Czynniki wpływające na występowanie ptaków w wyspach leśnych

Factors influencing the occurrence of birds in forest patches

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Spis treści

Spis artykułów

1. **Bełcik, M.**, Lenda, M., Amano, T., Skórka, P. (2020). Different response of the taxonomic, phylogenetic and functional diversity of birds to forest fragmentation. Scientific Reports, 10:20320, https://doi.org/10.1038/s41598-020-76917-2. (IF = 4.379 , 140 pkt MNiSW)

2. **Bełcik, M.**, Lenda, M., Amano, T., Pustkowiak, S., Skórka, P. (202x). Social information can alter the effect of habitat fragmentation on bird diversity and improve its stability. (maszynopis wysłany do Nature Communications)

3. **Bełcik, M.**, Lenda, M., Pustkowiak, S., Woźniak, B., Skórka, P. (202x). Lands of fear and uncertainty modify the effects of forest fragmentation on the abundance of a passerine bird. (maszynopis wysłany do Behavioral Ecology)

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Streszczenie

Różnorodność biologiczną można podzielić na bogactwo gatunkowe, różnorodność filogenetyczną oraz różnorodność funkcjonalną. Każda z tych miar może inaczej reagować na zmiany w środowisku. Jedną z najistotniejszych zmian środowiska jest fragmentacja siedlisk. Szczególnie uwidacznia się ona na przykładzie lasów w krajobrazie rolniczym, gdzie może wpływać na występowanie gatunków, a zatem bioróżnorodność. Jednak cechy strukturalne krajobrazu i siedlisk nie są jedynymi czynnikami wpływającymi na rozmieszczenie gatunków. Zwierzęta mogą wykorzystywać informację socjalną, czyli ślady aktywności osobników tego samego lub innych gatunków, jak również ich fizyczną obecność w danym miejscu. Dotychczas nie rozumiemy, jak informacja socjalna może modyfikować wpływ fragmentacji na różnorodność biologiczną i populacje poszczególnych gatunków.

Celem rozprawy doktorskiej jest próba odpowiedzi na pytanie w jaki sposób fragmentacja siedlisk wpływa na miary różnorodności biologicznej ptaków zasiedlających wyspy leśne w krajobrazie rolniczym. Kolejnym celem jest określenie wpływu informacji socjalnej na miary różnorodności biologicznej ptaków, liczebność wybranego gatunku ptaka (śpiewaka *Turdus philomelos*), oraz sprawdzenie czy informacja socjalna jest w stanie modyfikować wpływ Fragmentacji na ptaki.

Rozprawa doktorska stanowi zbiór trzech oryginalnych prac naukowych W pierwszej pracy **(Artykuł 1)** określiłem w jaki sposób fragmentacja płatów leśnych wpływa na różne miary bioróżnorodności ptaków. Przeprowadzone przeze mnie badania pokazały, że miary różnorodności w różnym stopniu reagują na fragmentację, gdyż najsilniej na fragmentację zareagowała różnorodność gatunkowa, a najsłabiej różnorodność funkcjonalna. Przykładowo, powierzchnia lasu była pozytywnie skorelowana z różnorodnością gatunkową, negatywnie z różnorodnością filogenetyczną, i nie miała wpływu na różnorodność funkcjonalną. Ten ostatni wynik może sugerować, że istnieje znaczna redundancja funkcji w obrębie zgrupowań ptaków w badanych lasach.

W drugiej pracy **(Artykuł 2)** opisuję w jaki sposób wpływ fragmentacji na wskaźniki bioróżnorodności ptaków może być modyfikowany przez informację socjalną. Pozytywna informacja socjalna (głos drozda śpiewaka) zwiększała różnorodność gatunkową i filogenetyczną w płatach lasu. Różnorodność funkcjonalna nie zareagowała na eksperyment. Pozytywna informacja zwiększała również tempo wymiany gatunków między latami, zaś informacja negatywa (głos jastrzębia) ją zmniejszała. Efekt eksperymentu utrzymywał się również w roku następnym. Pozytywna informacja socjalna potrafiła odwrócić efekt wpływu fragmentacji na miary różnorodności.

W trzeciej pracy **(Artykuł 3)** skupiam się na śpiewaku i testuję w jaki sposób informacja socjalna wpływa na jego liczebność w płatach leśnych o zróżnicowanym stopniuj fragmentacji. Uzyskane przeze mnie wyniki pokazały, iż największy wpływ na liczebność śpiewaka w lasach miała informacja negatywna, która wchodziła w interakcję z miarami fragmentacji płatów leśnych. W pierwszym roku trwania eksperymentu liczebność śpiewaka zwiększała się wraz ze wzrostem powierzchni płata lasu. Po emisji negatywnej informacji socjalnej, zależność ta uległa odwróceniu.

Wyniki uzyskane przeze mnie w ramach realizowania pracy doktorskiej pokazują, że informacja socjalna może mieć praktyczne znaczenie w utrzymaniu lokalnych populacji i bogactwa gatunkowego w warunkach zróżnicowanej fragmentacji siedlisk leśnych, potencjalnie tworząc nawet trwałą sieć nowych zależności międzygatunkowych.

Summary

Biodiversity can be described as species richness, phylogenetic diversity and functional diversity. Each of these metrics may respond differently to changes in the environment. One of the most significant of these changes is habitat fragmentation. Its effects are especially well visible in forest patches located in agricultural landscape, where forest fragmentation can influence the occurrence of species, and thus biodiversity. However, structural features of the landscape and habitats are not the only factors that influence species distribution. Animals may use social information, i.e. traces of the activity of other individuals or species, as well as their physical presence in a given place. We yet do not fully understand how social information can modify the impact of fragmentation on biodiversity and individual species.

The aim of this doctoral dissertation is an attempt to answer the question of how fragmentation of forest patches affects the measures of biodiversity of birds. Another goal of this dissertation is to determine the impact of social information on bird biodiversity metrics and the abundance of a selected bird species (song thrush *Turdus philomelos*), and to verify whether the social information is able to modify the impact of forest fragmentation on birds.

The doctoral dissertation is a collection of three original scientific manuscripts. In the first manuscript (**Article 1**) it is described how the fragmentation of forest patches affects various measures of bird biodiversity. The research has shown that three measures of bird diversity responded to fragmentation to a different extent with the species richness being most susceptible to forest fragmentation, and functional diversity the least. For example, forest area was positively correlated with species richness, negatively with phylogenetic diversity, and had no effect on functional diversity. These results may suggest that there is a significant redundancy of function within the bird community.

In the second manuscript (**Article 2**), I describe how the impact of fragmentation on bird biodiversity metrics can be modified by social information. Positive social information (songs of the song thrush) increased species and phylogenetic diversity in forest patches, but functional diversity showed no response to the experiment. Positive social information increased species turnover between years while negative social information (voice of the goshawk) decreased the turnover. The effect of the experiment was also maintained in the following year. Positive social information was able to reverse the effect of fragmentation on the diversity measures.

In the third paper (**Article 3**), I focus on the song thrush and test how social information influences its abundance in forest patches of varying fragmentation. The results have shown there was no simple effect of social information on the abundance of song thrush. Instead, the negative social information interacted with forest fragmentation. In the first year of the experiment, the number of the song thrushes was positively associated with the area of the forest patch. After the emission of negative social information, this relationship was reversed.

The results of this dissertation show that social information can be of practical importance in maintaining local populations and species richness in conditions of high fragmentation, potentially creating even a permanent network of new interspecies relationships.

Wstęp

Utrata różnorodności biologicznej jest głównym problemem w ekologii i ochronie przyrody na świecie (Cardinale i in. 2012, Hooper i in. 2012, Reich i in. 2012). Sama różnorodność biologiczna jest zjawiskiem wieloaspektowym i może być mierzona na różne sposoby, a każda z miar może reagować inaczej na zmiany środowiskowe. Tradycyjnie różnorodność biologiczną mierzy się bogactwem gatunkowym (Chesson, 2000). Taki wskaźnik jest intuicyjny, stosunkowo łatwy do oszacowania (Gotelli i Colwell 2001), oraz jest wykorzystywany w szeregu analiz (Magurran i McGill 2011). Jednak każdy gatunek nosi unikatową pulę genową, która koduje adaptacje zdobyte na drodze ewolucji, będące cechami pozwalającymi im przeżywać i rozmnażać się w określonych warunkach. Zatem różnorodność filogenetyczna jest kolejnym kluczowym składnikiem różnorodności biologicznej, odzwierciedlającym dziedzictwo ewolucyjne życia i potencjalnie jego zdolność do adaptacji do przyszłych, zmieniających się warunków (Vane-Wright i in. 1991, Cadotte i Davies 2010). Bogactwo gatunków i różnorodność filogenetyczna są również związane z różnorodnymi cechami funkcjonalnymi gatunków. Liczba tych cech może określać różnorodność funkcji pojedynczych gatunków lub zespołów gatunków w ekosystemie (Petchey i Gaston 2006, Duffy i in. 2007). Różnorodność funkcjonalna, będąca miarą liczebności gatunków mających odrębne cechy, jest ważną cechą zbiorowisk organizmów żywych (Naeem i Li 1997, Tilman i in. 1997, Mason i in. 2005).

W ochronie przyrody i ekologii dominuje pogląd, że fragmentacja siedlisk jest jednym z największych zagrożeń dla funkcjonowania populacji różnych gatunków, a tym samym różnorodności biologicznej (Wilson i in. 2016). Fragmentacja jest procesem definiowanym na wiele sposobów, najszerszym z nich jest zmniejszenie powierzchni i izolacja przestrzenna płatów siedlisk (Franklin i George 2002). Zmniejszenie powierzchni płatów siedlisk może skutkować mniejszym prawdopodobieństwem zajmowania i kolonizacji przez zwierzęta, przegęszczeniem lokalnych populacji, zwiększoną konkurencją o zasoby czy też zwiększoną podatnością populacji na efekty losowe. Wyjaśnienie efektu fragmentacji znajduje się w sformalizowanych koncepcjach metapopulacji (Levins, 1968) oraz biogeografii wysp (MacArthur i Wilson 2001). Mówią one, że tempo lokalnych ekstynkcji jest większe w małych i izolowanych płatach siedlisk, co z kolei powoduje zmniejszenie bogactwa gatunkowego. Liczne badania dowodzą, że fragmentacja wpływa na wiele procesów populacyjnych, takich jak dyspersję (Cote i in. 2017, Tischendorf i in. 2003), relacje drapieżnik – ofiara (Ryall i Fahrig 2006) czy też reprodukcję (Robinson i in. 1995, Stephens i in. 2003). Wpływ ten jest jednak zależny od badanej grupy gatunków – przykładowo, na zmniejszenie płatów siedlisk inaczej zareagują gatunki ubikwistyczne (generaliści siedliskowi), a inaczej będące specjalistami (Andren, 1994)

W myśl klasycznej ekologii występowanie gatunku w siedlisku ma zależeć głownie od jego cech fizycznych (np. fragmentacji siedlisk) oraz zasobów pokarmowych (Cody, 1985). Gatunki wchodzą jednak w liczne interakcje z innymi osobnikami tego samego lub innego gatunku, co również może mieć wpływ na ich występowanie. Samo środowisko jest często bardzo zmienne, co może sprawiać, że procesy decyzyjne, które miejsce wybrać (np. gdzie żerować, zakładać terytoria) mogą nie być optymalne, jeśli oparte są tylko na podstawie cech strukturalnych siedliska. Zwierzęta mogą jednakże wykorzystywać w wyborze siedliska tzw. informację socjalną, którą może być sama obecność innych osobników, wydawane przez nie odgłosy, ich zachowania lub zaledwie ślady ich obecności lub działalności (Fletcher 2007, Hromada i in. 2008). Może być ona niesiona przez inne osobniki tego samego lub różnych gatunków (Ward i in. 2010). Osobniki, które wykorzystują informację socjalną mogą znacznie podwyższyć swoje dostosowanie w porównaniu do osobników, które polegają wyłącznie na cechach strukturalno-fizycznych środowiska (Schmidt i in. 2010). Informacja socjalna może pochodzić z różnych źródeł, które mogą wzajemnie się osłabiać lub wzmacniać (np. odgłosy drapieżnika mogą osłabiać rolę głosów innych osobników tego samego gatunku). Informacja socjalna, poprzez oddziaływanie na osobniki różnych gatunków, może wpływać na występowanie poszczególnych gatunków, a zatem kształtować bogactwo gatunkowe. Ponadto, informacja socjalna, zwłaszcza jeśli pochodzi z różnych źródeł, może modyfikować wpływ cech fizycznych siedliska, przykładowo fragmentacji siedlisk, na populacje poszczególnych gatunków, a tym samym różnorodność zgrupowań zwierząt zamieszkujących te płaty siedlisk.

Środkowoeuropejskie ptaki, zwłaszcza gatunki leśnych, stanowią doskonałą grupę do zrozumienia wpływu fragmentacji na systemy biologiczne. Ptaki występują w krajobrazach silnie zmienionych poprzez rolnictwo i urbanizację, a jednak prezentujących różne stopnie fragmentacji siedlisk (Tellería i in. 2003, Tryjanowski i in. 2011). Obejmują one również szeroki zakres różnorodności gatunkowej, funkcjonalnej i filogenetycznej (Pearman i in. 2014). Dotychczasowe badania wskazują, że fragmentacja płatów siedlisk może być istotnym czynnikiem wpływającym na ich zajmowanie przez wybrane gatunki ptaków (Prugh i in. 2008, Hofmeister i in. 2017, Koivula i in. 2017). Silna izolacja płatów siedlisk może mieć zarówno negatywny, jak i pozytywny wpływ na bogactwo i skład gatunkowy awifauny, w zależności od szeregu czynników, w tym preferencji siedliskowych danego gatunku, gniazdowania, sposobu dyspersji lub taktyk żerowania (Stephens i in. 2003; Newbold i in. 2012). Odgłosy wydawane przez osobniki tego samego lub innych gatunków są z kolei czynnikiem, który może mieć ważny wpływ na podejmowanie przez ptaki decyzji o zasiedlaniu danego płata siedliska, przy czym, jak wspomniano powyżej, wpływ ten może być potencjalnie pozytywny jak i negatywny (Fletcher 2007, Suzuki 2015, Suzuki & Kutsukake 2017).

Cel badań

Celem rozprawy doktorskiej jest określenie wpływu miar fragmentacji wysp (płatów) leśnych na wskaźniki różnorodności biologicznej awifauny oraz liczebność wybranego gatunku leśnego ptaka, a także sprawdzenie jak ten wpływ może być modyfikowane poprzez informację socjalną. W ramach badań weryfikowane są dwie hipotezy:

Hipoteza 1: Fragmentacja lasów wpływa negatywnie na różnorodność biologiczną awifauny, wyrażoną różnymi miarami, przy czym efekt fragmentacji jest odmienny w przypadku różnych miar bioróżnorodności.

Przewidywałem, że jako pierwsza miara, na spadek powierzchni siedlisk i wzrost izolacji przestrzennej od siebie płatów leśnych, zareaguje bogactwo gatunkowe. Ponieważ rzadkie gatunki często znajdują się na odrębnych gałęziach drzewa filogenetycznego, przewidywałem, że jako druga na wzrost fragmentacji zareaguje spadkiem różnorodność filogenetyczna. W ugrupowaniach zwierząt występuje duża redundancja cech, a daną funkcję potrafi pełnić wiele gatunków, zatem przewidywałem, iż ze wzrostem fragmentacji różnorodność funkcjonalna spadnie ostatnia. Hipotezę tę testowałem w artykule 1.

Hipoteza 2: Pozytywna lub negatywna informacja socjalna może odpowiednio zniwelować lub pogłębiać efekt fragmentacji lasów na bioróżnorodność oraz liczebność wybranego gatunku.

Pozytywna informacja socjalna (głos ptaka wróblowego – śpiewaka *Turdus philomelos*) w płatach lasów może stanowić dodatkowy bodziec podczas podejmowania decyzji przez śpiewaki, jak i inne gatunki ptaków co do zasiedlenia wyspy leśnej, potencjalnie podnosząc jej wartość (liczebność śpiewaka jest pozytywnie skorelowana z liczebnością innych gatunków). Sprawia to, ze pozytywna informacja w małych oraz izolowanych lasach powinna zwiększać liczebność śpiewaka oraz bogactwo gatunkowe. Negatywne sygnały (głos jastrzębia *Accipiter gentilis* – drapieżnika polującego na wiele gatunków ptaków, w tym często na drozdy) mogą z kolei odstraszać śpiewaka, jak i inne gatunki ptaków przed zajmowaniem potencjalnie dogodnych małych oraz izolowanych siedlisk. Przewidywałem zatem, że negatywna informacja socjalna może pogłębiać efekty fragmentacji. Hipotezę tę testowałem w artykułach 2 i 3.

Metodyka badań

Badania zostały przeprowadzone w 163 lasach północnej części Małopolski, mającej charakter krajobrazu rolniczego (Fig.1.). Dla każdego lasu został określony zestaw parametrów siedliskowych (Tab.1.). Badania terenowe prowadzone były w latach 2017-2019. W tym czasie, corocznie pomiędzy 1.IV. a 31.V., prowadzone były kontrole lasów, podczas których liczono ptaki. Kontrola w roku 2017 miała na celu zapoznanie się ze stanem awifauny w wybranych lasach, w roku 2018 miała na celu ustalenie efektu eksperymentu, który przeprowadzono tuż przed sezonem lęgowym, a w roku 2019 miała na celu sprawdzenie czy efekt eksperymentu został utrwalony w wybranych lasach. W każdym lesie były przeprowadzone liczenia ptaków, w trzech dwudziestodniowych seriach. W każdej serii dany las kontrolowany była jeden raz, dając łącznie trzy kontrole w sezonie (pierwsza: 01.-20.IV, druga: 21.IV-10.V, trzecia 11.V-31.V). Obserwator poruszał się w drzewostanie, starając się podczas każdej kontroli iść inną trasą. Przed rozpoczęciem kontroli, notował czas rozpoczęcia, oraz warunki pogodowe panujące w danym momencie. Podczas każdej kontroli notowany był pierwszy osobnik danego gatunku, oraz czas obserwacji. Wyjątkiem od tej zasady był śpiewak, gdzie notowany był każdy osobnik (wraz z czasem obserwacji), a jego pozycja oznaczana na odbiorniku GPS. Jeśli przez 10 minut obserwator nie zanotował żadnego nowego gatunku, kończył kontrolę i przenosił się do innego lasu. Zastosowana metodyka jest zmodyfikowaną wersją modelu Michaelis-Menten i jest używana do oceny liczby gatunków zaobserwowanych podczas kontroli (Keating i Quinn 2012).

Eksperyment terenowy przeprowadzony został w okresie 17.III – 30.III 2018 r. Przed przystąpieniem do eksperymentu lasy zostały przyporządkowane do pięciu grup (po 30 lasów każda). Żadna z grup nie różniła się istotnie pod względem cech drzewostanu od innych. Grupy lasów to:

- lasy gdzie emitowany był głos śpiewaka (pozytywna informacja socjalna),
- lasy gdzie emitowany był głos jastrzębia (negatywna informacja socjalna),
- lasy gdzie emitowany był głos jastrzębia i śpiewaka (naprzemiennie na jednym nagraniu – informacja socjalna mieszana),
- lasy gdzie emitowany był odgłos tła (szum drzew, odgłosy dochodzące z otaczającego krajobrazu, itp. – tzw. kontrola proceduralna),
- lasy kontrolne (bez emisji sygnałów).

Liczba głośników była zależna od wielkości lasu i w każdym z nich emitowany był tylko jeden rodzaj sygnału. Emisje trwały codziennie od godziny 7 rano do 12. Po zakończeniu emisji głośniki były zbierane, w ciągu wieczora ładowane, i rozwieszane następnego dnia rano.

Dla każdej powierzchni obliczone zostały następujące wskaźniki różnorodności:

- Liczba gatunków jako miara różnorodności gatunkowej
- Średni dystans na drzewie filogenetycznym do najbliższego gatunku (MNTD) jako miara różnorodności filogenetycznej (Tucker i in. 2017)
- Bogactwo funkcjonalne (FRic) jako miara różnorodności funkcjonalnej (Mason i in. 2005)

W **artykule 1**, gdzie weryfikowałem **hipotezę 1**, sprawdziłem w jaki sposób miary fragmentacji płatów lasu wpływają na poszczególne miary bioróżnorodności zgrupowań ptaków. W tym celu stworzyłem uogólniony model addytywny (GAM), gdzie zmienną objaśnianą był każdy ze wskaźników różnorodności (obliczony dla wszystkich gatunków, oraz podzbioru gatunków będących leśnymi specjalistami). Zmienne objaśniające reprezentowały dwa rodzaje - te, które opisywały powierzchnię i izolację płatu siedliska (miary fragmentacji) oraz te, które opisywały parametry lasu, potencjalnie związane z jakością płatów leśnych (parametry drzewostanu - Tab.1).

W **artykule 2**, gdzie weryfikowałem **hipotezę 2**, wykorzystałem modele GAM stworzone dla każdego ze wskaźników różnorodności (obliczonego dla wszystkich gatunków, oraz podzbioru gatunków będących leśnymi specjalistami). Dla każdego z tych wskaźników różnorodności, obliczyłem zmianę w wyniku eksperymentu, poprzez odjęcie od wartości obliczonej dla roku 2018 wartości obliczonej dla roku 2017. Podobnie zrobiono dla danych z roku 2019. Jako zmienne objaśniające, modele zawierały miary fragmentacji (Tab.1.), rodzaj informacji socjalnej emitowanej w ramach eksperymentu na danej powierzchni, oraz interakcję między miarami fragmentacji i rodzajem informacji socjalnej. Różnice w odpowiedzi pomiędzy rodzajami informacji socjalnej zostały zbadane testem *a posteriori* Walda dla GAM. Dodatkowo zostały wykonane analizy ordynacyjne (kanonicza analiza korespondencji – CCA) mające ustalić, czy były istotne różnice w składzie gatunkowym w wyniku eksperymentu. Ponadto obliczono wskaźnik Jaccarda, który podaje jaki procent składu gatunkowego wymienił się w badanych lasach na skutek eksperymentu.

W **artykule 3** weryfikowałem **hipotezę 2**, wykorzystując śpiewaka do zbadania wpływu interakcji między informacją socjalną, a fragmentacją siedlisk na liczebność tego gatunku w płatach leśnych. Stworzyłem modele GAM uwzględniające wpływ rodzaju informacji socjalnej emitowanej w ramach eksperymentu, miar fragmentacji oraz interakcji miedzy tymi dwoma grupami czynników na liczebność śpiewaka. Różnice w odpowiedzi pomiędzy rodzajami informacji socjalnej zostały zbadane testem *a posteriori* Walda.

Wszystkie analizy były wykonane w środowisku statystycznym R, oprócz analiz ordynacyjnych wykonanych w programie Canoco.

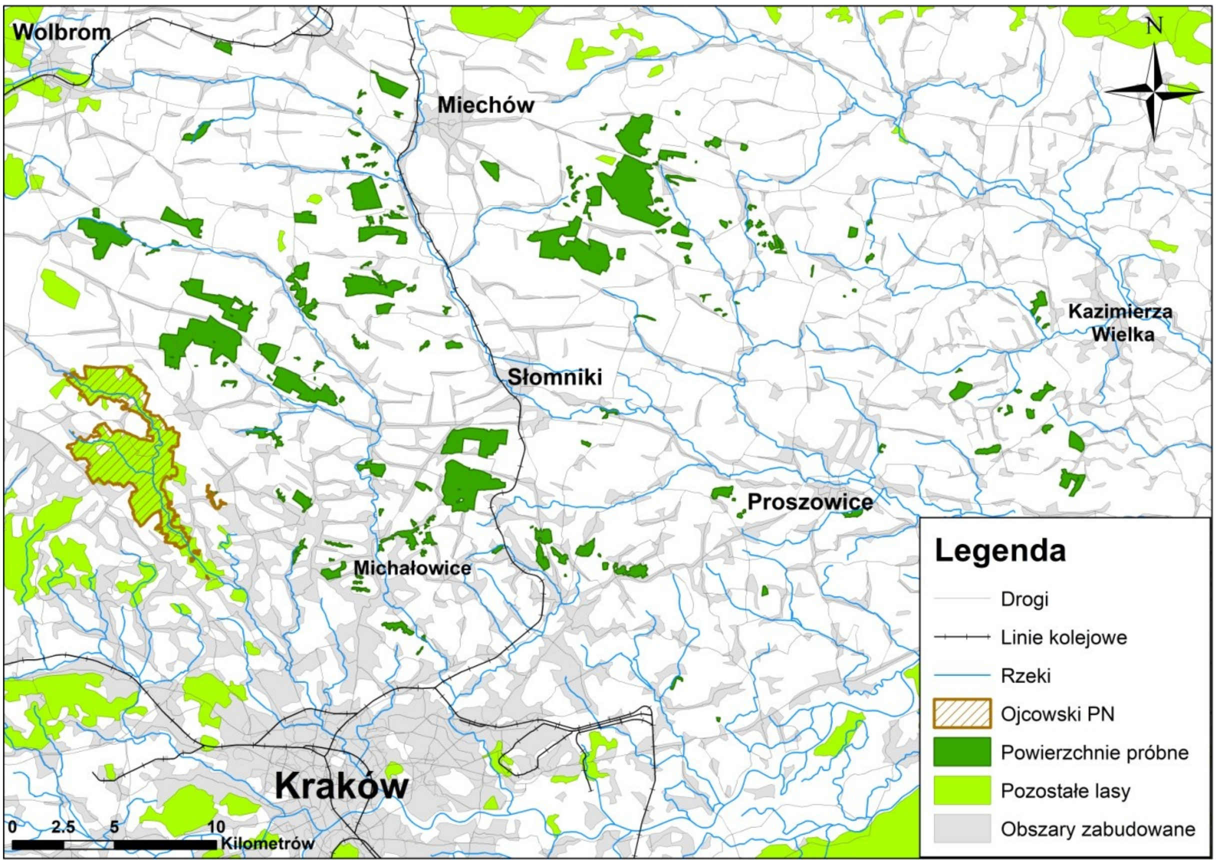

Figura 1. Mapa obszaru prac badawczych wykonywanych w ramach projektu, z zaznaczonymi leśnymi powierzchniami próbnymi.

Tabela 1. Zestaw parametrów wyliczonych dla każdego drzewostanu.

Parametr	**Rodzaj parametru**	**Opis**	**Zakres**	**Średnia ± SD**
Powierzchnia drzewostanu	Miara fragmentacji	Łączna powierzchnia drzewostanu (w hektarach)	0.4-582.3	37.3±89.5
Indeks kształtu	Miara fragmentacji	Miara skomplikowania kształtu granic drzewostanu	1.110-3.528	1.790±0.504
Odległość do najbliższego sąsiada	Miara fragmentacji	Najkrótsza odległość w linii prostej między brzegiem drzewostanu, a jego najbliższym sąsiadem (w metrach)	16-3509	269.3±701.4
Indeks izolacji	Miara fragmentacji	Suma powierzchni wszystkich drzewostanów których krawędzie mieszczą się w promieniu 2,5 km od brzegu danego drzewostanu, podzielonych przez kwadraty odległości do tego drzewostanu	0-1845	78.9±251.9
Wiek drzewostanu	Parametr drzewostanu	Średni wiek dominujących gatunków drzew w głównym piętrze drzewostanu (w latach)	10-112	58.2±24.3
Udział gatunku dominującego	Parametr drzewostanu	Wyrażony w skali całkowitej od 0 do 10 (gdzie 10 to najwyższy wynik), udział dominujących gatunków drzew w głównym piętrze drzewostanu	2-10	-
Zwarcie głównego piętra drzewostanu	Parametr drzewostanu	Średnia gęstość drzewostanu (reprezentująca procent dna lasu zacienionego przez koronę drzew – wyrażony w %)	30-100	66.1±15.8
Udział gatunków iglastych	Parametr drzewostanu	Odsetek gatunków iglastych w głównym piętrze drzewostanu (w%)	0-100	21.0±26.0

Wyniki

Wyniki modeli GAM wykazały różne reakcje wskaźników różnorodności ptaków na miary fragmentacji płatów leśnych, potwierdzając tym samym **hipotezę 1**. Różnorodność gatunkowa wzrastała nieliniowo, a różnorodność filogenetyczna spadała nieliniowo wraz z powierzchnią lasu (spadek ten przyspieszał wraz ze spadkiem powierzchni lasu – Fig.2. w artykule 1). Różnorodność funkcjonalna zgrupowań ptaków nie była związana ze zmianami powierzchni lasu. Różnorodność gatunkowa była najwyższa przy wysokiej i umiarkowanej wartości indeksu izolacji (Fig.3. w artykule 1). Wskaźniki różnorodności filogenetycznej i funkcjonalnej zmniejszały się liniowo wraz ze wzrostem izolacji lasu (Fig.3. w artykule 1). Inna miara fragmentacji (odległość do najbliższego sąsiada) była pozytywnie skorelowana z różnorodnością gatunkową.

Parametry drzewostanu były kolejną grupą czynników wpływających na miary różnorodności ptaków. Wiek lasu był pozytywnie związany z różnorodnością gatunkową i funkcjonalną, ale negatywnie z różnorodnością filogenetyczną dla wszystkich gatunków ptaków (Tab.2. w artykule 1). Zwarcie głównego piętra drzewostanu okazało się mieć pozytywny związek z różnorodnością funkcjonalną gatunków leśnych (Tab.3. w artykule 1). Udział gatunków iglastych był pozytywnie, a udział gatunku dominującego negatywnie skorelowany z różnorodnością gatunkową (Tab.2. w artykule 1).

Testowanie hipotezy 2 wykazało, iż różnorodność gatunkowa była większa na powierzchniach leśnych, gdzie emitowano pozytywną informację socjalną, niż w takich gdzie emitowano informację mieszaną lub negatywną (Tab.2. i Fig.2. w artykule 2). Część efektów eksperymentu utrzymała się w roku następnym (Tab.2. i Fig.2. w artykule 2). Jedyną zaobserwowaną reakcją różnorodności filogenetycznej na eksperyment była wyższa wartość różnorodności filogenetycznej w lasach gdzie emitowano informację pozytywną, niż w lasach gdzie emitowano informację negatywną w roku eksperymentu (Tab.2. i Fig.3. w artykule 2). Różnorodność funkcjonalna nie zareagowała na eksperyment (Tab.2. w artykule 2). Wyniki analiz CCA wskazywały, iż były istotne różnice w składzie gatunkowym pomiędzy lasami powstałe w wyniku eksperymentu, co zostało potwierdzone przez wskaźnik wymiany gatunków Jaccarda, który najbardziej wzrósł w lasach, gdzie emitowano pozytywną informację socjalną, a najbardziej zmalał w lasach gdzie emitowano negatywną informację socjalną (Fig.4. i Fig.5. w artykule 2).

Analizy potwierdziły również, iż informacja socjalna może modyfikować wpływ fragmentacji na miary różnorodności ptaków, potwierdzając tym samym **hipotezę 2.** Pozytywna informacja socjalna potrafiła zwiększyć różnorodność funkcjonalną w najmniejszych i największych płatach lasu, a efekt ten utrzymywał się w rok po eksperymencie (Tab.1., Tab.3. i Fig.6. w artykule 2). Pozytywna informacja socjalna zwiększała również indeks Jaccarda w najmniej i najbardziej izolowanych lasach zarówno w roku eksperymentu, jak i w roku następnym (Tab.4. i Fig.4. w artykule 2). Ponadto, pozytywna informacja socjalna zmniejszała różnorodność filogenetyczną wszystkich gatunków w najmniejszych płatach lasu i zwiększała w największych, osłabiając tym samym negatywny wpływ wzrostu wielkości lasu na różnorodność filogenetyczną wszystkich gatunków (Tab.1., Tab.3. i Fig.6 w artykule 2). Pozytywna informacja spowodowała również wzrost różnorodności filogenetycznej specjalistów leśnych w najbardziej izolowanych lasach w roku eksperymentu (Tab.1., Tab.3. i Fig.S1 w artykule 2).

Testowanie hipotezy na wybranym gatunku, wykazała, że liczebność śpiewaka nie zareagowała w żaden sposób na emitowaną informację socjalną, zarówno w roku eksperymentu, jak i rok później (Tab.1. i Fig.1. w artykule 3). Zaobserwowano jednak, że negatywna informacja socjalna modyfikowała związek między powierzchnią lasu, a liczebnością śpiewaka w obu latach eksperymentu (Tab.1. i Fig.2. w artykule 3), potwierdzający tym samym **hipotezę 2**. W pierwszym roku trwania eksperymentu liczebność śpiewaka zwiększała się wraz ze wzrostem powierzchni płata lasu, zaś po emisji negatywnej informacji socjalnej w tych lasach, zależność ta uległa odwróceniu (Tab.1. i Fig.2. w artykule 3). Z kolei mieszana informacja socjalna zwiększała liczebność śpiewaka w najmniej izolowanych lasach i zmniejszała w najbardziej izolowanych (Tab.1. i Fig.3. w artykule 3), również wspierając **hipotezę 2**.

Podsumowanie

Uzyskane przeze mnie wyniki pokazują, że fragmentacja siedlisk w różny sposób wpływa na różne miary bioróżnorodności (**Artykuł 1**), potwierdzając tym samym **hipotezę 1**. Najsilniej na fragmentację siedlisk zareagowała różnorodność gatunkowa, gdzie jej wzrost był pozytywnie skorelowany ze wzrostem wielkości płata lasu, oraz ze spadkiem izolacji przestrzennej tego płatu. Tendencja ta ustawała po osiągnięciu pewnej powierzchni płata lasu, a powyżej pewnej wartości wskaźnika izolacji przestrzennej lasów, następował spadek różnorodności gatunkowej. Najsłabiej na fragmentację siedlisk leśnych zareagowała różnorodność funkcjonalna, co jest zgodne z **hipotezą 1**, że istnieje znaczna redundancja funkcji w obrębie zespołu ptaków (Cadotte i in. 2011). Możliwe, iż w obrębie obszaru badań nawet niewielki płat lasu był w stanie utrzymać relatywnie szeroki zakres nisz ekologicznych, a tym samym cech funkcjonalnych (Hutchinson 1957; Wiens i in. 2010).

Wyniki otrzymane przeze mnie w **artykule 1** mogą wskazywać na to że fragmentacja siedlisk generuje duże zagęszczenie gradientów środowiskowych, co może być jednym z najważniejszych czynników wpływających na zróżnicowanie taksonomiczne zgrupowań gatunków (Cushman i McGarigal, 2003; Nord i Forslund, 2015). Możliwe, że duże zróżnicowanie siedliskowe pofragmentowanego krajobrazu może mieć pozytywny wpływ na bioróżnorodność ptaków zamieszkujących ten obszar pod warunkiem, że wielkość płatów lasu na tym obszarze nie spadnie poniżej pewnej wartości (Yahner i Rodewald 2001; Schippers i in. 2015; Koivula i in. 2017).

Jeśli uszeregować miary różnorodności zaczynając od najsilniej reagującej na informację socjalną, można je uporządkować w następujący sposób: różnorodność taksonomiczna > różnorodność filogenetyczna > różnorodność funkcjonalna. Jest to uszeregowanie podobne do tego które określałoby reakcję miar różnorodności na fragmentację. Podobnie jak w wypadku **artykułu 1**, potwierdzałoby to potencjalne występowanie dużej redundancji funkcji w zbiorowiskach ptaków zamieszkujących dany obszar (Cadotte i in. 2011; Sol i in. 2020). Zmiany w informacji socjalnej dostępnej w danym płacie siedlisk mogą wpływać na różnorodność taksonomiczną, ale niekoniecznie na funkcje ekosystemowe pełnione przez zgrupowania ptaków (Hutchinson 1957; Wiens i in. 2010).

Uzyskane wyniki wskazują, że wskaźniki różnorodności gatunkowej i filogenetycznej były wyższe w płatach leśnych gdzie emitowano pozytywną informację socjalną, niż w płatach gdzie emitowano mieszaną i negatywną informację (**Artykuł 2**). Wskazuje to, iż ptaki prawdopodobnie postrzegają takie płaty jako wysokie jakościowo potencjalne siedlisko (Seppänen i in. 2007; Szymkowiak i in. 2017). Głos śpiewaka miał wpływ zarówno na liczbę gatunków, jak i różnicował skład gatunkowy zgrupowań ptaków zamieszkujących dany las, a efekt ten utrzymywał się również w rok po przeprowadzeniu eksperymentu. Obecność śpiewaka mogła przyciągać inne gatunki, których obecność mogła z kolei działać przyciągająco na kolejne gatunki ptaków, co tłumaczyłoby dlaczego kompozycja gatunkowa zgrupowań ptaków była zmienna pomiędzy latami wykonania eksperymentu. Ponieważ efekt ten utrzymywał się również w rok po wykonaniu eksperymentu, możliwe jest, iż cała sieć nowych zależności międzygatunkowych, która najpewniej powstała poprzez wpływ pozytywnej informacji socjalnej, utrzymuje się również po tym jak informacja ta osłabnie lub zaniknie.

Obniżenie różnorodności gatunkowej i filogenetycznej przez mieszaną informację socjalną wskazywać może na to, że informacja negatywna ma silniejszy wpływ w procesie podejmowania decyzji co do wyboru siedliska przez ptaki, niż informacja pozytywna (Laundre i in. 2010; Gaynor i in. 2019). Twierdzenie to potwierdzałyby również wyniki uzyskane w ramach **artykułu 3**, gdzie mieszana informacja socjalna obniżała liczebność śpiewaka wraz z rosnącą izolacją danego płata lasu. Być może zwiększa ona niepewność w procesie podejmowania decyzji co do osiedlenia w danym miejscu przez osobniki wybranych gatunków. Sama informacja negatywna obniżała różnorodność gatunkową i filogenetyczną ptaków, a niższy wskaźnik wymiany gatunków w lasach gdzie ją emitowano (**Artykuł 2**) sugeruje, że drapieżniki mogą mieć stabilizujący wpływ na zgrupowania potencjalnych ofiar.

W swojej pracy wykazałem również, iż pozytywna (**Artykuł 2**) lub negatywna (**Artykuł 3**) informacja socjalna może zmodyfikować związek między wielkością płata siedlisk i izolacji na występowanie gatunków w danym płacie siedliska, potwierdzając tym samym **hipotezę 2**. Możliwe więc, iż gatunki odbierały obecność śpiewaka w danym lesie jako indykator wysokiej jakości siedliska, a głośność śpiewu tego drozda, rozciągającego się poza płat lasu, może stworzyć swoisty krajobraz bezpieczeństwa, będący przeciwieństwem krajobrazu strachu (**Artykuł 2**). Modyfikacja efektu wielkości płata lasu przez obecność jastrzębia pokazuje, że śpiewak uwzględnia wiele czynników (m.in. wielkość płata lasu czy obecność drapieżników) podejmując decyzję o zasiedleniu danego miejsca (**Artykuł 3**). Wyniki te sugerują, że efekty fragmentacji mogą być zmieniane przez informację socjalną, co może mieć praktyczne znaczenie w utrzymaniu lokalnych populacji i bogactwa gatunkowego, zwłaszcza, że efekty informacji socjalnej nierzadko utrzymują się po ustaniu sygnału.

Dotychczasowe badania sugerowały, iż osobniki mogą się kierować informacją socjalną pochodzącą od innych osobników tego samego gatunku, oraz że są zdolne do zapamiętania jej oraz powiązania z konkretnym obszarem (Seppänen i in. 2007; Kelly i Schmidt 2017). Zwierzęta tworzą w ten sposób mapy poznawcze, wykorzystując je m.in. w celu unikania potencjalnych drapieżników (Oriol-Cotterill i in. 2015; Gaynor i in. 2019), lub też nawigowania (Blaser i in. 2013; Liu i in. 2019). Wyniki uzyskane przeze mnie (**Artykuł 2** i **3**) wskazują na to, iż ptaki tworząc takie mapy mogą w sposób długotrwały uwzględniać na nich informacją socjalną pochodzącą od innych gatunków.

Literatura

Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions: a review. *Oikos*, *71*(3), 355–366.

Blaser, N., Dell'Omo, G., Dell'Ariccia, G., Wolfer, D. P. & Lipp, H. P. (2013). Testing cognitive navigation in unknown territories: Homing pigeons choose different targets. *Journal of Experimental Biology*, *216*(16), 3123–3131.

Cadotte, M. W., Carscadden, K. & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48(5)*, 1079–1087.

Cadotte, M. W. & Davies, T. J. (2010). Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions*, *16(3)*, 376–385.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M. & Grace, J. B. (2012). Biodiversity loss and its impacton humanity. *Nature*, *486*, 59–67.

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366.

Cody, M. L. (1985). *Habitat Selection in Birds* (M. L. Cody (ed.)). Academic Press.

Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D. & Baguette, M. (2017). Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography*, *40*(1), 56–73.

Cushman, S. A. & McGarigal, K. (2003). Landscape-level patterns of avian diversity in the Oregon coastal range. *Ecological Monographs*, *73*(2), 259–281.

Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thébault, E. & Loreau, M. (2007). The functional role of biodiversity in ecosystems: Incorporating trophic complexity. *Ecology Letters*, *10*(6), 522–538.

Fletcher, R. J. (2007). Species interactions and population density mediate the use. *Journal of Animal Ecology*, *76(3)*, 598–606.

Franklin, A. B. & George, T. L. (2002). What is habitat fragmentation? *Studies in Avian Biology*, *25,203-220*

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. & Brashares, J. S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology & Evolution*, *34*(4), 355–368.

Gotelli, N. J. & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, *4(4)*, 379–391.

Hofmeister, J., Hošek, J., Brabec, M. & Kočvara, R. (2017). Spatial distribution of bird communities in small forest fragments in central Europe in relation to distance to the forest edge, fragment size and type of forest. *Forest Ecology and Management*, *401*, 255–263.

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L. & Connor, M. I. O. (2012). A global synthesis reveals biodiversity loss as amajor driver of ecosystem change. *Nature*, *486*, 105–108.

Hromada, M., Antczak, M., Valone, T. J. & Tryjanowski, P. (2008). Settling decisions and heterospecific social information use in shrikes. *PLoS ONE*, *3*(12), e3930.

Hutchinson, E. G. (1957). "Concluding Remarks" on Animal Ecology and Demography. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427

Keating, K. A. & Quinn, J. F. (2012). Estimating species richness: the Michaelis-Menten model revisited. *Oikos*, *81*(2), 411–416.

Kelly, J. K. & Schmidt, K. A. (2017). Fledgling calls are a source of social information for conspecific, but not heterospecific, songbird territory selection. *Ecosphere*, *8*(2), e01512.

Koivula, M. J., Chamberlain, D. E., Fuller, R. J., Palmer, S. C. F., Bankovics, A., Bracken, F., Bolger, T., de Juana, E., Montadert, M., Neves, R., Rufino, R., Sallent, A., da Silva, L. L., Leitão, P. J., Steffen, M. & Watt, A. D. (2017). Breeding bird species diversity across gradients of land use from forest to agriculture in Europe. *Ecography*, *41(8)*, 1331–1344.

Laundre, J. W., Hernandez, L. & Ripple, W. J. (2010). The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecology Journal*, *3(3)*, 1–7.

Levins, R. (1968). Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bulletin of the Entomological Society of America*, *15*(3), 237–240.

Liu, Y., Day, L. B., Summers, K. & Burmeister, S. S. (2019). A cognitive map in a poison frog. *Journal of Experimental Biology*, *222*(11), 1–6.

MacArthur, R. H. & Wilson, E. O. (2001). *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Magurran, A. E. & McGill, B. J. (2011). *Biological Diversity: Frontiers in Measurement and Assessment*. Oxford University Press.

Mason, N. W. H., Mouillot, D., Lee, W. G. & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, *111*(1), 112–118.

McComb, B. & McGarigal, K. (1995). Relationships Between Landscape Structure and Breeding Birds in the Oregon Coast Range. *Ecological Monographs*, *65*(3), 235–260.

Naeem, S. & Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, *390*, 507–509.

Newbold, T., Scharlemann, J. P. W., Butchart, S. H. M., Sekercioglu, C. H., Alkemade, R., Booth, H. & Purves, D. W. (2012). Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proceedings of the Royal Society B*, *280(1750),20122131*

Nord, M. & Forslund, P. (2015). Environmental Gradients Explain Species Richness and Community Composition of Coastal Breeding Birds in the Baltic Sea. *PLoS ONE*, *10*(2), e0118455.

Oriol-Cotterill, A., Valeix, M., Frank, L. G., Riginos, C. & Macdonald, D. W. (2015). Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, *124*(10), 1263–1273.

Pearman, P. B., Lavergne, S., Roquet, C., Wüest, R., Zimmermann, N. E. & Thuiller, W. (2014).

Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage. *Global Ecology and Biogeography*, *23*(4), 414–424.

Petchey, O. L. & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, *9*(6), 741–758.

Prugh, L. R., Hodges, K. E., Sinclair, A. R. E. & Brashares, J. S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences*, *105*(52), 20770–20775.

Reich, P. B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S. E., Flynn, D. F. B., Eisenhauer, N., Reich, P. B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S. E., Flynn, D. F. B. & Eisenhauer, N. (2012). Impacts of Biodiversity Loss Escalate Through Time as Redundancy Fades. *Science*, *336*,589-592.

Robinson, S. K., Thompson, F. R., Donovan, T. M., Whitehead, D. R. & Faaborg, J. (1995). Regional Forest Fragmentation and the Nesting Success of Migratory Birds. *Science*, *267*(1987-1990).

Ryall, K. L. & Fahrig, L. (2006). Response of predators to loss and fragmentation of prey habitat: a review of theory. *Ecology*, *87*(5), 1086–1093.

Schippers, P., Koelewijn, H. P. & Smulders, M. J. M. (2015). Landscape diversity enhances the resilience of populations , ecosystems and local economy in rural areas. *Landscape Ecology*, *30(2)*, 193–202.

Schmidt, K. A., Dall, S. R. & van Gils, J. A. (2010). The ecology of information : an overview on the ecological significance of making informed decisions. *Oikos*, *119(2)*, 304–316.

Seppänen, J. T., Forsman, J. T., Monkkönen, M. & Thomson, R. L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology*, *88*(7), 1622–1633.

Sol, D., Trisos, C., Múrria, C., Jeliazkov, A., González-Lagos, C., Pigot, A. L., Ricotta, C., Swan, C. M., Tobias, J. A. & Pavoine, S. (2020). The worldwide impact of urbanisation on avian functional diversity. *Ecology Letters*, *23*(6), 962–972.

Stephens, S. E., Koons, D. N., Rotella, J. J. & Willey, D. W. (2003). Effects of habitat fragmentation on avian nesting success : a review of the evidence at multiple spatial scales. *Biological Conservation*, *115(1)*, 101–110.

Suzuki, T. N. (2015). Assessment of predation risk through referential communication in incubating birds. *Scientific Reports*, *5(1)*,10239.

Suzuki, T. N. & Kutsukake, N. (2017). Foraging intention affects whether willow tits call to attract members of mixed-species flocks. *Royal Society Open Science*, *4*(6), 170222.

Szymkowiak, J., Thomson, R. L. & Kuczynski, L. (2017). Interspecific social information use in habitat selection decisions among migrant songbirds. *Behavioral Ecology*, *28*(3), 767–775.

Tellería, J. L., Baquero, R. & Santos, T. (2003). Effects of forest fragmentation on European birds: Implications of regional differences in species richness. *Journal of Biogeography*, *30*(4), 621–628.

Tilman, D., Lehman, C. L. & Thomson, K. T. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Sciences*, *94(5)*, 1857–1861.

Tischendorf, L., Bender, D. J. & Fahrig, L. (2003). Evaluation of patch isolation metrics in mosaic landscapes for specialist vs . generalist dispersers. *Landscape Ecology*, *18(1)*, 41–50.

Tryjanowski, P., Hartel, T., Báldi, A., Szymański, P., Tobolka, M., Herzon, I., Goławski, A., Konvička, M., Hromada, M., Jerzak, L., Kujawa, K., Lenda, M., Orłowski, G., Panek, M., Skórka, P., Sparks, T. H., Tworek, S., & A. W. & Żmihorski, M. (2011). Conservation of Farmland Birds Faces Different Challenges in Western and Central-Eastern Europe. *Acta Ornithologica*, *46*(1), 1–12.

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., Grenyer, R., Helmus, M. R. & Lanna, S. (2017). A guide to phylogenetic metrics for conservation , community ecology and macroecology. *Biological Reviews*, *92(2)*, 698–715.

Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. (1991). What to Protect? Systematics and the Agony of Choice. *Biological Conservation*, *55(3)*, 235–254.

Ward, M. P., Benson, T. J., Semel, B. & Herkert, J. R. (2010). The Use of Social Cues in Habitat Selection by Wetland Birds. *The Condor*, *112*(2), 245–251.

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, T. J., Grytnes, J.-A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M. & Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13(10)*, 1310–1324.

Wilson, M. C., Richard, X. C., Didham, R. K., Ding, P., Holt, R. D., Holyoak, M., Hu, G., Hughes, A. C., Jiang, L., Laurance, W. F., Liu, J., Pimm, S. L., Robinson, S. K., Russo, S. E., Si, X., Wilcove, D. S., Wu, J. & Yu, M. (2016). Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landscape Ecology*, *31*(2), 219–227.

Yahner, A. D. & Rodewald, R. H. (2001). Influence of landscape compostion on avian community structure and associated mechanisms. *Ecology*, *82*(12), 3493–3504.

Artykuł 1

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Different response of the taxonomic, phylogenetic and functional diversity of birds to forest fragmentation

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Habitat fragmentation is considered as major threat to biodiversity worldwide. Biodiversity can be described as taxonomic, functional and phylogenetic diversity. However, the effect of forest fragmentation on taxonomic, phylogenetic and functional diversity is barely understood. We compare the response of taxonomic (species richness), phylogenetic and functional diversity of birds to forest fragmentation. We hypothesised that with increasing forest patch isolation and/or decreasing patch size the diversity of birds decreases but only if certain thresholds of fragmentation metrics are reached. Specifically, we hypothesized that out of the three diversity components the taxonomic diversity is the most sensitive to forest fragmentation, which means that it starts declining at larger patch size and higher connectivity values than phylogenetic and functional diversity do. We compared the three biodiversity metrics of central European bird species in a large set of forest patches located in an agricultural landscape. General additive modeling and segmented regression were used in analyses. Habitat fragmentation differentially affected studied biodiversity metrics. Bird taxonomic diversity was the most responsive towards changes in fragmentation. We observed an increase in taxonomic diversity with increasing patch area, which then stabilized after reaching certain patch size. Functional diversity turned out to be the least responsive to the fragmentation metrics and forest stand characteristics. It decreased linearly with the decreasing isolation of forest patches. Apart from the habitat fragmentation, bird taxonomic diversity but not phylogenetic diversity was positively associated with forest stand age. The lower share of dominant tree species, the highest taxonomic diversity was. While preserving a whole spectrum of forests (in terms of age, fragmentation and size) is important from the biodiversity perspective, forest bird species might need large, intact, old-growth forests. Since the large and intact forest becomes scarcer, our study underscore their importance for the preservation of forest specialist species.

In the Anthropocene land use changes such as intensive agriculture and urbanization have led to habitat fragmentation and loss which are primary drivers of species extinctions worldwide[1–4], however there is often disagreement to the extent to which fragmentation itself is to be blamed for the biodiversity loss[5]. The biodiversity decline may be initiated if the amount of available habitat falls below a certain, often species-specific, threshold level[6]. This may lead to the emergence of non-linear response of biodiversity to habitat fragmentation[7].

Traditionally, taxonomic diversity (species richness) has been the most commonly used index of the biodiversity[8]. Phylogenetic diversity is another key component of biodiversity, reflecting life's evolutionary heritage. Functional diversity is also an important feature of biological assemblages, having large impact on the rate and reliability of ecosystem processes[9,10]. There is often high redundancy in functional and phylogenetic diversity in species communities[11,12], in which case species loss may have no effect on ecosystem processes. Continued species extinction however invariably leads to irreversible degradation of ecosystem functions[13]. Thus, the three above-mentioned biodiversity components may show different responses to measures of fragmentation.

Several studies investigated the impact of habitat fragmentation on taxonomic, phylogenetic and functional diversity metrics. Some authors indicate a lack of significant impact of fragmentation on phylogenetic diversity[14,15], while other suggest that it might be affected by the edge effect and ecotone zones[16]. Functional diversity may be sensitive to a decrease in area and connectivity of habitat patches[17–20]. It is believed that fragmentation

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primarily affects specialist species and, to a lesser extent, generalists mostly via reduced connectivity[21,22]. However, those results may vary across different regions[23] and specialist groups[24].

Central European bird species, especially forest bird species, serve as an excellent group for understanding the effects of fragmentation on biological systems. They occur in landscapes highly affected by agriculture and urbanization, yet presenting different degrees of habitat fragmentation[25–28]. They also encompass a wide range of taxonomic functional and phylogenetic diversity[29]. Strong fragmentation favors generalists that are able to survive in smaller habitat patches than specialists[30,31]. In Europe, a decline of diversity of both farmland and woodland species is observed[32–34]. This decrease is more pronounced in species inhabiting farmlands than in species inhabiting forests[35] mostly because farmland is constantly changing[32] and is more prone to climate change. However, intensive forestry including salvage logging puts at risk forest birds, especially in Poland, where apparent conflict between government, foresters and conservationists have arisen in recent years[36,37].

Evidence from studies on bird assemblages suggests that forest size and isolation have negative effect on taxonomic diversity[38], functional diversity[18], and phylogenetic and functional diversity combined[39]. Moreover, those effects vary markedly between generalist and specialist species[40]. However, there have been only a few studies focusing on comparing the responses of different biodiversity components to changes in patch size and isolation in one complex study.

The aim of our study is to compare the response of taxonomic, phylogenetic and functional diversity of birds to forest fragmentation metrics. We have decided to study the response of all of the bird species found within those forest patches and forest specialist only. Following hypotheses were tested:

Hypothesis 1 With increasing patch isolation and/or decreasing patch size the diversity of birds decreases but only if certain thresholds of fragmentation metrics are reached. We expected that the diversity of forest specialists should be more sensitive to forest fragmentation (decrease faster) than the diversity of all of the bird species, since the latter also includes some farmland and ecotone species that may respond positively to fragmentation.

Hypothesis 2 Out of the three diversity components taxonomic diversity is the most sensitive to forest fragmentation, which means that it starts declining at larger patch size and higher connectivity values than phylogenetic and functional diversity do. We have formulated that hypothesis both for forest specialists and all of the bird species.

We expected this because there is often high redundancy in phylogeny and function in species assemblages. Moreover, we expected that phylogenetic diversity drops at larger patch size and higher connectivity values than functional diversity because there may be convergence in traits among phylogenetically-distant species and thus function in ecosystems.

Materials and methods

Study area.

The study has been conducted in the southern part of Poland, in the province of Małopolska, in an area encompassing 1097 square kilometres north of Cracow. We have chosen 163 forest patches located in an agricultural landscape (Fig. 1). Those were mostly mixed stands, both managed by the Polish State Forests Holding and private entities (supervised by the former entity). All these forest patches were habitat islands (not part of a larger continuous forest complex) and differed in size and isolation.

Forest characteristics.

For each forest patch, we collected a range of parameters to best capture the key characteristics of a forest stand which could possibly be important for local bird species (Table 1). They were measured and averaged for every single patch. Also, we used Forest Data Bank (www.bdl.lasy.gov.pl) as a data source for some of the forest patches. Where that data was not available, we have calculated those parameters in accordance to the guidelines of Forest Bureau for Forest Management and Geodesy[41]. Three the most commonly studied metrics of habitat fragmentation: patch size and two proximity indices were measures of forest fragmentation of primary interest. The isolation metrics were nearest neighbour distance (NND) and proximity index (PROX). Those were calculated using the Patch Analyst toolbox of the ArcGis ver. 10.1, which uses the same method to calculate landscape metrics as Fragstats software[42]. To avoid confounding effects, patch size and isolation metrics were selected in a way the correlation coefficients among them were low and non-significant (all values of the coefficient were below 0.2).

Bird observations.

Field surveys were carried out between the 1st of April and 31st of May 2017 by a team of three experienced birdwatchers. Each of those observers had the assigned set of forest patches Each forest was visited three times. We have divided that period into three 20-days rounds (1–20 April, 21 April–10 May, 11–31 May). In each of those periods, forest patches were surveyed once. Surveys started at around 5 a.m. and usually lasted till 11 a.m. During surveys an observer noted the starting time, then moved through forest in a random direction, trying to cover as much of the forest patch as possible. Each observer noted all species and the exact time of the first observation for each species heard or seen within a patch. From survey starting time in forest and time of observation of the first individual a species abundance index within a patch was estimated adopting the Michaelis-Mentien model[43] (Skórka et al. in prep). The survey ended if none new species was recorded for ten minutes (Skórka et al. in prep.). We have decided not to utilize a survey that assumes spending fixed time on every site since our forest patches varied markedly in size. We have instead decided to include both the effects of time and space in our models, which has been shown to increase the modelling accuracy[44].

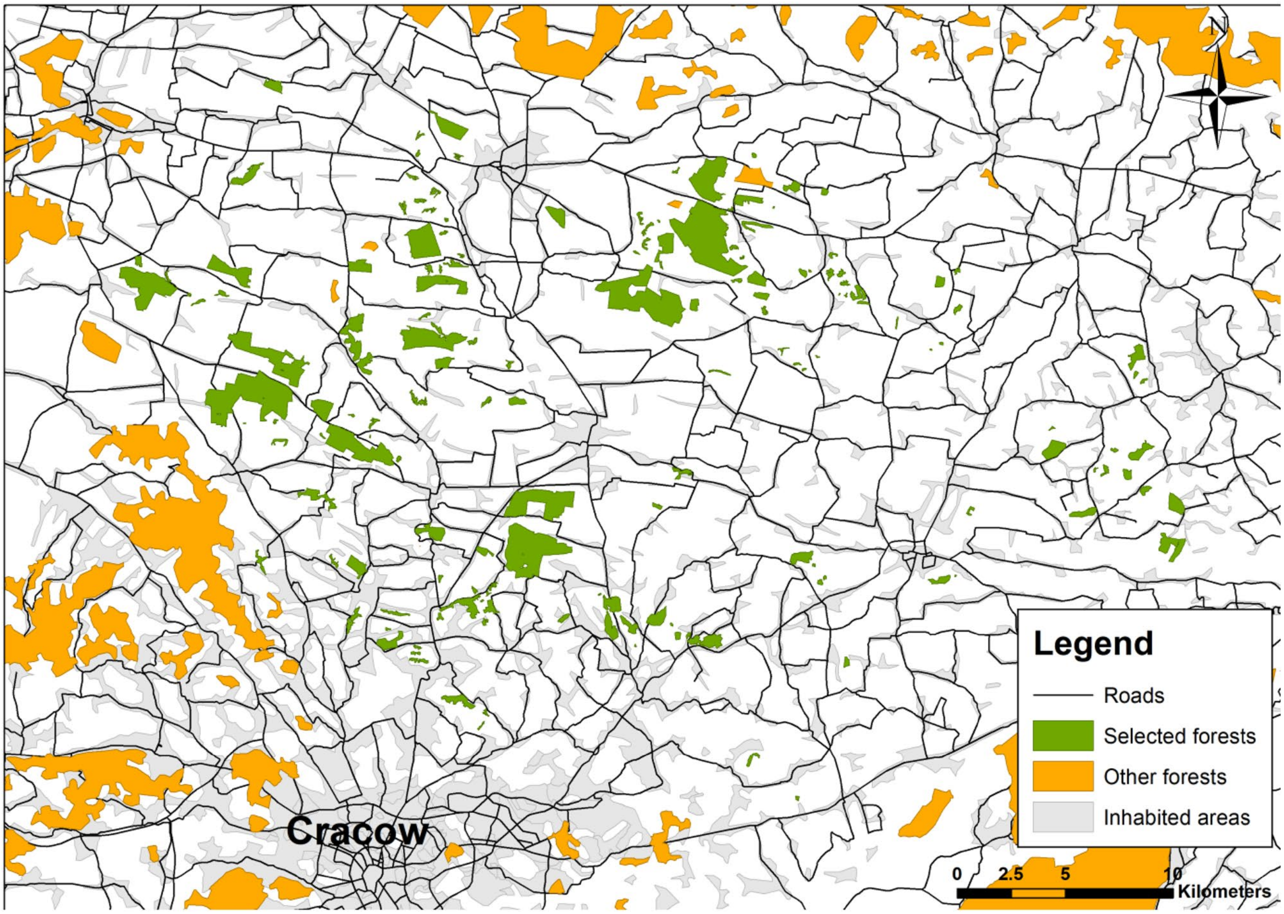

Figure 1. Map of the study area, with study forest patches marked in green, and other forests marked in orange. Created by Michał Bełcik using ArcMap 10.1.

Parameter	Type of parameter	Description	Log-transformed	Range	Mean ± SD
Forest area	Fragmentation variable	Total area of forest patch (in hectares)	Yes	0.38–582.33	37.28 ± 89.52
Forest age	Stand parameter	Mean age of dominant tree species in main stand storey (in years)	No	10–112	58.18 ± 24.30
Share of dominant species	Stand parameter	Expressed on the integer scale of 0–10 (with 10 being the highest result), the share of dominant tree species in main stand storey	No	2–10	–
Stand density	Stand parameter	Mean density of forest stand (representing percentage of forest bottom shaded by the tree canopy) (in %)	No	30–100	66.13 ± 15.80
Coniferous species	Stand parameter	Percentage of coniferous species in main stand storey (in %)	No	0.00–100.00	21.01 ± 26.04
Shape index (SI)	Fragmentation variable	Shape Index of forest stand	Yes	1.110–3.528	1.790 ± 0.504
Nearest neighbour distance (NND)	Fragmentation variable	Shortest straight-line distance between a focal patch and its nearest neighbour (in m)	Yes	16.53–3509.19	269.26 ± 701.36
Proximity index (PROX)	Fragmentation variable	Sum, over all patches whose edges are within the 2.5 km radius of the focal patch, of each patch size divided by the square of its distance from the focal patch	Yes	0.00–1845.83	78.86 ± 251.92

Table 1. Stand parameters and isolation metrics of studied forest patches.

We have divided our bird observations into two groups, for which we performed our analysis. The first was all of the bird species observed in those forest patches, including both forest specialists and generalist (further in this text—"all species"). The second group was a subset of forest specialists[45], which we created in accordance with the PanEuropean Common Bird Monitoring Scheme (www.ebcc.info). We refer to that group in this manuscript as "forest specialists".

Phylogenetic and functional diversity indices. As bird biodiversity metrics (for both all of the bird species and forest specialists) within each patch we computed: taxonomic diversity, phylogenetic diversity and functional diversity. Each of those metrics were computed for the alpha diversity level[46]. For measuring the phylogenetic diversity, we used the mean nearest taxon distance—MNTD[47]. This metric averages the subset of the possible pairwise distances extracted from a phylogenetic tree, where only the shortest distances between taxa are considered[47]. Phylogenetic tree was obtained from the BirdTree project website[48] (www.birdtree.org).

For measuring the functional diversity, we used the functional richness—Fric[10]. This measure quantifies the amount of a niche space occupied by the species within a community. This measure was chosen since it is independent of abundance, thus a section of niche space is considered to be occupied even if only low abundance occurs within it. This characteristic of this measure enabled us to fully capture the functional diversity of small forests and better study the possible effects of fragmentation on this measure. This metric was also chosen because it turned out to be the most sensitive to forest patch size and isolation as compared to other metrics (e.g. functional dispersion, functional evenness and functional divergence), as described by Mason et al.[10]. For calculating diversity measures, we used "picante"[50] and "FD" packages[51] in R. We used species traits linked with functioning of forest ecosystems (Table S1). These traits were related to diet, reproductive mode, lifespan, migratory behaviour, social behaviour. All these traits are linked e.g. with species interactions, nutrient cycling, seed dispersal, using space, thus have impact on forest ecosystem functioning.

Data preparation and analysis. All statistical analyses were performed in R statistical software[52,53]. The first step in our analysis was to test which patch characteristics and isolation metrics can be used as explanatory variables in modelling bird diversity in forest patches. For that, we have used the "mgcv" package[54]. We constructed a general additive model for each of the response variables: taxonomic diversity, functional richness, and phylogenetic diversity for bird assemblages including (1) all species and (2) only forest specialists. Models included all of the explanatory variables that we considered might be explaining that diversity variability (Table 1). The variance inflation factor was equal to 1.43 for the percentage of coniferous species, and below that value for other explanatory variables. Variables represented two groups – those that described patch size and isolation (fragmentation variables) and those that described the stand parameters potentially related to the quality of forest patches. For mean forest age and stand density a linear relationship was assumed, but for most, we have assumed a non-linear relationship between explanatory variables and response variables to identify threshold values We also included the interaction between geographic coordinates modeled as smoothed function for all models to control for spatial autocorrelation and abiotic heterogeneity[55], and the number of species as a covariate for models with functional diversity as the response variable, due to usually strong positive association between the number of species and functional diversity. Variables representing fragmentation indices were logarithmically transformed to avoid impact of detached observations (Table 1). To validate our models, we used a gam.check() function from the "mgcv" package[54], which produces diagnostic information, along with four residual plots. This function produces some diagnostic information about the fitting procedure and results, including a check whether the basis dimension for a smooth is adequate (not too low), along with four standard diagnostic plots. Our results showed that we had used a similar basis dimension (i.e. number of k-values) for our model as suggested, and plots produced showed a general good fit of the models. We also used the concurvity() function from the same package, which produces summary measures of concurvity between model components. All these checks revealed that the models were correctly constructed.

The second step in data analysis was to identify the response thresholds of diversity metrics to forest patch size and isolation with segmented regression. We calculated thresholds for each explanatory variable that showed a non-linear association with biodiversity metrics, using the lm.br() function from the "lm.br" package[56]. This function performs a significance tests for a changepoint in linear or multiple linear regression, and computes confidence intervals and confidence regions with exact coverage probabilities for the changepoint.

Results

Bird responses to fragmentation metrics. In total, 94 bird species were observed, of which 44 were forest bird species. The mean number of species per one survey at the given forest patch was 25 (SE = 7, min = 4, max = 42).

Results of general additive models showed varying biodiversity metrics responses to isolation metrics and stand parameters (Table 2). The area of a forest patch, proximity index and forest age had significant influences on diversity metrics. The taxonomic diversity (all species and forest specialists) increased non-linearly with the forest area (Fig. 2A,B). However, phylogenetic diversity decreased non-linearly with forest area and this decrease was rapid at low forest sizes (Fig. 2C,D). Functional diversity did not respond to the forest patch area. Taxonomic diversity of all species and forest specialist was highest at high (a low value of proximity index) and moderate habitat isolation (Fig. 3A,B). Phylogenetic and functional diversity indices for all bird species decreased linearly with decreasing habitat isolation (increasing values of proximity index, Fig. 3C,D). However, phylogenetic and functional diversity of forest specialists did not respond to this forest isolation index (Table 2). Another isolation metric, the nearest neighbor distance had a significant positive association with taxonomic diversity of all birds (Table 2, Fig. S1A).

Responses to forest parameters. Forest stand characteristic was another group of factors that influenced different components of bird diversity (Table 2). Forest age was positively associated with the species and functional diversity but negatively with the phylogenetic diversity of all bird species. Similar findings were found for taxonomic diversity of forest specialists (Table 2, Fig. S2B). Stand density turned out to have a positive association with the functional diversity of all bird species. Percentage of coniferous species had positive correlation with the taxonomic diversity of all birds and forest specialists, as well as positive non-linear association with the phylogenetic diversity of forest specialists (Table 2, Fig. S3A,B). Share of dominant species was negatively asso-

Explanatory variables	Response variables					
	Species richness of all birds	Functional diversity of all birds	Phylogenetic diversity of all birds	Species richness of forest bird specialists	Functional diversity of forest bird specialists	Phylogenetic diversity of forest bird specialists
GAM estimates of function slopes with standard errors (in brackets) for explanatory variables with assumed linear response						
Intercept	**19.06994 (2.051163)*****	**0.00596 (0.00085)*****	**63.23644 (3.35101)*****	**11.92428 (1.44099)*****	**0.07706 (0.01098)*****	**47.20254 (3.04480)*****
Forest age	**0.09464 (0.01640)*****	**0.00001 (0.00001) ’**	**– 0.09458 (0.02574)** ***	**0.06845 (0.01137)** ***	0.00002 (0.00009)	– 0.01585 (0.02487)
Stand density	0.00084 (0.02351)	**0.00002 (0.00001)***	0.00534 (0.03829)	0.02145 (0.01646)	0.00007 (0.00012)	– 0.01375 (0.03414)
Explanatory variables included as splines to control for potential non-linearity, with degrees of freedom presented						
NND	**Df = 1.000’**	Df = 1.000	Df = 1.000	Df = 3.033	Df = 1.000	Df = 1.000
PROX	**Df = 2.986***	**Df = 1.000’**	**Df = 1.000****	**Df = 3.073***	Df = 1.000	Df = 1.000
Forest area	**Df = 2.908*****	Df = 1.000	**Df = 1.801****	**Df = 3.225*****	Df = 1.903	**Df = 1.000*****
Number of species	Not included	**Df = 1.845*****	Not included	Not included	**Df = 1.000*****	Not included
Coniferous species	**Df = 1.496***	Df = 1.027	Df = 1.000	**Df = 1.000*****	**Df = 2.552****	Df = 1.003
Share of dominant species	**Df = 1.000***	Df = 2.401	Df = 1.000	**Df = 1.000***	Df = 2.021	Df = 1.000
SI	**Df = 1.000*****	Df = 1.000	Df = 1.000	**Df = 1.000****	**Df = 1.908***	Df = 1.000

Table 2. The effect of environmental variables on bird diversity components at patch characteristics and isolation metrics. Statistically significant effects are emboldened: ***P < 0.001, **P < 0.01, *P < 0.05, ‘P < 0.10.

ciated with taxonomic diversity of all birds and forest specialists and this relationship was linear in both cases (Table 2, Fig. S4A,B).

Threshold responses. Analysis of thresholds in the response of birds to fragmentation metrics and forest characteristics showed statistically significant changepoints for different bird biodiversity components (Table 3). Taxonomic diversity was the least sensitive metric to forest fragmentation and forest stand characteristics (Table 3). The threshold response of the phylogenetic diversity to forest patch size was different than expected, i.e. phylogenetic diversity decreased very quickly with increasing forest patch size but then stabilized at low diversity values and large forest patch size. There were no threshold responses of functional diversity to fragmentation metrics but there was a threshold response for a share of coniferous trees (Table 3).

Discussion

In our study we showed that habitat fragmentation affected the studied biodiversity components differently.. Taxonomic diversity was most sensitive to changes in fragmentation indices and forest parameters, compared to the functional and phylogenetic diversity (Table 2). We also observed that taxonomic diversity of all birds was susceptible to changes in a wider variety of forest parameters than taxonomic diversity of forest specialists. We suggest that it might be due to the fact that generalists are usually more taxonomically diverse and have wider ecological preferences than specialists[57]. However, against our previous assumption, it turned out that taxonomic diversity drop at lower patch size than phylogenetic diversity (Table 3). That effect was observed for all of the bird species and forest specialists as well. We were unable to verify the same assumption for the connectivity indices. Functional diversity, however, turned out to be the least responsive to the forest patch size and isolation metrics, as well as forest stand characteristics. That goes in line with our initial hypothesis that there is a significant redundancy of functions within bird assemblages. Moreover, according to Cadotte et al.[58], functional diversity is the least susceptible to the changes in forest cover and deforestation processes.

There are several possible explanations of the observed pattern of response to fragmentation metrics. Previous studies have shown a positive relationship between habitat patch area and taxonomic diversity[3,30,59]. In our study, we saw an increase in taxonomic diversity across both bird groups with increasing patch area, which then stabilized after reaching a certain patch size (Fig. 2A,B). It is interesting to note that beyond this threshold, an increase in patch area does not yield an increase in taxonomic nor phylogenetic diversity. This would suggest that large, undisrupted interior areas are vital to maintaining the diversity of both forest specialists and all of the bird taxa[60,61]. However, we did not observe habitat loss driving changes in phenotypic traits (i.e., no significant relationship between patch size and functional diversity was found, Table 2) as it was also reported elsewhere[11,38,59]. A possible explanation is that in our study area, even a relatively small forest patch was enough to harbor a range of niches[57,62], that could maintain a functionally diverse avian population. It could also indicate a high functional redundancy within bird communities[58].

The same process could explain a negative, linear relationship between the PROX and functional diversity of all bird species (Fig. 3D). However, this negative relationship could also be explained by the positive influence of fragmentation on biodiversity[5]. Furthermore, results for the phylogenetic diversity of all bird species (Fig. 3C) could indicate a rather opposite explanation[63]. For the taxonomic diversity (for both analyzed groups), we can see a non-linear relationship with proximity index (Table 2, Fig. 3A,B). The shape of the curve might indicate the influence of environmental gradients, dictated by the spatial composition and distance between the forest patches[64,65]. Evidence from other studies indicates that gradients of habitat cover can result in high taxonomic diversity at intermediate fragmentation level[30,66,67]. Nearest neighbour distance had a linear positive influence

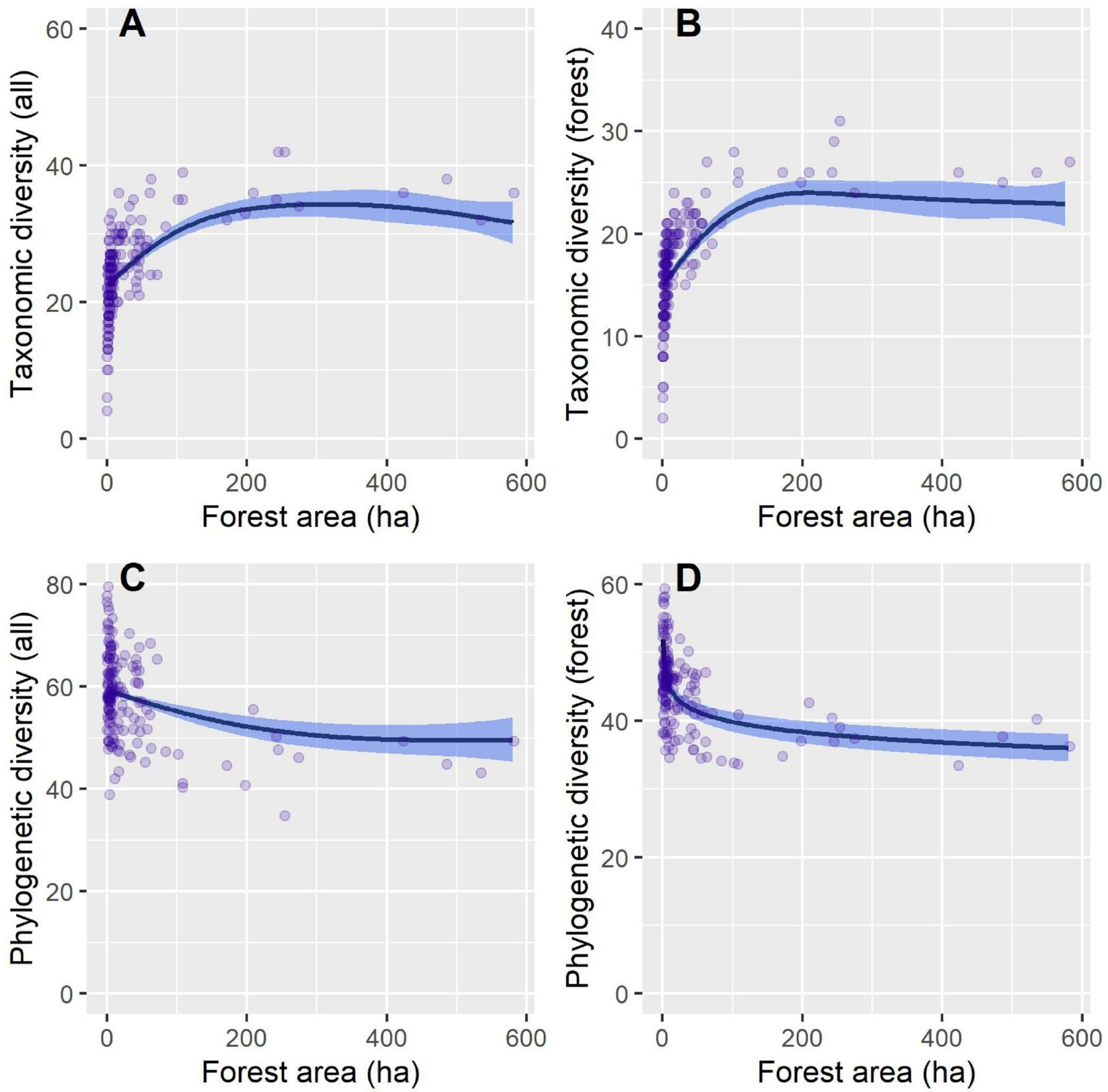

Figure 2. Response curves, derived from General Additive Modelling, showing the relationship between taxonomic and phylogenetic diversity (calculated for all of the bird species and forest specialist group) and forest patch area (in hectares).

on taxonomic diversity of all of the bird species. That could once again support the hypothesis of the positive influence of habitat fragmentation on taxonomic diversity[5].

The least important fragmentation metrics were shape index (SI) and NND (Table 2, Fig. S1). SI had a significant, positive linear influence on taxonomic diversity (for both groups) and a non-linear positive influence on the functional diversity of forest specialists. A possible explanation of this result could point to studies that indicated a high taxonomic diversity in the forest-field ecotone[60,68]. Higher SI means a longer, more complex border between a forest and field habitat, which generates a greater area of ecotone zones. Such zones are a highly heterogeneous environment (both in terms of structure and habitat composition), able to sustain a greater diversity of birds species[60].

Threshold responses. Prior to the analysis, we had expected the existence of forest patch area threshold for biodiversity of both all of the bird species and forest specialists[69,70]. We have also expected an existence of such threshold for forest canopy density[71] and forest age[72], especially for forest specialist species. Our analysis showed that patch size and isolation thresholds do exist. The most important thresholds describe the relationship between forest patch area and taxonomic diversity (of both studied bird subsets) and phylogenetic diversity

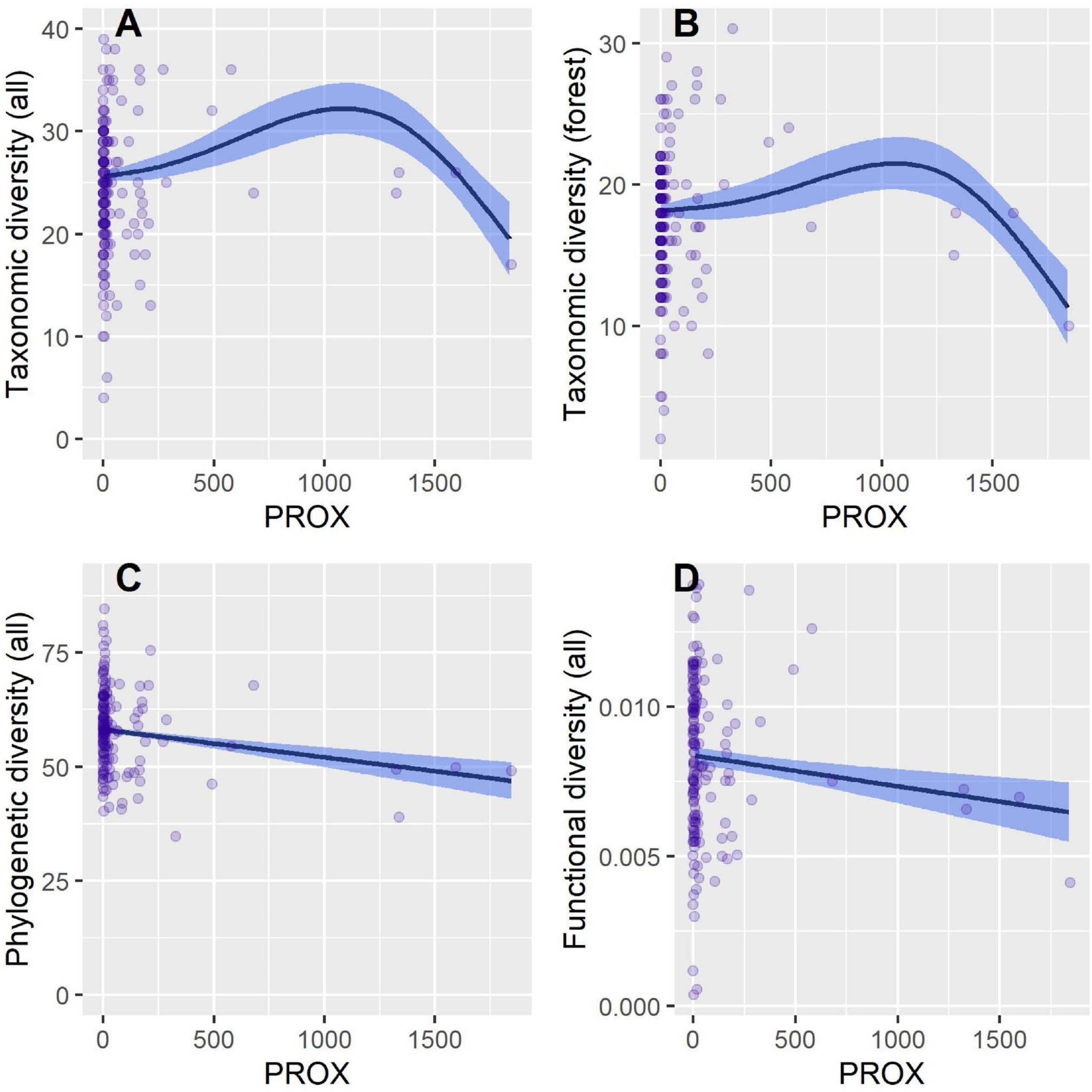

Figure 3. Response curves, derived from General Additive Modelling, showing the relationship between different metrics of bird diversity (for all of the study species and forest specialist group) and the amount of forest patches calculated for 2-km buffer (PROX).

Response variable	Explanatory variable	Changepoint	Significance level
Species richness of all bird species	Proximity Index (PROX)	570.005	0.185
	Forest patch area	**6.038**	**<0.001*****
	Percentage of coniferous species	**68.835**	**<0.001*****
Species richness of forest specialists	Proximity Index (PROX)	**451.550**	**0.051‘**
	Forest patch area	**10.426**	**<0.001*****
Phylogenetic diversity of all bird species	Forest patch area	**123.518**	**0.002****
Functional diversity of forest specialists	Percentage of coniferous species	**70.066**	**<0.001*****
	Shape Index (SI) of forest patch	2.474	0.452

Table 3. The response thresholds of diversity metrics to forest patch size and isolation. Thresholds were calculated only for variables that had statistically significant effect on diversity measures. Statistically significant effects are emboldened: ***P < 0.001, **P < 0.01, *P < 0.05, ‘P < 0.10.

of all bird species. It confirms our initial hypothesis that after the decrease to a certain patch size, taxonomic diversity metric will start to drop significantly. It also supports evidence from other studies showing that habitat specialists may be more severely impacted by habitat fragmentation than generalists[73,74]. It has a number of practical implications, because it shows that in order to preserve biodiversity of bird assemblages of mixed rural landscape (as it is a goal of many European conservation programmes), it is vital to ensure that certain size of patches must be maintained[75,76]. It is important to note that this threshold was definitely highest for phylogenetic diversity, and differs markedly between diversity metrics. That indicates phylogenetic susceptibility to fragmentation and underlines the need to take all of the diversity measures into account when designing efficient conservation plans.

The percentage of coniferous species, below which functional diversity of forest specialists started to decline, was about 70% (Table 3). This metric reflects homogeneity of the stand –the higher the amount of coniferous species is, the more homogeneous forest patch is. This underlines the need for maintaining diverse stands that would include a certain proportion of coniferous species in devising forest management strategies[60]. In spite of our initial assumptions, we found no evidence of existence of significant forest patch age or stand density thresholds on forest specialists. That may be due to the fact that most of the forest patches studied were of medium age and moderate canopy density, which are not usually characteristics of an old-growth forests that are favoured by a large proportions of woodland species.

Our results underscore the importance of considering the thresholds together with biodiversity metrics, because these measures may be differently related to the habitat fragmentation. So far, many studies suggest that the effect of habitat fragmentation on extinction thresholds to be as likely positive as negative[69,77–79]. Because biodiversity metrics differ in their response to changes in habitat features, a one process could trigger different kinds of responses between biodiversity metrics. For example, a taxonomic diversity may increase after exceeding a certain threshold of habitat patch area, and phylogenetic diversity may flatten after reaching similar threshold. It would indicate that between these two thresholds there is an optimum in which a high number of species and a large phylogenetic diversity persists.

Responses of other variables. Among other variables that were shown to have an influence on bird diversity metrics, the most important one was the age of forest stand. It had a positive influence on taxonomic, phylogenetic and functional diversity of all bird species, and on a taxonomic diversity of forest specialists. This is in line with the findings of other studies focusing on bird diversity in forest habitats[60]. Response curve was slightly steeper in case of the taxonomic diversity of all bird species, than in case of the taxonomic diversity of forest specialists (Fig. S2A,B). That would indicate that the older the tree stand is, the more specialized the forest bird species are in that stand. It is also important to note that the slope coefficient of the taxonomic diversity of all species was the highest among all three types of diversity. That leads to the conclusion that it is most susceptible to the changes in forest stand age caused by, for example, clearcuts and timber production.

According to classical niche-assembly models, the abundance and occurrence of species within communities are determined, among other factors, by the diversity of resources and habitats available[80]. The results from our study show that the most diverse forests were those with a high percentage of coniferous species in the main forest stand (Fig. S3) and with a low share of dominant species in forest stand (Fig. S4). This indicates the preference towards mixed, multi-species stands, which has already been signalled in previous studies[81,82].

It is noteworthy, however, that under different latitude, studies like our could yield potentially different results. Tropic ecosystems have higher diversity metrics and more complex biotic interactions among species than ones we see in temperate zones, which in turns leads to a wider variety of ecosystem functions in a given fauna pool. Therefore, reduction of some functional groups caused by fragmentation can be more apparent in tropical ecosystems. This could also create different thresholds of diversity metrics in tropics than in temperate zones. However, some similarities could also be observed. For example, studies have shown that disturbance caused by fragmentation also favours generalist species in tropics[83]. Possible frontiers for further studies stemming from our research could include a more complex analyses in which bird species would be grouped by their functional characteristics (e.g. foraging behaviour, nesting substrate). Calculating functional diversity metrics within such functional groups could reveal a new findings and show which functions are affected by the fragmentation the most.

Conclusions

Forest fragmentation is not universally negative on every aspect of bird communities diversity. It probably generates a high density of environmental gradients, which might be one of the most important drivers of diversity in community composition[65–67]. We believe that high habitat diversity of rural landscape caused by habitat fragmentation might be a positive feature for biodiversity provided that the size of the forest patches does not fall below certain area thresholds[61,84–86].

The differences of responses between biodiversity measures of either all bird species or forest specialists is more significant than the difference in responses of one diversity measures between all bird species and forest specialists. When we compare the responses of taxonomic diversity and shared evolutionary (both for all species and forest specialist) history to patch area, we see that the pattern of response is similar for both groups, and the response between taxonomic and phylogenetic diversity is non-consistent. The same could be observed for a number of other variables, like proximity index or forest stand age.

Understanding impact of habitat fragmentation on biological systems requires analyses that include various diversity components. We believe that a broader, more complex approach towards biodiversity is also necessary while studying natural (like population dynamics) or anthropogenic processes (like habitat fragmentation or invasion of alien species[87,88]). Focusing only on one diversity metric might lead to inaccurate conclusions since different metrics might respond in a different way to the same studied variable, as we have proven in case of proximity index. Our results also indicate that devising conservation strategies for various groups of birds is a multi-faceted dilemma, which should be important in decision making, at least in temperate zone. From the point of view of biodiversity as a whole, it may be important to maintain the full spectrum of forests that would represent different age, area, isolation or stand parameters. Considering this perspective, forest fragmentation might not necessarily be considered as a negative phenomenon, as it probably increases the density of ecotonic zones and thus the heterogeneity of the environment (both in terms of structure and habitat composition). This may allow for the penetration of typical farmland species into the forest patches, thus increasing the biodiversity in the given patch. From the point of view of forest specialists, however, it is necessary to preserve large and compact forests, consisting of old trees of different species composition and a dense canopy. Considering the scarcity of such large forests, our results underscore the importance of protecting those few that are still remaining across a lowland landscape of Central Europe.

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References

1. Foley, J. A. *et al.* Global Consequences of Land Use. *Science* **309**, 570–574 (2010).
2. Hansen, J., Sato, M., Russell, G. & Hansen, J. Climate sensitivity, sea level and atmospheric carbon dioxide. *Philos. Trans. R. Soc. A* **371**, 2–31 (2013).
3. Wilson, M. C. *et al.* Habitat fragmentation and biodiversity conservation : key findings and future challenges. *Landsc. Ecol.* **31**, 219–227 (2016).
4. Bovendorp, R. S. *et al.* Defaunation and fragmentation erode small mammal diversity dimensions in tropical forests. *Ecography* **42**, 23–35 (2019).
5. Fahrig, L. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515 (2003).
6. Macchi, L. *et al.* Thresholds in forest bird communities along woody vegetation gradients in the South American Dry Chaco. *J. Appl. Ecol.* **56**, 629–639 (2019).
7. Melo, I., Ochoa-quintero, J. M., Roque, F. D. O. & Dalsgaard, B. A review of threshold responses of birds to landscape changes across the world. *J. F. Ornithol.* **89**, 303–314 (2018).
8. Chesson, P. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–366 (2000).
9. Naeem, S. & Li, S. Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509 (1997).
10. Mason, N. W. H., Mouillot, D., Lee, W. G. & Wilson, J. B. Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* **111**, 112–118 (2005).
11. Flynn, D. F. B., Mirotchnick, N., Jain, M., Palmer, M. I. & Naeem, S. Functional and phylogenetic diversity as predictors of biodiversity: ecosystem-function relationships. *Ecology* **92**, 1573–1581 (2011).
12. Ricotta, C., Bacaro, G., Caccianiga, M., Cerabolini, B. E. L. & Pavoine, S. A new method for quantifying the phylogenetic redundancy of biological communities. *Oecologia* **186**, 339–346 (2017).
13. Ehrlich, P. R. & Ehrlich, A. H. *Extinction: The Causes and Consequences of Random, the Disappearance of Species.* (Random House, 1981).
14. Matos, F. A. R. *et al.* Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. *J. Ecol.* **105**, 265–276 (2017).
15. Grass, I., Brandl, R., Botzat, A., Neuschulz, E. L. & Farwig, N. Contrasting taxonomic and phylogenetic diversity responses to forest modifications : comparisons of taxa and successive plant life stages in South African Scarp Forest. *PLoS ONE* **10**, e0118722 (2015).
16. Magura, T. Ignoring functional and phylogenetic features masks the edge influence on ground beetle diversity across forest-grassland gradient. *For. Ecol. Manage.* **384**, 371–377 (2016).
17. Tscharntke, T. *et al.* Landscape contraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* **89**, 944–951 (2008).
18. Dias, D. F. C. *et al.* Beauty before age: Landscape factors influence bird functional diversity in naturally regenerating fragments, but regeneration age does not. *Restor. Ecol.* **24**, 259–270 (2016).
19. Barbaro, L. & Halder, I. Van. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography.* **32**, 321–333 (2009).
20. Moreno, C. E., Escobar, F., Halffter, G., Navarrete, D. & Barraga, F. Negative Impacts of Human Land Use on Dung Beetle Functional Diversity. *PLoS One* **6**, e17976(2011).
21. Leal, I. R., Filgueiras, B. K. C., Gomes, J. P., Iannuzzi, L. & Andersen, A. N. Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. *Biodivers. Conserv.* **21**, 1687–1701 (2012).
22. Horvath, R., Magura, T., Szinetar, C., Eichardt, J. & Tothmeresz, B. Large and least isolated fragments preserve habitat specialist spiders best in dry sandy grasslands in Hungary´. *Biodivers. Conserv.* **22**, 2139–2150 (2013).
23. Barbaro, L., Giffard, B., Charbonnier, Y., van Halder, I. & Brockerhoff, E. G. Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. *Divers. Distrib.* **20**, 149–159 (2014).
24. Sekercioglu, C. H. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *J. Ornithol.* **153**, 153–161 (2012).
25. Gaüzère, P. *et al.* Long-term effects of combined land-use and climate changes on local bird communities in mosaic agricultural landscapes. *Agric. Ecosyst. Environ.* **289**, 106722 (2020).
26. Smeraldo, S. *et al.* Modelling risks posed by wind turbines and power lines to soaring birds: the black stork (Ciconia nigra) in Italy as a case study. *Biodivers. Conserv.* **29**, 1959–1976 (2020).
27. Tellería, J. L., Baquero, R. & Santos, T. Effects of forest fragmentation on European birds: implications of regional differences in species richness. *J. Biogeogr.* **30**, 621–628 (2003).
28. Tryjanowski, P. *et al.* Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. *Acta Ornithol.* **46**, 1–12 (2011).
29. Pearman, P. B. *et al.* Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage. *Glob. Ecol. Biogeogr.* **23**, 414–424 (2014).
30. Andren, H. Effects of habitat fragmentation on birds and mammals of suitable habitat : a review landscapes with different proportions. *Oikos* **71**, 355–366 (1994).
31. Santos, T., Telleria, J. L. & Carbonell, R. Bird conservation in fragmented Mediterranean forests of Spain: effects of geographical location, habitat and landscape degradation. *Biol. Conserv.* **105**, 113–125 (2002).

32. Donald, P. F., Sanderson, F. J., Burfield, I. J. & van Bommel, F. P. J. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agric. Ecosyst. Environ.* **116**, 189–196 (2006).
33. Reif, J. Long-term trends in bird populations : a review of patterns and potential drivers in North America and Europe long-term trends in bird populations : a review of patterns and potential drivers in North America and Europe. *Acta Ornithol.* **48**, 1–16 (2013).
34. Bohning-Gaese, K. & Bauert, H. Changes in species abundance, distribution, and diversity in a Central European bird community. *Conserv. Biol.* **10**, 175–187 (1996).
35. Gregory, R. D. *et al.* Population trends of widespread woodland birds in Europe. *Ibis* **149**, 78–97 (2007).
36. Żmihorski, M., Chylarecki, P., Orczewska, A. & Wesołowski, T. Białowieża Forest: A new threat. *Science* **361**, 238 (2018).
37. Georgiev, K. B. *et al.* Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities. *J. Appl. Ecol.* **57**, 1103–1112 (2020)
38. Schütz, C. & Schulze, C. H. Functional diversity of urban bird communities: effects of landscape composition, green space area and vegetation cover. *Ecol. Evol.* **5**, 5230–5239 (2015).
39. Si, X. *et al.* Functional and phylogenetic structure of island bird communities. *J. Anim. Ecol.* **86**, 532–542 (2017).
40. Tischendorf, L., Bender, D. J. & Fahrig, L. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs . generalist dispersers. *Landsc. Ecol.* **18**, 41–50 (2003).
41. The State Forests Information Centre. Instrukcja urządzania lasu. (2012). Available at: https://www.lasy.gov.pl/pl/publikacje/copy_of_gospodarka-lesna/urzadzanie/iul.
42. McGarigal, K. FRAGSTATS 4 Tutorial Tutorial 1 . Setting Up Software and Inspecting Grids. 1–58 (2015).
43. Keating, K. A. & Quinn, J. F. Estimating species richness: the Michaelis-Menten model revisited. *Oikos* **81**, 411–416 (2012).
44. Adler, P. B. *et al.* Evidence for a general species-time-area relationship. *Ecology* **86**, 2032–2039 (2005).
45. Chylarecki, P. *Czynniki kształtujące zmiany liczebności pospolitych ptaków Polski w latach 2000–2012* (Muzeum i Instytut Zoologii PAN, Warszawa, 2016).
46. Whittaker, R. H. Evolution and measurement of species diversity. *Taxon* **21**, 213–251 (1972).
47. Tucker, C. M. *et al.* A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biol. Rev.* **92**, 698–715 (2017).
48. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
49. Mason, N. W. H., Mouillot, D., Lee, W. G., Wilson, J. B. & Functional, J. B. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* **1111**, 112–118 (2005).
50. Kembel, S. W. *et al.* Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464 (2010).
51. Laliberte, E. & Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305 (2010).
52. Swenson, N. G. *Functional and Phylogenetic Ecology in R.* (Springer, 2014)
53. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (2016). Available at: http://www.R-project.org/.
54. Wood, S. Package ' mgcv '. Available at: https://cran.r-project.org/web/packages/mgcv/index.html (2013).
55. Simmonds, J. S., Van Rensburg, B. J. & Maron, M. Non-random patterns of vegetation clearing and potential biases in studies of habitat area effects. *Landsc. Ecol.* **32**, 729–743 (2017).
56. Adams, M. lm.br: Linear Model with Breakpoint. (2017).
57. Wiens, J. J. *et al.* Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* **13**, 1310–1324 (2010).
58. Cadotte, M. W., Carscadden, K. & Mirotchnick, N. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* **48**, 1079–1087 (2011).
59. Legrand, D. *et al.* Eco-evolutionary dynamics in fragmented landscapes. *Ecography* **40**, 9–25 (2017).
60. Berg, Å. Diversity and abundance of birds in relation to forest fragmentation, habitat quality and heterogeneity. *Bird Study* **44**, 355–366 (1997).
61. Schippers, P., Koelewijn, H. P. & Smulders, M. J. M. Landscape diversity enhances the resilience of populations, ecosystems and local economy in rural areas. *Landsc. Ecol.* **30**, 193–202 (2015).
62. Hutchinson, E. G. "Concluding Remarks" on animal ecology and demography. *Cold Spring Harb. Symp. Quant. Biol.* **22**, 415–427 (1957).
63. Fletcher, R. J. *et al.* Is habitat fragmentation good for biodiversity ?. *Biol. Conserv.* **226**, 9–15 (2018).
64. Amarasekare, P. Competitive coexistence in spatially structured environments: a synthesis. *Ecol. Lett.* **6**, 1109–1122 (2003).
65. Nord, M. & Forslund, P. Environmental gradients explain species richness and community composition of coastal breeding birds in the Baltic Sea. *PLoS ONE* **10**, e0118455 (2015).
66. Jokimäki, J. & Suhonen, J. Effects of urbanization on the breeding bird species richness in Finland : a biogeographical comparison. *Ornis Fenn.* **70**, 71–77 (1993).
67. Cushman, S. A. & McGarigal, K. Landscape-level patterns of avian diversity in the Oregon coastal range. *Ecol. Monogr.* **73**, 259–281 (2003).
68. Rosin, Z. M. *et al.* Villages and their old farmsteads are hot spots of bird diversity in agricultural landscapes. *J. Appl. Ecol.* **53**, 1363–1372 (2016).
69. Fahrig, L. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecol. Appl.* **12**, 346–353 (2002).
70. Betts, M. G. *et al.* Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecol. Appl.* **20**, 2116–2130 (2010).
71. Guenette, J.-S. & Villard, M.-A. Thresholds in Forest bird response to habitat alteration as quantitative targets for conservation. *Conserv. Biol.* **19**, 1168–1180 (2005).
72. Moning, C. & Muller, J. Critical forest age thresholds for the diversity of lichens , molluscs and birds in beech (Fagus sylvatica L.) dominated forests. *Ecol. Indic.* **9**, 922–932 (2009).
73. Schmiegelow, F. K. A. & Monkkonen, M. Habitat loss and fragmentation in dynamic landscapes: Avian perspectives from the boreal forest. *Ecol. Appl.* **12**, 375–389 (2002).
74. Virkkala, R. & Rajasarkka, A. Spatial variation of bird species in landscapes dominated by old-growth forests in northern boreal Finland. *Biodivers. Conserv.* **15**, 2143–2162 (2006).
75. Fahrig, L. Relative effects of habitat loss and fragmentation on population extinction. *J. Wildl. Manage.* **61**, 603–610 (1997).
76. Brooks, T. M. *et al.* Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* **16**, 909–923 (2002).
77. Villard, M. A., Kurtis Trzcinski, M. & Merriam, G. Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. *Conserv. Biol.* **13**, 774–783 (1999).
78. McGarigal, K. & McComb, W. C. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecol. Monogr.* **65**, 235–260 (1995).
79. Trzcinski, M. K., Fahrig, L. & Merriam, G. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecol. Appl.* **9**, 586–593 (1999).
80. Rahbek, C. & Graves, G. R. Multiscale assessment of patterns of avian species richness. *Proc. Natl. Acad. Sci.* **98**, 4534–4539 (2001).

81. Jansson, G. & Andrén, H. Habitat composition and bird diversity in managed boreal forests. *Scand. J. For. Resour.* **18**, 225–236 (2003).
82. Mikusiński, G., Villero, D., Herrando, S. & Brotons, L. 5 - Macroecological Patterns in Forest Bird Diversity in Europe. in *Ecology and Conservation of Forest Birds* 137–182 (Cambridge University Press, 2018).
83. Rivera, L. F., Armbrecht, I. & Calle, Z. Silvopastoral systems and ant diversity conservation in a cattle-dominated landscape of the Colombian Andes. *Agric. Ecosyst. Environ.* **181**, 188–194 (2013).
84. McComb, B. & McGarigal, K. Relationships Between Landscape Structure and Breeding Birds in the Oregon Coast Range. *Ecol. Monogr.* **65**, 235–260 (1995).
85. Yahner, A. D. & Rodewald, R. H. Influence of landscape compostion on avian community structure and associated mechanisms. *Ecology* **82**, 3493–3504 (2001).
86. Koivula, M. J. *et al.* Breeding bird species diversity across gradients of land use from forest to agriculture in Europe. *Ecography* **41**, 1331–1344 (2017).
87. Rutt, C. L., Mokross, K., Kaller, M. D. & Stouffer, P. C. Experimental forest fragmentation alters Amazonian mixed-species flocks. *Biol. Conserv.* **242**, 108415 (2020).
88. Bertolino, S. *et al.* Spatially explicit models as tools for implementing effective management strategies for invasive alien mammals. *Mamm. Rev.* **50**, 187–199 (2020).

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Author contributions

All authors participated in writing and reviewing the manuscript. M.B. prepared all of the figures and tables.

Competing interests

The authors declare no competing interests.

Additional information

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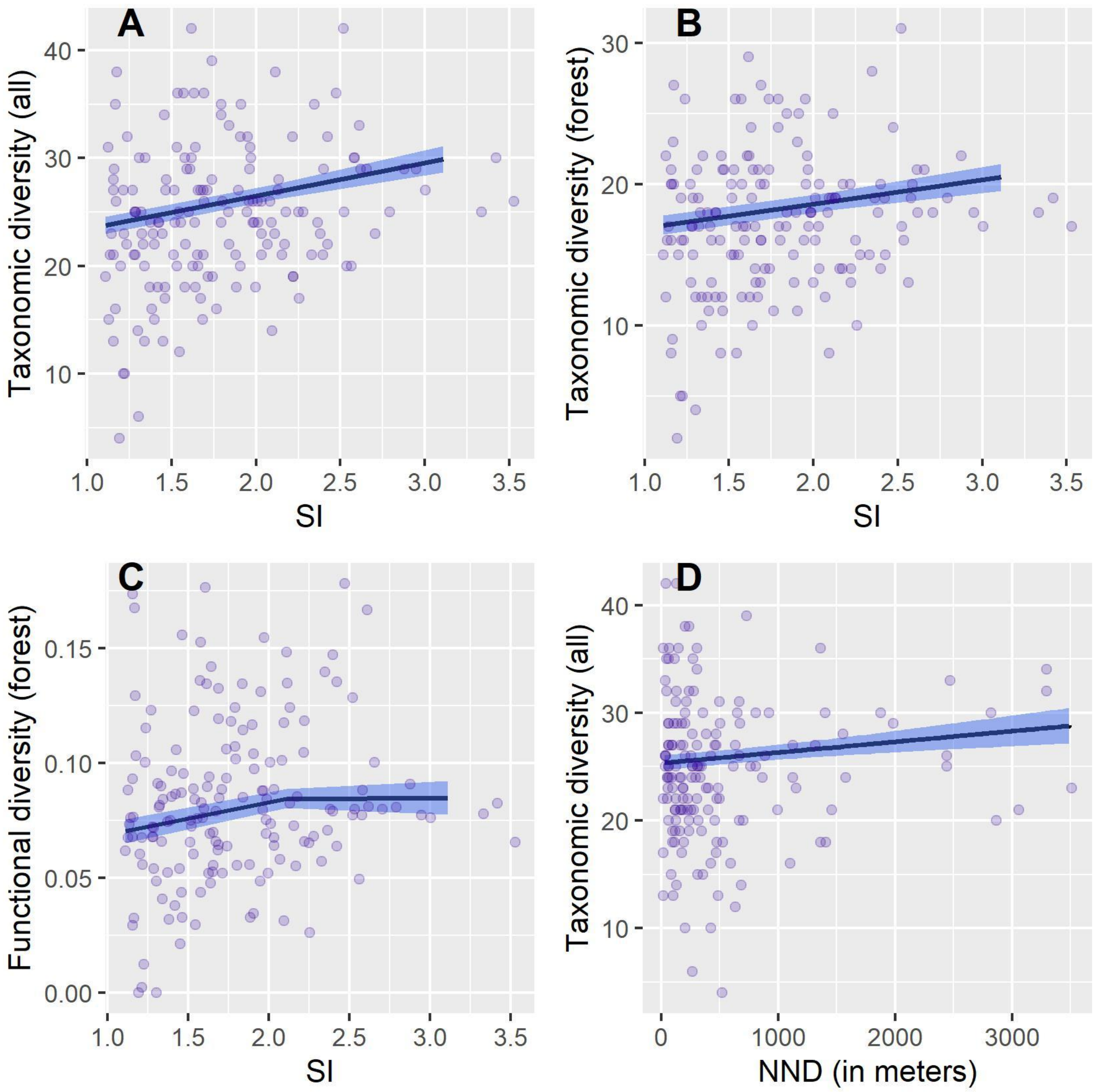

Figure S1. Response curves, derived from General Additive Modelling, showing the relationship between taxonomic and functional diversity (calculated for all of the bird species and forest specialist group) and forest patch shape index (SI) and nearest neighbour distance (NND).

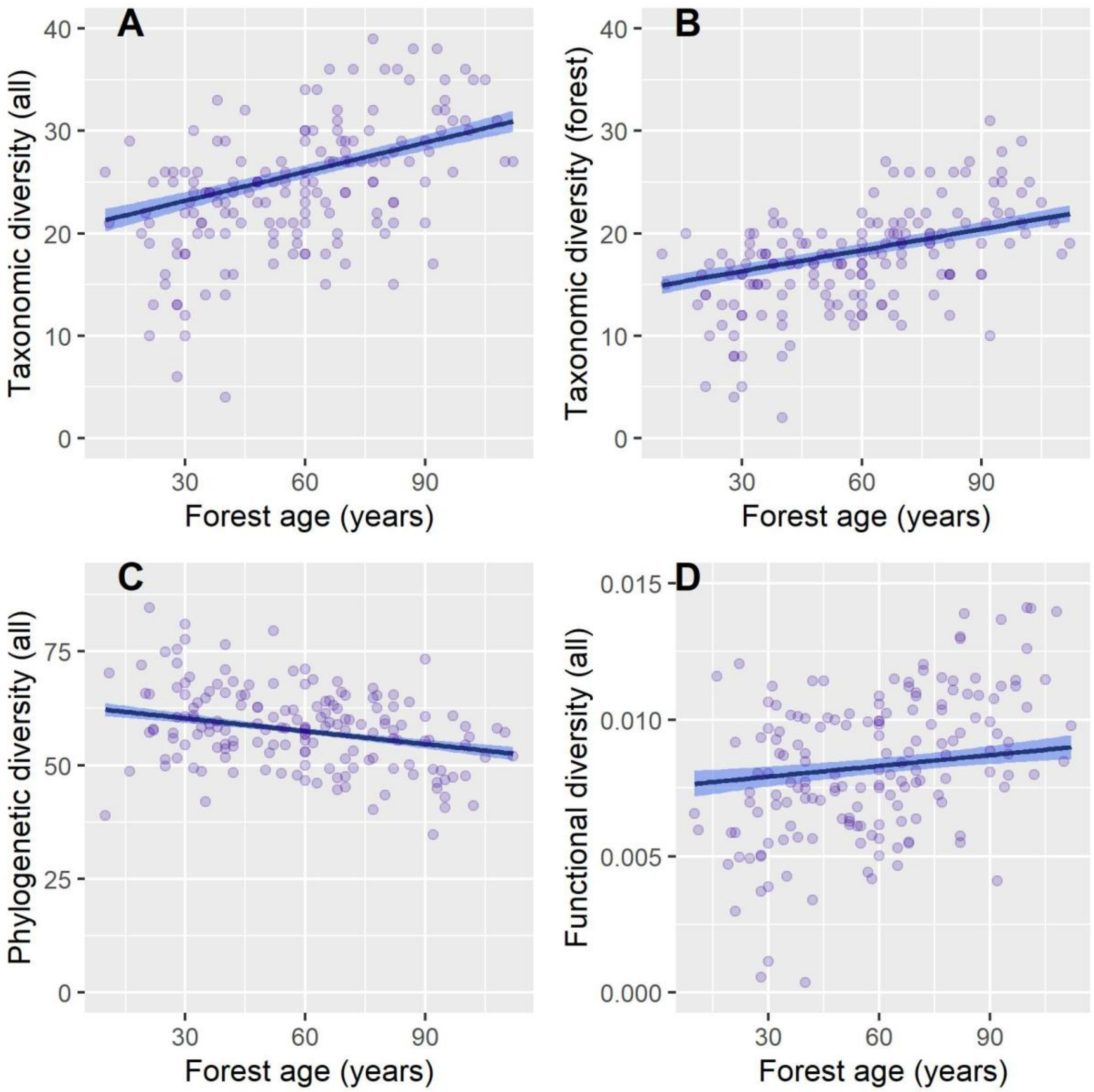

Figure S2. Response curves, derived from General Additive Modelling, showing the relationship between different metrics of bird diversity (for all of the study species and forest specialist group) and age of the forest patches.

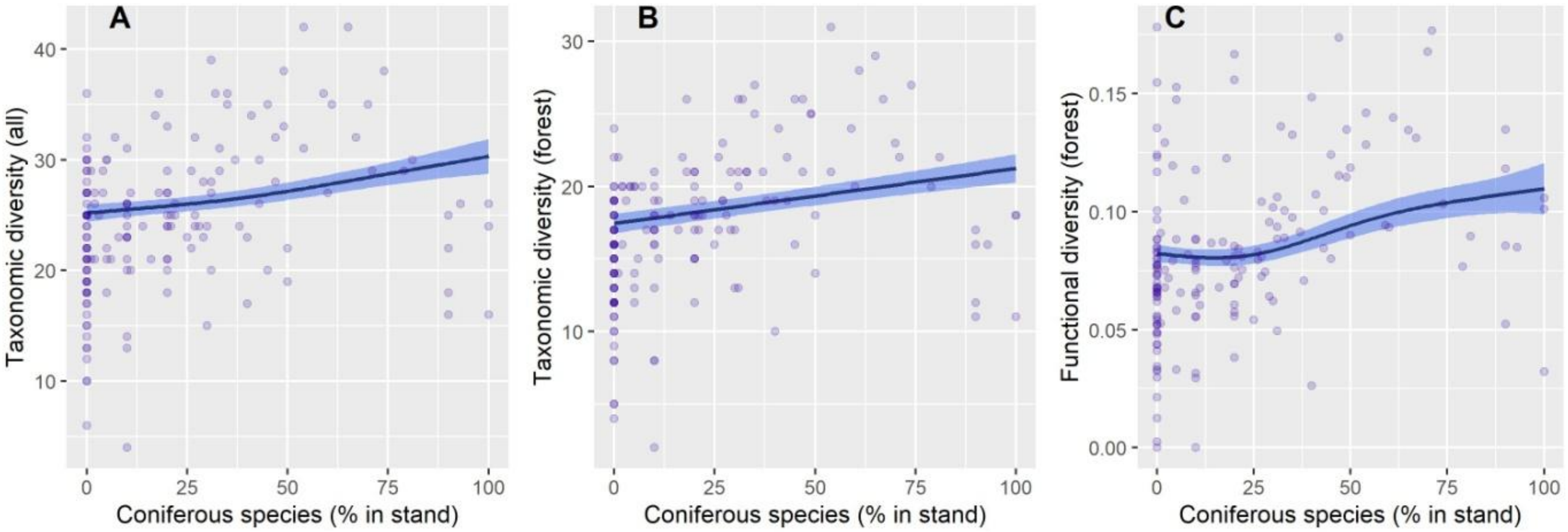

Figure S3. Response curves, derived from General Additive Modelling, showing the relationship between taxonomic and functional diversity (calculated for all of the bird species and forest specialist group) and percentage of coniferous species within a forest stand.

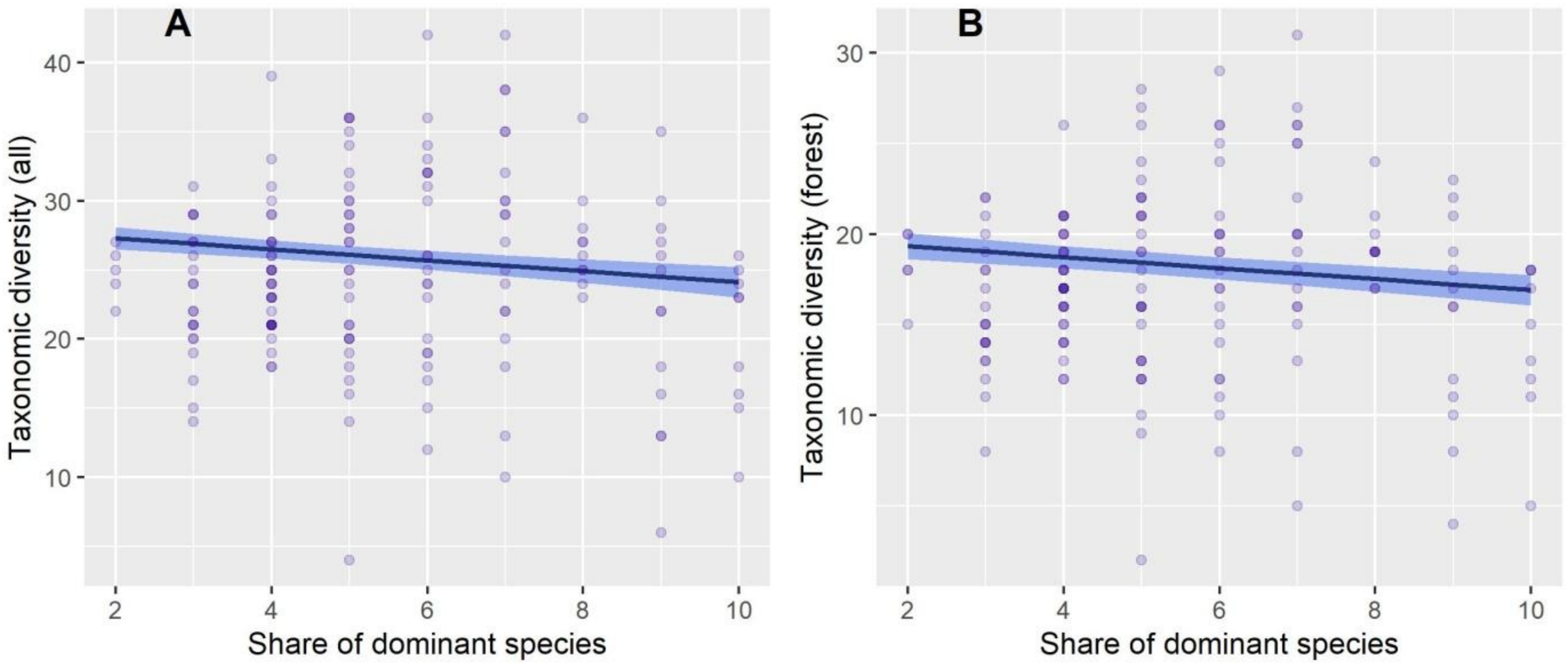

Figure S4. Response curves, derived from General Additive Modelling, showing the relationship between taxonomic diversity (calculated for all of the bird species and forest specialist group) and share of dominant species within a forest stand (ranging from 0 to 10).

Different response of the taxonomic, phylogenetic and functional diversity of birds to forest fragmentation

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Table S1. Functional traits used for calculating functional diversity metrics

Variable	**Description**	**Units**
LengthU_MEAN	Mean length of the bird, unsexed	cm
WingU_MEAN	Mean length of the wing, unsexed	mm
WingM_MEAN	Mean length of the wing, male	mm
WingF_MEAN	Mean length of the wing, female	mm
TailU_MEAN	Mean length of the tail, unsexed	mm
TailM_MEAN	Mean length of the tail, male	mm
TailF_MEAN	Mean length of the tail, female	mm
BillU_MEAN	Mean length of the bill, unsexed	mm
BillM_MEAN	Mean length of the bill, male	mm
BillF_MEAN	Mean length of the bill, female	mm
TarsusU_MEAN	Mean length of tarsus, unsexed	mm
TarsusM_MEAN	Mean length of tarsus, male	mm
TarsusF_MEAN	Mean length of tarsus, female	mm
WeightU_MEAN	Mean weight in breeding season, unsexed	grams
WeightM_MEAN	Mean weight in breeding season, male	grams
WeightF_MEAN	Mean weight in breeding season, female	grams
Sexual dimorphism	Difference between male and female in size and plumage colour	1: yes; 0: no
Clutch_MIN	Minimum clutch size	number of eggs

Clutch_MAX	Maximum clutch size	number of eggs
Clutch_MEAN	Mean clutch size	number of eggs
Broods per year	Mean number of broods per breeding season (replaced broods are not included)	number of broods
EggL_MEAN	Mean length of the egg	mm
EggW_MEAN	Mean width of the egg	mm
Egg mass	Mean weight of the egg	grams
Young	Type of young	AL = altricial, SA = semi-altricial, PR = precocial
Association during nesting	Association of adults during nesting	S = solitary, SC = semi-colonial, C = colonial
Nest type	Type of nest	G = ground, on ground directly; H = hole, in tree, bank, ground, crevice; OA = open-arboreal, cup in bush, tree, on cliff ledge; CA = closed-arboreal; GC = ground close, nest in tussock very close to ground but not directly on ground, hidden in surrounded vegetation
Nest building	Sex building the nest	M = male, F = female, B = both, N = none
Mating system	Type of mating system	M = monogamous, PG = polygynous, PA = polyandrous, PM = promiscuous
Incubation period	Mean length of eggs´ incubation	days
Incubation sex	Sex incubating eggs	M = male, F = female, B = both, N = none
Hatching	Type of hatching	AS = asynchronous young hatch within 2 days or more, SY = synchronous, young hatch within 1 day
Eggshells	Eggshells are left in the nest or not	1: yes; 0: no
Nestling period	Average age of young when leaving nest	days
Fledging period	Average age of young when fledging	days
Parental feeding	Average age when young are not regularly fed by parents	NA = birds which feed young but the period is unknown, 0 = birds which do not feed young, days
Age of independence	- Average age when young totally separate off parents - young are not fed or protected by parents	days
Feeding independence	Average age when young are independent of feeding by	days

	parents, calculated as mean from Parental feeding and Age of independence	
Age of first breeding	Average age of the first breeding	years
Life span	Maximum life span recorded in wild	years
Post-fledging mortality	Mean mortality of young in the first year of their life	%
Mortality of adults	Mean annual mortality of adults	%
Association outside the breeding season	Association of adults outside breeding season	GR = gregarious, PA = in pairs, SO = solitary
Territoriality	Defence of a territory (defended area occupied exclusively by a single bird, pair or larger social unit)	1: yes; 0: no
Sedentary	Species lives in the same area in both breeding and non-breeding season	1: yes; 0: no
Facultative migrant	Species makes irregular shifts in non-breeding season	1: yes; 0: no
Short distance migrant	Species migrates within the range of the Western Palearctic in non-breeding season	1: yes; 0: no
Long distance migrant	Species migrates beyond the range of the Western Palearctic in non- breeding season	1: yes; 0: no
Deciduous forest	Species occupies deciduous forest in breeding area	1: yes; 0: no
Coniferous forest	Species occupies coniferous forest in breeding area	1: yes; 0: no
Woodland	Species occupies woodland, i.e. habitat with disperse vegetation, edge of forest, etc. with presence of full-grown trees in breeding area	1: yes; 0: no
Shrub	Species occupies shrub. i.e. habitat with disperse vegetation, bush, shrub, scrub, etc. without presence of full-grown trees in breeding area	1: yes; 0: no
Savanna	Species occupies savanna in breeding area	1: yes; 0: no
Tundra	Species occupies tundra in breeding area	1: yes; 0: no
Grassland	Species occupies grassland (lowland meadows and fields) in breeding area	1: yes; 0: no

Mountain meadows	Species occupies mountain meadows in breeding area	1: yes; 0: no
Reed	Species occupies swamps with reed in breeding area	1: yes; 0: no
Swamps	Species occupies swamps without reed in breeding area	1: yes; 0: no
Desert	Species occupies desert and semi-desert habitats in breeding area	1: yes; 0: no
Freshwater	Species occupies static and flowing freshwaters in breeding area	1: yes; 0: no
Marine	Species occupies marine habitats in breeding area	1: yes; 0: no
Rocks	Species occupies rocks (stony habitats, cliffs, crags etc.) in breeding area	1: yes; 0: no
Human settlements	Species occupies human settlements in breeding area	1: yes; 0: no
Folivore_Y	At least 10% of diet throughout the year composed of grass, leaves, small plants etc.	1: yes; 0: no
Frugivore_Y	At least 10% of diet throughout the year composed of fruits	1: yes; 0: no
Granivore_Y	At least 10% of diet throughout the year composed of grains, seeds and nuts	1: yes; 0: no
Arthropods_Y	At least 10% of diet throughout the year composed of arthropod	1: yes; 0: no
Other invertebrates_Y	At least 10% of diet throughout the year composed of invertebrates excepting arthropods	1: yes; 0: no
Fish_Y	At least 10% of diet throughout the year composed of fish	1: yes; 0: no
Other vertebrates_Y	At least 10% of diet throughout the year composed of vertebrates excepting fish	1: yes; 0: no
Carrion_Y	At least 10% of diet throughout the year composed of carrion	1: yes; 0: no
Omnivore_Y	Diet throughout the year composed of similar amount of plants and animals	1: yes; 0: no
Folivore_B	At least 10% of diet	1: yes; 0: no

	throughout the breeding season composed of grass, leaves, small plants etc.	
Frugivore_B	At least 10% of diet throughout the breeding season composed of fruits	1: yes; 0: no
Granivore_B	At least 10% of diet throughout the breeding season composed of grains, seeds and nuts	1: yes; 0: no
Arthropods_B	At least 10% of diet throughout the breeding season composed of arthropods	1: yes; 0: no
Other invertebrates_B	At least 10% of diet throughout the breeding season composed of invertebrates excepting arthropods	1: yes; 0: no
Fish_B	At least 10% of diet throughout the breeding season composed of fish	1: yes; 0: no
Other vertebrates_B	At least 10% of diet throughout the breeding season composed of vertebrates excepting fish	1: yes; 0: no
Carrion_B	At least 10% of diet throughout the breeding season composed of carrion	1: yes; 0: no
Omnivore_B	Diet throughout the breeding season composed of similar amount of plants and animals	1: yes; 0: no

Artykuł 2

Bełcik, M., Lenda, M., Amano, T., Pustkowiak, S., Skórka, P. (202x). Social information can alter the effect of habitat fragmentation on bird diversity and improve its stability.

Social information can alter the effect of habitat fragmentation on bird diversity and improve its stability

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Abstract

Habitat loss and fragmentation are the primary drivers of biodiversity loss worldwide; however, their effects may be altered by both abiotic and biotic factors. Many animal species use social information, such as the presence of other individuals, while deciding where to settle; however, how the variability in social information alters the effects of habitat loss and fragmentation is unknown. Thus, using a large-scale field experiment, we demonstrated that adding positive social information (the song of a passerine bird) increased species diversity and adding negative social information (voices of predators) decreased species diversity while increasing community stability. Furthermore, positive social information altered the relationship between forest area and biodiversity metrics, for example, by drastically increasing species diversity in small forest patches; this effect persisted even after one year of the experiment. Thus, social information plays a key role in shaping biodiversity and ecological laws (e.g. species-area relationships). Manipulation of social information may be an important conservation tool as it may increase species diversity in less utilised, yet suitable habitats, thereby reducing the negative effects of habitat fragmentation.

Introduction

Habitat fragmentation and habitat loss are now recognised as the primary causes of biodiversity loss and decline worldwide [1–3]. Island biogeography [4] and metapopulation [5] predict that in fragmented landscapes the isolation of habitat patches negatively affects local biodiversity. The mechanism underlying this phenomenon is that the relative ratio between local colonisation and extinction leads to a lower species population density and occupancy in small and isolated habitat patches than in large and less isolated patches [4,5].

However, local biodiversity may depend not only on the spatial configuration and structural features of the habitat patches but also on various interactions among individuals of the same or different species (e.g. social, competitive, and predator-prey interactions) [6,7]. Therefore, relying only on structural features of the landscape can be misleading while making vital decisions [8], such as where to forage or reproduce. Thus, animals often use social public information (hereafter referred to as "social information"), including the presence of other individuals, their sounds, traces of their presence, their behaviour or their activities that relate to habitat quality, suitability, and available resources, while selecting and settling in a new habitat [6,9–11]. Individuals who utilise social information can significantly increase their fitness compared to individuals who rely solely on the structural and physical characteristics of the environment [8,12]. Social information can be carried by other individuals of the same species or different species [13] and can affect the whole community [14,15]. Moreover, social information may come from multiple sources, which may weaken or reinforce one another. For example, the presence of predators may create a landscape of fear, which is a continuous spatial variation in an animal's perception of predation risk, including places where an animal avoids predation risk [16]. Therefore, the signs of presence of a predator in an area may deter prey species from setting territories in that area [17–19] and thus decrease the level of local biodiversity [15]. In contrast, the presence of conspecifics or different species may attract individuals to settle in those habitat patches [14,17–19]. Calls produced by conspecifics and heterospecifics may be perceived as positive social information, which attracts more individuals and thus increases patch occupancy and local density [6,20]. Further, animals can also use the presence of a successfully established individual as an indicator of high-quality of the habitat [21,22]. Therefore, social information may be perceived as negative (e.g. the voice of predators), positive (e.g. the voice of conspecifics), or mixed (both predators and conspecifics) depending on the recipient [6,23].

Although the impact of social information on population density and habitat occupancy is relatively well documented, its interaction with habitat fragmentation and temporal extent is barely understood [25]. Different types of social information may alter the impact of habitat fragmentation by diminishing or augmenting the positive association of patch area and negative association of isolation with biodiversity, respectively. For example, providing positive social information, such as the presence of other individuals, in suitable but small habitat patches may increase patch occupancy and, thus, taxonomic diversity within a given area. In contrast, negative social information cues, such as the presence of predators, could diminish the number of species per unit area as prey species might respond negatively to the cues that indicate negative consequences for their fitness [24]. This effect of negative social information is expected to be especially strong in small habitat patches where there may not be enough shelter from predators [25]. Thus, negative social information may augment the impact of habitat fragmentation on taxonomic diversity. In reality, it is rare for only one type of social information to exist in the field. However, it is unknown how mixed antagonistic (positive and negative) sources of social information affect the distribution and diversity of animal species. To date, only one study has shown that social information can augment or diminish the effect of habitat patch size on a single bird species [6]. As social information may be utilised by a wide range of other species, it may shape the composition of the whole species community [26] and further, it may also be remembered over longer periods.

However, only a few studies have investigated the possibility of a temporal carryover effect of social information, mostly showing negative results [27].

Here, we experimentally investigated the interactive effect of different types of social information and forest fragmentation on the species composition and biodiversity metrics of bird assemblages. Birds communicate mostly by vocalisations, creating acoustic social information, which makes them a suitable model for studying the effect of social information on local communities. They also encompass a wide range of taxonomic, functional, and phylogenetic diversity [28,29]. In Central Europe, many bird species occur in landscapes highly altered by agriculture and urbanisation, yet present different degrees of habitat fragmentation [30,31]. A majority of European forests has a form of isolated habitat patches surrounded by arable fields and human settlements, with 60% of forest edges located along intensive land uses [32]. Since strong fragmentation favours generalists who are able to survive in smaller patches of habitats than specialists [33,34], we focused on the biodiversity components of all bird species and forest specialists. We tested the following three hypotheses (our specific predictions for each hypothesis are included in Table S1):

Hypothesis 1. Bird taxonomic, phylogenetic and functional diversity and community temporal dissimilarity are affected differently by the presence, absence, and coexistence of different types of social information (i.e. negative, positive, and mixed) in fragmented habitat patches.

Hypothesis 2. The effect of negative (voices of predator), positive (song of a passerine bird), and mixed (both) social information on bird diversity has different long-lasting effects and may persist until the following year.

Hypothesis 3. The presence, absence, and coexistence of different types of social information modifies the effects of habitat patch size and isolation on bird taxonomic, phylogenetic, and functional diversity in habitat patches.

Results

A total of 94 (44 forest species), 98 (47 forest species), and 94 (47 forest species) bird species were observed in 2017, 2018, and 2019, respectively. The mean number of species observed per survey in a given forest patch was 25 (SE = 7, range 4–42) in 2017, 25 (SE = 7, range 4–43) in 2018, and 25 (SE = 6, range 7–40) in 2019.

In 2017 (one year prior to the experiment), there was no difference in biodiversity metrics between forests assigned as control groups and those assigned as treatment groups (Figs. 2 and 3). However, there was a slightly higher taxonomic diversity of all species in forests subjected to positive information than those subjected to negative information (Fig. 2). Partial-canonical correspondence analysis (CCA) indicated that in 2017, species composition was similar among different forest groups for all the species (first axis: F = 1.92, P = 0.092; all axes: F = 1.00, P = 0.476, Fig. 4) and forest specialists (first axis: F = 2.00, P = 0.200; all axes: F = 0.90, P = 0.741, Fig. 4). The CCA explained only 3.4% and 3.1% of variation in species composition for all species and forest specialists, respectively.

Hypothesis 1: Effect of social information type on biodiversity metrics

The results of our experiment support our first hypothesis since taxonomic, phylogenetic, and functional diversity metrics, indeed, showed different responses to different types of social information (Tables 1–3, Figs. 2, 3). Taxonomic diversity (both species and forest specialists) was higher in forest patches subjected to positive social information than those subjected to mixed or negative social information (Tables 1–3, Fig. 2). However, taxonomic diversity in control forests was significantly higher than that in forests subjected to mixed social information (for all the species and forest specialists) and marginally higher than forests subjected to negative social information for all the species (Tables 1–3, Fig. 2). For both all species and forest specialists, partial-CCA indicated that the species communities separated due to the experiment, as indicated by a significant pseudo F-test on the first ordination axis (all species F = 7.4, *P* = 0.002; forest species: F = 11.2, *P* = 0.002) and on all axes (all species: F = 2.3, *P* = 0.002; forest species: F =3.2, *P* = 0.002). The ordination axes explained 7.4% and 10% variation in species composition for all species and forest specialists, respectively (Fig. 4). The variables that contributed the most to community differentiation were mixed social information (all species: F = 1.4, *P* = 0.022; forest species: F = 2.0, *P* = 0.004) and forest patch size (all species: F = 7.4, *P* = 0.002; forest species: F = 11.0, *P* = 0.002; Fig. 4). The experimental treatment also affected the species dissimilarity between 2017 and 2018 (Table 4, Fig. 5). Furthermore, temporal dissimilarity increased in forests with positive social information and decreased in forests with negative social information as compared to the control forest patches, for all species and forest specialists (Table 4, Fig. 5). Moreover, dissimilarity was significantly higher in forest patches with positive social information than in patches with negative and mixed social information (the latter for all species only; Fig. 5). Furthermore, the dissimilarity in forest patches with mixed information did not differ from that in the control forest patches (Table 4, Fig. 5). Phylogenetic diversity in the control group of forest patches did not differ from that in forest patches with broadcasted social information (Tables 1 and 2, Fig. 3); however, we found marginally significant differences between forests with positive and negative social information for all the species (Tables 1 and 2, Fig. 3). On the contrary, functional diversity did not show any significant response to the experimental broadcasts (Tables 1 and 2, Fig. 3).

Hypothesis 2: Temporal carry-over effect of social information

Our results also partially supported our second hypothesis as there were no differences in biodiversity metrics between the control forest patches and treatment forest patches for both all species and forest specialists, one year after the experiment (Table 3, Figs. 2 and 3); however, the taxonomic diversity of all the species was higher in forest patches subjected to positive social information a year after the experiment than in those subjected to mixed social information (Table 2, Fig. 2). Moreover, partial-CCA indicated that ordination axes still separated species composition of birds and explained 7.9% and 9.5% of variation in all the species (first axis: F = 7.8, *P* = 0.002; all axes: F = 2.4, *P* = 0.002) and forest specialists (first axis: F = 10.7, *P* = 0.002; all axes: F = 3.0, *P* = 0.003) composition, respectively. The variables contributing to the differences were forest patch area (all species: F = 7.9, *P* = 0.002; forest species: F = 10.6, *P* = 0.002) and the isolation index for all the species (F = 1.5, *P* = 0.024), with a marginal effect of mixed social information (F = 1.3, *P* = 0.076) for all the species (Fig. 4). Forest patches subjected to positive information still had a higher Jaccard dissimilarity index than control forest patches for all the species and forest specialists (Table 4, Fig. 5).

The phylogenetic diversity of forest specialists in forest patches subjected to mixed social information was slightly higher than that of forest patches subjected to positive and negative social information (Table 2, Fig. 3). In contrast, functional diversity did not show any significant reaction to the experimental broadcast one year after the experiment (Table 3).

Hypothesis 3: Impact of social information on the effect of forest fragmentation

Our results also partially support our third hypotheses. Our analyses showed that social information could modify the effects of fragmentation metrics on bird diversity and that this effect could persist for one year after the experiment. In 2017 (the year before the experiment) and 2018 (the year of the experiment), the taxonomic diversity of forest specialists showed little change with forest patch area; however, in 2019 (one year after the experiment), there was a strong negative relationship between forest specialist richness and forest patch area (Table 3, Fig. 6). As these analyses were based on differences in species richness between the years, this indicates that positive information had the largest positive effect in small forest patches and negative or no effect in larger patches (Fig. 6). Species temporal dissimilarity (for all species and forest specialists) between 2017 and 2018 was the highest at the low and high values of forest isolation in patches subjected to positive social information, whereas dissimilarity was independent of the isolation index in the other experimental groups (Table 4). Similar findings were obtained while comparing species temporal dissimilarity between 2017 and 2019 (Table 4).

Differences in the phylogenetic diversity of forest specialists between 2017 and 2018 and 2017 and 2019 increased with increasing nearest neighbour distance; however, this effect was statistically not significant in the year following the experiment (Tables 1 and 3, Fig. S1). This indicates that phylogenetic diversity increased in the most isolated habitat patches. Furthermore, differences in functional diversity of all bird species in 2018 and 2019, compared to 2017, increased the most in small forest patches subjected to positive social information; however, this effect decreased along with an increase in forest area only up to a certain level (Fig. 6, Tables 1 and 3). The same pattern was observed for the functional and phylogenetic diversity of all bird species one year after the experiment (Table 3, Fig. 6). The other types of interactions were statistically not significant (Tables 1 and 3).

Discussion

In this study, we demonstrated that social information can change the spatial distribution, diversity, composition, and temporal dissimilarity of bird species at the landscape scale. Biodiversity metrics showed varied responses to different types of social information. For instance, providing positive social information (passerine bird songs) increased species diversity, but decreased temporal stability in species composition. In contrast, providing negative (voices of predators) and mixed social information decreased species diversity and increased temporal stability in species composition.

Our first hypothesis was supported by the experiment. Based on their responsiveness to social information, the biodiversity metrics can be ordered as taxonomic diversity > phylogenetic diversity > functional diversity. A possible explanation for this result is the high potential redundancy of functions within the avian community that occupies a specific habitat patch [35]. Therefore, changes in social information may affect taxonomic diversity but not necessarily ecosystem functions performed by avian communities [36,37].

We observed that the taxonomic diversity (all the bird species and forest specialists) and phylogenetic diversity were both higher in forest patches with positive information than in forest patches with negative and mixed social information. Positive social information also altered species composition, as shown by the canonical correspondence ordination of species and an increase in temporal dissimilarity. Since positive social information is generally perceived as an indicator of a high-quality habitat, the observed changes in taxonomic diversity suggest that indications of such habitats could have a significant effect on birds' decision to settle, as predicted by the interspecific attraction hypothesis [38]. Thus, these results indicate that birds might view forest patches with positive social information as low-risk patches [39]. It is worth noting that adding songs of only one passerine species had a pronounced and long-lasting effect on changes in species number and community composition indicating that the songs of *Turdus philomelos,* used in this study, can have a cascading effect on other species. Therefore, it is possible that the song of the thrush attracted other species, which in turn acted as social attractors. This would explain why the species composition in forests subjected to positive information was unstable even after a year of the experiment.

In contrast, negative social information seemed to decrease both taxonomic and phylogenetic diversity in forest patches as well as the temporal dissimilarity. The reduced dissimilarity confirms the idea that predators can stabilise bird communities in fragmented forests. Contrary to our hypothesis, mixed social information decreased both the taxonomic and phylogenetic diversity. This result indicates that the effect of negative social information (e.g. predator presence) is stronger than that of the positive social information (i.e. signs of a high-quality patch), instead of the two effects cancelling each other, as has been suggested in previous studies [40]. Therefore, the perceived risk of predation could be the main behavioural factor underlying species distribution across suitable habitat patches [18,41].

Moreover, our second hypothesis was also partly supported and we observed a carryover effect of social information on the taxonomic diversity of all bird species, phylogenetic diversity of forest specialists, species composition, and temporal dissimilarity in species composition. Social information use has been suggested to extend across temporal, spatial, and ecological dimensions [39] and our results indicate that the temporal dimension may extend to at least the following year. This was already suggested for the effect of social information from conspecifics [27]; however, the carry-over effect of heterospecific social information has been poorly documented. This suggests that avian cognitive abilities and memory capacity allow birds to connect a given social information type and intensity to a certain habitat patch. Moreover, it is possible that changes in species composition due to social information creates a network of inter- and intra-specific interactions that are sustained even after the social cues terminate.

Lastly, our third hypothesis was also supported to a limited extent by our experimental results. We observed that only positive social information modified the functional and phylogenetic diversity of all bird species and the taxonomic diversity of forest specialists with the increasing area of forest patches. Complying with our first hypothesis, positive social information increased the number of forest species in small habitat patches in 2019 compared to the base year (2017). However, compared to 2017, it seems that positive social information decreased species diversity in 2019 in large forest patches. For the phylogenetic diversity of all bird species, positive social information seemed to have altered the negative effect of forest patch area to a positive effect after the experiment. Among the diversity indices, positive social information increased phylogenetic diversity the most in large forest patches in 2018 and in both small and large forest patches in 2019, compared to 2017. This could provide further evidence that there is a carryover effect in social information use by different species and that information obtained in a given year, along with other indicators for the quality of the habitat, could serve as one of the factors shaping the diversity-area association [39]. However, positive social information had an opposite effect on functional diversity of all the bird species as it increased the most in small forests in both 2018 and 2019. A possible explanation for this result is that the presence of song thrush can be associated with high-quality forest patches. The high intensity and loudness of song thrush calls that extend outside a forest patch might create a landscape of social attraction, even for non-forest species. Thus, positive social information might have influenced the heterospecifics' (farmland species) decision to settle in such forests.

Positive social information also modified the effect of another forest fragmentation metric, nearest neighbour distance, on temporal dissimilarity (for both species and forest species) and the phylogenetic diversity of forest specialists. Interestingly, dissimilarity was highest in the less isolated forest patches. The latter contradicts the idea that species composition is stable in large and well-connected forest patches. These changes in species composition also likely explain the disappearance of the negative association between the phylogenetic diversity of forest specialists and habitat isolation in forests with positive social information.

Contrary to our hypothesis, negative social information did not moderate the effects of habitat fragmentation metrics. This probably results from the decreased temporal dissimilarity in forests with negative social information. Lower species turnover due to predator presence may make bird communities more stable, and thus less responsive to forest fragmentation.

Study limitations

The biggest limitation of our study was that, in our experimental approach, we focused on the social information that was artificially broadcasted in the forest patches. However, these forest patches were already occupied by many different species; therefore, conspecific and interspecific social information must have already been present prior to and during our experiment. However, our analyses did not account for other social information due to the difficulty in quantifying pre-existing social information networks. This was well beyond the scope of our study, and even if situation and resources permitted, the methodology and framework for quantifying all social information is lacking. Therefore, posing an opportunity for future studies, quantifying social information networks (or, at least, acoustic networks) in a given habitat patch could greatly advance our understanding of behavioural and landscape ecology.

Further, we could not estimate the fitness, such as breeding success, of individuals and species that were attracted by positive social information and therefore this aspect could also be explored in future studies. However, we observed that biodiversity remained high in forest patches with positive social information even in the year following the experiment. Therefore, we suspect that there was no immediate decrease in individual fitness due to the increased species density. Previous studies have demonstrated that an increased density of conspecifics may have positive associations with individual components of fitness [42,43].

Practical recommendations

This study has several important practical implications. Firstly, our results indicate that generating positive social information may increase the taxonomic diversity of birds in fragmented landscapes. This may help build species-rich habitats, especially in case of newly created or restored habitats of high quality, and may facilitate such habitats in reaching their maximum sustaining capacity. Moreover, using positive social information may help overcome the negative effects of small habitat patches and habitat isolation on species diversity. Thus, providing positive social information in small habitat patches may conserve or restore the local biodiversity. As the effect of social information seems to be partially sustained in the following year, the manipulation of social information in a habitat might be a cost-effective tool to increase species diversity. This also creates an entirely new frontier of study that might broaden our understanding of how animals adapt to environmental changes under increasing human pressure and habitat fragmentation.

Methods

Study system

Positive, negative, and mixed social information

In this study, we considered three types of social information—positive, negative, and mixed. Positive social information was provided by songs from the song thrush, *Turdus philomelos* (L). It is a medium-sized (20–23 cm in length and weighs 50–100 g) forest specialist species occurring in different forest types. In Central Europe, it is mostly a migratory bird which starts singing and setting territories in March. Its songs are loud and are audible from distant locations, even outside the forest habitat patch [47]. The song thrush forages a variety of food sources, including both invertebrates and plants (e.g. fruits) [45]. Moreover, it is one of the primary prey species of Northern Goshawk *Accipiter gentilis* (L.) [44]. Thus, its presence may be a good indicator for a suitable habitat type that is rich in food resources and free of predators. Our preliminary analysis revealed a significant positive association between the abundance of the song thrush and the taxonomic diversity of birds ($r = 0.601$). Negative social information included the territorial calls of the Northern Goshawk,. It is a large sized (male and female body length and mass are 46–61 cm and 360–1000 g and 59–70 cm and 770–2200 g, respectively) opportunistic predator preying upon diverse range of birds [44,45]. It breeds in various forests and even in small habitat patches. Therefore, presenting cues for the presence of this predator may deter many birds from setting territories in such forest habitat patches [46]. Furthermore, it vocalises early during the breeding season, usually in March. Lastly, mixed social information was emitted interchangeably by the voices of both the Northern Goshawk and song thrush.

Our research was carried out from 2017 to 2019 and consisted of two tasks (Fig. 1). The first task was to conduct annual field surveys in select forest patches, and the second task was to perform a behavioural landscape-wide experiment manipulating social information in select forest patches.

Study sites

Our study area of 1097 km^2 was located in the southern part of Poland, in the province of Lesser Poland, north of Cracow. In this region, we selected 150 forest patches located in an agricultural landscape, which were mostly mixed stands managed or supervised by the Polish State Forests Holding. The selected forest patches were not part of a larger continuous forest complex and differed in size and isolation.

Field surveys

Field surveys were conducted between 1 April and 31 May from 2017 to 2019. They were conducted by a team of three experienced birdwatchers, each with more than ten years of experience in performing bird censuses. Each of these observers had an assigned set of forest patches, with each patch being visited three times, once during each 20-days round (1-20 April, 21 April – 10 May, 11-31 May). Surveys commenced at approximately 5 a.m. and usually lasted until 11 a.m. During surveys, an observer noted the starting time and then moved through the forest in random directions, trying to cover maximum area. The observer made notes of all the species and the exact time the first individual in each species was heard or seen within a patch [29]. Species abundance index within a patch was estimated using the Michaelis-Menten model using the survey starting time and the time of observation of the first individual [48] (Skórka et al. in prep.). The survey was terminated if no new species were observed for ten minutes [29] (Skórka et al., in prep.).

Experimental manipulation of social information

The field experiments were conducted from 17 March to 30 March 2018. A group of 30 forest patches, having similar characteristics (Table S2), were assigned to one of the five groups:

- forest subjected to positive social information (song thrush, *Turdus philomelos*)
- forest subjected to negative social information (Northern Goshawk, *Accipiter gentilis* (L.))
- forest subjected to mixed social information (both the song thrush songs and Goshawk calls)
- forest constituting the procedural control subjected to background noise (i.e. sound of moving trees and surrounding landscape)
- forest constituting the control group with no broadcast

In each of these groups, the assigned broadcast was played every day from 7 am to 12 pm. The number of loudspeakers varied from one to five depending on the forest patch area. After 12 pm the speakers were collected and charged and were hung again the next morning.

The broadcast consisted of five minutes of songs/calls and fifteen minutes of silence played alternately for five hours. The procedural playback was constructed similarly, except that it contained a neutral ambient sound instead of songs/calls. Bird song/call recordings having "A" mark (highest quality) were obtained from the Xeno Canto portal (https://www.xeno-canto.org/). JAM HX-P710 speaker (set for maximum loudness) paired with a Philips GoGear Azure SA5AZU08KF mp4 player was used as the broadcasting device.

Data analysis

Taxonomic, phylogenetic, and functional diversity indices

We computed species richness, phylogenetic diversity, and functional diversity to measure the bird biodiversity in each forest patch. These metrics were computed for all the bird species observed within each patch and for a subset of species which were considered to be forest specialists [49]. Forest bird specialists were defined in accordance with the PanEuropean Common Bird Monitoring Scheme (https://pecbms.info/). We used the mean nearest taxon distance (MNTD) to measure phylogenetic diversity [50]. MNTD averages the subset of the possible pairwise distances extracted from a phylogenetic tree, where only the shortest distances between taxa are considered [50]. A phylogenetic tree was constructed on the BirdTree project website (http://birdtree.org/) [51]. Further, to measure functional diversity, we used functional richness (Fric) [52] which is a measure that quantifies the niche space occupied by species within a community. As this measure is independent of abundance, niche space is considered to be occupied even under low abundance of a species [52]. This characteristic of this measure enabled us to fully capture the functional diversity of small forests and better assess the possible effects of fragmentation on functional diversity.

After calculating the diversity metrics for each patch from 2017 to 2019, we computed the immediate effect of the behavioural experiment, as well as the carry-over effect of the experimental results. To assess the immediate effect of the experiment, we subtracted the values of a given biodiversity metric (i.e. species richness, functional diversity, and phylogenetic diversity) of a patch for the base year 2017 from the corresponding value for the year 2018. This represented the effect of our experimental treatment, as bird observations in 2018 were performed after ending the broadcast of sounds and control treatments (procedural control and no broadcast). The control group allowed us to monitor changes in biodiversity indices without manipulations between the two years, thus accounting for potential temporal and random changes in biodiversity. The carry-over effect of the experiment in the following year was computed in a similar manner, with a given biodiversity metric for the base year 2017 being subtracted from the corresponding value for the year 2019. This allowed us to determine whether biodiversity indices continued to be influenced by the experimental manipulation of social information a year after the experiment. For calculating all of the diversity measures, we have used “picante” [53] and “FD” packages [54] in R [55].

Species composition and dissimilarity

The species composition was analysed using partial-canonical correspondence analysis (CCA) implemented in CANOCO 5.0 software [56]. This analysis was based on the species occurrence in each forest patch and was conducted for each year of the study (2017–2019).

Species dissimilarity (Jaccard index) among years was calculated using “beta.temp()” function in “betapart” R package [57,58]. Species dissimilarity was calculated between 2017 and 2018 to determine the effect of the experimental treatment and between 2017 and 2019 to determine the temporal carry-over effect of the experimental treatment.

Fragmentation metrics

We calculated the habitat patch size (in ha) and habitat patch isolation. To measure patch isolation, we computed two metrics: the nearest neighbour distance (NND) and proximity index (PROX) which were significantly correlated ($r = -0.203$). However we chose NND for analysis as it had a less skewed distribution and no outliers after log transformation. Patch size, PROX, and NND remained constant throughout all the years of experiment. All fragmentation metrics were calculated using the Patch Analyst toolbox in ArcGis ver. 10.1 [59].

Statistical models

We constructed a series of generalised additive models (GAM) using the “mgcv” package ver. 1.8-38 [60] in R ver. 4.1.2 [55,61] to explain whether social information experiment, fragmentation metrics, or their interactions influenced biodiversity indices and temporal community dissimilarities in each of the forest patches. GAMs were constructed for each of the following response variables: differences in species richness, functional richness, and phylogenetic diversity between 2017 and 2018 and 2017 and 2019 and the temporal dissimilarity in species composition between the years. These variables were calculated for all the bird species recorded in a given patch and for forest specialists. We also built models for the base year (2017), with the raw values of these indices as the response variables. The models included all the explanatory variables that we considered might explain the diversity variability, such as information type used during the experiment (positive, negative, mixed, or none), fragmentation metrics (NNDist, patch area), and factor-smooth interactions between them (Table 1). Since the dependent variables for 2018 and 2019 were differences in the values of diversity metrics between these years and that of 2017, significant interaction denotes changes in the association between the diversity metric and habitat fragmentation metric after different social information types were emitted. The data for procedural control and no broadcast control were pooled together at one level (labelled "none") in the variable information type as there were no differences in bird biodiversity metrics between the two groups. Further, we included the interaction between geographic coordinates as a smoothed function for all models to account for spatial autocorrelation [62]. We log-transformed fragmentation metrics to avoid the impact of outlying data points and assumed a non-linear relationship for all the explanatory variables except for information type. To validate our models, we used the "model.check()" function from the "mgcv" R package ver. 1.8-38 [60] which yielded k-values (i.e. number of basic functions) similar to those used in model building. We also used the "concurvity()" function from the same package to measure the concurvity between the model components. All of these checks revealed that the model was correctly constructed. Thereafter, we performed a post-hoc Wald test to check the differences in given biodiversity metric responses between each of the information types, using the "itsadug" package ver. 2.4 [60].

A partial-CCA was built separately for each year. The explanatory variables were social information type and log-transformed fragmentation metrics (NNDist, patch area) and geographic coordinates were assigned as covariates. Rare species were downweighed [56]. CCA was performed for 2017 to determine differences in species composition among predefined experimental groups (no differences were expected for these groups in 2017).

To test our first hypothesis, we checked the statistical significance of the information-type variable, accompanied by the Wald test results. Furthermore, to test our second hypothesis, we also compared the statistical significance of the information type variable revealed by the GAM and CCAs for comparisons made between 2017 and 2018 and 2017 and 2019. Lastly, to test our third hypothesis, we checked the statistical significance of interactions between information type and fragmentation metrics and inspected plots showing the relationship between the given biodiversity metric between the years, as well as species composition and fragmentation metrics for a given type of social information.

References

1. Newbold, T. *et al.* Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50 (2015).
2. Thompson, P. L., Rayfield, B. & Gonzalez, A. Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography* **40**, 98–108 (2017).
3. Brondízio, E. S., Settele, J., Díaz, S. & Ngo, H. T. (eds). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. *IPBES* (2019).
4. MacArthur, R. H. & Wilson, E. O. *The theory of island biogeography*. (Princeton University Press, Princeton, 2001).

5. Levins, R. Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bull. Entomol. Soc. Am.* **15**, 237–240 (1968).

6. Fletcher, R. J. Species interactions and population density mediate the use of social cues for habitat selection. *J. Anim. Ecol.* **76**, 598–606 (2007).

7. Dormann, C. F. *et al.* Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. *Glob. Ecol. Biogeogr.* **27**, 1004–1016 (2018).

8. Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Anim. Behav.* **66**, 973–988 (2003).

9. Hromada, M., Antczak, M., Valone, T. J. & Tryjanowski, P. Settling decisions and heterospecific social information use in shrikes. *PLoS One* **3**, e3930 (2008).

10. Fletcher, R. J. & Sieving, K. E. Social-information use in heterogeneous landscapes: A prospectus. *Condor* **112**, 225–234 (2010).

11. Suzuki, T. N. Assessment of predation risk through referential communication in incubating birds. *Sci. Rep.* **5**, 10239 (2015).

12. Schmidt, K. A., Dall, S. R. & van Gils, J. A. The ecology of information : an overview on the ecological significance of making informed decisions. *Oikos* **119**, 304–316 (2010).

13. Ward, M. P., Benson, T. J., Semel, B. & Herkert, J. R. The Use of Social Cues in Habitat Selection by Wetland Birds. *Condor* **112**, 245–251 (2010).

14. Forsman, J. T., Hjernquist, M. B. & Gustafsson, L. Experimental evidence for the use of density based interspecific social information in forest birds. *Ecography* **32**, 539–545 (2009).

15. Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D. & Zanette, L. Y. Fear of large

carnivores causes a trophic cascade. *Nat. Commun.* **7**, 10698 (2016).

16. Kohl, M. T. *et al.* Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* **88**, 638–652 (2018).

17. Smith, J. A. *et al.* Fear of the human ‘super predator’ reduces feeding time in large carnivores. *Proc. R. Soc. B* **284**, 20170433 (2017).

18. Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. & Brashares, J. S. Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends Ecol. Evol.* **34**, 355–368 (2019).

19. Ciuti, S. *et al.* Human selection of elk behavioural traits in a landscape of fear. *Proc. R. Soc. B* **279**, 4407–4416 (2012).

20. Suzuki, T. N. & Kutsukake, N. Foraging intention affects whether willow tits call to attract members of mixed-species flocks. *R. Soc. Open Sci.* **4**, 170222 (2017).

21. Valone, T. J. & Giraldeau, L.-A. Patch estimation by group of foragers: what information is used? *Anim. Behav.* **45**, 721–728 (1993).

22. Houston, A. I. & Lang, A. The ideal free distribution with unequal competitors: the effects of modelling methods. *Anim. Behav.* **56**, 243–251 (1998).

23. Seppänen, J. T., Forsman, J. T., Monkkönen, M. & Thomson, R. L. Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* **88**, 1622–1633 (2007).

24. Rodríguez, A., Andrén, H. & Jansson, G. Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos* **95**, 383–396 (2001).

25. Morrison, E. B., Lindell, C. A., Holl, K. D. & Zahawi, R. A. Patch size effects on avian foraging behaviour: Implications for tropical forest restoration design. *J. Appl. Ecol.* **47**, 130–138 (2010).

26. DeJong, L. N., Cowell, S. D., Nguyen, T. N. N. & Proppe, D. S. Attracting songbirds

with conspecific playback: A community approach. *Behav. Ecol.* **26**, 1379–1388 (2015).

27. Kelly, J. K. & Schmidt, K. A. Fledgling calls are a source of social information for conspecific, but not heterospecific, songbird territory selection. *Ecosphere* **8**, e01512 (2017).

28. Pearman, P. B. *et al.* Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage. *Glob. Ecol. Biogeogr.* **23**, 414–424 (2014).

29. Bełcik, M., Lenda, M., Amano, T. & Skórka, P. Different response of the taxonomic, phylogenetic and functional diversity of birds to forest fragmentation. *Sci. Rep.* **10**, 20320 (2020).

30. Tellería, J. L., Baquero, R. & Santos, T. Effects of forest fragmentation on European birds: Implications of regional differences in species richness. *J. Biogeogr.* **30**, 621–628 (2003).

31. Tryjanowski, P. *et al.* Conservation of Farmland Birds Faces Different Challenges in Western and Central-Eastern Europe. *Acta Ornithol.* **46**, 1–12 (2011).

32. Estreguil, C., Caudullo, G., de Rigo, D. & San-Miguel-Ayanz, J. *Forest Landscape in Europe: Pattern, Fragmentation and Connectivity*. *EUR – Scientific and Technical Research* **25717**, (2013).

33. Andren, H. Effects of habitat fragmentation on birds and mammals of suitable habitat : a review landscapes with different proportions. *Oikos* **71**, 355–366 (1994).

34. Santos, T., Telleria, J. L. & Carbonell, R. Bird conservation in fragmented Mediterranean forests of Spain: effects of geographical location, habitat and landscape degradation. *Biol. Conserv.* **105**, 113–125 (2002).

35. Sol, D. *et al.* The worldwide impact of urbanisation on avian functional diversity. *Ecol. Lett.* **23**, 962–972 (2020).

36. Hutchinson, E. G. “Concluding Remarks” on Animal Ecology and Demography. *Cold Spring Harb. Symp. Quant. Biol.* **22**, 415–427 (1957).

37. Wiens, J. J. *et al.* Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* **13**, 1310–1324 (2010).

38. Szymkowiak, J., Thomson, R. L. & Kuczynski, L. Interspecific social information use in habitat selection decisions among migrant songbirds. *Behav. Ecol.* **28**, 767–775 (2017).

39. Seppanen, J.-T., Forsman, J. T., Monkonnen, M. & Thomson, R. L. Social Information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* **88**, 1622–1633 (2007).

40. Hof, A. R., Snellenberg, J. & Bright, P. W. Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. *Anim. Behav.* **83**, 1099–1106 (2012).

41. Laundre, J. W., Hernandez, L. & Ripple, W. J. The Landscape of Fear: Ecological Implications of Being Afraid. *Open Ecol. J.* **3**, 1–7 (2010).

42. Reed, D. H. Relationship between population size and fitness. *Conserv. Biol.* **19**, 563–568 (2005).

43. Stephens, P. A. & Sutherland, W. J. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* **14**, 401–405 (1999).

44. Krauze, D., Gryz, J. & Goszczyński, J. Food composition of the goshawk (Accipiter gentilis L. 1758) during the nesting season in the Rogów Forest (central Poland). *Folia For. Pol. Ser. A - For.* 45–53 (2005).

45. Snow, D., Perrins, C. M. & Gillmor, R. *The Birds of the Western Palearctic; Volume 1 Non-Passerines*. (Oxford University Press, Oxford, 1998).

46. Hua, F., Fletcher, R. J., Sieving, K. E. & Dorazio, R. M. Too risky to settle: Avian community structure changes in response to perceived predation risk on adults and

offspring. *Proc. R. Soc. B Biol. Sci.* **280**, 20130762 (2013).

47. Clement, P., Hathway, R., Byers, C. & Wilczur, J. *Thrushes (Helm Identification Guides)*. (Helm, London, 2010).

48. Keating, K. A. & Quinn, J. F. Estimating species richness: the Michaelis-Menten model revisited. *Oikos* **81**, 411–416 (2012).

49. Chylarecki, P. *Czynniki kształtujące zmiany liczebności pospolitych ptaków Polski w latach 2000 – 2012*. (Muzeum i Instytut Zoologii PAN, Warszawa, 2016).

50. Tucker, C. M. *et al.* A guide to phylogenetic metrics for conservation , community ecology and macroecology. *Biol. Rev.* **92**, 698–715 (2017).

51. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).

52. Mason, N. W. H., Mouillot, D., Lee, W. G. & Wilson, J. B. Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* **111**, 112–118 (2005).

53. Kembel, S. W. *et al.* Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464 (2010).

54. Laliberte, E. & Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305 (2010).

55. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (2016).

56. Šmilauer, P. & Lepš, J. *Multivariate Analysis of Ecological Data using CANOCO 5*. (Cambridge University Press, Cambridge, 2014).

57. Baselga, A. & Orme, C. D. L. Betapart: An R package for the study of beta diversity. *Methods Ecol. Evol.* **3**, 808–812 (2012).

58. Baselga, A. *et al.* Package ‘betapart’. (2021).

59. McGarigal, K. FRAGSTATS 4 Tutorial Tutorial 1 . Setting Up Software and Inspecting Grids. (2015).

60. Wood, S. Package ' mgcv '. (2021). doi:10.1007/s10853-011-5868-y

61. Swenson, N. G. *Functional and Phylogenetic Ecology in R*. (Springer, Berlin, 2014).

62. Simmonds, J. S., Rensburg, B. J. Van & Maron, M. Non-random patterns of vegetation clearing and potential biases in studies of habitat area effects. *Landsc. Ecol.* **32**, 729–743 (2017).

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Author contributions

P.S. conceived the study and, organised the fieldwork procedures with the assistance of M.B. S.P. prepared the voice recordings. M.B. and P.S. performed the data analysis, M.B., M.L. and T.A. drafted the manuscript. All the authors discussed the results and commented on the manuscript.

Additional information

Competing interests: The authors declare no competing interests.

Materials & Correspondence: Correspondence should be addressed to M. B. (e-mail: belcik@iop.krakow.pl)

Data availability statement

All data have been attached to the manuscript and will be made publicly available in Dryad after the manuscript is accepted for publication.

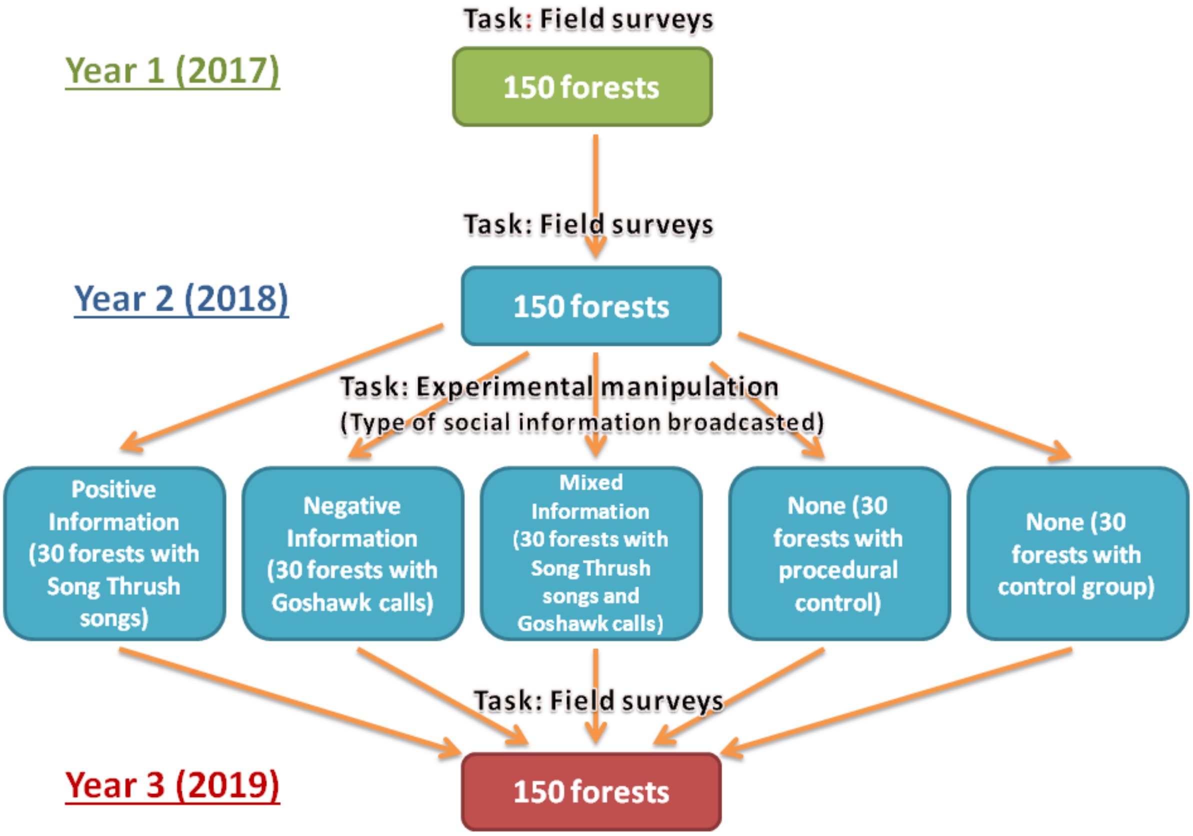

Fig. 1. A conceptual model of the research project

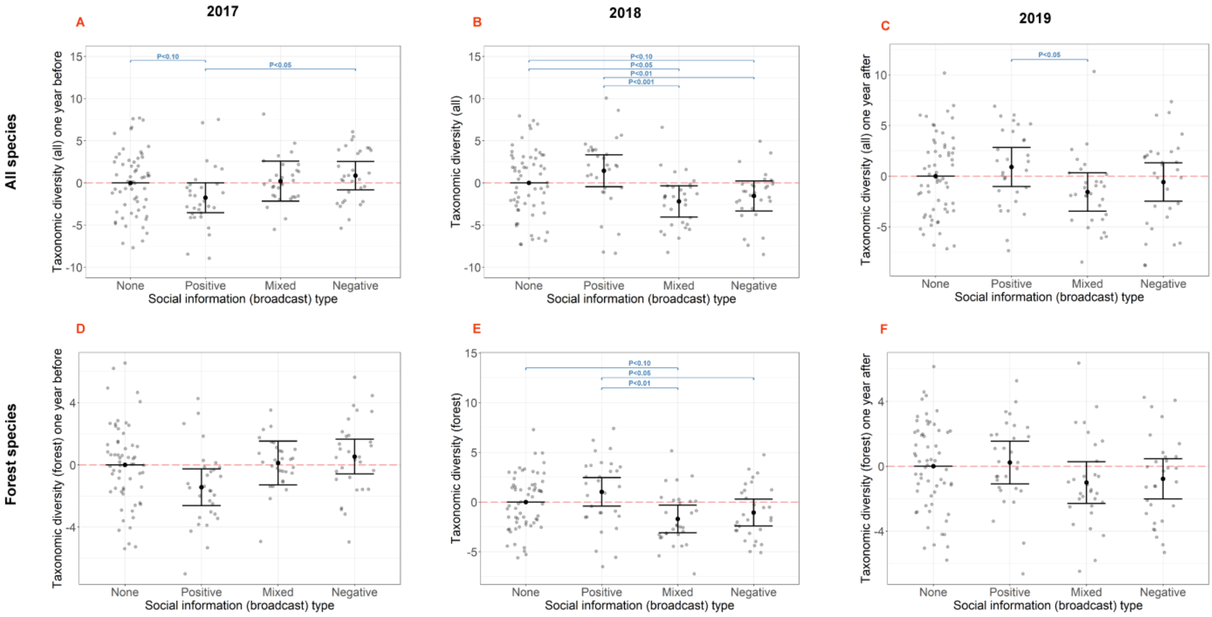

Fig. 2. Influence of social information types on taxonomic diversity of all bird species (subplots A, B, and C) and forest specialists (subplots D, E, and F). Results for 2017 (one year prior the experiment), 2018 (experimental year), and 2019 (one year post experiment) are shown in subplots A and D, B and E, and C and F, respectively. Statistically significant results are marked with blue lines on the subplots. Data for 2018 and 2019 are differences in diversity metrics from those of 2017.

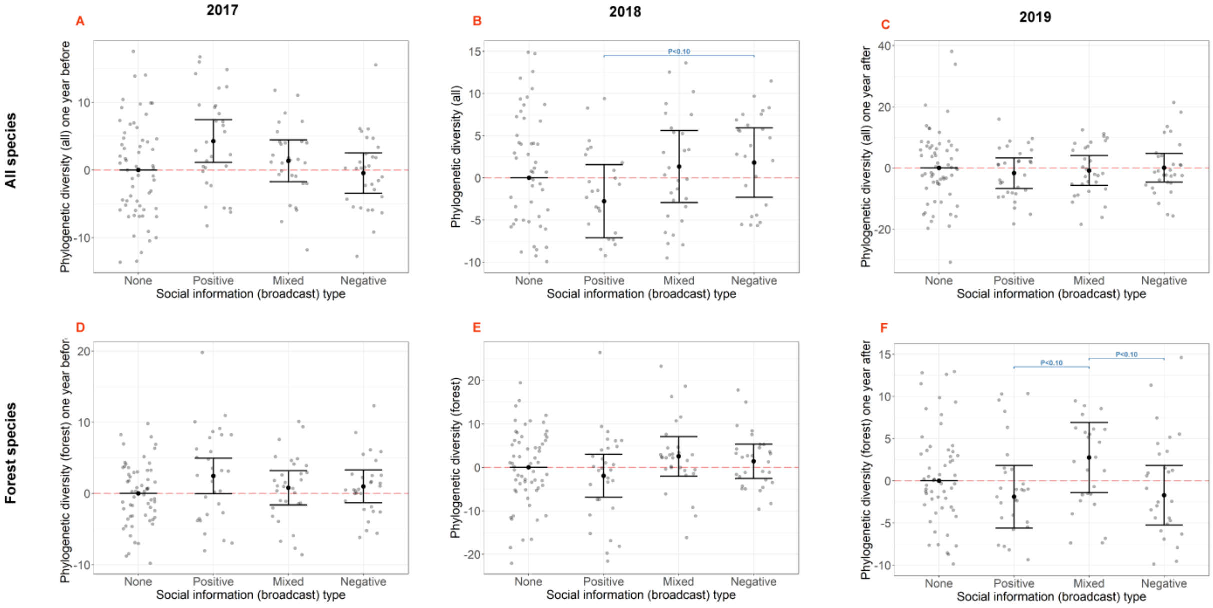

Fig. 3. Influence of social information types on phylogenetic diversity of all bird species (subplots A, B, and C) and forest specialists (subplots D, E, and F). Results for 2017 (one year prior the experiment), 2018 (experimental year), and 2019 (one year post experiment) are shown in subplots A and D, B and E, and C and F, respectively. Statistically significant results are marked with blue lines on the subplots. For further explanations see Fig. 2.

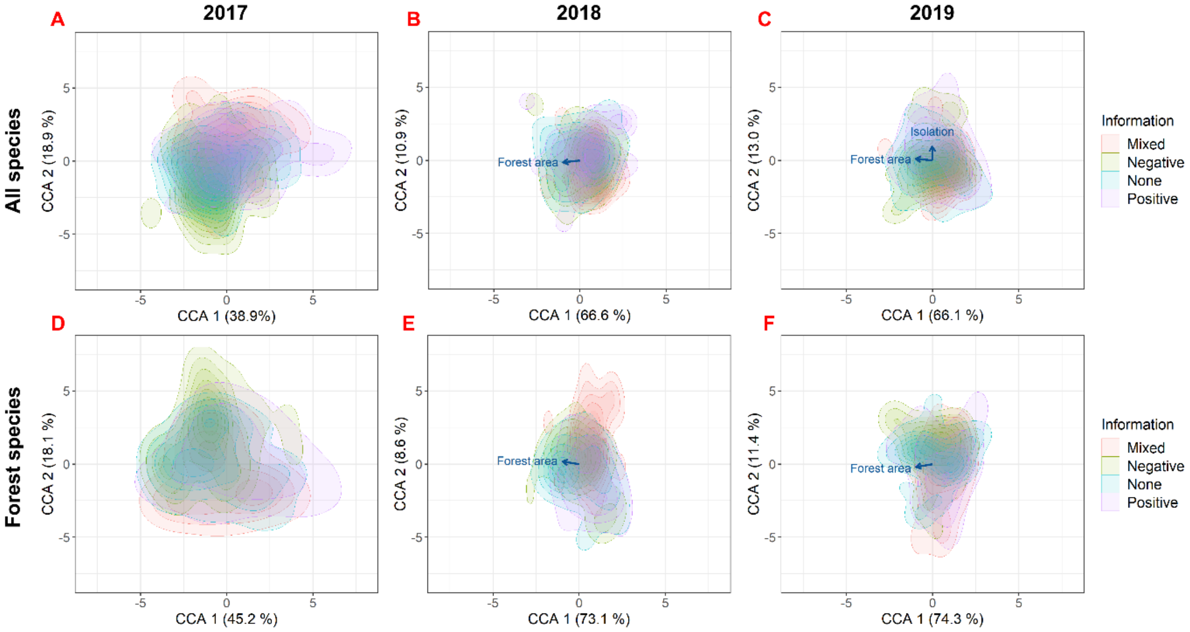

Fig. 4. Ordination of bird communities in forest patches belonging to different experimental groups depicted via kernel density estimations of site-specific scores along the two first axes of partial-Canononical Correspondence Analysis (CCA). Analyses were performed for all the species (subplots A, B, and C) and forest specialists (subplots D, E, and F). Percentages in brackets indicate contribution of the axis to the explained variance in species composition.

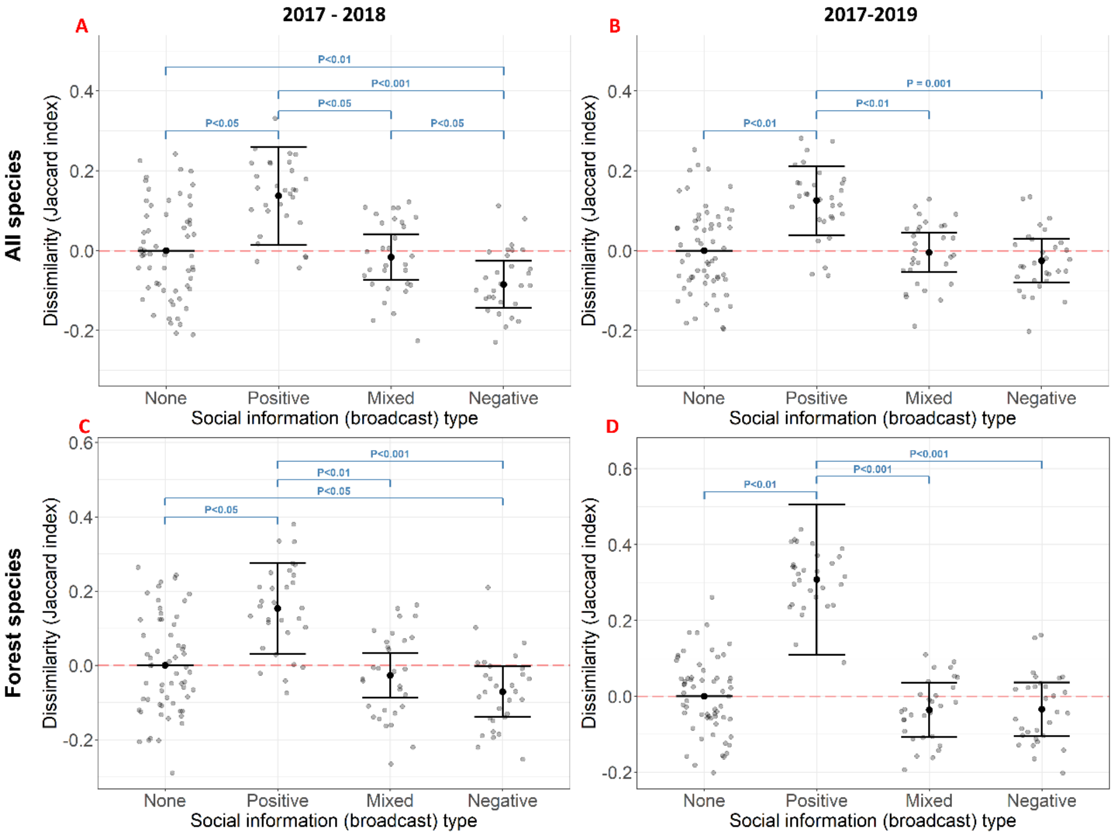

Fig. 5. Estimates of temporal dissimilarity (Jaccard index) of bird species compositions in forest patches belonging to different experimental groups resulting from general additive models. Scaled means with 95% confidence intervals are presented. Analyses were done for all the species (subplots A and B) and forest specialists (subplots C and D). Statistically different levels are connected with blue line segments associated with *P*-values.

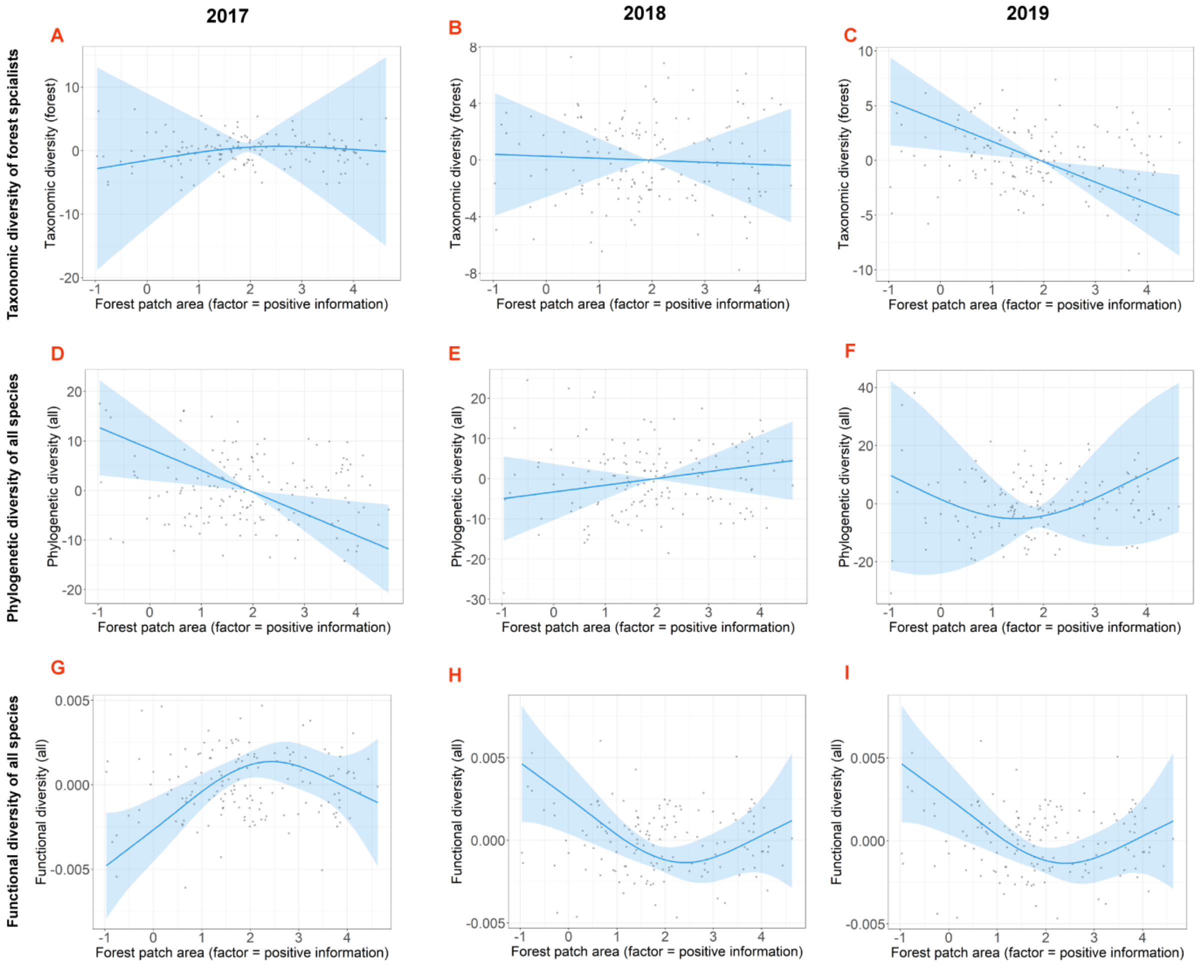

Fig. 6. Modification of the effect of habitat fragmentation on the taxonomic diversity of forest specialists (subplots A, B, and C), phylogenetic diversity of all birds (subplots D, E, and F), and functional diversity of all birds (subplots G, H, and I) by positive social information. The results for 2017 (before the experiment), 2018 (the year of experiment), and 2019 (a year after the experiment) are shown in subplots A, D, and G; B, E, and H; and C, F, and I, respectively. For further explanations see Fig. 2.

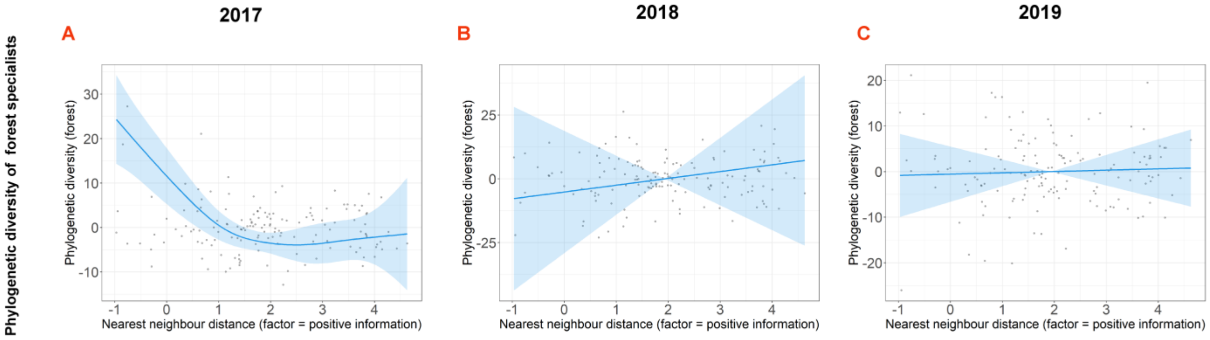

Fig. S1. Modification of the effect of the nearest neighbour distance on the functional diversity of forest specialists. The results for 2017 (before the experiment), 2018, and 2019 are shown in in subplots A, B, and C, respectively. For further explanations see Fig. 2.

Tables

Table 1. The effect of broadcasted social information types and isolation metrics on bird diversity components in the year of the experiment. Response variables were differences between the values of diversity metrics in 2017 and 2018. Statistically significant effects are emboldened: *** - P < 0.001, ** - P < 0.01, * - P < 0.05, ‘- P < 0.10.

Explanatory variables	Response variables					
	Species richness of all birds	Phylogenetic diversity of all birds	Functional diversity of all birds	Species richness of forest bird specialists	Phylogenetic diversity of forest bird specialists	Functional diversity of forest bird specialists
GAM estimates of function slopes with standard errors (in brackets) for social information types with assumed linear response						
Intercept	**1.066 (0.518)***	**-2.963 (1.237)***	**-0.008*** (<0.001)**	0.168 (0.393)	**7.939*** (1.154)**	**-0.075*** (0.004)**
InformationPositive	1.436 (0.967)	-2.766 (2.208)	<0.001 (<0.001)	1.033 (0.732)	-1.939 (2.515)	-0.002 (0.007)
InformationMixed	**-2.197 (0.945)***	1.336 (2.178)	< -0.001 (<0.001)	**-1.690* (0.7133)**	2.534 (2.321)	-0.007 (0.007)
InformationNegative	**-1.546 (0.908)’**	1.814 (2.101)	< -0.001 (<0.001)	-1.048 (0.688)	1.384 (2.011)	-0.005 (0.007)
Approximate significance of smooth terms:						
log(NNDist)	Df = 1.000	Df = 1.000	Df = 1.000	Df = 1.000	Df = 1.000	Df = 1.002
log(Forest area)	Df = 1.000	Df = 1.000	**Df = 1.000***	Df = 1.000	Df = 1.000	Df = 1.817
log(NNDist):InformationNone	Df = 1.761	Df = 1.000	Df = 1.367	Df = 1.000	Df = 1.000	Df = 1.153
log(NNDist):InformationPositive	Df = 2.299	Df = 1.000	Df = 1.000	Df = 2.004	**Df = 4.535***	Df = 1.000
log(NNDist):InformationMixed	Df = 0.499	Df < 0.001	Df = 1.146	Df < 0.001	Df < 0.001	Df = 1.000
log(NNDist):InformationNegative	Df = 2.064	Df = 1.000	Df < 0.001	Df = 1.746	Df = 1.000	Df = 0.507
log(Forest area):InformationNone	Df = 1.000	Df = 2.149	Df = 1.000	Df = 1.000	Df = 1.000	Df = 1.000
log(Forest area):InformationPositive	Df = 1.000	Df = 1.000	**Df = 2.488****	Df = 1.000	Df = 1.000	Df = 1.000
log(Forest area):InformationMixed	Df = 1.000	Df = 1.000	Df < 0.001	Df < 0.001	Df = 0.977	Df = 1.000
log(Forest area):InformationNegative	Df < 0.001	Df < 0.001	Df = 1.000	Df = 1.000	Df = 1.000	Df = 0.296

Table 2. Results of comparison between predictor levels for different biodiversity metrics. Response variables were differences between the values of diversity metrics in 2017 and 2018 (for experiment results in 2018) and between the values of diversity metrics in 2017 and 2019 (for experiment results holding in 2019). Statistically significant effects are emboldened: *** - P < 0.001, ** - P < 0.01, * - P < 0.05, ’- P < 0.10.

Types of social information compared	*Biodiversity metric*					
	Species richness of all birds	*Phylogenetic diversity of all birds*	*Functional diversity of all birds*	*Species richness of forest bird specialists*	*Phylogenetic diversity of forest bird specialists*	*Functional diversity of forest bird specialists*
For experiment results in 2018						
Comparing Positive with Mixed	**X2(1.000)*** =0.131**	X2(1.000) =2.528	X2(1.000) =2.289	**X2(1.000)** =9.946**	X2(1.000) =2.185	X2(1.000) =0.384
Comparing Positive with Negative	**X2(1.000)** =7.158**	**X2(1.000) =3.324’**	X2(1.000) =1.607	**X2(1.000)* =6.114**	X2(1.000) =1.420	X2(1.000) =0.170
Comparing None with Mixed	**X2(1.000)* =5.413**	X2(1.000) =0.377	X2(1.000) =1.655	**X2(1.000)* =5.612**	X2(1.000) =1.192	X2(1.000) =0.942
Comparing None with Negative	**X2(1.000)’ =2.896**	X2(1.000) =0.745	X2(1.000) =0.974	X2(1.000) =2.319	X2(1.000) =0.474	X2(1.000) =0.554
Comparing Mixed with Negative	X2(1.000) =0.365	X2(1.000) =0.038	X2(1.000) =0.087	X2(1.000) =0.616	X2(1.000) =0.196	X2(1.000) =0.050
Comparing None with Positive	X2(1.000) =2.211	X2(1.000) =1.569	X2(1.000) =0.282	X2(1.000) =1.993	X2(1.000) =0.595	X2(1.000) =0.056
For experiment results holding in 2019						
Comparing Positive with Mixed	**X2(1.000)* =4.482**	X2(1.000)=0.081	X2(1.000)=2.289	X2(1.000)=2.407	**X2(1.000)=3.555’**	X2(1.000)=0.346
Comparing Positive with Negative	X2(1.000) =2.609	X2(1.000)=0.355	X2(1.000)=1.607	X2(1.000)=1.679	X2(1.000)=0.007	X2(1.000)=0.182
Comparing None with Mixed	X2(1.000) =1.632	X2(1.000)=0.115	X2(1.000)=1.655	X2(1.000)=2.335	X2(1.000)=1.669	X2(1.000)=0.842
Comparing None with Negative	X2(1.000) =0.368	X2(1.000)=0.001	X2(1.000)=0.973	X2(1.000)=1.493	X2(1.000)=0.915	X2(1.000)=0.555
Comparing Mixed with Negative	X2(1.000) =0.749	X2(1.000)=0.099	X2(1.000)=0.088	X2(1.000)=0.094	**X2(1.000)=3.560’**	X2(1.000)=0.031
Comparing None with Positive	X2(1.000) =0.834	X2(1.000)=0.441	X2(1.000)=0.282	X2(1.000)=0.114	X2(1.000)=1.006	X2(1.000)=0.050

Table 3. The effect of broadcasted information types on bird diversity components at isolation metrics one year after the experiment (2019) was performed. Response variables were differences between the values of diversity metrics in 2017 and 2019. Statistically significant effects are emboldened: *** - P < 0.001, ** - P < 0.01, * - P < 0.05, ‘- P < 0.10.

Explanatory variables	Response variables					
	Species richness of all birds	Phylogenetic diversity of all birds	Functional diversity of all birds	Species richness of forest bird specialists	Phylogenetic diversity of forest bird specialists	Functional diversity of forest bird specialists
GAM estimates of function slopes with standard errors (in brackets) for social information types with assumed linear response						
Intercept	**1.870***** **(0.5347)**	**2.619’** **(1.379)**	**-0.008***** **(<0.001)**	**1.318***** **(0.363)**	**5.617***** **(1.028)**	**-0.076***** **(0.004)**
InformationPositive	0.898 (0.984)	-1.694 (2.551)	<0.001 (<0.001)	0.227 (0.673)	-1.896 (1.891)	-0.002 (0.007)
InformationMixed	-1.567 (0.970)	-0.842 (2.479)	<0.001 (<0.001)	-1.006 (0.658)	2.746 (2.126)	-0.006 (0.007)
InformationNegative	-0.586 (0.965)	0.047 (2.393)	<0.001 (<0.001)	-0.775 (0.635)	-1.718 (1.796)	-0.005 (0.007)
Approximate significance of smooth terms:						
log(NNDist)	Df = 1.000	Df = 1.000	Df = 1.000	Df = 1.000	Df = 1.000	Df = 1.001
log(Forest area)	Df = 1.000	Df = 1.000	**Df = 1.000***	**Df = 1.000***	Df = 1.000	Df = 1.864
log(NNDist):InformationNone	Df = 1.000	Df = 1.000	Df = 1.368	Df = 1.000	Df = 1.000	Df = 1.202
log(NNDist):InformationPositive	Df = 1.000	Df = 1.002	Df = 1.000	Df = 1.776	Df = 1.000	Df = 1.000
log(NNDist):InformationMixed	Df < 0.001	Df = 1.000	Df = 0.147	Df = 1.000	Df = 1.558	Df = 1.000
log(NNDist):InformationNegative	Df = 1.000	Df < 0.001	Df = 1.000	Df < 0.001	Df < 0.001	Df = 0.477
log(Forest area):InformationNone	Df = 1.000	Df = 1.218	Df = 1.000	Df = 1.000	Df = 1.000	Df = 1.000
log(Forest area):InformationPositive	Df = 1.000	**Df = 2.299***	**Df = 2.488****	**Df = 1.000****	Df = 1.000	Df = 1.000
log(Forest area):InformationMixed	Df = 1.000	Df < 0.001	Df < 0.001	Df < 0.001	Df = 2.096	Df = 0.302
log(Forest area):InformationNegative	Df = 1.172	Df = 1.000	Df = 1.000	Df = 1.000	Df < 0.001	Df = 2.001

Table 4. The effect of broadcasted information types on temporal dissimilarity of birds (Jaccard dissimilarity index) in year of experiment and one year after the experiment was performed.
Statistically significant effects are emboldened: *** - $P < 0.001$, ** - $P < 0.01$, * - $P < 0.05$, ‘- $P < 0.10$.

Explanatory variables	Response variables			
	Dissimilarity 2017 vs 2018 all species	Dissimilarity 2017 vs 2019 all species	Dissimilarity 2017 vs 2018 forest bird specialists	Dissimilarity 2017 vs 2019 forest bird specialists
GAM estimates of function slopes with standard errors (in brackets) for social information types				
Intercept	**0.521*** (0.017)**	**0.498*** (0.015)**	**0.453 *** (0.019)**	**0.439*** (0.019)**
Information Positive	**0.137* (0.063)**	**0.126** (0.044)**	**0.153* (0.063)**	**0.308** (0.101)**
Information Mixed	-0.016 (0.029)	-0.004 (0.025)	-0.027 (0.031)	-0.036 (0.037)
Information Negative	**-0.085** (0.030)**	-0.026 (0.028)	**-0.071* (0.035)**	-0.034 (0.036)
Approximate significance of smooth terms:				
log(NNDist)	Df = 0.800	Df = 1.047	Df = 0.800	Df = 0.800
log(Forest area)	Df = 0.800	Df = 0.800	Df = 1.231	Df = 0.800
log(NNDist):Information None	Df = 0.800	Df = 0.800	Df = 0.800	Df = 1.559
log(NNDist):Information Positive	**Df = 5.326****	**Df = 4.484***	**Df = 4.912****	**Df = 6.749*****
log(NNDist):Information Mixed	Df = 4.547	Df = 0.800	Df = 0.800	Df = 0.800
log(NNDist):Information Negative	Df = 0.800	Df = 0.800	Df = 2.270	Df = 0.832
log(Forest area):Information None	Df = 0.800	Df = 0.800	Df = 0.801	Df = 2.281
log(Forest area):Information Positive	Df = 1.156	Df = 0.800	Df = 0.800	Df = 0.800
log(Forest area):Information Mixed	Df = 0.800	Df = 0.800	Df = 0.800	Df = 0.800
log(Forest area):Information Negative	Df = 0.800	Df = 0.898	Df = 0.800	Df = 0.800
X:Y	Df = 2.000	Df = 5.147	Df = 2.000	Df = 21.382

Table S1. Predicted effect of positive, mixed, and negative social information on taxonomic, phylogenetic, and functional diversity of bird communities

	Social information type		
	Positive social information	*Mixed social information*	*Negative social information*
Effect on bird diversity metrics in the year of the experiment (Hypothesis 1)			
Taxonomic diversity	We expected that positive social information would **increase** bird taxonomic diversity	We expected **no effect**, because of positive and negative effects cancelling out each other	We expected that negative social information would **decrease** bird taxonomic diversity
Phylogenetic diversity	We expected that positive social information would **decrease** phylogenetic diversity as the receivers of the information would mostly be conspecifics or related, similar species	We expected **no effect**, because of positive and negative effects cancelling out each other	We expected **no effect**, assuming that the predator is opportunistic and there is phylogenetic redundancy in bird communities
Functional diversity	We expected that positive social information would **decrease** functional diversity as the receivers of the information would mostly be conspecifics or related, similar species	We expected **no effect**, because of positive and negative effects cancelling out each other	We expected **no effect**, assuming that the predator is opportunistic and there is functional redundancy in bird communities
Lasting effect on bird diversity metrics (Hypothesis 2)			
Bird diversity metrics	We expected that species turnover (dissimilarity) over the years will be **high** in forest patches subjected to positive social information added	We expected that mixed social information, carrying contrasting value should have **no lasting effect** on diversity indices	We expected the effect of negative social information to be **aversive** and that it would affect bird species diversity for a longer period than positive or mixed signals. We expected that species turnover over the years should be **highes**t in these patches
Modification of effect of habitat fragmentation on bird diversity metrics (Hypothesis 3)			
Effect of habitat patch size and isolation on bird diversity	We expected that positive social information may **alleviate** the effects of patch size and isolation on **taxonomic** diversity by attracting more individuals to small habitat patches	We expected **no effect**, because of positive and negative effects cancelling out each other	We expected that negative social information could further **reinforce** the effects of habitat fragmentation on **all** diversity metrics, by posing higher predatory pressure on local populations in small and isolated habitat patches than in large and non-isolated patches

Table S2. Results for Tukey HSD test for differences between experimental forest group patches in regard to isolation metrics.
Statistically significant effects are emboldened: ***P <0.001, **P <0.01, *P <0.05, ’P <0.10.

Isolation metric	**Compared groups**	***P* adj**
Nearest neighbour distance	Positive-None	0.471
Nearest neighbour distance	Mixed-None	0.870
Nearest neighbour distance	Negative-None	0.996
Nearest neighbour distance	Mixed-Positive	0.225
Nearest neighbour distance	Negative-Positive	0.718
Nearest neighbour distance	Negative-Mixed	0.824
Forest patch area	Positive-None	0.945
Forest patch area	Mixed-None	0.778
Forest patch area	Negative-None	0.616
Forest patch area	Mixed-Positive	0.986
Forest patch area	Negative-Positive	0.418
Forest patch area	Negative-Mixed	0.242

Artykuł 3

Bełcik, M., Lenda, M., Pustkowiak, S., Woźniak, B., Skórka, P. (202x). Lands of fear and uncertainty modify the effects of forest fragmentation on the abundance of a passerine bird.

Lands of fear and uncertainty modify the associations between forest fragmentation and the abundance of a passerine bird

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Lay Summary

The occurrence and abundance of species in a landscape may depend on habitat patch size and isolation. However, the interactions with animals belonging to the same or different species may also play an important role. Based on a large-scale experimental study, we demonstrated that cues regarding the presence of predators, but not conspecifics, could modify the effect of habitat fragmentation on song thrush abundance in forest patches. Such effect also lasted one year after the end of the experiment.

Abstract

Habitat loss and fragmentation are the main factors driving the occurrence and abundance of species in the landscape. However, the local occurrence and abundance of species may also depend on heterospecific and conspecific interactions among individual animals. In this large-scale experimental study, we investigated the impact of the interaction between different types of social information and forest fragmentation on the abundance of the song thrush, *Turdus philomelos*, in Central Europe. A large-scale behavioral experiment in which three types of social information (positive, negative, and mixed) were broadcasted in forest patches that varied in size and isolation metrics was performed. Negative social information (cues of presence of predator) was found to reverse the positive association between habitat patch size and song thrush abundance to a negative association that lasted one year after the end of the experiment. Further, mixed social information (cues of the presence of conspecifics and predators alike) generated a negative association between habitat patch isolation and song thrush abundance in habitat patches, which persisted until the next year. Overall, our findings indicate that lands of fear and uncertainty could modify the effect of habitat fragmentation on species abundance. Notably, such effect may be long-lasting.

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Key words

Song thrush, landscape of fear, social information, information uncertainty, animal cognitive map

Introduction

Habitat loss and fragmentation drive major ecological processes (e.g., dispersal, population viability, and species interactions) across the globe (Fahrig 1997; Newbold et al. 2015; Betts et al. 2017). According to the classic concepts of island biogeography (Kirkby et al., 1968) and metapopulation theory (Hanski & Ovaskainen, 2003; Levins, 1968), the isolation of habitat patches negatively affects the occurrence and abundance of species in a fragmented landscape. In these concepts, larger and less isolated habitat patches should have a greater chance of being occupied by a given species and harbor a greater population density than smaller and more isolated patches (Hanski & Ovaskainen, 2003; Kirkby et al., 1968).

The spatial configuration of habitat patches is not the only factor that influences the local occurrence and abundance of species. In fact, these population characteristics may also depend on heterospecific and conspecific interactions among individual animals (Ward et al., 2010). Owing to the high heterogeneity of habitat patches (Tews et al., 2004), individuals may need to gather information on the environment to correctly assess local habitat quality (Doligez et al., 2002). As information gathered by one individual regarding the structural features of the landscape may be misleading for making vital decisions, animals may use social public information during their assessment of the local habitat quality and selection of their subsequent breeding site (Doligez et al., 2003; Schmidt et al., 2010).

The term, social public information (hereafter in this study just "social information"), may refer to the presence of other individuals, their behavior, the sounds they make, or other traces of their presence or activity (Fletcher, 2007; Hromada et al., 2008; Suzuki, 2015). As social information can be carried by other heterospecific or conspecific individuals (Ward et al., 2010), it might be perceived as negative (e.g., voice of predators), positive (e.g., voice of conspecifics), or mixed (both predators and conspecifics) by the recipient (Seppanen et al., 2007), and may weaken or reinforce each other.

Negative social information is an important characteristic describing the landscape of fear, a mental map describing continuous spatial variation in an animal's perception of predation risk, including places where an animal avoids minimizing risk (Kohl et al., 2018). Signs of the presence of predators might affect how potential prey utilize the landscape (Suraci et al., 2016) and may deter prey species from settling in a given area (Ciuti et al. 2012; Smith et al. 2017; Kaitlyn et al. 2019). On the other hand, calls produced by conspecifics and heterospecifics may be perceived as positive information, increasing the social attraction of the area and thus its population density (Fletcher, 2007; Suzuki & Kutsukake, 2017); this is because animals can use the presence of a successfully established individual as an indicator of the location of a high-quality habitat or vital resources (Houston & Lang, 1998; Valone & Giraldeau, 1993).

Although a recent study investigated the role of social information on patch occupancy by local populations (Fletcher 2009), very few studies have addressed the relative role of social information derived from different sources on the abundance in local populations. In the real world, the existence of only one type of social information is rare, as different species create a network of direct and indirect interactions (Rigal et al., 2022). This differential value of social information may modify the distribution of animals and their abundance depending on whether different types of social information cues occur jointly or alone. Different types of social information may also alter the impact of habitat fragmentation by diminishing or augmenting the effects of patch area and isolation on species occurrence and abundance. For example, providing positive social information in suitable but small habitat patches may lead to the disappearance of the patch area effect and increase patch occupancy and the local abundance of a species. In contrast, social information on the presence of a predator should markedly diminish the abundance of habitat patches as prey species should respond very rapidly to cues that strongly (negatively) correlate with their fitness (Rodriguez et al. 2001). This effect should be especially strong in small habitat patches, where shelter from predators may be insufficient (Morrison et al. 2010) relative to that of large habitat patches.

The duration of the effects of social information in the environment is unknown. To date, the possibility of a carryover effect of social information affecting the distribution of species has been addressed in few studies, mainly with negative results (Kelly & Schmidt, 2017). However, the existence of such effect would significantly broaden our understanding of the role played by social information in shaping species distribution and population density.

Song thrush *Turdus philomelos* (L.) is a good species for investigating the impact of social information on the distribution of individuals in a fragmented landscape. Song thrush is a medium-sized passerine bird that has a very distinctive mating call, allowing it to easily detect and locate territories, thereby determining its abundance (Tomiałojć & Lontkowski, 1989). Song thrush breeds at relatively high densities in its respective habitat in Poland (Kuczyński & Chylarecki, 2012), and has been demonstrated to display a high degree of breeding philopatry (Davies & Snow, 1965).

In this large-scale experimental study, we investigated the impact of the interaction between different types of social information and forest fragmentation metrics on the abundance of song thrush by testing the following hypothesis:

Hypothesis 1. Different types of social information (i.e., negative, positive, and mixed) create different types of land with different impacts on song thrush abundance. Land of fear (caused by negative social information) has a negative effect on the abundance of song thrushes. The land of uncertainty (caused by mixed social information) has no effect on song thrush abundance. Land of social attraction (caused by positive social information) has a positive effect on the abundance of song thrush. Such effect is maintained in the following year.

Hypothesis 2. By creating an acoustic space that differs in its potential impact on song thrush abundance, social information modifies the association between habitat patch size and isolation and Song thrush abundance in forest patches. Land of fear (caused by negative social information) increases the positive association between habitat patch size and song thrush abundance, and the negative association between isolation and abundance. Land of uncertainty (caused by mixed social information) does not modify the effect of habitat patch size and isolation on song thrush abundance. Land of social attraction (caused by positive social information) decreases the positive association between habitat patch size and song thrush abundance, but decreases the negative association between isolation and abundance. This effect is maintained in the following year.

Materials and methods

Study system

In this study, we considered three types of social information. The negative social information that created the land of fear was the territorial voices of the northern goshawk *Accipiter gentilis* (L.). This large sized (male body length and mass are 46–61 cm and 360-1000 grams, respectively; females are 59-70 cm in length and 770-2200 grams in weight) top predator preys on different birds (Burgas et al., 2021; Krauze et al., 2005; Snow et al., 1998) and breeds in various forests and even in small patches. Therefore, presenting cues for the presence of this predator may deter many birds from settling in territories in forest habitat patches (Hua et al., 2013). Norther goshawk vocalizes early during the breeding season, usually in March.

Positive social information, which creates a land of social attraction, comprises songs of the song thrush. Song thrush is a medium-sized (20-23 centimeters in length and weighs 50–100 g) forest specialist species that occurs in different forest types. In Central Europe, song thrush is mainly a migratory bird that starts singing and settling in territories in March. Its songs are loud and can be heard from a distance, even outside the forest habitat patch (Clement et al., 2010). The song thrush forages different food sources, both invertebrates and plants (e.g., fruit) (Snow et al., 1998), and is one of the main prey species of northern goshawk (Krauze et al., 2005). Thus, presence of song thrush may be a good cue of a good habitat type that is rich in food resources and free of predators.

Mixed social information, which creates a land of uncertainty, is the voice of both the northern goshawk and song thrush emitted alternately.

Our research was carried out from 2017-2019, and mainly consisted of two tasks. The first task involved the performance of field surveys on the abundance of song thrush in all selected forest patches, and the second involved a behavioral landscape experiment in which social information was manipulated in selected forest patches.

Study sites

A study area in the southern part of Poland, in the province of Lesser Poland, north of Cracow, covering an area of 1,097 square kilometers, was selected. A total of 150 forest patches located in an agricultural landscape were employed. These patches were mainly mixed stands managed by the Polish State Forests Holding and private entities (supervised by the former entity). Of note, most of these forest patches are not part of a larger continuous forest complex and differ in size and isolation. The characteristics of the forest patch size were (in hectares) as follows: mean = 14.91, SD = 19.15, range 0.38 - 102.28. The forest patch isolation characteristics were (as meters): mean = 557,67, SD = 772.07, range 16.53 – 3509.19.

Field surveys

Field surveys to estimate song thrush abundance were conducted between April 1 and May 31 in 2017-2019. The surveys were conducted by a team of three experienced birdwatchers, each with more than ten years of experience in performing bird censuses. Each observer had an assigned set of forest patches, with each patch being visited three times, once during each 20-day round (April 1-20, April 21 – May 10, May 11-31). Surveys began at approximately 5 AM and usually lasted until 11 AM. During the surveys, an observer recorded the starting time and then moved through the forest in a random direction, attempting to cover as much of the forest patch as possible. The observer recorded the exact time of every individual song thrush heard or seen within a patch and marked its location on a handheld GPS device.

Experimental manipulation in social information

The field experiment was conducted from March 17 to March 30, 2018, just before the breeding period of the song thrush. Before the experiment was initiated, the forest patches were assigned to one of five groups. None of the patches differed significantly from the other patches in terms of stand characteristics. The groups were as follows:

- Group of 30 patches where song thrush (*Turdus philomelos*) songs were broadcasted, which constituted positive social information;
- Group of 30 patches where goshawk calls were broadcasted, which constituted negative social information;
- Group of 30 patches where both song thrush and goshawk calls were broadcasted, which constituted mixed social information;
- Group of 30 patches where background noise (i.e., sound of moving trees, wind, and sounds from the surrounding landscape) were broadcasted, serving as a procedural control;
- Group of 30 patches with no broadcast, serving as the control.

In each group, the assigned single type of broadcast was played every day from 7 AM to 12 PM. The number of loudspeakers depended on the forest patch area, varying from a single loudspeaker in small forest patches to five loudspeakers in large forest patches. After the broadcast ended for a given day, the speakers were collected, charged, and hung the next morning.

The broadcast consisted of five minutes of songs/voices and fifteen minutes of silence, which occurred alternately for five hours. Bird song/voice recordings were obtained from the Xeno Canto portal, a website created for sharing bird voices from around the world (https://www.xeno-canto.org/). Only recordings that had an "A" mark for quality (indicating the highest quality available for this portal) were used. A JAM HX-P710 speaker (set for maximum loudness) paired with a Philips GoGear Azure SA5AZU08KF mp4 player was employed as the broadcasting device.

Data analysis

Fragmentation metrics

We calculated the habitat patch size and habitat patch isolation. Patch size was calculated in hectares. To measure isolation, two metrics were computed: the nearest neighbor distance (NND) and proximity index (PROX). These metrics were found to be significantly correlated (r = -0.203); however, NND was selected for the analysis as it had less skewed distribution and no outliers after log transformation, in contrast to PROX. All fragmentation metrics were calculated using the Patch Analyst toolbox in ArcGis ver. 10.1.

Statistical models

All statistical analyses were performed using R statistical software (Swenson 2014, R Core Team 2016). We constructed a series of models that would explain whether social information, fragmentation metrics, or interaction between the social information type and fragmentation metrics influenced the maximum abundance (out of three surveys) of song thrush in each of the studied forest patches. These models were constructed using the "mgcv" package (S. N. Wood, 2011). A generalized additive model was constructed for each of the response variables: maximum abundance in 2017 and the difference in maximum abundance between 2017 and 2018 and between 2017 and 2019. The models included all explanatory variables that might explain the song thrush abundance variability: information type used during the experiment (positive, negative, mixed, or none), fragmentation metrics (NNDist, patch area), and factor-smooth interactions between each information type and fragmentation metric. The data for procedural control and no sound emissions were pooled as one level (labeled “none) in the variable information type as no differences in song thrush abundance were found between the two groups. The interaction between geographic coordinates modeled as a smoothed function for all models was also included to account for spatial autocorrelation (Simmonds et al., 2017). The fragmentation metrics were log-transformed to avoid the impact of outlying data points and a non-linear relationship was assumed for all explanatory variables, except information type. To validate our models, the ‘model.check()’ function from the “mgcv” package (S. Wood, 2021), which produces diagnostic information and four residual plots was used. The results yielded k-values (i.e., number of basic functions) similar to those used in model building. The ‘concurvity()’ function from the same package, which produces summary measures of the concurvity between model components, was also employed. These checks collectively revealed correct construction of the model. A post-hoc Wald test was subsequently performed to check the differences in the given abundance metric responses to each of the information types, using the ‘wald_gam()’ function from the “itsadug” package (van Rij et al., 2020).

To test our first hypothesis, we checked the statistical significance of the information-type variable and the Wald test results. To test our second hypothesis, we checked the statistical significance of interactions between information type and fragmentation metrics and inspected plots showing the relationship between differences in abundance among years and fragmentation metric at a given type of social information.

Results

The mean number of song thrush individuals observed at a given forest patch per survey was 2.83 (SE = 0.19, min = 0, max = 14) in 2017, 2.48 (SE = 0.15, min = 0, max = 14) in 2018, and 3.06 (SE = 0.19, min = 0, max = 10) in 2019. At least one thrush was observed in 133 forest patches in 2017, 130 in 2018, and 135 in 2019.

Hypothesis 1: Effect of different types of social information on song thrush abundance

Our results did not support our initial hypothesis. Herein, song thrush abundance did not display a statistically significant response to the different social information types (Table 1, Figure 1). The results of the Wald post hoc test between predictor levels for song thrush abundance also revealed no statistically significant differences between predictor levels (Table 2, Figure 1). Of note, the effect of the experimental manipulation did not appear in the year after the experiment was performed (Table 2, Figure 1).

Hypothesis 2: Modification of the effect of habitat fragmentation on song thrush abundance

Our results partially supported our initial hypothesis. There was no statistically significant relationship between song thrush abundance in 2017 or differences in abundance among years and interactions with positive social information, forest patch area, or nearest distance (Table 1).

There was no statistically significant association between song thrush abundance in 2017 and relative abundance in 2018 and 2019 and the interaction between negative social information and nearest neighbor distance (Table 1). However, a statistically significant response of relative abundance to negative social information interacting with forest patch area was found (Table 1, Figure 2). This response was significant for every year of the project (Table 1 and Figure 2). In the initial year of the project, song thrush abundance increased with increasing forest patch area in patches subjected to negative social information in the year of the experiment. However, the relative abundance of song thrush decreased in the largest forest patches and increased in the smallest ones where the negative information was broadcasted; this effect was similar for the year following the experiment (Figure 2). This result supported our second hypothesis, as land of fear related to negative social information was predicted to modify the effect of forest patch area or song thrush abundance; however, the effects opposed our expectations.

The relative abundance of song thrush in 2018 was associated with the interaction between forest isolation and mixed social information (Table 1). In 2017, no association was found between the abundance of the song thrush and forest isolation and mixed social information (emitted in 2018). However, the relative abundance in 2018 increased in the least isolated forest patches and decreased in the most isolated ones, where mixed information was broadcasted in the year of the experiment (Table 1, Figure 3). Of note, the effect was visible in 2019, but was not statistically significant. These results contradict our expectations for the second hypothesis.

Discussion

In this study, deciding on a settling area was demonstrated to be a complex process for song thrush. However, social landscape is one of the factors considered by this species, and may influence other factors, such as the structural characteristics of a habitat patch. Therefore, song thrushes may adjust the risk of setting up a territory near the predator territory, depending on the size of the habitat patch. Among the social information types, land of fear is recognized to be the most significant, surpassing land of uncertainty or land of social attraction.

Northern goshawks play an important role in shaping the composition of bird communities in large forests, especially bird species, including song thrush, which constitutes most of their diet. According to previous studies, the abundance of potential prey species in large forest patches increases with increasing distance from goshawk nests (Burgas et al., 2021). However, whether the same phenomenon can be observed in fragmented forests in an agricultural landscape is unclear. A negative association was found between the forest patch area and song thrush abundance in patches where negative social information was broadcasted. This result might be due to the lower chance of a thrush becoming a prey to a goshawk in small habitat patches than larger habitat patches. Based on previous studies, goshawks do not hunt in the vicinity nearest to their nest (Mönkkönen et al., 2007; Sokołowski, 1972). The size of the goshawk territory varies from 300 ha to 1000 ha in the study region (Wiehle et al., 2020). Therefore, in small forest patches, a goshawk could forage outside of these patches, thereby decreasing predation risk and increasing patch attractiveness as a nesting location for a song thrush. In such situations, the risk of immediate predation from a goshawk can be outweighed by the possible benefit of reduced nest predation (Mönkkönen et al., 2007). In a smaller habitat patch, goshawks could also catch more mammals, including hares, than birds (Toyne, 1998).

Goshawk is regarded as a forest species (Burgas et al., 2021; Penteriani & Faivre, 2001), and in Poland, this species nests in lower density agricultural landscape and starts to colonize the agricultural landscape after its population size increases to that found in a typical forest landscape. The population of goshawks inhabiting agricultural landscapes in Poland is declining (Buczek et al., 2007; Chylarecki et al., 2018). Traditional occupancy models suggest that the decline in a species population always starts with the species leaving the suboptimal habitat (Newton, 1998). As a result, goshawks in agricultural areas are even rarer than those in forests. Even in forest habitats, goshawks can abandon areas where the share of clear cuttings exceeds 30% of their territory (Penteriani & Faivre, 2001). As song thrush is a philopatric species (Davies & Snow, 1965), individuals nesting in smaller forest patches may not be used in the goshawk's voice and might not recognize it as a threat. Goshawks most often use their voice in the direct vicinity of their nest in the prelaying period, mainly to scare nest predators; therefore, thrushes breeding inside the territory of a goshawk in small forest patches may not be related to the predation threat.

In our study, land of uncertainty (formed by mixed social information) caused a decrease in song thrush abundance with an increase in the spatial isolation of a given forest patch. As mixed information is a combination of attractive (positive information) and deterrent (negative information) factors, it may not (unlike positive or negative information) be a factor that can clearly outweigh the song thrush decision-making process. Thus, mixed information might increase the uncertainty in the bird decision-making process. Combined with another factor that reduces the attractiveness of a given habitat patch, namely increasing spatial isolation, this information would result in song thrushes more often rejecting such sites as potential breeding habitats. This result might also be due to the deterring value of negative information outweighing the attractive value of positive information. Therefore, when presented with both types of information simultaneously (such as the mixed social information), a given song thrush individual might be deterred by the negative component of the mixed social information. Combined with the increasing value of spatial isolation, this deterrent could influence the song thrush to avoid settling in a given forest patch.

To date, studies on the landscape of fear suggest that prey species not only modify their behavior in accordance with traces of the predator's presence, which they can detect at a given time, but also according to the perceived risks of predation in a given area (Luttbeg & Trussell, 2013). In such situations, prey species might create a cognitive map of areas with differing risks of predator encounters to navigate the landscape (Gaynor et al., 2019; Oriol-Cotterill et al., 2015). The existence of cognitive navigational maps has been suggested in studies on navigating home ranges and finding food resources across landscapes by vertebrates (Blaser et al. 2013; Skórka et al. 2016; Liu et al. 2019). The confirmed existence of the carryover effect of negative social information could reinforce these results, suggesting the use of such cognitive maps by certain avian species. Those maps might also be developed across the lifetime of a given individual and such individuals could link a given habitat patch with a certain degree of predation risk, even one year after encountering cues of high predator activity in that habitat patch.

In our experimental design, we did not account for social information that already existed in any of the studied forest patches, which serves as the main limitation of this study. Song thrush and goshawk had already resided in the area prior to our study. However, full control of the already present social information (e.g., capturing and removing birds from forest patches) was beyond the available means and raised serious ethical issues. Therefore, all conclusions drawn from this study can only be interpreted as the social information added to a given forest patch during the experiment.

Herein, we did not account for the detectability of song thrush in our analyses, thereby serving as another limitation of our study. However, we partially addressed this issue beforehand; of the three visits to a certain habitat patch, the maximum number of detected song thrushes during any of those visits was used for further analysis. Further, any clear cuts that could influence the abundance and spatial distribution of song thrushes within a forest patch were not mapped. However, clear-cuts alter the median age of the trees within the forest patch by introducing areas where the median age drops to zero (or to a single digit value, after a new tree generation has already been introduced). Therefore, the issue of clear-cuts and commercial felling was addressed by accounting for the median age of the trees in the main forest story, weighted by the area occupied by each of the similar-aged tree groups. For this experiment, forest patch groups were selected to ensure no difference in the weighted median age between the groups.

References

Blaser, N., Dell'Omo, G., Dell'Ariccia, G., Wolfer, D. P. & Lipp, H. P. (2013). Testing cognitive navigation in unknown territories: Homing pigeons choose different targets. *Journal of Experimental Biology*, *216*(16), 3123–3131.

Buczek, T., Keller, M. & Różycki, A. Ł. (2007). Lęgowe ptaki szponiaste Falconiformes Lasów Parczewskich – zmiany liczebności i rozmieszczenia w latach 1991 – 1993 i 2002 – 2004. *Notatki Ornitologiczne*, *48*, 217–231.

Burgas, D., Ovaskainen, O., Blanchet, F. G. & Byholm, P. (2021). The Ghost of the Hawk: Top Predator Shaping Bird Communities in Space and Time. *Frontiers in Ecology and Evolution*, *9*(638039).

Chylarecki, P., Chodkiewicz, T., Neubauer, G., Sikora, A., Meissner, W., Woźniak, B., Wylegała, P., Ławicki, Ł., Marchowski, D., Betleja, J., Bzoma, S., Cenian, Z., Górski, A., Korniluk, M., Moczarska, J., Ochocińska, D., Rubacha, S., Wieloch, M., Zielińska, M., … Kuczyński, L. (2018). *Trendy liczebności ptaków w Polsce*. GIOŚ.

Ciuti, S., Muhly, T. B., Paton, D. G., Mcdevitt, D., Musiani, M. & Boyce, M. S. (2012). Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B*, *279*(September), 4407–4416.

Clement, P., Hathway, R., Byers, C. & Wilczur, J. (2010). *Thrushes (Helm Identification Guides)* (1st ed.). Helm, London.

Davies, P. W. & Snow, D. W. (1965). Territory and food of the Song Thrush. *British Birds*, *58*(5), 161–175.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. (2003). When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour*, *66*(5), 973–988.

Doligez, B., Doligez, B., Danchin, E. & Clobert, J. (2002). Public Information and Breeding Habitat

Selection in a Wild Bird Population. *Science*, *297*, 1168–1170.

Fletcher, R. J. (2007). Species interactions and population density mediate the use. *Journal of Animal Ecology*, *76*, 598–606.

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. & Brashares, J. S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology & Evolution*, *34*(4), 355–368.

Hanski, I. & Ovaskainen, O. (2003). Metapopulation theory for fragmented landscapes. *Theoretical Population Biology*, *64*(1), 119–127.

Houston, A. I. & Lang, A. (1998). The ideal free distribution with unequal competitors: the effects of modelling methods. *Animal Behaviour*, *56*, 243–251.

Hromada, M., Antczak, M., Valone, T. J. & Tryjanowski, P. (2008). Settling decisions and heterospecific social information use in shrikes. *PLoS ONE*, *3*(12), e3930.

Hua, F., Fletcher, R. J., Sieving, K. E. & Dorazio, R. M. (2013). Too risky to settle: Avian community structure changes in response to perceived predation risk on adults and offspring. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1764), 20130762.

Kelly, J. K. & Schmidt, K. A. (2017). Fledgling calls are a source of social information for conspecific, but not heterospecific, songbird territory selection. *Ecosphere*, *8*(2), e01512.

Kirkby, M. J., MacArthur, R. H. & Wilson, E. O. (1968). *The Theory of Island Biogeography*. Princeton University Press.

Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., White, P. J., Smith, D. W. & MacNulty, D. R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs*, *88*(4), 638–652.

Krauze, D., Gryz, J. & Goszczyński, J. (2005). Food composition of the goshawk (Accipiter gentilis L. 1758) during the nesting season in the Rogów Forest (central Poland). *Folia Forestalia Polonica, Series A - Forestry*, *47*, 45–53.

Kuczyński, L. & Chylarecki, P. (2012). *Atlas pospolitych ptaków lęgowych Polski. Rozmieszczenie, wybiórczość siedliskowa, trendy*. GIOŚ.

Levins, R. (1968). Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bulletin of the Entomological Society of America*, *15*(3), 237–240.

Liu, Y., Day, L. B., Summers, K. & Burmeister, S. S. (2019). A cognitive map in a poison frog. *Journal of Experimental Biology*, *222*(11), 1–6.

Luttbeg, B. & Trussell, G. C. (2013). How the informational environment shapes how prey estimate predation risk and the resulting indirect effects of predators. *American Naturalist*, *181*(2), 182–194.

Mönkkönen, M., Husby, M., Tornberg, R., Helle, P. & Thomson, R. L. (2007). Predation as a landscape effect: The trading off by prey species between predation risks and protection benefits. *Journal of Animal Ecology*, *76*(3), 619–629.

Newton, I. (1998). *Population Limitation in Birds* (1st ed.). Academic Press.

Oriol-Cotterill, A., Valeix, M., Frank, L. G., Riginos, C. & Macdonald, D. W. (2015). Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, *124*(10), 1263–1273.

Penteriani, V. & Faivre, B. (2001). Effects of harvesting timber stands on goshawk nesting in two European areas. *Biological Conservation*, *101*, 211–216.

R Core Team. (2016). *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.*

Rigal, S., Devictor, V., Gaüzère, P., Kéfi, S., Forsman, J. T., Kajanus, M. H., Mönkkönen, M. & Dakos, V. (2022). Biotic homogenisation in bird communities leads to large-scale changes in species associations Stanislas. *Oikos*, *2022*(e08756).

Schmidt, K. A., Dall, S. R. & van Gils, J. A. (2010). The ecology of information : an overview on the ecological significance of making informed decisions. *Oikos*, *119*(2), 304–316.

Seppanen, J.-T., Forsman, J. T., Monkonnen, M. & Thomson, R. L. (2007). Social Information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology*, *88*(7), 1622–1633.

Simmonds, J. S., Rensburg, B. J. Van & Maron, M. (2017). Non-random patterns of vegetation clearing and potential biases in studies of habitat area effects. *Landscape Ecology*, *32*(4), 729–743.

Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y. & Wilmers, C. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores. *Proceedings of the Royal Society B*, *284*(20170433).

Snow, D., Perrins, C. & Gillmor, R. (1998). *The Birds of the Western Palearctic; Volume 5 Tyrant flycatchers to thrushes*. Oxford University Press.

Sokołowski, J. (1972). *Ptaki Ziem Polskich tom 2* (2nd ed.). Państwowe Wydawnictwo Naukowe.

Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D. & Zanette, L. Y. (2016). Fear of large carnivores causes a trophic cascade. *Nature Communications*, *7*, 10698.

Suzuki, T. N. (2015). Assessment of predation risk through referential communication in incubating birds. *Scientific Reports*, *5*(10239).

Suzuki, T. N. & Kutsukake, N. (2017). Foraging intention affects whether willow tits call to attract members of mixed-species flocks. *Royal Society Open Science*, *4*(6), 170222.

Swenson, N. G. (2014). *Functional and Phylogenetic Ecology in R*. Springer, Berlin.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M. C., Schwager, M. & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, *31*, 79–92.

Tomiałojć, L. & Lontkowski, J. (1989). A technique for censusing territorial song thrushes Turdus philomelos. *Annales Zoologici Fennici*, *26*(3), 235–244.

Toyne, E. P. (1998). Breeding season diet of the Goshawk Accipiter gentilis in Wales. *Ibis*, *140*(4), 569–579.

Valone, T. J. & Giraldeau, L.-A. (1993). Patch estimation by group of foragers: what information is used? *Animal Behaviour*, *45*, 721–728.

van Rij, J., Wieling, M., Baayen, R. H. & van Rijn, H. (2020). *itsadug: Interpreting Time Series and Autocorrelated Data Using GAMMs.*

Ward, M. P., Benson, T. J., Semel, B. & Herkert, J. R. (2010). The Use of Social Cues in Habitat Selection by Wetland Birds. *The Condor*, *112*(2), 245–251.

Wiehle, D., Wyka, J., Matysek, M., Sobas, P., Kusal, B. & Kajtoch, Ł. (2020). Rozmieszczenie i liczebność jastrzębia Accipiter gentilis w środkowej części województwa małopolskiego. *Ornis Polonica*, *61*, 47–56.

Wood, S. (2021). *Package ' mgcv .'*

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, *73*(1), 3–36.

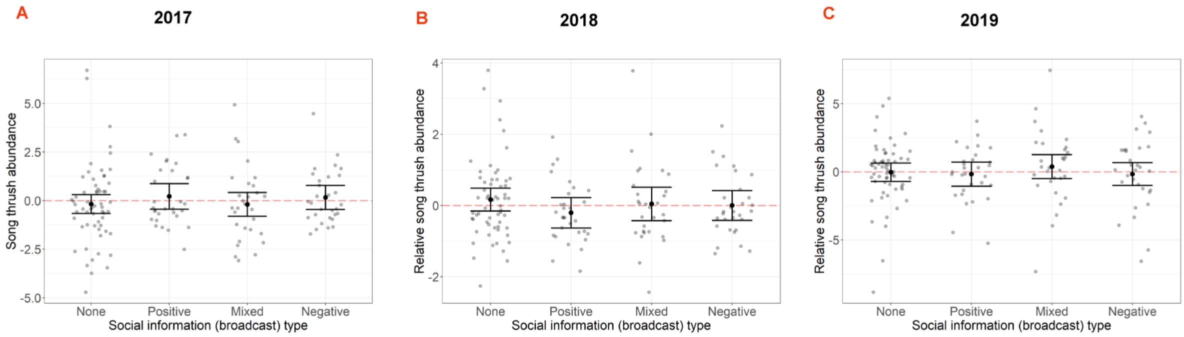

Figure 1. Influence of the types of social information on song thrush abundance (subplot A) and relative song thrush abundance (subplots B and C). The results were obtained before the experiment (2017: subplot A), in the year of the experiment (2018: subplot B), and a year after the experiment (2019: subplot C). No result was statistically significant.

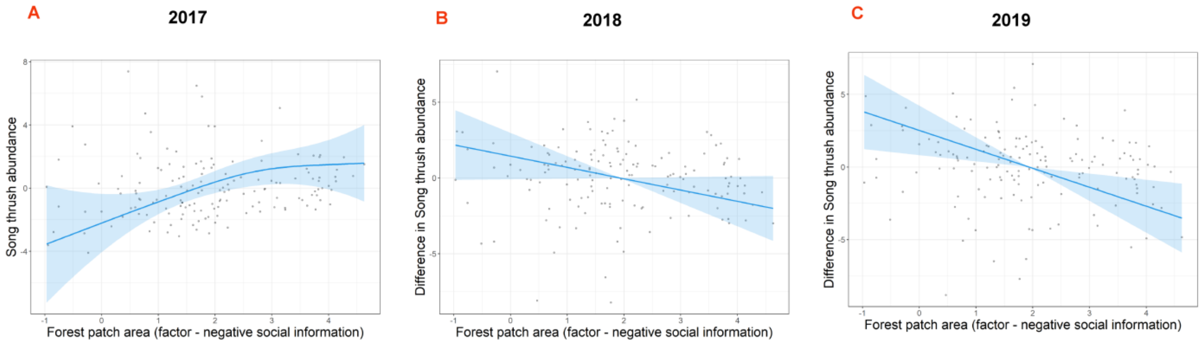

Figure 2. Modification of the effect of forest patch area on the song thrush abundance (subplot A) and relative song thrush abundance (subplots B and C) by negative social information. The results were obtained before the experiment (subplot A), in the year of the experiment (subplot B), and the year after the experiment (subplot C). All relationships were statistically significant.

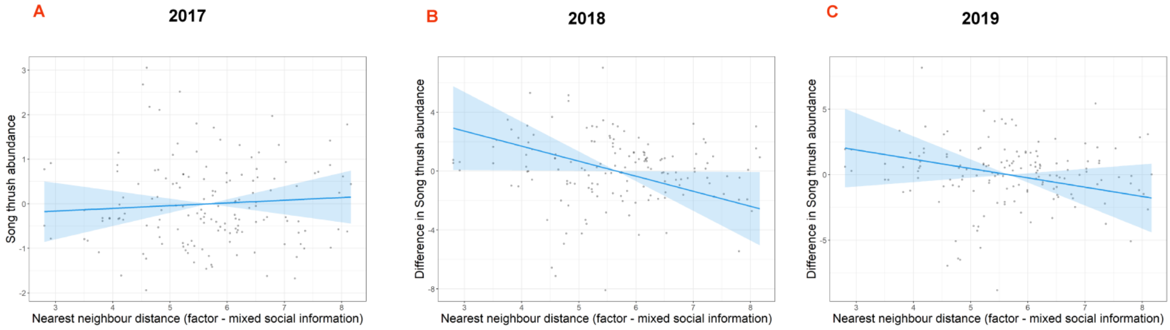

Figure 3. Modification of the effect of nearest neighbor distance on the song thrush abundance (subplot A) and relative song thrush abundance (subplots B and C) by mixed social information. The results were obtained before the experiment (subplot A), in the year of the experiment (subplot B), and the year after the experiment (subplot C). Only the relationship displayed in subplot B was statistically significant.

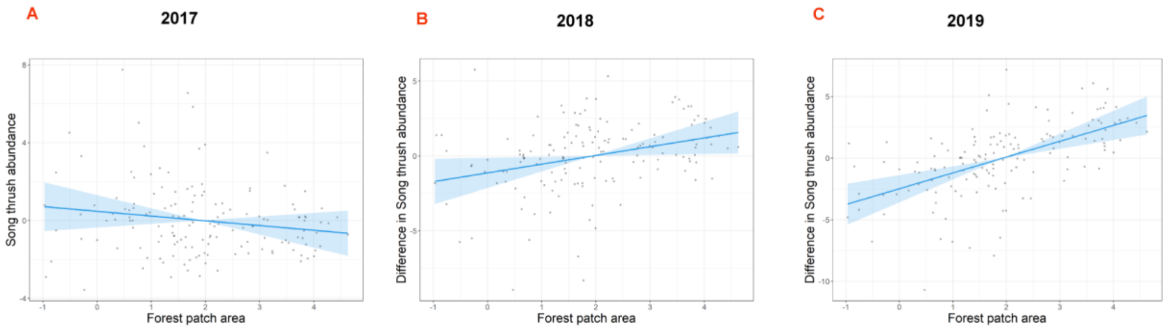

Figure 4. Effect of forest patch area on the song thrush abundance (subplot A) and relative song thrush abundance (subplots B and C). The results were obtained before the experiment (subplot A), in the year of the experiment (subplot B), and the year after the experiment (subplot C). Relationships displayed in subplots B and C were statistically significant.

Table 1. The effect of broadcasted information types and isolation metrics on Song thrush abundance and relative abundance (difference in abundance between 2018 and 2017, and 2019 and 2017).
Statistically significant effects are emboldened: *** - P < 0.001, ** - P < 0.01, * - P < 0.05, ‘- P < 0.10.

Explanatory variables	*Song thrush abundance in 2017*	*Song thrush relative abundance in 2018 (the year of the experiment)*	*Song thrush relative abundance in 2019 (one year after the experiment)*
GAM estimates of function slopes with standard errors (in brackets) for social information types with assumed linear response			
Intercept	**2.9412** *** **(0.1831)**	**0.0296** * **(0.2243)**	0.2315 (0.2333)
InformationPositive	0.1219 (0.3534)	0.7375 (0.4211)	0.0339 (0.4472)
InformationMixed	-0.0023 (0.3926)	0.7072 (0.4819)	-0.2038 (0.4844)
InformationNegative	0.0236 (0.4048)	0.5773 (0.5056)	-0.4022 (0.5272)
Approximate significance of smooth terms:			
log(NNDist)	Df = 2.845	Df = 1.000	Df = 1.000
log(Forest area)	Df = 1.000	**Df = 1.000** *	**Df = 1.000** ***
log(NNDist):InformationNone			
log(NNDist):InformationPositive	Df = 1.000	Df = 1.000	Df = 1.000
log(NNDist):InformationMixed	Df = 1.000	**Df = 1.000** *	Df = 1.000
log(NNDist):InformationNegative	Df = 1.826	Df = 1.000	Df = 1.278
log(Forest area):InformationNone			
log(Forest area):InformationPositive	Df = 1.000	Df = 1.000	Df = 1.000
log(Forest area):InformationMixed	Df = 1.000	Df = 1.510	Df = 1.000
log(Forest area):InformationNegative	**Df = 1.713** *	**Df = 1.000 ‘**	**Df = 1.000** **

Table 2. Results of comparison between categorical predictor levels for song thrush abundance. None of the results turned out to be statistically significant.

Types of social information compared	*Song thrush abundance in 2017*	*Song thrush relative abundance in 2018 (the year of the experiment)*	*Song thrush relative abundance in 2019 (one year after the experiment)*
Comparing Positive with Mixed	$\chi2$ (1.000) = 0.002	$\chi2$ (1.000) = 0.185	$\chi2$ (1.000) = 0.528
Comparing Positive with Negative	$\chi2$ (1.000) = 0.026	$\chi2$ (1.000) = 0.065	$\chi2$ (1.000) = 0.000
Comparing None with Mixed	$\chi2$ (1.000) = 0.041	$\chi2$ (1.000) = 0.082	$\chi2$ (1.000) = 0.417
Comparing None with Negative	$\chi2$ (1.000) = 0.131	$\chi2$ (1.000) = 0.307	$\chi2$ (1.000) = 0.048
Comparing Mixed with Negative	$\chi2$ (1.000) = 0.016	$\chi2$ (1.000) = 0.035	$\chi2$ (1.000) = 0.563
Comparing None with Positive	$\chi2$ (1.000) = 0.024	$\chi2$ (1.000) = 0.674	$\chi2$ (1.000) = 0.049

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DECLARATION

I declare that in the chapter **Different response of the taxonomic, phylogenetic and functional diversity of birds to forest fragmentation** my contribution represented a 20% of the publication and consisted of:

- **Significantly contributing to the drafts written by Michał Bełcik**
- **Approving the last version of the manuscript**

Additionally I declare that the largest contribution to the manuscript was made by Michał Bełcik

天野達也

(signature of co-author)

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Social information can alter the effect of habitat fragmentation on bird diversity and improve its stability.

Mój udział był następujący:

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Place and data: **Brisbane, June 2022**

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DECLARATION

I declare that in the chapter **Social information can alter the effect of habitat fragmentation on bird diversity and improve its stability** my contribution represented a 20% of the publication and consisted of:

- **Significantly contributing to the drafts written by Michał Bełcik**
- **Approving the last version of the manuscript**

Additionally I declare that the largest contribution to the manuscript was made by Michał Bełcik

天野達也

(signature of co-author)

Oświadczenie współautorów o zakresie udziału merytorycznego we wspólnych publikacjach, z których fragment stanowi samodzielną i wyodrębnioną część rozprawy doktorskiej mgr inż. Michała Bełcika

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Wykonałam nagrania audio niezbędne do wykonania eksperymentu. Udzielałam krytycznych uwag i sugestii w całym procesie powstawania pracy.

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Dr hab. Piotr Skórka,

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Oświadczenie Kandydata o zakresie wkładu merytorycznego
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Mój udział był następujący:

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Jestem głównym autorem koncepcji pracy i wszystkich jej założeń metodycznych. Koordynowałem realizację terenowej część badań, wykonałem wszystkie analizy statystyczne wyników oraz ich prezentację graficzną. Przygotowałem pierwszą wersję manuskryptu, a następnie naniosłem poprawki zasugerowane przez współautorów. Jako autor korespondencyjny uczestniczyłem we wszystkich etapach procesu redakcyjnego.

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Dr Magdalena Lenda,

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Oświadczam, że w pracy:

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Sylwia
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....

(data, podpis współautora)

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dr Bartłomiej Woźniak,

Samodzielny Zakład Zoologii Leśnej i Łowiectwa, Instytut Nauk Leśnych, Szkoła Główna Gospodarstwa Wiejskiego w Warszawie

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