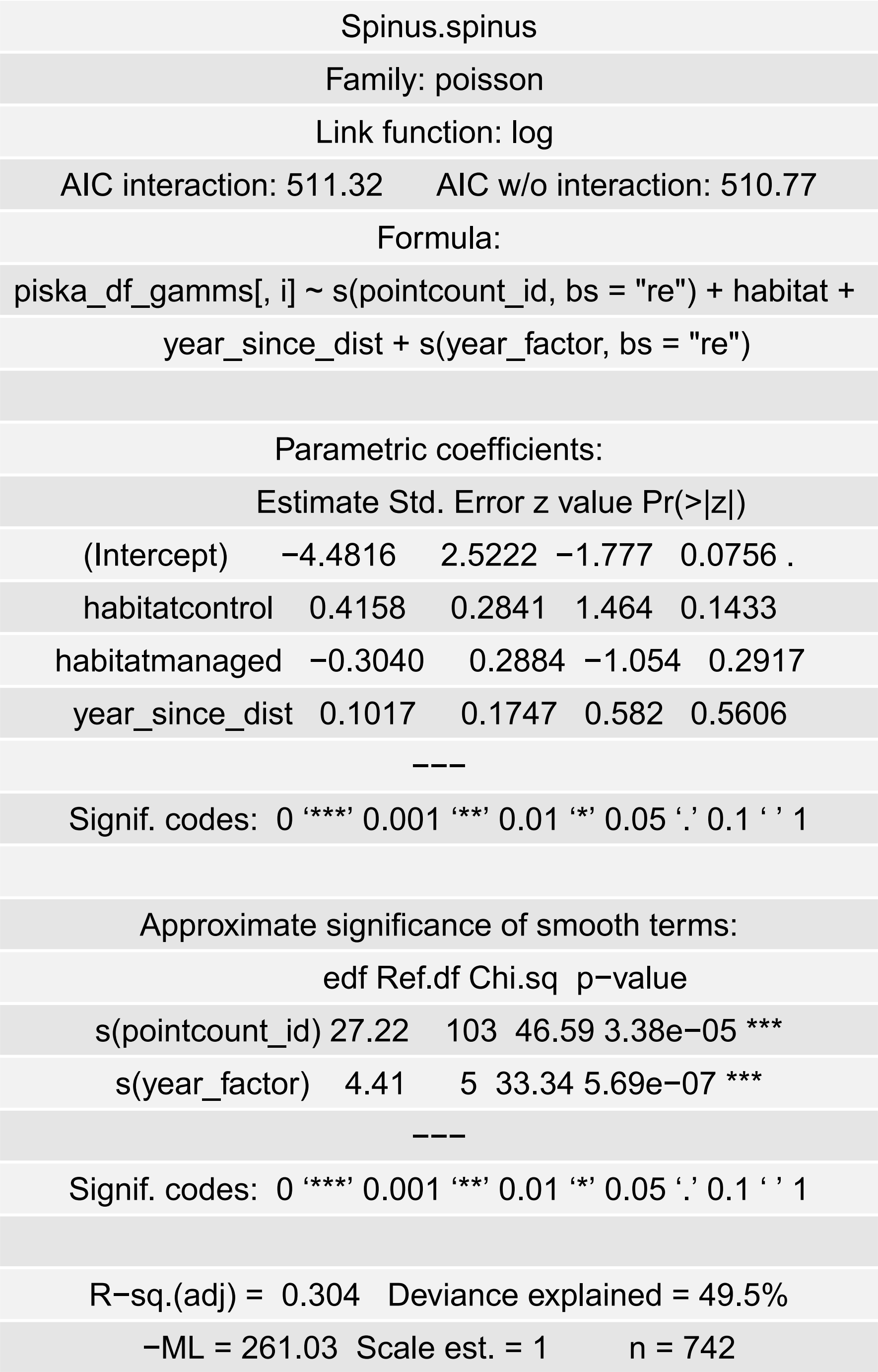
```
Phylloscopus.trochilus
Family: poisson
Link function: log
AIC interaction: 1838.96      AIC w/o interaction: 1851.45
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                    Estimate Std. Error z value Pr(>|z|)
(Intercept)                         1.044866   0.725623   1.440 0.149879
habitatcontrol                     −0.908294   0.343050  −2.648 0.008104 **
habitatmanaged                     −0.797656   0.246057  −3.242 0.001188 **
year_since_dist                    −0.065409   0.052153  −1.254 0.209778
habitatcontrol:year_since_dist      0.002973   0.025903   0.115 0.908618
habitatmanaged:year_since_dist      0.066433   0.017891   3.713 0.000205 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq p−value
s(pointcount_id) 32.041    103  47.05 0.00198 **
s(year_factor)    4.875      5 188.97 < 2e−16 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.504   Deviance explained = 46.4%
−ML =    927  Scale est. = 1         n = 742
```

```
Poecile.montanus
Family: poisson
Link function: log
AIC interaction: 999.51      AIC w/o interaction: 999.16
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)     −0.912191   0.380186  −2.399  0.01643 *
habitatcontrol  −0.581767   0.189178  −3.075  0.00210 **
habitatmanaged  −0.467626   0.161180  −2.901  0.00372 **
year_since_dist −0.001365   0.026518  −0.051  0.95894
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq  p−value
s(pointcount_id) 8.872    103  10.09 0.166620
s(year_factor)   3.480      5  16.20 0.000314 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.063   Deviance explained = 8.73%
−ML = 493.63  Scale est. = 1         n = 742
```



```
Prunella.modularis
Family: poisson
Link function: log
AIC interaction: 669.93      AIC w/o interaction: 666.39
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      0.480024   0.503640   0.953    0.341
habitatcontrol   0.003009   0.270619   0.011    0.991
habitatmanaged  −0.203753   0.251295  −0.811    0.417
year_since_dist −0.195592   0.038209  −5.119 3.07e−07 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                  edf Ref.df Chi.sq  p−value
s(pointcount_id) 32.19    103  51.18 0.000216 ***
s(year_factor)    2.95      5  17.25  7.4e−05 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.274   Deviance explained = 35.4%
−ML = 333.15  Scale est. = 1        n = 742
```

```
Regulus.regulus
Family: poisson
Link function: log
AIC interaction: 990.81      AIC w/o interaction: 992.32
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                   Estimate Std. Error z value Pr(>|z|)
(Intercept)                        −3.33250    0.84465  −3.945 7.97e−05 ***
habitatcontrol                      2.34650    0.71308   3.291   0.0010 ***
habitatmanaged                      1.23929    0.73247   1.692   0.0907 .
year_since_dist                     0.11842    0.05704   2.076   0.0379 *
habitatcontrol:year_since_dist     −0.10393    0.04691  −2.215   0.0267 *
habitatmanaged:year_since_dist     −0.06330    0.04787  −1.322   0.1861
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq p−value
s(pointcount_id) 21.876    103  28.75  0.0222 *
s(year_factor)    4.408      5  76.42  <2e−16 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.239   Deviance explained = 26.7%
−ML = 494.32  Scale est. = 1         n = 742
```

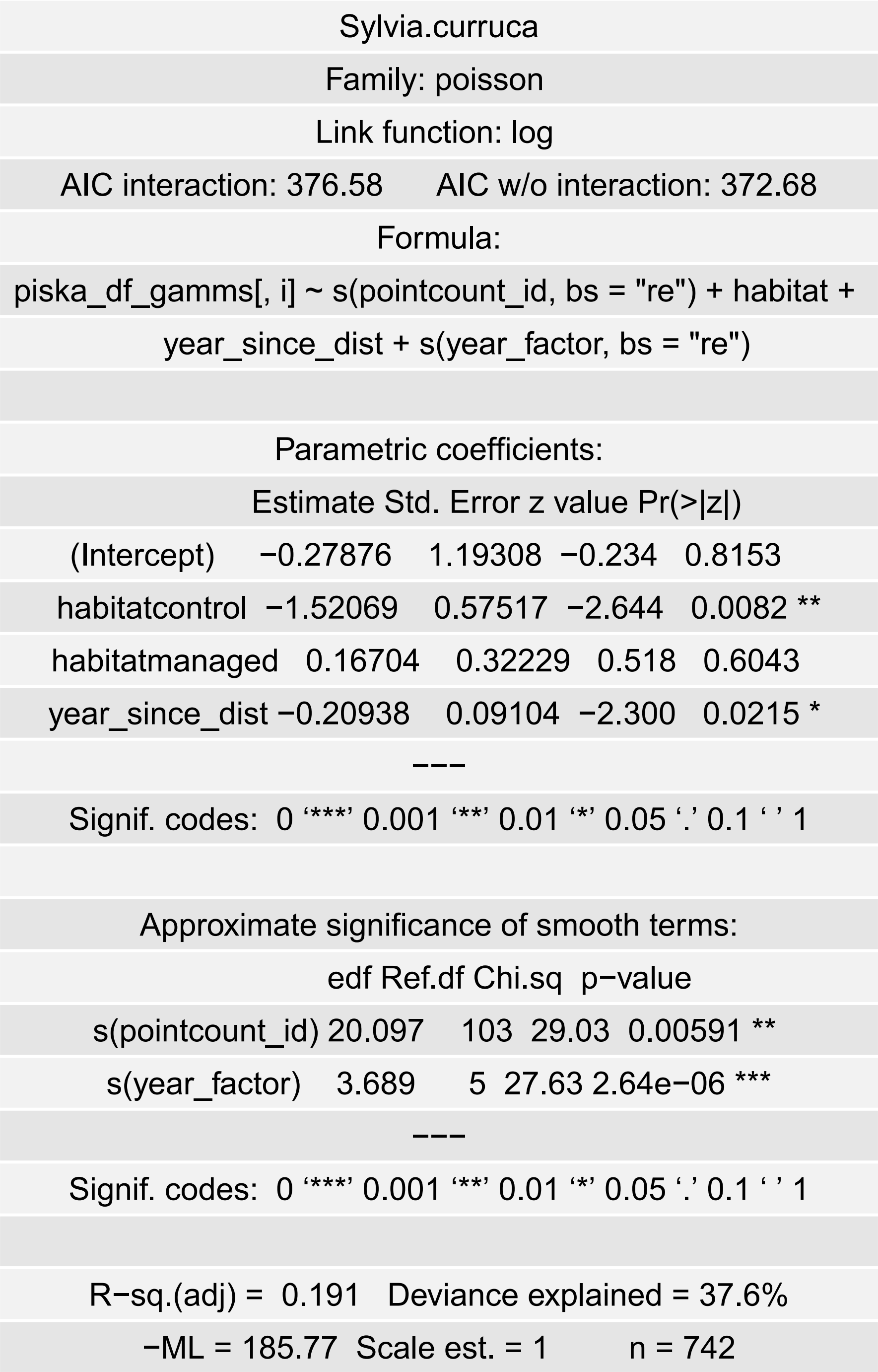


```
Spinus.spinus
Family: poisson
Link function: log
AIC interaction: 511.32      AIC w/o interaction: 510.77
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      −4.4816     2.5222  −1.777   0.0756 .
habitatcontrol    0.4158     0.2841   1.464   0.1433
habitatmanaged   −0.3040     0.2884  −1.054   0.2917
year_since_dist   0.1017     0.1747   0.582   0.5606
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq  p−value
s(pointcount_id) 27.22    103  46.59 3.38e−05 ***
s(year_factor)    4.41      5  33.34 5.69e−07 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.304   Deviance explained = 49.5%
−ML = 261.03  Scale est. = 1         n = 742
```

```
Sturnus.vulgaris
Family: poisson
Link function: log
AIC interaction: 417.12      AIC w/o interaction: 417.92
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                 Estimate Std. Error z value Pr(>|z|)
(Intercept)                    −4.068e−01  1.057e+00  −0.385   0.7002
habitatcontrol                 −3.625e+01  9.828e+06   0.000   1.0000
habitatmanaged                  7.031e−01  8.128e−01   0.865   0.3870
year_since_dist                −1.304e−01  7.849e−02  −1.662   0.0965 .
habitatcontrol:year_since_dist  1.467e−01  7.283e+05   0.000   1.0000
habitatmanaged:year_since_dist −1.462e−01  7.450e−02  −1.962   0.0497 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq p−value
s(pointcount_id) 33.917     75  75.61  <2e−16 ***
s(year_factor)    3.865      5  36.39  <2e−16 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =    0.4   Deviance explained = 56.4%
−ML = 212.33  Scale est. = 1         n = 742
NA
```

CAUTION: estimates for control unreliable: inflated standard errors (due to 0 observations in control)

```
Sylvia.atricapilla
Family: poisson
Link function: log
AIC interaction: 952.73      AIC w/o interaction: 952.53
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)     −1.05360    0.32467  −3.245  0.00117 **
habitatcontrol   0.29959    0.22238   1.347  0.17791
habitatmanaged   0.37263    0.20102   1.854  0.06378 .
year_since_dist −0.03879    0.02130  −1.821  0.06858 .
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq p−value
s(pointcount_id) 27.067    103 40.502 0.00108 **
s(year_factor)    2.647      5  7.931 0.01082 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.138   Deviance explained = 16.1%
−ML = 473.78  Scale est. = 1         n = 742
```



```
Sylvia.curruca
Family: poisson
Link function: log
AIC interaction: 376.58      AIC w/o interaction: 372.68
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
    year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)     −0.27876    1.19308  −0.234   0.8153
habitatcontrol  −1.52069    0.57517  −2.644   0.0082 **
habitatmanaged   0.16704    0.32229   0.518   0.6043
year_since_dist −0.20938    0.09104  −2.300   0.0215 *
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                   edf Ref.df Chi.sq  p−value
s(pointcount_id) 20.097    103  29.03  0.00591 **
s(year_factor)    3.689      5  27.63 2.64e−06 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.191   Deviance explained = 37.6%
−ML = 185.77  Scale est. = 1         n = 742
```

```
Troglodytes.troglodytes
Family: poisson
Link function: log
AIC interaction: 733.35      AIC w/o interaction: 730.79
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)     −0.59759    0.26156  −2.285  0.02233 *
habitatcontrol   0.47380    0.23257   2.037  0.04163 *
habitatmanaged  −0.88299    0.26854  −3.288  0.00101 **
year_since_dist −0.07903    0.01725  −4.583 4.59e−06 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq  p−value
s(pointcount_id) 27.0597    103 42.278 0.000848 ***
s(year_factor)    0.1912      5  0.278 0.202124
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.205   Deviance explained = 26.4%
−ML = 360.23  Scale est. = 1         n = 742
```

```
Turdus.merula
Family: poisson
Link function: log
AIC interaction: 1447.86      AIC w/o interaction: 1448
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat *
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                                 Estimate Std. Error z value Pr(>|z|)
(Intercept)                      −0.563042   0.343574  −1.639   0.1013
habitatcontrol                    0.621497   0.374378   1.660   0.0969 .
habitatmanaged                    0.480304   0.331018   1.451   0.1468
year_since_dist                   0.003181   0.024593   0.129   0.8971
habitatcontrol:year_since_dist −0.055573   0.027976  −1.986   0.0470 *
habitatmanaged:year_since_dist −0.025394   0.024040  −1.056   0.2908
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                        edf Ref.df Chi.sq  p−value
s(pointcount_id) 0.001775    103  0.001    0.929
s(year_factor)   3.596273      5 20.718 2.54e−05 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.0661   Deviance explained = 6.07%
−ML = 720.76  Scale est. = 1         n = 742
```

```
Turdus.philomelos
Family: poisson
Link function: log
AIC interaction: 1644.64      AIC w/o interaction: 1641.77
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
    year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      0.052425   0.217169   0.241   0.8092
habitatcontrol   0.037245   0.097060   0.384   0.7012
habitatmanaged  −0.184821   0.092046  −2.008   0.0447 *
year_since_dist −0.006478   0.015024  −0.431   0.6663
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                     edf Ref.df Chi.sq  p−value
s(pointcount_id) 0.001187    103  0.001 0.997566
s(year_factor)   3.576554      5 17.821 0.000147 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =  0.0787   Deviance explained = 6.62%
−ML = 819.63  Scale est. = 1         n = 742
```

```
Turdus.viscivorus
Family: poisson
Link function: log
AIC interaction: 1040.24      AIC w/o interaction: 1039.98
Formula:
piska_df_gamms[, i] ~ s(pointcount_id, bs = "re") + habitat +
year_since_dist + s(year_factor, bs = "re")

Parametric coefficients:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)      0.12382    1.08910   0.114 0.909481
habitatcontrol  −0.58590    0.16247  −3.606 0.000311 ***
habitatmanaged  −0.38618    0.13458  −2.870 0.004110 **
year_since_dist −0.08450    0.07887  −1.071 0.284009
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                    edf Ref.df Chi.sq p−value
s(pointcount_id) 0.01216    103  0.012   0.546
s(year_factor)   4.70015      5 66.818  <2e−16 ***
−−−
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R−sq.(adj) =   0.16   Deviance explained =   20%
−ML = 525.89  Scale est. = 1         n = 742
```

Figure S7 - Results of PERMANOVA analysis (balanced design)

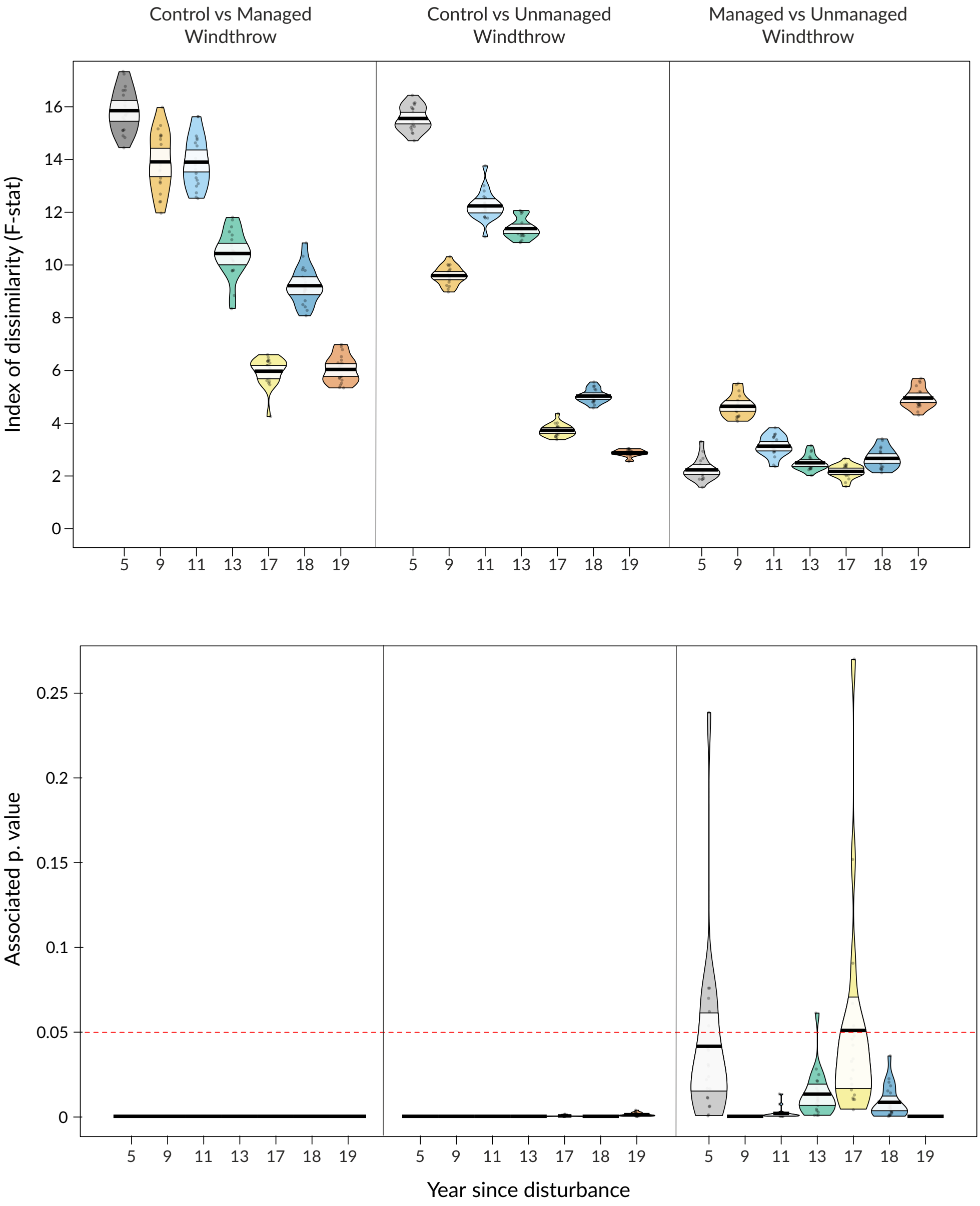

Control vs Managed Windthrow
Control vs Unmanaged Windthrow
Managed vs Unmanaged Windthrow
Index of dissimilarity (F-stat)
0
2
4
6
8
10
12
14
16
5
9
11
13
17
18
19
Associated p. value
0
0.05
0.1
0.15
0.2
0.25
Year since disturbance

TABLE S1

(summary of abundances)

species_name	habitat_PECBMC	abundance_total	abundance_unmanaged	abundance_managed	abundance_control
Fringilla coelebs	other	1915	553	661	701
Phylloscopus trochilus	forest	936	325	487	124
Dendrocopos major	other	686	258	262	166
Turdus philomelos	forest	681	219	256	206
Erithacus rubecula	other	677	193	262	222
Anthus trivialis	forest	541	183	218	140
Cuculus canorus	other	496	183	193	120
Garrulus glandarius	forest	482	159	213	110
Turdus merula	other	469	135	221	113
Lullula arborea	other	464	148	282	34
Phylloscopus collybita	forest	395	114	165	116
Parus major	other	379	147	154	78
Periparus ater	forest	367	97	123	147
Phylloscopus sibilatrix	forest	347	102	83	162
Columba palumbus	other	339	112	143	84
Emberiza citrinella	farmland	331	93	232	6
Lophophanes cristatus	forest	304	99	96	109
Turdus viscivorus	forest	278	113	108	57
Regulus regulus	forest	249	49	95	105
Corvus corax	other	236	84	105	47
Poecile montanus	forest	217	91	80	46
Sylvia atricapilla	forest	211	49	102	60
Oriolus oriolus	other	211	84	107	20
Dryocopus martius	forest	160	67	63	30
Troglodytes troglodytes	forest	149	50	28	71
Alauda arvensis	farmland	140	34	106	0
Prunella modularis	forest	137	45	52	40
Spinus spinus	forest	110	31	34	45
Columba oenas	forest	85	27	29	29
Sturnus vulgaris	farmland	84	49	35	0
Phoenicurus phoenicurus	forest	79	53	18	8
Corvus cornix	other	71	11	56	4
Grus grus	other	70	22	33	15
Certhia familiaris	forest	68	20	13	35
Sylvia curruca	other	60	21	35	4
Lanius collurio	farmland	50	22	26	2
Pyrrhula pyrrhula	forest	48	18	17	13
Muscicapa striata	forest	45	30	6	9
Oenanthe oenanthe	other	41	10	31	0
Sylvia communis	farmland	41	7	34	0
Upupa epops	other	39	26	13	0
Chloris chloris	other	39	29	10	0
Tringa ochropus	forest	38	15	20	3
Poecile palustris	forest	36	16	10	10
Streptopelia turtur	farmland	36	18	17	1
Sitta europaea	forest	25	11	5	9
Sylvia borin	other	24	4	19	1
Gallinago gallinago	other	24	0	23	1
Aegithalos caudatus	other	14	4	4	6
Coccothraustes coccothraustes	forest	13	1	10	2
Crex crex	NA	12	2	10	0
Apus apus	other	11	10	1	0
Buteo buteo	other	11	4	3	4
Cyanistes caeruleus	other	10	5	4	1
Ficedula hypoleuca	forest	10	4	2	4
Motacilla alba	other	10	0	10	0
Coturnix coturnix	NA	10	6	4	0
Anas platyrhynchos	other	9	4	5	0
Vanellus vanellus	farmland	8	0	8	0
Caprimulgus europaeus	NA	8	8	0	0

species_name	habitat_PECBMC	abundance_total	abundance_unmanaged	abundance_managed	abundance_control
Regulus ignicapilla	forest	8	2	0	6
Jynx torquilla	other	7	2	5	0
Accipiter nisus	forest	7	1	4	2
Accipiter gentilis	NA	6	1	1	4
Turdus pilaris	other	6	1	5	0
Phoenicurus ochruros	other	5	2	2	1
Loxia sp.	NA	5	3	1	1
Strix aluco	NA	5	0	2	3
Lanius excubitor	NA	5	2	3	0
Lyrurus tetrix	NA	4	1	3	0
Falco subbuteo	NA	4	1	3	0
Scolopax rusticola	NA	4	1	2	1
Anthus campestris	other	4	0	4	0
Botaurus stellaris	NA	3	0	2	1
Saxicola rubetra	farmland	3	0	3	0
Hippolais icterina	other	3	0	3	0
Haliaeetus albicilla	NA	2	2	0	0
Dendrocopos minor	forest	2	2	0	0
Bucephala clangula	NA	2	0	2	0
Fringilla montifringilla	NA	2	0	2	0
Acrocephalus palustris	other	2	0	2	0
Nucifraga caryocatactes	forest	2	1	0	1
Acrocephalus arundinaceus	other	2	1	1	0
Pernis apivorus	NA	2	1	1	0
Circus aeruginosus	other	1	0	1	0
Ciconia nigra	NA	1	0	0	1
Turdus iliacus	NA	1	0	1	0
Dendrocopos medius	NA	1	0	0	1
Picus canus	forest	1	0	1	0
Picus viridis	forest	1	1	0	0
Ficedula albicollis	forest	1	0	0	1
Aquila pomarina	NA	1	0	1	0
Emberiza calandra	farmland	1	0	1	0

TABLE S2

(marginal means pairwise comparison results)

contrast	year_since_dist	estimate	SE	df	t.ratio	p.value	pair
control - managed	5	0.410	0.069	678.050	5.929	0.000	abundance_for
control - unmanaged	5	0.110	0.071	678.050	1.536	0.275	abundance_for
managed - unmanaged	5	-0.301	0.068	678.050	-4.425	0.000	abundance_for
control - managed	6	0.372	0.064	678.050	5.802	0.000	abundance_for
control - unmanaged	6	0.087	0.066	678.050	1.312	0.389	abundance_for
managed - unmanaged	6	-0.285	0.063	678.050	-4.526	0.000	abundance_for
control - managed	7	0.335	0.060	678.050	5.617	0.000	abundance_for
control - unmanaged	7	0.064	0.062	678.050	1.044	0.550	abundance_for
managed - unmanaged	7	-0.270	0.059	678.050	-4.618	0.000	abundance_for
control - managed	8	0.297	0.055	678.050	5.355	0.000	abundance_for
control - unmanaged	8	0.042	0.058	678.050	0.726	0.748	abundance_for
managed - unmanaged	8	-0.255	0.054	678.050	-4.687	0.000	abundance_for
control - managed	9	0.259	0.052	678.050	4.993	0.000	abundance_for
control - unmanaged	9	0.019	0.054	678.050	0.354	0.933	abundance_for
managed - unmanaged	9	-0.240	0.051	678.050	-4.719	0.000	abundance_for
control - managed	10	0.221	0.049	678.050	4.510	0.000	abundance_for
control - unmanaged	10	-0.004	0.051	678.050	-0.069	0.997	abundance_for
managed - unmanaged	10	-0.224	0.048	678.050	-4.690	0.000	abundance_for
control - managed	11	0.183	0.047	678.050	3.896	0.000	abundance_for
control - unmanaged	11	-0.026	0.049	678.050	-0.530	0.857	abundance_for
managed - unmanaged	11	-0.209	0.046	678.050	-4.579	0.000	abundance_for
control - managed	12	0.145	0.046	678.050	3.160	0.005	abundance_for
control - unmanaged	12	-0.049	0.048	678.050	-1.008	0.572	abundance_for
managed - unmanaged	12	-0.194	0.044	678.050	-4.367	0.000	abundance_for
control - managed	13	0.107	0.046	678.050	2.336	0.052	abundance_for
control - unmanaged	13	-0.071	0.049	678.050	-1.472	0.305	abundance_for
managed - unmanaged	13	-0.179	0.044	678.050	-4.052	0.000	abundance_for
control - managed	14	0.069	0.047	678.050	1.479	0.302	abundance_for
control - unmanaged	14	-0.094	0.050	678.050	-1.894	0.141	abundance_for
managed - unmanaged	14	-0.164	0.045	678.050	-3.650	0.001	abundance_for
control - managed	15	0.032	0.049	678.050	0.645	0.795	abundance_for
control - unmanaged	15	-0.117	0.052	678.050	-2.255	0.063	abundance_for
managed - unmanaged	15	-0.148	0.046	678.050	-3.194	0.004	abundance_for
control - managed	16	-0.006	0.052	678.050	-0.122	0.992	abundance_for
control - unmanaged	16	-0.139	0.055	678.050	-2.547	0.030	abundance_for
managed - unmanaged	16	-0.133	0.049	678.050	-2.721	0.018	abundance_for
control - managed	17	-0.044	0.055	678.050	-0.800	0.703	abundance_for
control - unmanaged	17	-0.162	0.058	678.050	-2.774	0.016	abundance_for
managed - unmanaged	17	-0.118	0.052	678.050	-2.262	0.062	abundance_for
control - managed	18	-0.082	0.059	678.050	-1.381	0.351	abundance_for
control - unmanaged	18	-0.185	0.063	678.050	-2.947	0.009	abundance_for
managed - unmanaged	18	-0.103	0.056	678.050	-1.835	0.159	abundance_for
control - managed	19	-0.120	0.064	678.050	-1.873	0.147	abundance_for
control - unmanaged	19	-0.207	0.067	678.050	-3.075	0.006	abundance_for
managed - unmanaged	19	-0.087	0.060	678.050	-1.452	0.315	abundance_for

contrast	year_since_dist	estimate	SE	df	t.ratio	p.value	pair
control - managed	5	0.463	0.074	693.741	6.293	0.000	richness_for
control - unmanaged	5	0.151	0.075	693.741	2.009	0.111	richness_for
managed - unmanaged	5	-0.312	0.073	693.741	-4.258	0.000	richness_for
control - managed	6	0.429	0.068	693.741	6.347	0.000	richness_for
control - unmanaged	6	0.132	0.069	693.741	1.896	0.141	richness_for
managed - unmanaged	6	-0.298	0.067	693.741	-4.425	0.000	richness_for
control - managed	7	0.396	0.062	693.741	6.371	0.000	richness_for
control - unmanaged	7	0.112	0.064	693.741	1.750	0.188	richness_for
managed - unmanaged	7	-0.284	0.062	693.741	-4.598	0.000	richness_for
control - managed	8	0.362	0.057	693.741	6.345	0.000	richness_for
control - unmanaged	8	0.092	0.059	693.741	1.562	0.263	richness_for
managed - unmanaged	8	-0.270	0.057	693.741	-4.767	0.000	richness_for
control - managed	9	0.328	0.053	693.741	6.239	0.000	richness_for
control - unmanaged	9	0.072	0.054	693.741	1.323	0.383	richness_for
managed - unmanaged	9	-0.256	0.052	693.741	-4.914	0.000	richness_for
control - managed	10	0.295	0.049	693.741	6.013	0.000	richness_for
control - unmanaged	10	0.052	0.051	693.741	1.024	0.562	richness_for
managed - unmanaged	10	-0.243	0.048	693.741	-5.011	0.000	richness_for
control - managed	11	0.261	0.046	693.741	5.628	0.000	richness_for
control - unmanaged	11	0.032	0.048	693.741	0.665	0.784	richness_for
managed - unmanaged	11	-0.229	0.046	693.741	-5.021	0.000	richness_for
control - managed	12	0.227	0.045	693.741	5.062	0.000	richness_for
control - unmanaged	12	0.012	0.047	693.741	0.260	0.963	richness_for
managed - unmanaged	12	-0.215	0.044	693.741	-4.905	0.000	richness_for
control - managed	13	0.194	0.045	693.741	4.331	0.000	richness_for
control - unmanaged	13	-0.008	0.047	693.741	-0.164	0.985	richness_for
managed - unmanaged	13	-0.201	0.043	693.741	-4.643	0.000	richness_for
control - managed	14	0.160	0.046	693.741	3.491	0.001	richness_for
control - unmanaged	14	-0.028	0.048	693.741	-0.572	0.835	richness_for
managed - unmanaged	14	-0.187	0.044	693.741	-4.249	0.000	richness_for
control - managed	15	0.126	0.048	693.741	2.623	0.024	richness_for
control - unmanaged	15	-0.047	0.051	693.741	-0.937	0.617	richness_for
managed - unmanaged	15	-0.174	0.046	693.741	-3.766	0.001	richness_for
control - managed	16	0.093	0.051	693.741	1.798	0.171	richness_for
control - unmanaged	16	-0.067	0.054	693.741	-1.244	0.428	richness_for
managed - unmanaged	16	-0.160	0.049	693.741	-3.251	0.003	richness_for
control - managed	17	0.059	0.056	693.741	1.057	0.541	richness_for
control - unmanaged	17	-0.087	0.058	693.741	-1.491	0.296	richness_for
managed - unmanaged	17	-0.146	0.053	693.741	-2.751	0.017	richness_for
control - managed	18	0.025	0.061	693.741	0.416	0.909	richness_for
control - unmanaged	18	-0.107	0.064	693.741	-1.686	0.211	richness_for
managed - unmanaged	18	-0.132	0.058	693.741	-2.291	0.058	richness_for
control - managed	19	-0.008	0.066	693.741	-0.128	0.991	richness_for
control - unmanaged	19	-0.127	0.069	693.741	-1.838	0.158	richness_for
managed - unmanaged	19	-0.119	0.063	693.741	-1.883	0.144	richness_for
control - managed	5	-4.851	0.791	688.114	-6.131	0.000	abundance_farm
control - unmanaged	5	-4.716	0.795	688.114	-5.930	0.000	abundance_farm
managed - unmanaged	5	0.135	0.154	688.114	0.875	0.656	abundance_farm
control - managed	6	-4.656	0.722	688.114	-6.450	0.000	abundance_farm

contrast	year_since_dist	estimate	SE	df	t.ratio	p.value	pair
control - unmanaged	6	-4.471	0.726	688.114	-6.163	0.000	abundance_farm
managed - unmanaged	6	0.184	0.144	688.114	1.284	0.405	abundance_farm
control - managed	7	-4.460	0.655	688.114	-6.814	0.000	abundance_farm
control - unmanaged	7	-4.226	0.658	688.114	-6.424	0.000	abundance_farm
managed - unmanaged	7	0.234	0.135	688.114	1.731	0.194	abundance_farm
control - managed	8	-4.265	0.590	688.114	-7.229	0.000	abundance_farm
control - unmanaged	8	-3.981	0.593	688.114	-6.711	0.000	abundance_farm
managed - unmanaged	8	0.283	0.129	688.114	2.197	0.072	abundance_farm
control - managed	9	-4.069	0.529	688.114	-7.690	0.000	abundance_farm
control - unmanaged	9	-3.736	0.533	688.114	-7.015	0.000	abundance_farm
managed - unmanaged	9	0.333	0.126	688.114	2.647	0.023	abundance_farm
control - managed	10	-3.874	0.474	688.114	-8.180	0.000	abundance_farm
control - unmanaged	10	-3.491	0.478	688.114	-7.309	0.000	abundance_farm
managed - unmanaged	10	0.382	0.125	688.114	3.047	0.007	abundance_farm
control - managed	11	-3.678	0.425	688.114	-8.649	0.000	abundance_farm
control - unmanaged	11	-3.246	0.431	688.114	-7.541	0.000	abundance_farm
managed - unmanaged	11	0.432	0.128	688.114	3.366	0.002	abundance_farm
control - managed	12	-3.483	0.387	688.114	-8.999	0.000	abundance_farm
control - unmanaged	12	-3.001	0.394	688.114	-7.620	0.000	abundance_farm
managed - unmanaged	12	0.481	0.134	688.114	3.593	0.001	abundance_farm
control - managed	13	-3.287	0.362	688.114	-9.082	0.000	abundance_farm
control - unmanaged	13	-2.756	0.371	688.114	-7.429	0.000	abundance_farm
managed - unmanaged	13	0.531	0.142	688.114	3.735	0.001	abundance_farm
control - managed	14	-3.092	0.353	688.114	-8.760	0.000	abundance_farm
control - unmanaged	14	-2.511	0.364	688.114	-6.891	0.000	abundance_farm
managed - unmanaged	14	0.580	0.152	688.114	3.807	0.000	abundance_farm
control - managed	15	-2.896	0.361	688.114	-8.020	0.000	abundance_farm
control - unmanaged	15	-2.267	0.375	688.114	-6.043	0.000	abundance_farm
managed - unmanaged	15	0.630	0.164	688.114	3.830	0.000	abundance_farm
control - managed	16	-2.701	0.385	688.114	-7.006	0.000	abundance_farm
control - unmanaged	16	-2.022	0.401	688.114	-5.035	0.000	abundance_farm
managed - unmanaged	16	0.679	0.178	688.114	3.821	0.000	abundance_farm
control - managed	17	-2.505	0.423	688.114	-5.920	0.000	abundance_farm
control - unmanaged	17	-1.777	0.441	688.114	-4.030	0.000	abundance_farm
managed - unmanaged	17	0.729	0.192	688.114	3.791	0.000	abundance_farm
control - managed	18	-2.310	0.471	688.114	-4.903	0.000	abundance_farm
control - unmanaged	18	-1.532	0.490	688.114	-3.125	0.005	abundance_farm
managed - unmanaged	18	0.778	0.208	688.114	3.750	0.001	abundance_farm
control - managed	19	-2.114	0.526	688.114	-4.017	0.000	abundance_farm
control - unmanaged	19	-1.287	0.547	688.114	-2.354	0.049	abundance_farm
managed - unmanaged	19	0.828	0.224	688.114	3.703	0.001	abundance_farm
control - managed	5	-5.589	0.941	674.323	-5.941	0.000	richness_farm
control - unmanaged	5	-5.360	0.943	674.323	-5.684	0.000	richness_farm
managed - unmanaged	5	0.228	0.176	674.323	1.300	0.395	richness_farm
control - managed	6	-5.404	0.886	674.323	-6.102	0.000	richness_farm
control - unmanaged	6	-5.146	0.888	674.323	-5.798	0.000	richness_farm
managed - unmanaged	6	0.258	0.165	674.323	1.569	0.260	richness_farm
control - managed	7	-5.219	0.834	674.323	-6.257	0.000	richness_farm
control - unmanaged	7	-4.931	0.836	674.323	-5.901	0.000	richness_farm

contrast	year_since_dist	estimate	SE	df	t.ratio	p.value	pair
managed - unmanaged	7	0.288	0.156	674.323	1.852	0.154	richness_farm
control - managed	8	-5.035	0.787	674.323	-6.399	0.000	richness_farm
control - unmanaged	8	-4.716	0.788	674.323	-5.986	0.000	richness_farm
managed - unmanaged	8	0.319	0.149	674.323	2.135	0.084	richness_farm
control - managed	9	-4.850	0.744	674.323	-6.516	0.000	richness_farm
control - unmanaged	9	-4.501	0.745	674.323	-6.040	0.000	richness_farm
managed - unmanaged	9	0.349	0.145	674.323	2.399	0.044	richness_farm
control - managed	10	-4.665	0.708	674.323	-6.593	0.000	richness_farm
control - unmanaged	10	-4.287	0.709	674.323	-6.048	0.000	richness_farm
managed - unmanaged	10	0.379	0.144	674.323	2.623	0.024	richness_farm
control - managed	11	-4.481	0.678	674.323	-6.611	0.000	richness_farm
control - unmanaged	11	-4.072	0.679	674.323	-5.995	0.000	richness_farm
managed - unmanaged	11	0.409	0.146	674.323	2.792	0.015	richness_farm
control - managed	12	-4.296	0.656	674.323	-6.554	0.000	richness_farm
control - unmanaged	12	-3.857	0.658	674.323	-5.865	0.000	richness_farm
managed - unmanaged	12	0.439	0.151	674.323	2.901	0.011	richness_farm
control - managed	13	-4.111	0.642	674.323	-6.406	0.000	richness_farm
control - unmanaged	13	-3.643	0.645	674.323	-5.649	0.000	richness_farm
managed - unmanaged	13	0.469	0.159	674.323	2.954	0.009	richness_farm
control - managed	14	-3.926	0.637	674.323	-6.163	0.000	richness_farm
control - unmanaged	14	-3.428	0.641	674.323	-5.346	0.000	richness_farm
managed - unmanaged	14	0.499	0.168	674.323	2.962	0.009	richness_farm
control - managed	15	-3.742	0.642	674.323	-5.832	0.000	richness_farm
control - unmanaged	15	-3.213	0.647	674.323	-4.966	0.000	richness_farm
managed - unmanaged	15	0.529	0.180	674.323	2.938	0.010	richness_farm
control - managed	16	-3.557	0.655	674.323	-5.429	0.000	richness_farm
control - unmanaged	16	-2.998	0.662	674.323	-4.529	0.000	richness_farm
managed - unmanaged	16	0.559	0.193	674.323	2.894	0.011	richness_farm
control - managed	17	-3.372	0.677	674.323	-4.979	0.000	richness_farm
control - unmanaged	17	-2.784	0.686	674.323	-4.060	0.000	richness_farm
managed - unmanaged	17	0.589	0.207	674.323	2.838	0.013	richness_farm
control - managed	18	-3.188	0.707	674.323	-4.508	0.000	richness_farm
control - unmanaged	18	-2.569	0.717	674.323	-3.583	0.001	richness_farm
managed - unmanaged	18	0.619	0.223	674.323	2.777	0.016	richness_farm
control - managed	19	-3.003	0.744	674.323	-4.038	0.000	richness_farm
control - unmanaged	19	-2.354	0.755	674.323	-3.118	0.005	richness_farm
managed - unmanaged	19	0.649	0.239	674.323	2.714	0.019	richness_farm

TABLE S3

(PERMANOVA results)

pairs	F.val	P	year	year_since_dist
control vs unmanaged	15.90784958	3.00E-04	2007	5
control vs managed	18.11097325	3.00E-04	2007	5
unmanaged vs managed	2.534265574	0.0036	2007	5
control vs unmanaged	9.910906518	3.00E-04	2011	9
control vs managed	15.66629812	3.00E-04	2011	9
unmanaged vs managed	5.604767111	3.00E-04	2011	9
control vs unmanaged	12.63750346	3.00E-04	2013	11
control vs managed	15.92727812	3.00E-04	2013	11
unmanaged vs managed	3.704805906	3.00E-04	2013	11
control vs unmanaged	11.7217317	3.00E-04	2015	13
control vs managed	11.88918991	3.00E-04	2015	13
unmanaged vs managed	2.931994636	0.0012	2015	13
control vs unmanaged	3.887422821	3.00E-04	2019	17
control vs managed	6.912233947	3.00E-04	2019	17
unmanaged vs managed	2.549265657	0.0066	2019	17
control vs unmanaged	5.206987205	3.00E-04	2020	18
control vs managed	11.01374853	3.00E-04	2020	18
unmanaged vs managed	3.073309883	9.00E-04	2020	18
control vs unmanaged	2.896939757	9.00E-04	2021	19
control vs managed	6.988284421	3.00E-04	2021	19
unmanaged vs managed	6.022283571	3.00E-04	2021	19

Chapter III

Active post-disturbance management in Białowieża Forest shifts bird communities toward farmland assemblages

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Abstract

Ecological disturbances, such as insect outbreaks, shape animal communities in forest ecosystems – for example, by promoting open-habitat species. Active post-disturbance management can lead to additional changes, facilitating further influx of open-habitat species, including those typical of farmland. However, these community shifts are rarely quantified or evaluated, especially in natural forest ecosystems with limited history of past management. We assessed breeding bird communities in the disturbed landscape of Białowieża Forest, a highly natural forest ecosystem located in North-Eastern Poland. We recorded fifteen 1-minute samples of bird sounds within a 4-hour window during two time periods (April and May–June) at 137 point-count sites. The point-count sites were located within two types of Norway spruce-dominated forest habitats disturbed by a bark beetle outbreak: (1) unmanaged after disturbance, and (2) actively managed after disturbance (primarily through salvage logging), as well as two reference habitats: (3) unaffected spruce forest and (4) nearby farmland. We compared bird communities across these four habitats to assess the ecological consequences of bark beetle outbreaks and post-disturbance management on bird richness, diversity, and community similarity. The bark beetle disturbance caused a shift in bird community composition, moving from a typical undisturbed forest assemblage toward one more characteristic of farmland, with increased farmland bird richness. Active post-disturbance management led to a further shift in the same direction, resulting in even greater richness of farmland species and closer resemblance to farmland bird assemblages. Notably, active management of the disturbed areas produced a greater deviation from the forest-typical bird communities than the initial bark beetle disturbance. Our results suggest that active post-disturbance management substantially alters bird communities and thus may disrupt natural successional processes in forest ecosystems. We recommend limiting such management interventions to protect unique forest communities, particularly in forests of high conservation value. However, we also propose that managed disturbances could be considered potentially important habitats for farmland birds.

Key words

salvage logging; avian communities; intensive management; forest disturbance

1. Introduction

Ecological disturbances, such as insect outbreaks, storms and fires, are key factors shaping the dynamics of temperate European forests (Senf and Seidl, 2021; Turner, 2010). By killing trees and opening the canopy, they create early-successional habitats characterized by high structural diversity (Swanson et al., 2011). In Europe, such disturbance-induced gaps are usually managed through "salvage logging" (i.e., removal of dead and damaged trees), often followed by additional activities such as tilling and tree replanting (Lindenmayer et al., 2012a; Sanginés de Cárcer et al., 2021). While this approach is aimed at mitigating economic losses in timber production, it often leads to the degradation of other ecosystem services, such as biodiversity, soil quality and water regulation (Leverkus et al., 2020). Therefore, the structurally heterogeneous gaps created by natural disturbances are increasingly left unaltered by forest management operations, especially in protected areas (Müller et al., 2018). As both natural disturbances and active post-disturbance management have important impacts on ecosystem functioning, understanding their consequences is becoming increasingly important for developing evidence-based forest management and restoration policies (Hlásny et al., 2021; Patacca et al., 2023; Rabesandratana, 2023).

Natural disturbances substantially alter forest structure and thus affect most organisms within the ecosystem. Increased canopy openness and greater sunlight exposure in disturbance-induced gaps lead to an influx of open-habitat taxa, including many farmland-associated species (Ram et al., 2020; Żmihorski et al., 2019). However, the presence of various disturbance legacies (e.g., surviving trees, snags, and dead wood) provides critical refuges for saproxylic organisms and other forest-dependent species (Cours et al., 2023; Franklin et al., 2000; Thorn et al., 2018). By removing these legacies, active post-disturbance management triggers an additional shift in community composition, often characterized by increases in open-habitat and farmland-related taxa and declines in closed-canopy forest species (Thorn et al., 2018; Walesiak et al., 2024; Wermelinger et al., 2025). It also sets community succession on a distinct pathway, leading to long-term changes in species composition (Walesiak et al., 2024). Thus, active post-disturbance management may be considered a "post-disturbance disturbance", altering regeneration processes within the ecosystem (Orczewska et al., 2019; Walesiak et al., 2024; Żmihorski, 2010). In natural forest ecosystems, where the protection of characteristic communities and ecological processes is a key conservation priority, this may represent a significant threat (Mikusiński et al., 2018).

However, the community changes induced by disturbances are rarely evaluated in the context of natural forest ecosystems, which are increasingly uncommon in Europe (Sabatini et al., 2018). In natural temperate forests – typically more heterogeneous and structurally complex – disturbances often occur as small-scale events, since disturbance agents are constrained by environmental complexity. This contrasts with the large-scale disturbances more typical of managed forests (Aszalós et al., 2022; Janda et al., 2025; Maroschek et al., 2024). Small-scale gaps in natural forests may follow distinct successional pathways as their suitability to host open-canopy species may be limited (Fuller, 2000; Kuuluvainen and Aakala, 2011; Ram et al., 2023). In contrast to managed forests, biotic communities of natural forests often host high species richness and abundance of forest specialists prior to the disturbance event (Bengtsson et al., 2000; Moning and Müller, 2009; Nirhamo et al., 2025). Furthermore, existing studies often lack reference ecosystems (e.g., undisturbed forest), making it difficult to compare the community shifts triggered by natural disturbances and post-disturbance management. Overall, the community changes caused by disturbances and post-disturbance management in natural forests remain largely unexplored.

In this study, we examined the effects of European spruce bark beetle (*Ips typographus*) outbreak and subsequent active management on the bird community composition in Norway spruce (*Picea abies*)-dominated stands in the Białowieża Forest, Poland. Birds were chosen as model organisms because they are sensitive to changes in forest composition and successional stages, making them effective indicators of habitat transformation resulting from both natural and anthropogenic disturbances (Wesołowski et al., 2018; Winter and Brambach, 2011). The large-scale bark beetle outbreak that occurred in Białowieża Forest between 2012 and 2019 led to significant dieback of spruce stands, creating semi-open forest gaps (Stereńczak et al., 2020). Some of these gaps were subjected to salvage logging and other management actions (Mikusiński et al., 2018), allowing for a comparison between two distinct disturbed forest habitats: actively managed and unmanaged. We assessed bird community composition across these two habitats and compared them with two control habitats: undisturbed spruce stands and adjacent, extensively managed open habitats (farmlands). This habitat mosaic provided a rare opportunity to empirically assess the ecological impacts of both disturbance and post-disturbance management in a forest of high naturalness.

Based on previous studies in managed forest ecosystems, we hypothesized that: First, the bark beetle outbreak would shift bird communities toward assemblages typical of farmland, with active management amplifying this effect. Second, given the high naturalness of the studied forest and the presence of rich disturbance legacies (Jaroszewicz et al., 2019), we expected that active management would produce a greater deviation from forest-typical bird communities than the bark beetle disturbance. Third, we predicted a gradual increase in the richness of farmland bird species along the habitat gradient – from undisturbed forest through unmanaged and managed disturbed stands, to farmland ecosystems.

2. Methods

2.1. Study site

Our study took place in the Białowieża Forest, located in northeastern Poland, which is recognized as both a UNESCO World Heritage Site and a Natura 2000 area (52°41’36.4”N 23°53’50.4”E; Figure 1). Białowieża Forest is among the largest remaining fragments of the ancient temperate lowland forests that once covered the European plain. It encompasses a wide variety of habitats, including mainly mixed forests rich in deciduous species, but also coniferous forests dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (Jaroszewicz et al., 2019). The most common tree species include common hornbeam (*Carpinus betulus*), pedunculate oak (*Quercus robur*), small-leaved lime (*Tilia cordata*), black alder (*Alnus glutinosa*), Scots pine, Norway spruce, and two birch species (*Betula pendula* and *Betula pubescens*; Faliński, 2003). Despite some parts being subject to limited forest management in the past (e.g., timber extraction and localized tree planting), the whole Białowieża Forest retains a high level of naturalness and old-growth characteristics. This includes complex and heterogeneous forest structure, a high volume of dead wood, a diverse array of microhabitats, and a high proportion of old trees (Jaroszewicz et al., 2019; Przepióra and Ciach, 2023; Samojlik et al., 2013). The surroundings of the Białowieża Forest are dominated by a mosaic of extensively managed pastures, fields, meadows, and fallow lands, interspersed with trees, shrubs, and small woodland patches.

Białowieża Forest is recognized as an Important Bird Area, hosting a total of 180 recorded breeding bird species. These include rare forest passerines such as the red-breasted flycatcher (*Ficedula parva*) and the collared flycatcher (*Ficedula albicollis*), as well as an almost complete European woodpecker community, including the grey-headed woodpecker (*Picus canus*), white-backed woodpecker (*Dendrocopos leucotos*), middle spotted woodpecker (*Dendrocoptes medius*), and three-toed woodpecker (*Picoides tridactylus*). The forest also supports a rich owl community, featuring species such as the pygmy owl (*Glaucidium passerinum*), boreal owl (*Aegolius funereus*), Ural owl (*Strix uralensis*), and Eurasian eagle-owl (*Bubo bubo*; BirdLife International, 2025). The open landscapes surrounding the Białowieża Forest also harbor a diverse community of birds, including many protected and declining species dependent on open habitats. Notable examples include the lesser spotted eagle (*Clanga pomarina*), corn crake (*Crex crex*), Eurasian skylark (*Alauda arvensis*), red-backed shrike (*Lanius collurio*) and northern lapwing (*Vanellus vanellus*; BirdLife International, 2021).

From 2012 to 2019 (peaking in 2015-2018), Białowieża Forest experienced the largest spruce bark beetle outbreak in modern history, leading to the death of about 40% of Norway spruce trees, particularly large and old individuals (Kamińska et al., 2021; Stereńczak et al., 2020; Figure 1). This outbreak had profound effects on forest structure, transforming previously closed-canopy stands into more open habitats characterized by a high proportion of standing dead trees and large amounts of dead wood. Immediately after the outbreak, salvage logging was conducted in many affected areas of the forest, during which both standing dead trees and downed woody debris were removed. These operations were mostly conducted in patches of around 1 hectare, totaling 675 hectares – including 230 hectares of old-growth stands. As a result, these patches were left completely open and treeless, with nearly all dead wood removed. In some of these areas, additional management practices such as tilling, tree planting, and fencing were implemented, further transforming the ecosystem. In 2017, following intervention by the European Union, all the post-disturbance management operations in Białowieża Forest were halted (Mikusiński et al., 2018). Thus, the ecosystem underwent two major disturbances: first, the bark beetle outbreak, and second, the subsequent active management applied in part of the affected area. This resulted in a mosaic of undisturbed and disturbed forest patches (varying in disturbance severity and implemented management strategy) across the spruce-dominated stands of Białowieża Forest. This disturbed landscape provided a unique experimental setting to assess the impacts of bark beetle outbreak and post-disturbance management on bird communities.

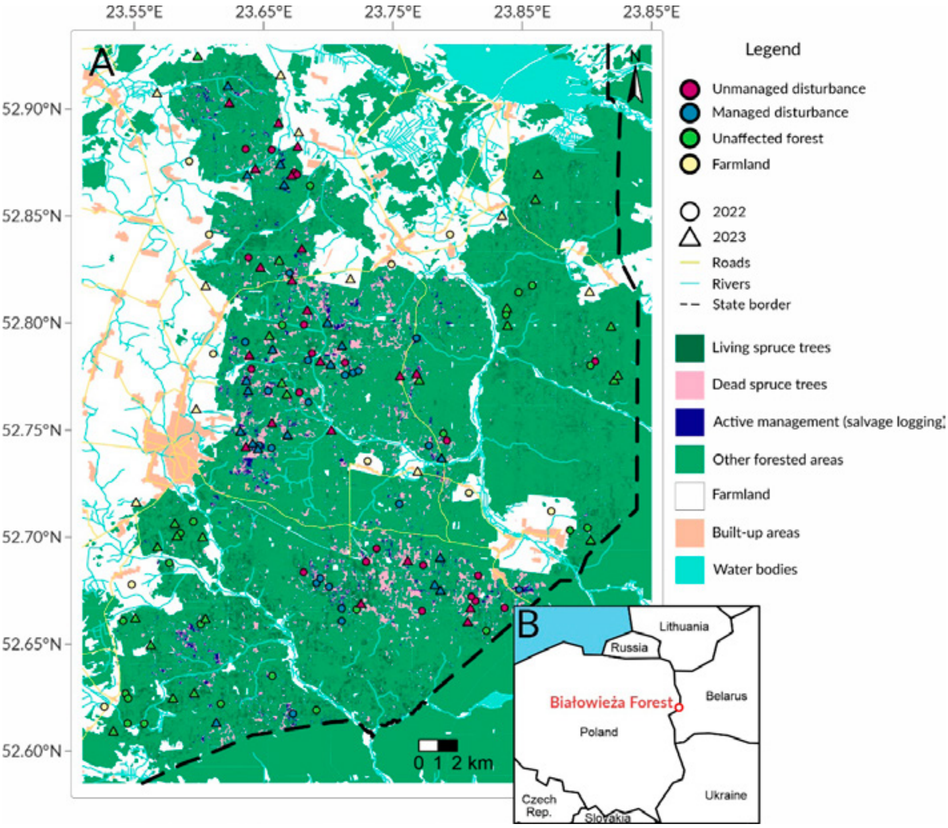


Figure 1: Distribution of point-count sites in Białowieża Forest. The landscape of spruce trees (both living and dead) and the extent of salvage logging are shown for 2017, the period immediately after the bark beetle outbreak peak and the logging ban, based on Mikusiński et al. (2018) and Stereńczak et al. (2020).

2.2. Site selection

For our bird counts, we selected Białowieża Forest subcompartments in which Norway spruce was the dominant species in the canopy and spruce made up at least 30% of all trees (1824 out of 17773 subcompartments; State Forests National Forest Holding, 2025; Stereńczak et al., 2020). From this group, we identified 323 subcompartments unaffected by the outbreak, where more than 80% of spruces were still alive after the in 2019 (after the outbreak peak; “unaffected forest”, UA), 507 subcompartments where most spruce trees (>80%) died within the period of bark beetle outbreak and no management operations were conducted (“unmanaged disturbance”, UD), and 177 subcompartments where most spruces (<80%) died and at least 2000m^2 of the area was actively managed in response (“managed disturbance”, MD; Mikusiński et al., 2018; Stereńczak et al., 2020).

From these subcompartments, we randomly chose a subset of 49 unaffected forest subcompartments (Figure 2A), 41 unmanaged disturbance subcompartments (Figure 2B) and 40 managed disturbance subcompartments (Figure 2C with selection probability proportional to their total area. These 130 subcompartments were verified in the field, and if they did not meet our criteria (e.g., partial logging in unmanaged disturbances) or were nearly inaccessible, we replaced them with other subcompartments that matched our criteria – either the next in the random selection order, the nearest suitable site, or based on our prior knowledge of the area. Within each selected forest subcompartment, we established a point-count site at least 50 meters from the subcompartment borders, choosing a location that best represented the assigned habitat. In addition to the 130 point-count sites placed within the forest, we selected 20 point-count sites distributed across open areas near the Białowieża Forest complex (farmland; FL). These open areas included a diversity of habitats, such as meadows, fallow land and pastures (Figure 2D). Due to technical problems identified during data analysis (i.e., high distortion possibly affecting species identification), three of the original 150 point-count sites were excluded. Therefore, the final dataset consisted of 147 point-count sites, categorized as follows: 41 unmanaged disturbance (UD), 39 managed disturbance (MD), 47 unaffected forest (UA) and 20 farmland (FL; Figure 1).

2.3. Data collection

Point-count sites were divided into two groups, with half surveyed in 2022 and half in 2023. In each of the 147 point-count sites, we hung a single Audiomoth recording unit (hardware version 1.2.0/1.1.0, firmware version 1.7.1; Hill et al., 2019) on a randomly chosen tree, at a height of approximately 2 m, facing away from the northwest to minimize distortion caused by the wind. Each Audiomoth recorded bird sounds during two study periods (April and May–June) to cover the peak of the breeding season for both sedentary and migratory species. In each study period and each point-count site, we recorded birds during on the same day (to reduce possible weather effect on bird activity) for 4 hours, starting 1 hour before sunrise and continuing until 3 hours after sunrise, thus covering the peak of bird vocal activity. In a few cases of technical problems (e.g., recorder malfunction), we repeated the recording on the next suitable occasion (within two weeks) and used those data for subsequent analyses. Field recordings were conducted only in good weather conditions (no heavy rain nor strong wind).

From each 4-hour recording, we extracted a 1-minute sample every 20 minutes, except during the first hour after sunrise, when samples were taken every 10 minutes to better capture the period of highest bird activity. In total, 30 minutes were sampled for each point-count site (15 minutes in each of the two periods). Random names were assigned to each of the 1-minute samples to prevent prior knowledge of habitat type associated with the recording. Each 1-minute file was listened to by a single expert ornithologist, who identified all bird species heard in the recording. Only bird vocalizations that could be reliably identified to the species level were included in subsequent analyses. For each of the 147 point-count sites, we pooled species information from all 30 minutes (15 minutes x two study periods), producing a single presence/absence value for each species at each point-count site.

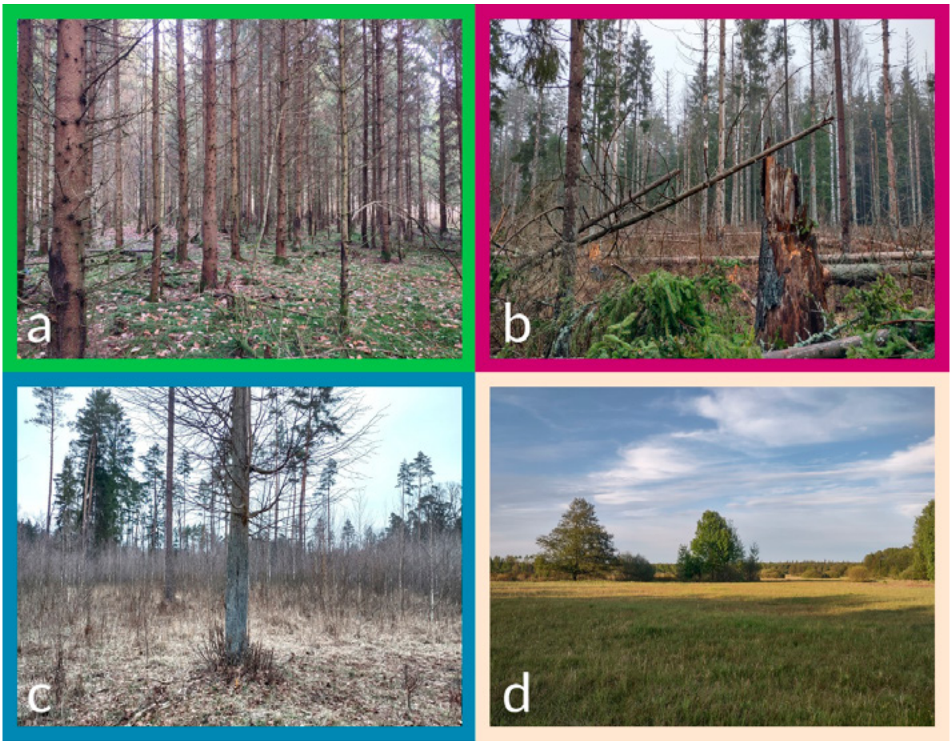


Figure 2: Examples of the four habitat types selected in our study – Unaffected forest (a), Unmanaged disturbance (b), Managed disturbance (c), Farmland (d).

2.4 Data analysis

To test whether the bird communities differed between the four habitats, we performed pairwise PERMANOVA with year as a strata and Bonferroni's p-value correction, using "pairwiseAdonis" package in R (Martinez Arbizu, 2017; R Core Team, 2024). To visualize the data, we performed Canonical Correspondence Analysis, a method well suited method to visualize species occurrences based on presence/absence data ("vegan" package; Oksanen et al., 2024). We did not visualize species occurring in less than five point-count sites, as their associations with habitats were considered unreliable.

To test the dissimilarities between the four habitats, we calculated Jaccard dissimilarity matrix based on all our 147 point-count sites. We visualized only the comparisons between the two disturbed habitats (”unmanaged disturbance” and “managed disturbance”) and two control habitats (”unaffected forest” and “farmland”). We added two more comparisons to serve as references: between unaffected forest and farmland and between unaffected forest and unaffected forest (i.e., dissimilarity within the unaffected forest habitat). We created a Generalized Additive Mixed Model (GAMM) with dissimilarity values as a response variable and habitat-pair identity as the explanatory variable (Wood, 2017). As each dissimilarity value is a distance between a pair of point-count sites, we added point-count site as two separate random effects in the model. The model was fitted with a normal distribution using the “mgcv” package (Wood, 2017). We tested differences in dissimilarity values (contrasts) among habitat pairs using the predict_response() and test_predictions() functions from the “ggeffects” package (Lüdecke, 2018).

To test whether the richness of typical farmland bird species differed across the four habitats, each bird species was attributed to a habitat type based on the classification used in PanEuropean Common Bird Monitoring Scheme (2022). We selected the subset of species belonging to “farmland” and calculated their richness for each point-count site. Based on that, we created a Generalized Additive Mixed Model (GAMM) with farmland richness as response variable, habitat as the explanatory variable as well as year and point-count site as two random variables. The model was fitted using a Poisson distribution and “mgcv” package. All visualization were produced using “ggplot2”, “gridExtra” and “patchwork” packages (Auguie, 2017; Pedersen, 2024; Wickham, 2016). All analyses were conducted in R (R Core Team, 2024).

3. Results

We detected 104 bird species in total. The ten most frequently recorded species were blackbird *Tudrus merula* (147; 100% of our study point-count sites), song thrush *Turdus philomelos* (146), wood pigeon *Columba palumbus* (146), chaffinch *Fringilla coelebs* (144), European robin *Erithacus rubeula* (142), Eurasian blackcap *Sylvia atricapilla* (141), common cuckoo *Cuculus canorus* (137), common chiffchaff *Phylloscopus collybita* (136), great tit *Parus major* (135) and great-spotted woodpecker *Dendrocopos major* (131). We identified 13 farmland species, with most common being yellowhammer *Emberiza citrinella* (66), Common starling *Sturnus vulgaris* (32), Eurasian skylark (28) and red-backed shrike (28). Detailed frequencies of point count sites occupied by all species in the four habitats are presented in Appendix Table 1.

Bird communities were distinct between all four habitats (PERMANOVA, $p < 0.001$ for all comparisons; Appendix Table 2). The CCA revealed the largest separation of bird communities and species preferences between farmland and the three forest habitats (unaffected forest, unmanaged disturbance and managed disturbance; Figure 3-4). CCA1 explained 27% of the variation, while CCA2 explained 5%.

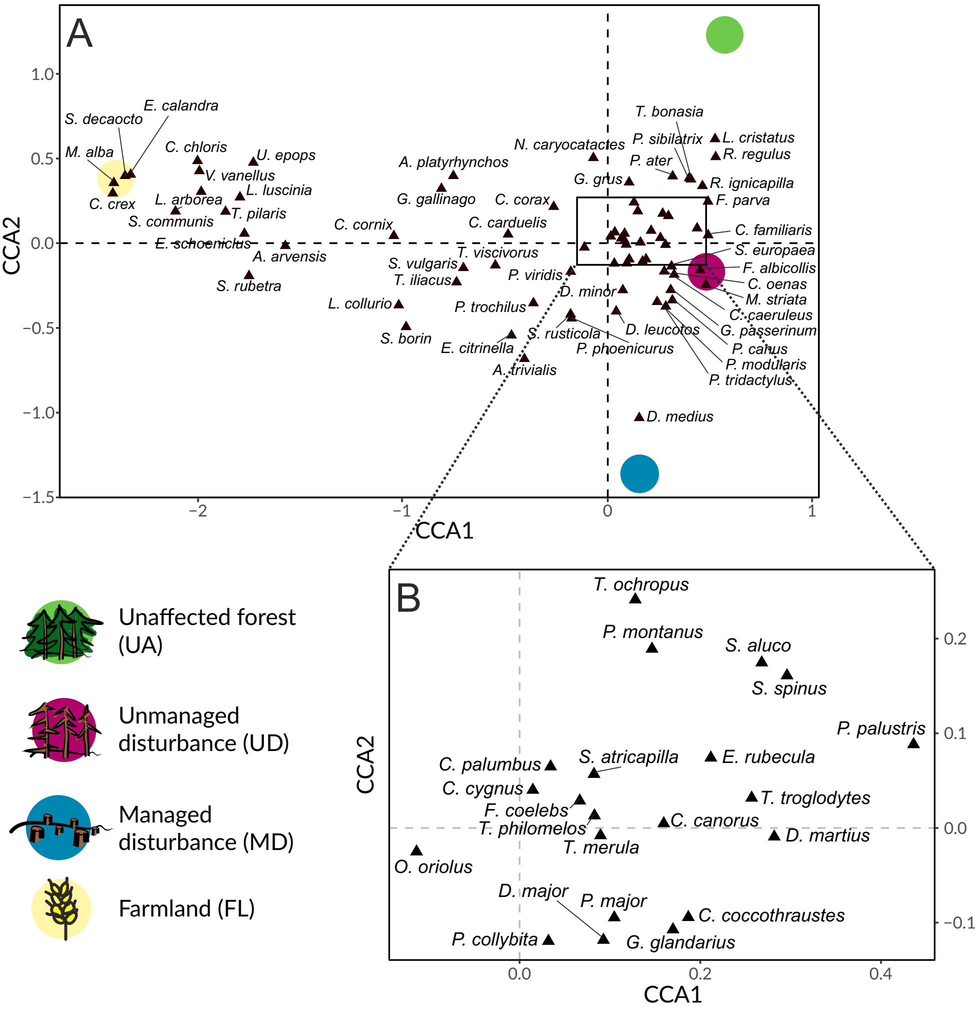


Figure 3: Canonical Correspondence Analysis plots: (A) Species present in at least 5 point-count sites are shown alongside centroids of all four habitats (colored dots). (B) A detailed view of the area around 0 is presented separately for increased clarity. CCA1 explained 27% of the variation, while CCA2 explained 5%.

Bark beetle disturbance resulted in bird communities shifting towards the communities recorded in the farmland habitat (UA-FL vs UD-FL contrast = 0.02, p = 0.016; Figure 5A and Appendix Table 3) and away from the forest communities (UD-UA vs UA-UA contrast = 0.03, p < 0.001; Figure 5B). Active post-disturbance management pushed the communities further in the same direction, even closer to those recorded in farmland (UD-FL vs MD-FL contrast = 0.03, p < 0.001) and further away from the communities recorded in the forest (MD-UA vs UD-UA contrast = 0.05, p < 0.001).

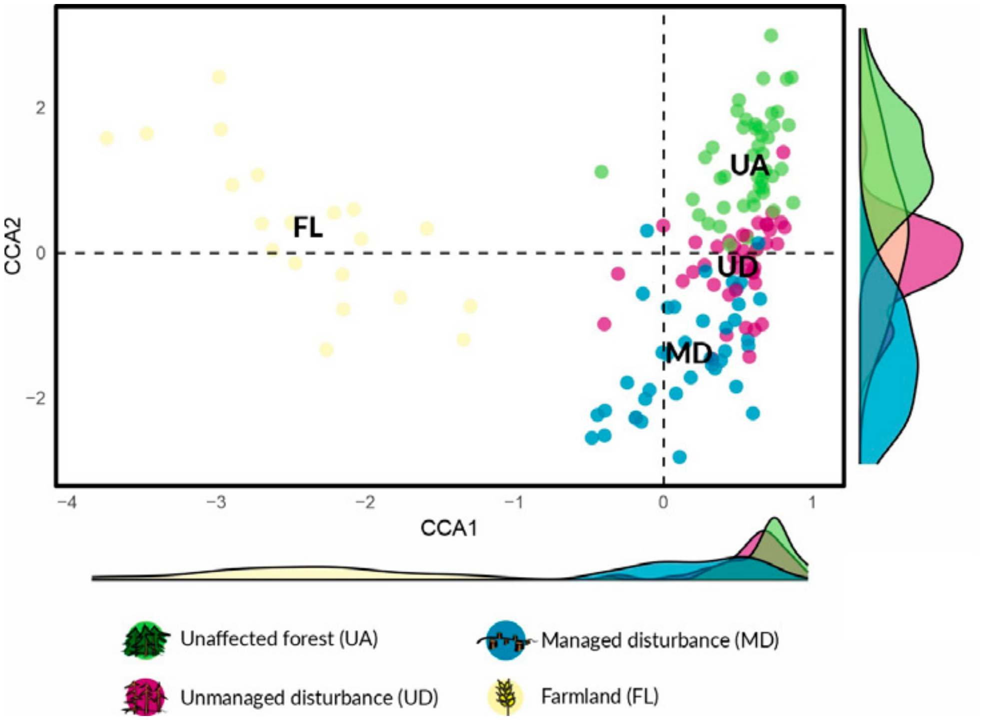


Figure 4: Canonical Correspondence Analysis plot: Sites are shown alongside centroids of all four habitats. Density curves are displayed for both axes and all four habitats. CCA1 explained 27% of the variation, while CCA2 explained 5%.

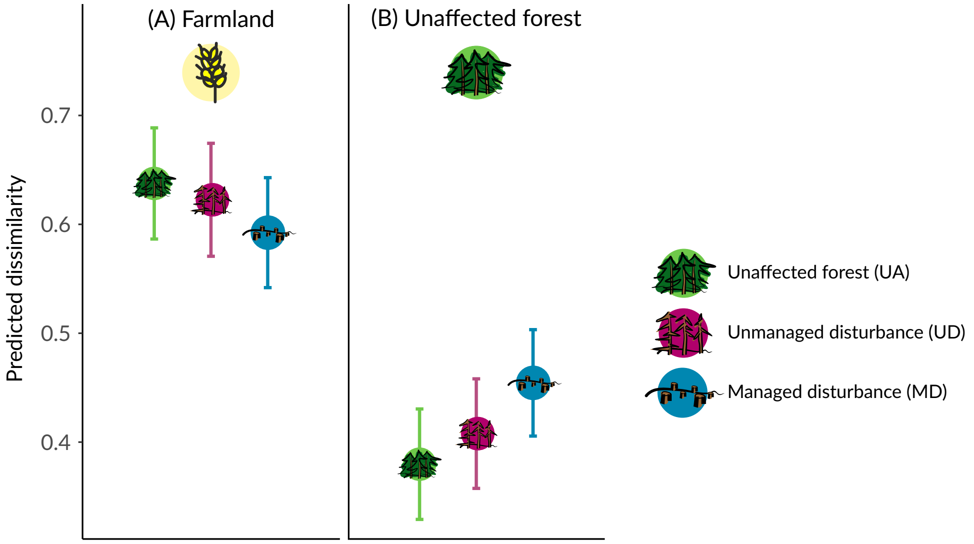
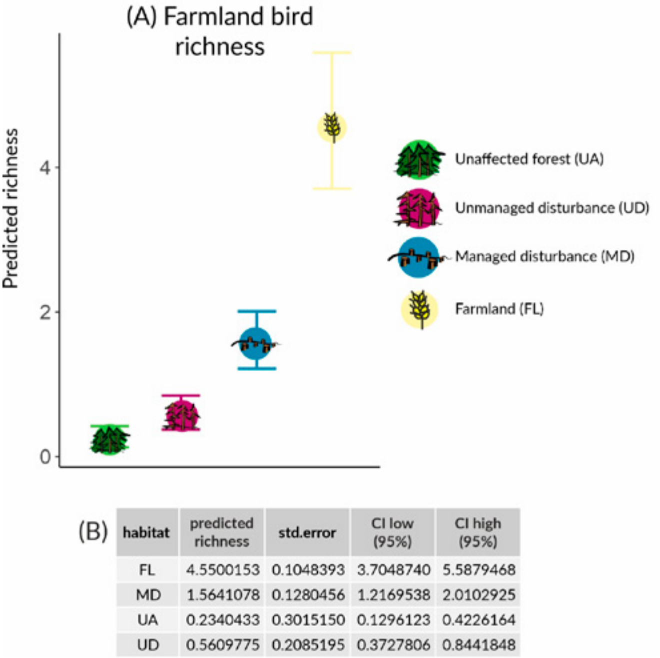


Figure 5: Bird community differences between pairs of habitats as derived from GAMM model: Predicted Jaccard dissimilarities between the three forest habitats (unaffected forest, unmanaged disturbance and managed disturbance) and farmland (A) as well as unaffected forest (B). All predicted dissimilarities for the habitat pairs differ from each other (see Appendix table 2 for details).

The comparison of contrast values reveals that active management produced a larger deviation from forest bird communities than the initial bark beetle disturbance (Figure 5A, B and Appendix Table 3). Nonetheless, bird communities in both disturbed forest habitats still more closely resembled forest communities than those of farmland. Detailed model outputs, predictions, and contrasts are provided in Appendix Tables 3–4.



habitat	predicted richness	std.error	CI low (95%)	CI high (95%)
FL	4.5500153	0.1048393	3.7048740	5.5879468
MD	1.5641078	0.1280456	1.2169538	2.0102925
UA	0.2340433	0.3015150	0.1296123	0.4226164
UD	0.5609775	0.2085195	0.3727806	0.8441848

Figure 6: Predicted richness of farmland birds based on the GAMM model for each of the four habitats: unaffected forest, unmanaged disturbance, managed disturbance, and farmland (A-B). All habitats differed from each other in terms of farmland bird richness (contrast, $p < 0.01$). For details and model outputs, see Appendix Tables 3 and 5.

4. Discussion

Out of 13 farmland species identified in total, 7 were detected in the disturbed forest areas within Białowieża Forest (UD and MD). The number of farmland species per point-count site was higher in the unmanaged spruce stands affected by the bark beetle outbreak as compared to the unaffected forest (UA vs UD contrast = 0.33, $p=0.018$; Figure 6A). Disturbed point-count sites that were subjected to active management harbored a higher richness of farmland birds compared to unmanaged disturbance stands (MD vs UD contrast = -1, $p < 0.001$). Farmland habitats hosted the richest farmland bird communities among all the four habitats, roughly three times richer than the managed disturbance (Figure 6B). Detailed model outputs, predictions, and contrasts are provided in Appendix Tables 3 and 5.

We found that the bark beetle outbreak caused a shift in bird communities from typical forest assemblages toward those more characteristic of farmland, and that active post-disturbance management amplified this effect, confirming our first hypothesis. This result suggests that natural disturbance and post-disturbance management have an additive effect on the breeding bird community shift. Moreover, the community shift away from the forest was greater between unmanaged and managed disturbances than between unmanaged disturbance and the unaffected forest, confirming our second hypothesis. This finding indicates that bark beetle disturbance may have had a smaller impact on forest bird communities than the active post-disturbance management. Additionally, farmland bird richness was higher in managed disturbances compared to unmanaged ones, supporting our third hypothesis. Nevertheless, despite all the community shifts, bird communities in disturbed habitats remained more similar to those in forests than to those in farmland.

The observed shift in bird communities at both managed and unmanaged disturbed forest habitats toward communities typical of farmland ecosystems was partly driven by the immigration of typical farmland species. Many species present in a nearby farmland (e.g., Eurasian skylark, yellowhammer, hooded crow *Corvus cornix*, and common starling) were recorded also in both of our disturbed habitats. However, there were species present in the farmland that did not utilize our forest gaps (e.g., corn crake, European greenfinch *Chloris chloris*, corn bunting *Emberiza calandra,* northern lapwing*).* The suitability of forest gaps for farmland birds depends on several factors, including gap size, the proportion of open areas in the surrounding landscape, and proximity to the forest edge (Bakx et al., 2020; Graser et al., 2025; Hofmeister et al., 2017; Żmihorski et al., 2016). In Białowieża Forest, the disturbance-induced gaps are generally small, located far from forest edges, and surrounded by closed-canopy stands – conditions that are suboptimal for many farmland species, including those known to colonize disturbed areas in other temperate forests (e.g. corn bunting, northern lapwing; Walesiak et al., 2024). Nevertheless, even with a limited influx of farmland birds, the shift in bird communities toward farmland assemblages following both disturbance and active post-disturbance management was clearly evident in Białowieża Forest.

Active management caused a greater shift in bird communities away from the forest and toward communities typical of farmland than did the bark beetle disturbance. Farmland birds can colonize gaps created after natural disturbances, both unmanaged and managed (Bakx et al., 2020; Żmihorski et al., 2016). However, managed sites often support higher farmland bird diversity (Graser et al., 2024; Walesiak et al., 2024). In contrast, unmanaged disturbances may retain suitable habitat features for many forest species that are lost following active management (Thorn et al., 2020; Walesiak et al., 2024). This is because conditions following natural disturbances (e.g., bark beetle outbreaks) often resemble those of undisturbed forests: surviving trees provide partial canopy cover, the ground layer remains mostly intact, and dead wood is abundant. These features can support forest bird communities by offering nesting sites (van Eupen et al., 2025) and a food base, as dead wood provides refuge for forest invertebrates (Cours et al., 2023). In contrast, active management after natural disturbances typically results in complete habitat opening and the removal of dead wood, eliminating resources important for forest species while creating conditions more favorable to open-habitat birds (e.g., increased sunlight exposure and grassland vegetation). These changes likely explain why we observed a greater shift away from the forest assemblages due to active management compared with the bark beetle outbreak.

In our study, we focused on the effects of a bark beetle outbreak and post-disturbance management 3–7 years after the peak of the disturbance event (Stereńczak et al., 2020). On one hand, this time frame allows species from outside the forest to detect and colonize suitable habitats within the forest, even those located several kilometers from the edge. On the other hand, the gaps may already be too old to support species that prefer early successional habitats with short vegetation, such as wheatear (*Oenanthe oenanthe*) or Eurasian skylark. Nevertheless, this period may coincide with the peak of relative farmland bird richness in temperate forest gaps (Walesiak et al., 2024; Żmihorski et al., 2016), potentially influencing the observed patterns of community shifts. Since our study captures only a snapshot in the long-term trajectory of bird communities in response to disturbance and post-disturbance management, long-term studies are urgently needed to provide a full understanding of the post-disturbance succession.

Finally, our survey method – using autonomous recording units (ARUs) instead of human observers – offers important advantages but also has certain limitations. First of all, it is difficult to confirm whether a recorded vocalization originated from within the surveyed habitat. Although our recorders were placed at least 50 meters from habitat borders to minimize edge effects, this approach did not eliminate the influence of adjacent habitats entirely. For example, skylarks were recorded at two point-count sites in unaffected forest, even though such closed-canopy habitats are unsuitable for this species. Moreover, recording units cannot distinguish species flying over the canopy from birds occupying any given habitat patch. For instance, the common crane *Grus grus*, a typical open-habitat species, was recorded more frequently in unaffected forest sites than in farmland, likely because they vocalize frequently during flight (Appendix Table 1).

Finally, species that vocalize infrequently (e.g., raptors) or whose calls are difficult to identify (e.g., contact calls of tits) may be underrepresented in our data. Overall, while the general shift in bird communities following disturbance and post-disturbance management is evident and our conclusions are robust, some results (particularly species-specific patterns) should be interpreted with caution.

Conservation implications

We demonstrated that active post-disturbance management in Białowieża Forest caused a significant shift in bird communities, in some ways greater than the bark beetle outbreak. These findings support the view of active management as a "post-disturbance disturbance", with negative consequences for forest ecosystem functioning (Hotta et al., 2021; Mikusiński et al., 2018; Thorn et al., 2018). As community shifts result in altered succession trajectories, post-disturbance management could also hinder forest regeneration, leading to habitats impoverished in both structure and biodiversity (Walesiak et al., 2024). For these reasons, in forests where the protection of forest-typical biodiversity and natural processes is among key objectives (i.e., Białowieża Forest), active post-disturbance management should be avoided whenever possible. In cases where it has to be performed for a certain reason (Lindenmayer et al., 2012b), we recommend concentrating it in parts of the disturbed area of lowest value in terms of disturbance legacies (e.g., youngest stands with limited abundance of snags or coarse dead wood). In this way, we believe some biodiversity conservation goals can be achieved in disturbed forests alongside other objectives for the area.

Active management facilitated an influx of farmland birds and increased farmland bird richness within the forest area. In many parts of Europe, farmland birds represent one of the most rapidly declining species groups (Gregory et al., 2007). Some of these species find suitable habitats within disturbed forest landscapes, including areas subjected to active management (Graser et al., 2024; Walesiak et al., 2024; Żmihorski et al., 2016). In some cases, those areas may benefit species of high conservation concern (Rost et al., 2012; but see Titeux et al., 2020). For these reasons, actively managed disturbances should also be recognized as potentially important from a biodiversity conservation perspective (Rost et al., 2012; Sielezniew et al., 2019).

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AUTHOR CONTRIBUTIONS

Michał Walesiak: Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Conceptualization; **Beata Bramorska:** Conceptualization, Methodology; **Dominika Koprowska:** Methodology, Data curation; **Rosanne Michielsen:** Conceptualization, Visualization, Data curation; **Grzegorz Mikusiński:** Writing – review & editing, Conceptualization, Supervision; **Michał** Żmihorski**:** Writing – review & editing, Conceptualization, Supervision.

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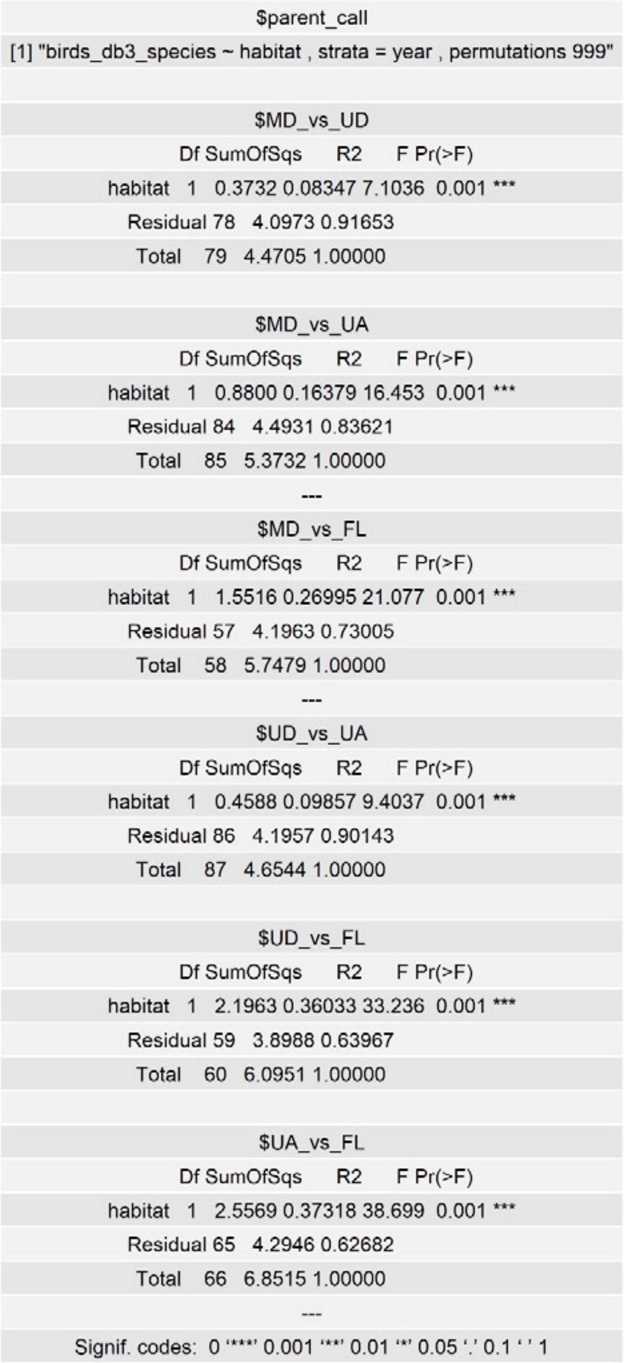
Appendix Table 1: Occurrences of all bird species in the four habitats. Due to uneven number of point-count sites within each habitat, occurrences are presented as percent of occupied point-count sites by a given species. Farmland species are presented in bold font (PanEuropean Common Bird Monitoring Scheme, 2022).

species	unaffected forest	unmanaged disturbance	managed disturbance	farmland
Accipiter gentilis	2.1	2.4	0.0	0
Accipiter nisus	6.4	0.0	0.0	0
Acrocephalus arundinaceus	0.0	0.0	0.0	10
Acrocephalus schoenobaenus	0.0	0.0	0.0	5
Acrocephalus scirpaceus	0.0	0.0	0.0	5
Aegolius funereus	0.0	0.0	2.6	0
Alauda arvensis	4.3	4.9	12.8	95
Anas platyrhynchos	6.4	2.4	2.6	20
Anthus pratensis	0.0	0.0	2.6	10
Anthus trivialis	6.4	12.2	61.5	50
Ardea cinerea	2.1	0.0	0.0	0
Asio otus	0.0	0.0	2.6	10
Botaurus stellaris	0.0	0.0	0.0	5
Caprimulgus europaeus	0.0	2.4	0.0	0
Carduelis carduelis	6.4	0.0	7.7	15
Carpodacus erythrinus	0.0	2.4	2.6	10
Certhia familiaris	68.1	97.6	56.4	5
Chloris chloris	2.1	0.0	0.0	25
Ciconia ciconia	0.0	0.0	0.0	5
Coccothraustes coccothraustes	68.1	75.6	71.8	40
Columba oenas	31.9	22.0	43.6	10
Columba palumbus	100.0	97.6	100.0	100
Corvus corax	38.3	31.7	23.1	65
Corvus cornix	4.3	2.4	10.3	40
Corvus monedula	0.0	0.0	0.0	5
Crex crex	0.0	0.0	0.0	45
Cuculus canorus	95.7	100.0	94.9	70
Cyanistes caeruleus	48.9	85.4	92.3	20
Cygnus cygnus	8.5	2.4	10.3	5
Cygnus olor	0.0	0.0	0.0	5
Dendrocopos leucotos	6.4	24.4	33.3	20
Dendrocopos major	85.1	97.6	100.0	60
Dendrocoptes medius	2.1	7.3	28.2	0
Dryobates minor	25.5	56.1	61.5	30
Dryocopus martius	80.9	65.9	79.5	40
Emberiza calandra	0.0	0.0	0.0	45
Emberiza citrinella	10.6	22.0	84.6	95
Emberiza schoeniclus	0.0	2.4	2.6	35
Erithacus rubecula	100.0	100.0	100.0	75
Ficedula albicollis	19.1	34.1	20.5	0
Ficedula parva	23.4	14.6	12.8	0

species	unaffected forest	unmanaged disturbance	managed disturbance	farmland
Fringilla coelebs	100.0	97.6	100.0	90
Gallinago gallinago	10.6	9.8	5.1	45
Garrulus glandarius	61.7	65.9	74.4	30
Glaucidium passerinum	4.3	7.3	7.7	0
Grus grus	68.1	48.8	35.9	60
Hippolais icterina	0.0	0.0	5.1	15
Hirundo rustica	0.0	0.0	0.0	5
Jynx torquilla	0.0	2.4	0.0	10
Lanius collurio	2.1	2.4	30.8	70
Linaria cannabina	0.0	0.0	0.0	5
Locustella fluviatilis	0.0	0.0	0.0	5
Locustella naevia	0.0	0.0	0.0	15
Lophophanes cristatus	55.3	22.0	15.4	0
Loxia curvirostra	2.1	0.0	2.6	5
Lullula arborea	0.0	2.4	2.6	65
Luscinia luscinia	2.1	4.9	2.6	60
Motacilla alba	0.0	0.0	0.0	30
Muscicapa striata	12.8	51.2	17.9	0
Nucifraga caryocatactes	6.4	2.4	2.6	5
Oriolus oriolus	53.2	70.7	56.4	80
Parus major	93.6	100.0	97.4	60
Passer montanus	0.0	0.0	0.0	5
Periparus ater	40.4	29.3	17.9	5
Phoenicurus ochruros	0.0	0.0	2.6	10
Phoenicurus phoenicurus	2.1	14.6	17.9	15
Phylloscopus collybita	83.0	100.0	100.0	85
Phylloscopus sibilatrix	95.7	56.1	38.5	5
Phylloscopus trochiloides	2.1	2.4	5.1	0
Phylloscopus trochilus	6.4	9.8	28.2	25
Pica pica	0.0	2.4	0.0	10
Picoides tridactylus	10.6	19.5	25.6	0
Picus canus	12.8	22.0	25.6	0
Picus viridis	4.3	14.6	10.3	15
Poecile montanus	40.4	31.7	23.1	20
Poecile palustris	72.3	63.4	51.3	10
Porzana porzana	0.0	0.0	0.0	10
Prunella modularis	25.5	58.5	51.3	5
Pyrrhula pyrrhula	4.3	4.9	2.6	0
Regulus ignicapilla	36.2	26.8	12.8	0
Regulus regulus	97.9	43.9	38.5	0
Remiz pendulinus	0.0	0.0	0.0	5
Saxicola rubetra	0.0	0.0	5.1	25
Scolopax rusticola	12.8	7.3	33.3	25
Sitta europaea	36.2	61.0	38.5	5
Spinus spinus	53.2	31.7	41.0	5

species	unaffected forest	unmanaged disturbance	managed disturbance	farmland
Streptopelia decaocto	0.0	0.0	0.0	30
Streptopelia turtur	0.0	2.4	0.0	0
Strix aluco	38.3	34.1	30.8	20
Sturnus vulgaris	4.3	24.4	20.5	60
Sylvia atricapilla	93.6	100.0	97.4	90
Sylvia borin	2.1	0.0	25.6	40
Sylvia communis	0.0	0.0	2.6	35
Sylvia curruca	4.3	2.4	2.6	0
Tetrastes bonasia	23.4	7.3	12.8	0
Tringa ochropus	38.3	29.3	25.6	30
Troglodytes troglodytes	83.0	100.0	94.9	30
Turdus iliacus	2.1	9.8	12.8	35
Turdus merula	100.0	100.0	100.0	100
Turdus philomelos	100.0	97.6	100.0	100
Turdus pilaris	2.1	0.0	2.6	40
Turdus viscivorus	12.8	9.8	23.1	50
Upupa epops	2.1	2.4	0.0	35
Vanellus vanellus	2.1	0.0	0.0	35

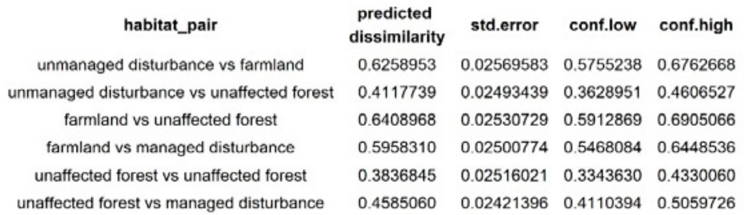
Appendix Table 2: Results of PERMANOVA comparisons between all habitat pairs.



```
$parent_call
[1] "birds_db3_species ~ habitat , strata = year , permutations 999"

$MD_vs_UD
         Df SumOfSqs      R2      F Pr(>F)
habitat   1   0.3732 0.08347 7.1036  0.001 ***
Residual 78   4.0973 0.91653
Total    79   4.4705 1.00000

$MD_vs_UA
         Df SumOfSqs      R2      F Pr(>F)
habitat   1   0.8800 0.16379 16.453  0.001 ***
Residual 84   4.4931 0.83621
Total    85   5.3732 1.00000
---
$MD_vs_FL
         Df SumOfSqs      R2      F Pr(>F)
habitat   1   1.5516 0.26995 21.077  0.001 ***
Residual 57   4.1963 0.73005
Total    58   5.7479 1.00000
---
$UD_vs_UA
         Df SumOfSqs      R2      F Pr(>F)
habitat   1   0.4588 0.09857 9.4037  0.001 ***
Residual 86   4.1957 0.90143
Total    87   4.6544 1.00000

$UD_vs_FL
         Df SumOfSqs      R2      F Pr(>F)
habitat   1   2.1963 0.36033 33.236  0.001 ***
Residual 59   3.8988 0.63967
Total    60   6.0951 1.00000

$UA_vs_FL
         Df SumOfSqs      R2      F Pr(>F)
habitat   1   2.5569 0.37318 38.699  0.001 ***
Residual 65   4.2946 0.62682
Total    66   6.8515 1.00000
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

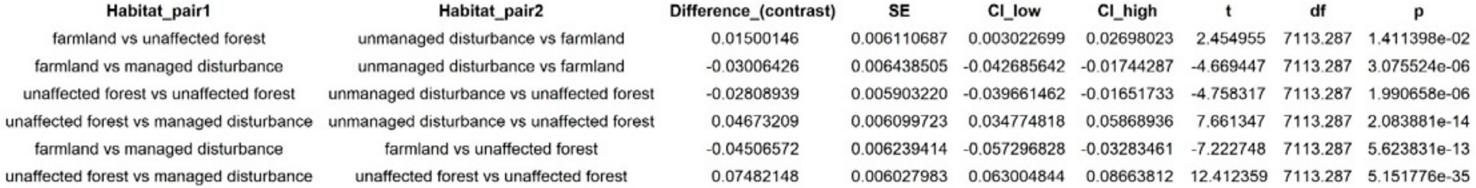
Appendix Table 3: Predicted dissimilarities between habitats as derived from GAMM models (A) and contrasts between those predicted dissimilarities (B). Only dissimilarities for pairs of habitats of interest are presented to increase readability.

(A) Predicted dissimilarities for forest habitat pairs



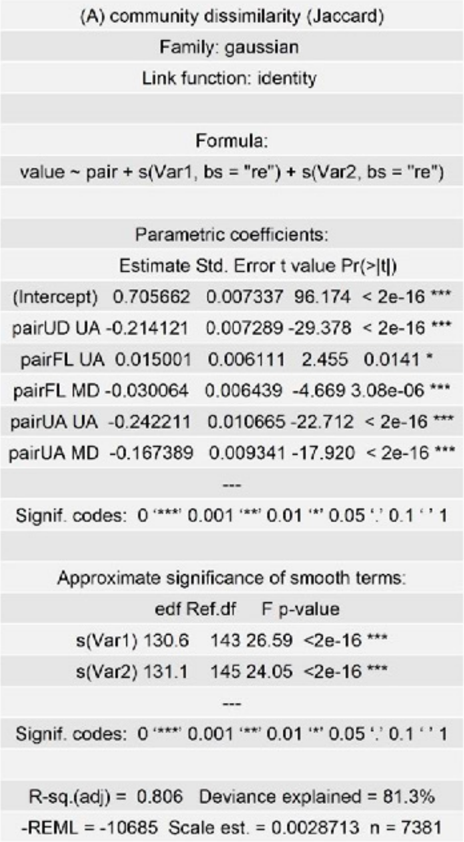
habitat_pair	predicted dissimilarity	std.error	conf.low	conf.high
unmanaged disturbance vs farmland	0.6258953	0.02569583	0.5755238	0.6762668
unmanaged disturbance vs unaffected forest	0.4117739	0.02493439	0.3628951	0.4606527
farmland vs unaffected forest	0.6408968	0.02530729	0.5912869	0.6905066
farmland vs managed disturbance	0.5958310	0.02500774	0.5468084	0.6448536
unaffected forest vs unaffected forest	0.3836845	0.02516021	0.3343630	0.4330060
unaffected forest vs managed disturbance	0.4585060	0.02421396	0.4110394	0.5059726

(B) Contrasts between the predicted dissimilarities with associated p-values

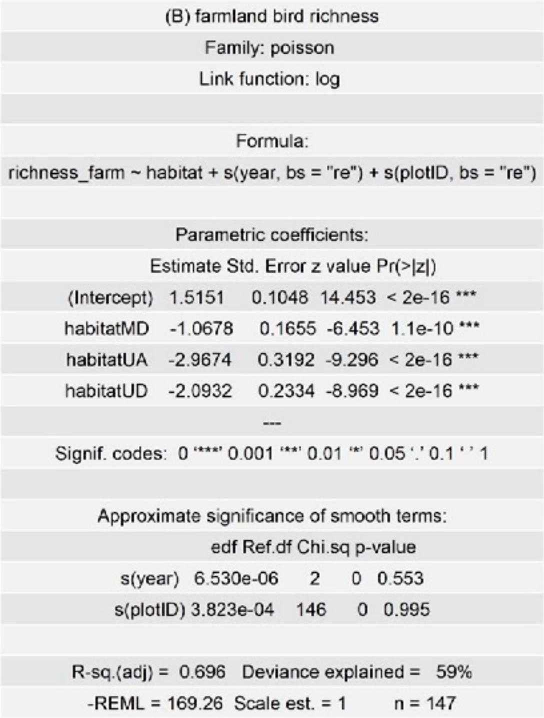


Habitat_pair1	Habitat_pair2	Difference_(contrast)	SE	CI_low	CI_high	t	df	p
farmland vs unaffected forest	unmanaged disturbance vs farmland	0.01500146	0.006110687	0.003022699	0.02698023	2.454955	7113.287	1.411398e-02
farmland vs managed disturbance	unmanaged disturbance vs farmland	-0.03006426	0.006438505	-0.042685642	-0.01744287	-4.669447	7113.287	3.075524e-06
unaffected forest vs unaffected forest	unmanaged disturbance vs unaffected forest	-0.02808939	0.005903220	-0.039661462	-0.01651733	-4.758317	7113.287	1.990658e-06
unaffected forest vs managed disturbance	unmanaged disturbance vs unaffected forest	0.04673209	0.006099723	0.034774818	0.05868936	7.661347	7113.287	2.083881e-14
farmland vs managed disturbance	farmland vs unaffected forest	-0.04506572	0.006239414	-0.057296828	-0.03283461	-7.222748	7113.287	5.623831e-13
unaffected forest vs managed disturbance	unaffected forest vs unaffected forest	0.07482148	0.006027983	0.063004844	0.08663812	12.412359	7113.287	5.151776e-35

Appendix Table 4: Model outputs of two Generalized Additive Mixed Models (GAMMs) from our study: Community dissimilarity (A) and farmland bird richness (B).



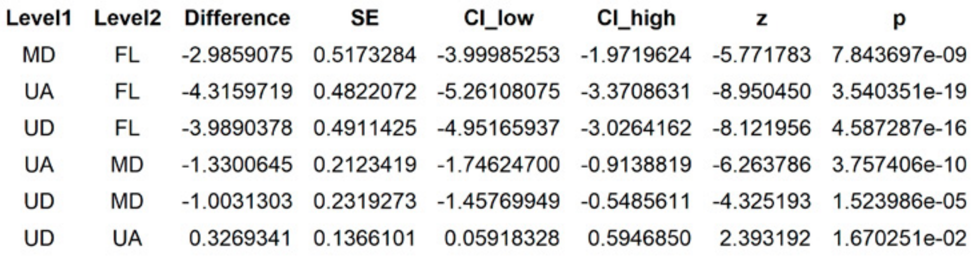
```
(A) community dissimilarity (Jaccard)
Family: gaussian
Link function: identity

Formula:
value ~ pair + s(Var1, bs = "re") + s(Var2, bs = "re")

Parametric coefficients:
Estimate Std. Error t value Pr(>|t|)
(Intercept)   0.705662   0.007337  96.174  < 2e-16 ***
pairUD UA -0.214121   0.007289 -29.378  < 2e-16 ***
pairFL UA  0.015001   0.006111   2.455   0.0141 *
pairFL MD -0.030064   0.006439  -4.669 3.08e-06 ***
pairUA UA  -0.242211   0.010665 -22.712  < 2e-16 ***
pairUA MD  -0.167389   0.009341 -17.920  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
edf Ref.df     F p-value
s(Var1) 130.6     143 26.59  <2e-16 ***
s(Var2) 131.1     145 24.05  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.806   Deviance explained = 81.3%
-REML = -10685  Scale est. = 0.0028713  n = 7381
```



```
(B) farmland bird richness
Family: poisson
Link function: log

Formula:
richness_farm ~ habitat + s(year, bs = "re") + s(plotID, bs = "re")

Parametric coefficients:
Estimate Std. Error z value Pr(>|z|)
(Intercept)   1.5151     0.1048  14.453  < 2e-16 ***
habitatMD    -1.0678     0.1655  -6.453  1.1e-10 ***
habitatUA    -2.9674     0.3192  -9.296  < 2e-16 ***
habitatUD    -2.0932     0.2334  -8.969  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
edf Ref.df Chi.sq p-value
s(year)   6.530e-06      2      0   0.553
s(plotID) 3.823e-04    146      0   0.995

R-sq.(adj) =  0.696   Deviance explained =   59%
-REML = 169.26  Scale est. = 1         n = 147
```

Appendix Table 5: Contrasts between predicted values for farmland bird richness in each habitat, as derived from GAMM models.

Farmland bird richness (contrasts)



Level1	Level2	Difference	SE	CI_low	CI_high	z	p
MD	FL	-2.9859075	0.5173284	-3.99985253	-1.9719624	-5.771783	7.843697e-09
UA	FL	-4.3159719	0.4822072	-5.26108075	-3.3708631	-8.950450	3.540351e-19
UD	FL	-3.9890378	0.4911425	-4.95165937	-3.0264162	-8.121956	4.587287e-16
UA	MD	-1.3300645	0.2123419	-1.74624700	-0.9138819	-6.263786	3.757406e-10
UD	MD	-1.0031303	0.2319273	-1.45769949	-0.5485611	-4.325193	1.523986e-05
UD	UA	0.3269341	0.1366101	0.05918328	0.5946850	2.393192	1.670251e-02

4. Discussion

My results clearly demonstrate that natural disturbances significantly impact bird community composition, abundance, and species richness. The shift in species composition was recorded after wetland fire (Chapter I), windthrow in a managed forest (Chapter II) and bark beetle outbreak in a highly natural forest (Chapter III). The direction and magnitude of this community shift vary depending on the type of disturbance, habitat, post-disturbance management strategy, and the timescale considered. For example, I show that natural disturbances can cause short-term declines in bird communities, as observed in the Biebrza Valley following a fire (Chapter I). Within a year, the community largely returned to its initial state (Walesiak et al., in prep.), consistent with studies showing that both vegetation and birds in open wetlands often recover to pre-disturbance conditions within a year (Grzywaczewski et al., 2014; Heim et al., 2019). In contrast, disturbances in forest ecosystems may lead to long-term changes in bird community composition. I show that in managed forests, these changes can benefit bird communities over extended periods, for example by increasing species richness. However, this impact strongly relies on the post-disturbance management strategy, and the positive effects dwindle when the disturbed area is subjected to intensive forest management.

Despite the variability in bird diversity responses to natural disturbance events, I was able to identify several consistent patterns. For example, disturbances favored certain open-habitat species, particularly ground-feeding birds (Chapters I, II and III; see also Viljur et al., 2022). This trend was observed regardless of whether the disturbed habitat was a closed-canopy forest or a more open environment such as a peatland. Conversely, some habitat specialists were negatively affected by disturbance events, especially in the initial phase (see also Fuller, 2000; Heim et al., 2019). In forests, this included species dependent on a closed canopy (Chapter II); in peatlands, it included those reliant on tall grasses, tussocks or reedbeds (Chapter I). When looking at a total biodiversity outcome, disturbances may both increase, or decrease it, depending on the temporal and spatial context. However, regardless of the net effect on biodiversity, it is essential to recognize that the impact of disturbance can never be classified simply as positive or negative. Even when species diversity increases, certain species or groups inevitably decline (Thorn et al., 2018; Viljur et al., 2022). Conversely, even when overall diversity decreases, some species benefit from the disturbance. This complexity must always be taken into account when developing management or conservation strategies aimed at supporting biodiversity following natural disturbance events.

Naturally disturbed areas are often rare in modern Europe, as they are either actively prevented from forming or immediately altered by forest management (Müller et al., 2018; Sanginés de Cárcer et al., 2021; Swanson et al., 2011). However, such areas appear to be crucial for many organisms, some of which may rely on them as their primary habitat (Thorn et al., 2020). Before large-scale, human-induced transformations of terrestrial ecosystems, natural disturbances likely played a major role in creating forest openings, serving as essential habitats for species now associated with open landscapes (Pearce et al., 2025; Wesołowski et al., 2018). My studies revealed that they still form important habitats for many species and ecological groups. For example, in both disturbed peatlands and managed forests, the tree pipit (*Anthus trivialis*) was recorded in higher numbers than in undisturbed reference habitats (Chapters I and II). In natural forests, disturbances facilitated the occurrence of species related to farmland that are otherwise rare or absent in closed-canopy environments (e.g., yellowhammer, *Emberiza citrinella,* and red-backed shrike, *Lanius collurio*; Chapter III). Similarly, in managed forests, woodpeckers and thrushes were found in exceptionally high numbers within disturbed areas (Chapter II). Some of these species (e.g., black woodpecker *Dryocopus martius*) are recognized as important ecosystem engineers, providing nesting opportunities for other birds in the form of cavities and thus enhancing local bird diversity (Trzcinski et al., 2022). This, in turn, can lead to natural disturbances becoming localized biodiversity hotspots in both natural and managed forests (Chapter II; Przepióra et al., 2020). Overall, my results prove that naturally disturbed habitats are unique in terms of their biodiversity and cannot be fully substituted by any human-modified habitats (Chapters I, II and III). Therefore, in landscapes largely devoid of natural disturbances, habitats created by such disturbances should be recognized as valuable, even if certain components of biodiversity are reduced within them (see also Chapter I; Thom and Seidl, 2016).

Natural disturbances can also be viewed as important tools in ecosystem management and restoration and may serve as templates for specific management strategies (see also Hobbs et al., 2007). For example, prescribed fires in wetlands and prairies may help maintain non-climax habitats of high conservation value, along with their associated biodiversity (Clark and Wilson, 2001; Kotze, 2013). Such human-induced fires can act as ecological substitutes for natural fires or traditional human activities like mowing (Conway et al., 2010; Vermeire et al., 2020). Similarly, intentional tree damage that mimics natural disturbances (i.e., ‘veteranisation’) may be applied in forests to accelerate wood decay and decomposition, thereby benefiting organisms dependent on damaged trees and tree-related microhabitats (Cizek et al., 2025). Beyond these targeted practices, natural disturbances may increase structural complexity and biodiversity of affected ecosystems, which can facilitate the transformation of landscapes into more desirable ecological states (Szwagrzyk et al., 2018). In my work, I demonstrate that the complex forest structures shaped by natural disturbances more closely resemble natural forest ecosystems and support increased bird-species diversity (Chapter II). This capacity of natural disturbances to promote structurally rich and biodiverse ecosystems is especially relevant in light of the current European Union policy, which requires member states to restore at least 20% of degraded ecosystems by 2030 (European Commission’s Directorate-General for Environment, 2024). Forests previously degraded by intensive management but subsequently affected by natural disturbance events could contribute significantly toward meeting this restoration target. Such outcomes could be achieved without the high costs often associated with active restoration programs (Swezy et al., 2021). Overall, in certain contexts, natural disturbances offer a cost-effective means to achieve management and conservation objectives.

However, in certain situations, natural disturbance events can pose a serious threat to biodiversity. This is particularly true for ecosystems that were once resilient but have become more vulnerable due to climate change (Kettridge et al., 2015; Sulwiński et al., 2020). In other cases, increased disturbance frequency may prevent ecosystems from returning to their pre-disturbance states, leading instead to alternative ecosystem states that threaten associated biodiversity (Johnstone et al., 2016; Turner and Seidl, 2023). Even temporary ecosystem changes induced by a single disturbance event may pose risks to biodiversity in specific context. For example, I recorded the immediate disappearance of four avian species of high conservation concern after wetland fire, including *Acrocephalus paludicola*, the rarest migratory bird in Europe (Świętochowski et al., 2010, chapter I). As succession progresses, these affected species should recolonize disturbed areas from nearby undisturbed patches, as the surface vegetation returns to its pre-disturbance state (see also Heim et al., 2019). However, such post-disturbance recolonization may be hindered, especially in the case of taxa with limited mobility, such as certain arthropods (Mutz et al., 2017). Many animals in heavily fragmented temperate European ecosystems exist as metapopulations, in which individual high-quality habitat patches can be crucial for sustaining populations across the broader landscape (Pulliam, 1988). In such dynamics, a sufficiently large disturbance may eliminate single key patches, effectively reducing species densities on a landscape level (Thomas et al., 1996). Even relatively small disturbances can destroy critical “stepping-stone” habitats that maintain connectivity within metapopulations, disrupting their persistence (Ancrenaz et al., 2021; Hanski, 1999). In extreme cases, a disturbance might be extensive enough to eliminate most of the suitable habitat for localized species, effectively driving them to extinction (Arvidson, 2023). Therefore, in some contexts, suppressing natural disturbances is justified from a biodiversity conservation perspective.

The impact of natural disturbances on biodiversity is altered by post-disturbance management decisions. Forest ecosystems are particularly affected, as interventions (e.g., salvage logging, soil tilling, replanting, fencing, and thinning) are commonly implemented to mitigate timber-related economic losses and to secure the future production value of regenerating stands. My research demonstrates that these management actions alter bird community composition in both natural and managed forests (Chapters II and III; see also Thorn et al., 2018). In managed forests, these interventions redirect bird succession toward trajectories resembling clearcuts rather than natural ecosystems, leading to sustained biodiversity loss (Chapter II). In natural forests, active management caused even greater deviations from forest-typical bird communities than the initial natural disturbance itself, potentially disrupting forest regeneration processes (Chapter III). These findings highlight the need to critically reassess post-disturbance management strategies within European forests (Müller et al., 2018). In managed forests, portions of disturbed areas could be left unmanaged to promote the regeneration of structurally complex, biodiversity-rich stands. In natural forests, management interventions should be avoided whenever possible, as disrupting recovery processes may undermine conservation goals (see also Mikusiński et al., 2018).

Perspectives for future studies

My PhD thesis provided new insights about the natural disturbance effects on bird diversity in temperate climate zone. However, many aspects of their diversity response remain unexplored. For example, in my thesis I focus on changes in bird abundance in disturbed areas during the breeding season as a proxy for assessing disturbance impacts on bird populations. Indeed, abundance-based diversity metrics remain the most widely used approach to describe the effects of disturbances on biotic communities (Gaillard et al., 2003). However, abundance data alone are insufficient to fully capture the complex impacts of disturbances on animal communities (Cordeiro Pereira et al., 2024; Runge et al., 2006). Many species exist in the form of metapopulations, where habitat patches may function as “sources” or “sinks” depending on their reproductive output (Pulliam, 1988; Runge et al., 2006). Correctly classifying a habitat patch in the context of its role in source-sink dynamics is often critical for effective management and conservation. Yet, source–sink dynamics cannot be detected using abundance data alone and may therefore be overlooked if reproductive data are not collected (Runge et al., 2006). Natural disturbances may influence various aspects of bird biology, including habitat use, diet, adult mortality and stress levels, which in turn may change their reproductive output (Diamond and Ross, 2020; Jones et al., 2001; Waide, 1991). In some cases, this may cause disturbed areas to function as population sinks, but empirical evidence remains limited (Boves et al., 2013; Hollander et al., 2015). Although most studies on mammals show little to no evidence of changes in reproductive output following large-scale disturbances (e.g., Banks et al., 2011; Gaillard et al., 2003), without comprehensive studies on the reproductive output of birds, our understanding of how disturbances affect avian communities remains incomplete (Cordeiro Pereira et al., 2024).

Birds are often considered reliable indicators of disturbance effects, but extrapolating their responses to other taxa should be executed with caution. Biodiversity responses are highly taxon-dependent, as groups occupying different ecological niches may react to disturbances in contrasting ways (Żmihorski and Durska, 2011). For example, saproxylic organisms tend to thrive in disturbed forests, primarily due to the increased availability of diverse deadwood structures (Thorn et al., 2017; Wermelinger et al., 2025). However, their diversity typically declines following post-disturbance management, which often involves the removal of dead wood. In contrast, taxa that prefer open habitats (e.g., hoverflies and epigeal spiders) may benefit from both natural disturbances and subsequent management operations (Thorn et al., 2018; Viljur et al., 2022). As I demonstrate in my work, even among bird communities, disturbance can have divergent effects depending on the species or functional group considered (Chapters I & II). To capture broader-scale patterns and make informed management decisions, monitoring multiple taxa simultaneously is recommended. One promising tool for monitoring multiple taxa while remaining cost-effective is Passive Acoustic Monitoring, which allows simultaneous detection of vocalizing groups such as birds, mammals, insects, and amphibians (Sugai et al., 2019; Chapter III). However, Passive Acoustic Monitoring is limited to sound-producing species and therefore cannot detect plants, fungi, and other silent groups that may respond strongly to disturbances and play vital roles in ecosystem functioning (Gibb et al., 2019; Thorn et al., 2018). An alternative approach could involve shifting the focus from specific taxonomic groups to key habitat features and structural indicators of biodiversity. Tree-related microhabitats, for example, show promise as biodiversity indicators, as they are used by a wide range of ecological groups and can be surveyed in a cost-effective manner (Asbeck et al., 2021; Dutta et al., 2025; Martin et al., 2022). They are also sensitive to natural disturbance events (Augustynczik et al., 2020; Zemlerová et al., 2023), as also demonstrated by our study in Białowieża Forest (van Eupen et al., 2025). Overall, a multifaceted approach to biodiversity monitoring in naturally disturbed areas is needed – one that integrates both species-level data and structural habitat indicators to provide a reliable picture of disturbance impact at both local and global scales.

Finally, even extremely large disturbed areas never function as isolated entities – they exist within a broader landscape context. Thus, their biodiversity and succession trajectories depend highly on their surrounding environment. For example, tree regeneration in disturbed areas of Białowieża Forest was primarily shaped by species composition in adjacent undisturbed habitat patches (Dobrowolska et al., 2022). Naturally disturbed areas may provide optimal habitat for certain open-habitat species, but these species may struggle to colonize such areas if they are limited by the distance from source populations, such as other disturbed sites or farmland (Żmihorski et al., 2016). Large animals, such as mammals and birds, often have home ranges that extend beyond individual disturbed areas and hence use nearby undisturbed sites as integral parts of their territories (Gryz et al., 2025; Reiner et al., 2023). Moreover, disturbed areas often lack clearly defined boundaries (with the exception of fires) and typically affect ecosystems unevenly, creating a mosaic of impacts ranging from minimal damage to complete ecosystem transformation (Turner, 2010). Despite the importance of landscape context for disturbance dynamics, landscape-scale effects are rarely assessed, even in bird studies (but see Graser et al., 2025, 2024). This represents a significant gap in our understanding of the dynamics of natural disturbances and their effect on biodiversity.

5. Conclusions

Natural disturbances are usually perceived as catastrophes due to their significant economic impacts, potential to disrupt ecosystem services and, in some cases, their adverse effects on human health (Cascio, 2018; Schuck and Schelhaas, 2013; Thom and Seidl, 2016). However, my research confirms that they also play an important role in shaping biodiversity, as demonstrated in birds. The effects of disturbances on bird diversity are complex and depend on multiple factors, including disturbance frequency, the type of ecosystem affected, and management decisions. These effects also change over time as ecological succession unfolds. Moreover, disturbance events rarely affect all bird species in the same way – some species benefit, while others inevitably decline.

Because of this complexity and their multi-faceted influence on biodiversity, natural disturbances can be considered double-edged swords: their outcomes can only be evaluated within the broader context of management and conservation goals for a given area (Brambila et al., 2023; Thom and Seidl, 2016). I argue that, when managed appropriately, natural disturbances can contribute to achieving conservation and management goals across many regions of Europe without severely compromising other ecosystem functions. They may also facilitate ecosystem restoration by fostering structurally complex and resilient forests, while supporting the objectives prioritized in European Union environmental policies (European Commission's Directorate-General for Environment, 2024; Selwyn et al., 2025).

The pressure exerted by natural disturbances on ecosystems has increased in recent years and is expected to continue rising (Patacca et al., 2023; Schelhaas et al., 2003; Seidl et al., 2017). As a result, we will increasingly face both their occurrence and consequences for ecosystems. Such situations demand timely management decisions, often made under pressure. Only a deep understanding of natural disturbance impacts can enable us to develop effective responses, helping us to coexist with these fascinating, yet controversial, phenomena in the uncertain future of the Anthropocene.

6. References

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7. Other works, not included in the thesis

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Ej, wykorzystam też to miejsce na autoreklamę, bo mnie rozbawił ten pomysł – nagrywam muzykę jako Zakochane Kundle i myślę, że to jest moja fajniejsza aktywność życiowa niż nauka, więc zapraszam do posłuchania np. na Spotify albo Bandcampie. Jeżeli dla Ciebie nauka jest najważniejsza to też fajnie, ale dla mnie nie jest.

Teraz – dla mojej najbliższej rodziny. Dla rodziców (**Małgorzaty** i **Cezarego Walesiaków**) – za bliskość, ciepło i nieustające wsparcie przez całe życie. Co tu dużo mówić – bez Was nie byłbym tu, gdzie jestem (w ogóle nigdzie bym nie był, hehe). Dla moich braci – **Tomasza Walesiaka** (za inspirację we wzniosłych i pomoc w przyziemnych sprawkach!) i **Krzysztofa Antoniaka** (za wszystkie śmieszne żarty, kozackie historie i chwile wytchnienia). Również dla **Iwony Furman**, **Bartłomieja Antoniaka**, **Haliny Furman** i Łucji Doradzińskiej – czyli całej mojej najbliższej rodziny. „Silnej rodziny”!

Chciałbym też osobno podziękować mojej Mamie – **Małgorzacie Walesiak**, która w mojej naukowej drodze wspierała mnie przez całe życie jak nikt inny. Przez wiele lat nie wyobrażałem sobie, dlaczego w ogóle miałbym zostać naukowcem – a Ty miałaś dobrą „kobiecą intuicję”! Bardzo Ci, Mamo, dziękuję!

Ha, no i na koniec przyszedł ten moment…

Dla **Zinki** i **Witka Walesiaków**, bo są kochani i słodcy. Teraz nie umiecie jeszcze czytać, ale kiedyś to sobie przeczytacie.

Dla **Alicji Walesiak**. Za to, że moje życie dzięki Tobie jest piękne.