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Looking for indicator bird species in the context of forest fragmentation and isolation in West Kalimantan, Indonesia

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ABSTRACT

In the context of Borneo's drastic landscape fragmentation, we assessed the role of diverse forest and land uses—swidden agriculture, mixed garden, smallholder rubber and oil palm plantations—in determining (1) diversity levels and composition of bird species in different vegetation types; (2) the potential for bird species to act as indicators of habitat quality; and (3) the agricultural matrix's contribution to preserving forest-dependent species. Field campaigns across West Kalimantan sites were conducted during both rainy and dry seasons, using mist nets and 10-min point count recordings along transects. We used four diversity indices, non-metric multidimensional scaling (NMDS) and the Indicator Value index (IndVal) for our analysis. Our results endorsed the general trend found across the tropics of a significant reduction in bird species richness, from the complex natural and old secondary forest structures to the simplified monoculture habitats. We recorded 10,519 individuals across 214 bird species, representing almost 90% of Borneo's lowland forest species. NMDS differentiated intact forest from forest fragments and land under different agriculture uses. Eighty percent of the bird species preferred an intact forest environment. Industrial oil palm sites were the most 'avoided' vegetation type. Using IndVal, we found six indicator species significantly associated with forest, three indicator species for depleted forest, one for mixed garden, and none for oil palm plantation. Farm-dependent species richness was strikingly low, and species had little conservation value as per IUCN standards; industrial oil palm plantations were poorest in bird species. Notable exceptions were traditional mixed gardens and old fallows associated with swidden agriculture, when in proximity to forest. These traditional agroforestry systems have higher conservation value than industrial and smallholder monoculture plantations, however, their long-term preservation is uncertain, and monitoring programs are lacking that can contribute to long-term biodiversity conservation and ecosystem service maintenance. More data are needed to determine the viable population sizes for the bird indicator species identified in our study. Such knowledge on population trends can be used to monitor habitat quality and health of forest agriculture landscape mosaics and improve the effectiveness of management, conservation and monitoring in future.

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1. Introduction

Deforestation and habitat fragmentation are viewed as a harsh threat to global biodiversity (Fischer and Lindenmayer, 2007; Foley et al., 2005; Sala et al., 2000), particularly in Southeast Asia, where the rate of extinction is predicted to reach 26% in 2030 if the deforestation trend of the 1990–2000s remains unchanged (Brook et al., 2006). Borneo, the third largest island in the world, is no exception. Considered a significant biodiversity evolutionary hotspot (De Bruyn et al., 2014), and containing the highest species richness level of Southeast Asian plants (Kier et al., 2005; Roos et al., 2004) and mammals (Phillipps and Phillipps, 2016), Borneo (including its Indonesian part known as Kalimantan) is also home to some 670 bird species, of which 42 are endemic and 46 have near-threatened status globally (Lepage, 2019). Logging, mining and conversion to monoculture agriculture have drastically impacted Borneo's rainforests (Curran et al., 2004; Gaveau et al., 2014; Koh and Sodhi, 2010; Miettinen et al., 2011), and modified landscape structure through fragmentation and habitat loss (Cushman and Wasserman, 2017).

Indicator species, that is species that are sensitive to change, whose abundance in a given area indicates certain environmental conditions (Lindenmayer et al., 2000; Miller et al., 1998; Simberloff, 1998; Thompson et al., 2013), are used to monitor these changes or the efficacy of environmental management. The concept is not unanimously accepted, however, having been criticized for the lack of justification behind the choice of a particular indicator, which is not always clearly defined (Siddig et al., 2015). In Indonesia, it has primarily been used to monitor pollution or contamination levels, sometimes referred to as "bioindicators" (Adam et al., 2019; Farantika et al., 2020 [using macro zoobenthos]; Hasairin et al., 2020 [lichen]; Ihsan et al., 2018; Kleinertz et al., 2016; Neubert et al., 2016 [fish]; Prasetia et al., 2018 [trees]). Aoyagi et al. (2017) looked for indicators of forest disturbance at the genus level, but besides a few indicator value index (IndVal) attempts using soil bacterial communities (Berkelmann et al., 2018) or tree plantation species (Siswo et al., 2019a, 2019b), no attempt has ever been made to find potential indicators for landscape level management and monitoring.

Birds, butterflies or ground beetles are the most used indicators, mainly because of data availability, relative ease of collection and identification, and because many have known susceptibility to environmental changes or have ecosystem functions such as pest reduction, pollination or seed dispersal (Bibby, 1999; Brown and Freitas, 2000; Koivula, 2011; Lawton et al., 1998; Morrison, 1986; Peh et al., 2006; Rainio and Niemelä, 2003; Schulze et al., 2004). Much has been written on birds as highly effective indicators of the impacts of environmental changes, notably in the search for global indices to monitor ecosystem health in Europe and North America (Gregory and van Strien, 2010), and as proxy for overall biodiversity and environmental planning (Kati et al., 2004).

In this study, birds were also the preferred study focus because they are relatively easy to monitor in the field, frequently addressed as important taxa in habitat disturbance studies in Indonesia, and there was significant availability of local and global expertize (BirdLife International, 2020; MacKinnon et al., 1993; Phillipps and Phillipps, 2016; Planqué et al., 2020). With future environmental monitoring programs in Kalimantan (Indonesian Borneo)'s forest and agriculture landscapes in mind, we aimed to study bird species richness and composition along a gradient of habitat fragmentation and degradation, looking for species that distinctly relate to specific vegetation types or with particular habitat preferences, as well as species that could be used as indicators of habitat degradation, using relatively intact forests as control sites. We were interested to know, forest intactness aside, if the presence of any particular species could be used to monitor habitat quality of specific vegetation, and if this information could be used in monitoring and managing landscape structure. Vulnerable, sensitive species within the landscape mosaic need to be identified and distinguished from those that would be able to persist in the current land management system.

With the ultimate goal of setting up a baseline for future monitoring of the impact of changes on landscape structure and ecosystems using bird species, in this study we set out to: (1) compare the diversity levels and composition of bird species across different types of vegetation; (2) look for potential indicator bird species for monitoring the quality of specific vegetation habitat; and (3) evaluate the contribution of the agricultural matrix to the preservation of forest-dependent species in Bornean landscape.

2. Material and methods

2.1. Study area and sampling design

This study was located in West Kalimantan Province (Indonesian Borneo). We selected this province because it represents an ancient deforestation front (see the map of the Planning Department of Forest Service, 1950) and illustrates a gradient of fragmentation, from the more forested interior to the more developed central and west regions (Fig. 1). Apart from the still-forested remote areas of the eastern and southern parts of the province, most forests have been converted to agriculture under various processes of fragmentation and transformation, with a strong emphasis on industrial-level monoculture plantations (mainly oil palm) influencing land use since the 1980s. Such a landscape represents an excellent opportunity to examine how bird communities change across a gradient of fragmentation and the isolation of forest patches, investigating the relative conservation value of various mosaics of vegetation within a non-forest matrix. The mean annual temperature is 27.2 °C (lowest monthly mean 22.1 °C and highest 31.9 °C), with a mean annual precipitation of 4154 mm (driest annual mean 2673 mm, wettest 5550 mm) (Worldclim, 2018).

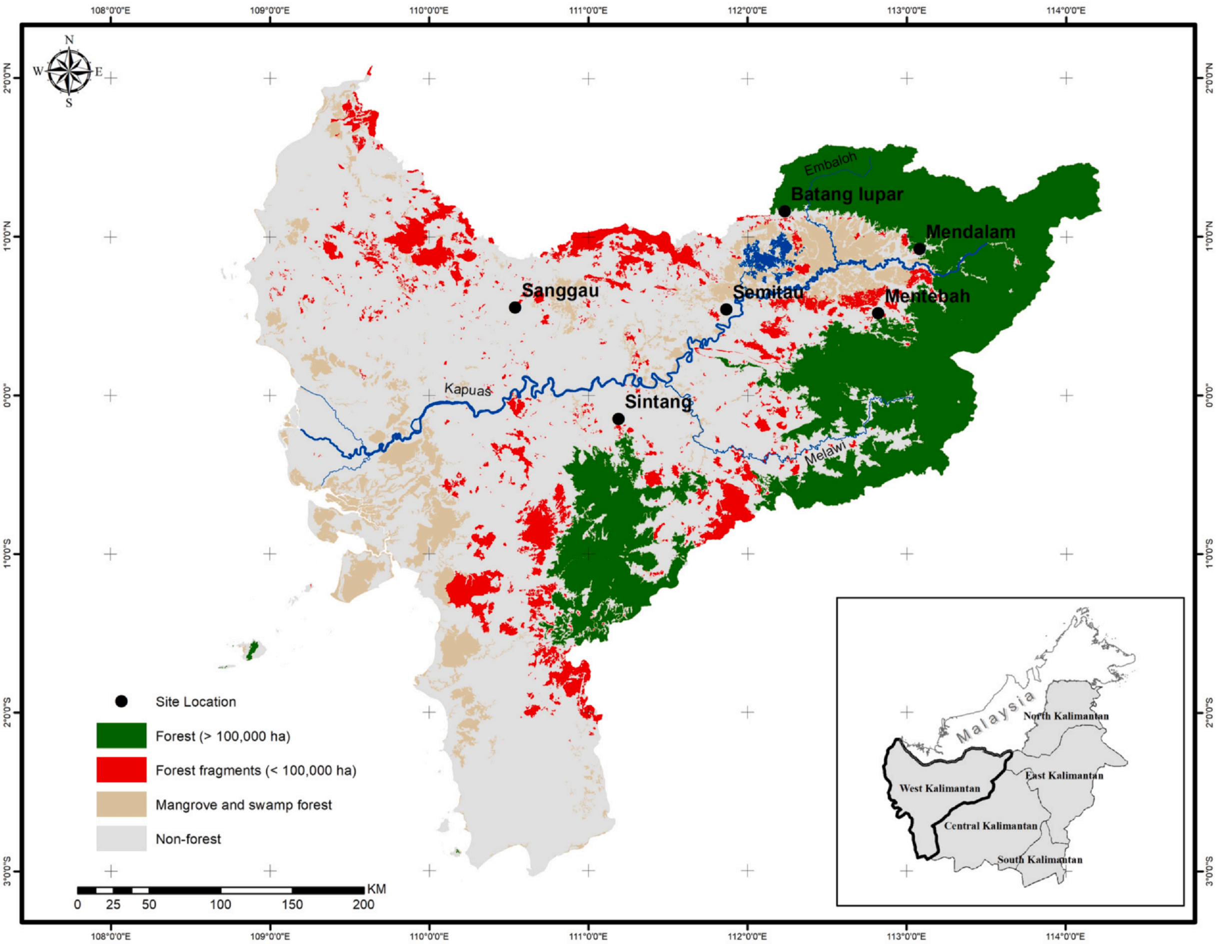

Fig. 1. Sampling sites in West Kalimantan Province. Names are those of the corresponding regencies or districts. Details for sites are given in Table 1. Forest cover was extracted from Pribadi et al. (2020) and Laumonier et al. (2020a). Based on Lucey et al. (2017) findings on the relationship between species richness with core forest patches (continuous forest equivalence threshold at 165,000 ha) and the findings of Marshall et al. (2009) indicating a minimal forest area of 50 000–100,000 ha for viable orangutan population, we defined a critical threshold in forest fragmentation at 100,000 ha in our study.

The selection of our six study sites was made by studying the distribution of vegetation types on large-scale ecological vegetation maps and the corresponding classification available for that area (Laumonier et al., 2020a; Pribadi et al., 2020). From these data, we selected: two sites representing the traditional long-cycle swidden agriculture, old fallows and agroforestry system mosaic in the proximity of a national park (Batang Lupar, Mendalam); two sites representing a mosaic landscape of oil palm concessions (RSPO-certified, including forest patches within) and smallholder rubber (Mentebah, Semitau); and two sites that were isolated from natural forest, representing mixed gardens, and smallholder rubber and oil palm plantations, with communities still relying on their locally preserved isolated forest fragment, but now practicing just short-cycle swidden agriculture in areas where old fallows are difficult to find (Sintang, Sanggau). Within each of these sites (approximately 10 × 10 km), we used the same maps to pre-stratify and design an equally stratified sampling protocol covering the main vegetation types. This sampling strategy is considered to be robust, with many advantages over pure random or proportionally stratified sampling (Hirzel and Guisan, 2002; Rolecek et al., 2007).

We ultimately sampled a total of 23 locations, representing: various forest types (including well-drained lowland mixed dipterocarp, but also nutrient-poor peat swamp and sandy soil *kerangas* forests); forest fragments within oil palm plantations (peat swamp, *kerangas*, and mixed dipterocarp forest); swidden agriculture mosaics of food crop fields and fallows of different age representing successional stages of the regeneration of vegetation after clear felling and burning (young 2–10 years, old 10–20 years, old secondary forest ≥ 20 years old); smallholder rubber/oil palm farms, and mixed gardens; and industrial oil palm plantations (Table 1 and SI 1). Selected ecological attributes, to which the bird indicator species may be responsive, were vegetation and broad soil types (mineral clay, pure sand, or peaty soils).

Table 1
Study sites, vegetation (habitat) and locations surveyed.

District and Regency	Vegetation (habitat) type*	Coordinates (Lat/Long)	Elevation ASML (m)	Distance (km) to nearest continuous forest ≥ 100,000 ha	Soil type
Batang Lupar (Kapuas Hulu)	Mixed dipterocarp forest	1° 8′ 0″ N–112° 15′ 20″ E	50–150	0	Mineral clay
	Old fallow	1° 8′ 27″ N-112° 15′ 7″ E		1	Mineral clay
	Young fallow	1° 8′ 17″ N-112° 15′ 18″ E		0.8	Mineral clay
Mendalam (Kapuas Hulu)	Mixed dipterocarp forest	0° 55′ 23″ N-113° 4′ 51″ E	30–100	0	Mineral clay
	Riparian forest	0° 54′ 7″ N-113° 2′ 22″ E		0	Mineral clay
	Kerangas	0° 53′ 57″ N-113° 3′ 39″ E		0	Pure sand
	Old fallow	0° 53′ 57″ N-113° 4′ 32″ E		1.5	Mineral clay
	Young fallow	0° 53′ 48″ N-113° 5′ 6″ E		1.5	Mineral clay
Mentebah (Kapuas Hulu)	Mixed dipterocarp forest	0° 31′ 11″ N-112° 49′ 13″ E	50–100	0	Mineral clay
	Kerangas	0° 34′ 38″ N-112° 47′ 02″ E		0	Pure sand
	Jungle rubber	0° 31′ 45″ N-112° 46′ 33″ E		2	Mineral clay
	Old fallow	0° 32′ 4″ N-112° 48′ 33″ E		1	Mineral clay
	Young fallow	0° 29′ 35″ N-112° 49′ 5″ E		1	Mineral clay
Semitau (OP) (Kapuas Hulu)	Kerangas fragment (780 ha)	0° 32′ 22″ N-111° 46′ 21″ E	30–100	8	Pure sand
	MDF fragment (85 ha)	0° 32′ 36″ N-111° 52′ 7″ E		8	Mineral clay
	Peat swamp fragment (280 ha)	0° 27′ 14″ N-111° 51′ 6″ E		14	Peat soil
Sanggau	Depleted MDF (2210 ha)	0° 33′ 17″ N-110° 32′ 28″ E	50–550	67	Mineral clay
	Smallholder rubber	0° 34′ 14″ N-110° 28′ 12″ E		57	Mineral clay
	Mixed garden	0° 34′ 10″ N-110° 28′ 22″ E		57	Mineral clay
Sintang	Depleted MDF (1400 ha)	0° 8′ 32″ S-111° 11′ 17″ E	20–200	7	Mineral clay
	Smallholder rubber	0° 8′ 21″ S-111° 13′ 50″ E		9	Mineral clay
	Industrial oil palm	0° 8′ 27″ S-111° 13′ 56″ E		9.4	Mineral clay
	Smallholder oil palm	0° 8′ 50″ S-111° 13′ 48″ E		8.2	Mineral clay

* Mixed dipterocarp forest: intact lowland mixed dipterocarp forest (MDF) characteristic of Southeast Asia; Depleted mixed dipterocarp forest: remnant forest, depleted through local use of timber (often the ‘reserve forest’ of the village); Riparian forest: distinctive forest type present along river banks; Kerangas: forest on nutrient-poor sandy soil; Peat swamp: forest developed on semi-decomposed nutrient-poor organic matter accumulated in depressions, with a depth of up to 7 m in our survey sites; Old fallows and young fallows: successional stages, natural regrowth after slash and burn, upland paddy cultivation for 2 years and field abandonment.

2.2. Data collection

Following vegetation sampling representing different habitats in the area (Laumonier et al., 2020b), two bird species surveys were conducted per year for 3 years between 2017 and 2019, during both the rainy and drier seasons, at the six sites where vegetation sampling had been previously performed (Table 1). Although some El Niño years experience prolonged dry seasons, the difference between rainy and dry seasons is rarely striking in West Kalimantan, with typically high rainfall throughout the year (Inoue et al., 1993; Kumagai et al., 2005). Point count surveys were only conducted in clear weather and stopped during the rain. Point count recordings, performed by a team of two persons, occurred between 6 and 9 am and 3–6 pm, every 100 m along 1000 m transects and 200 m away from of each vegetation edge to control edge effects (Restrepo and Gómez, 1998). All bird species seen and heard within a 50 m fixed radius from the point were recorded visually and by standardized tape recordings (Parker, 1991). Each transect was sampled twice back and forth in a day, resulting in 40 point counts in a day. Sample replication was carried out for the same transect over the following 4 days. In addition, three mist nets were placed in each transect (at the beginning, middle, and end) for 5 days; nets were 5 × 10 m in size, placed 2 m above the ground, and monitored between 6 and 9 am and 3–6 pm. Full body images were taken of captured birds, which were marked before released, to avoid double-counting. The mist net data was treated as additional data for particular point count locations. The total amount of birds captured using mist nets accounted for less than 2% of the whole dataset; data was mainly used for taxonomic purposes. Birds flying over the canopy, migratory birds, birds of prey and swifts were disregarded because of their long-range behavior and mobility. For the nomenclature and identification of species traits, we followed Wilman et al. (2014).

2.3. Analysis

2.3.1. Diversity indices

To compare the diversity of sites—besides species richness (sr), which is a common biodiversity surrogate measure that has the disadvantage of being sampling dependent—we used four diversity indices: Shannon–Weiner (H) index for both species richness and evenness or equitability; Fisher's alpha parameter for its relative robustness at low sample completeness and relative independence of sample size (Beck and Schwanghart, 2010); and Berger–Parker index, looking at the proportion of the most abundant species in the population, since it is also an effective index for monitoring biodiversity deterioration in ecosystems (Berger and Parker, 1970; Caruso et al., 2007). All indices were computed using the Vegan package (Oksanen et al., 2019) in R version 4.0.2 (R Core Team, 2020). We also assessed beta diversity looking at the Sørensen indices of total dissimilarity (β_{SOR}), that is the sum of the turnover (β_{SIM}), and the nestedness (β_{SNE}), using the Betapart package (Baselga et al., 2020) in R version 4.0.2 (R Core Team, 2020).

2.3.2. Ordination: non-metric multidimensional scaling

Non-metric multidimensional scaling (NMDS) of the point count dataset was used to explore potential birds' community similarities among different vegetation types. Unlike other ordination techniques that rely on (primarily Euclidean) distances, NMDS uses rank orders, and thus is an extremely flexible technique that can accommodate a variety of different kinds of data. NMDS was performed using the first two dimensions and random starting iterations to obtain the lowest stress value. NMDS was complemented by an analysis of similarities (ANOSIM) to test the significance of observed differences between identified bird associations. We used the Vegan package (Oksanen et al., 2019) in R version 4.0.2 (R Core Team, 2020).

2.3.3. Specialization and potential indicator species

Specialization is intuitively linked to indicator concepts, but is difficult to assess. The concept is highly context-dependent and suffers from a great variability of existing definitions and methods (Devictor et al., 2010). Some authors argue that a species is more specialized to a certain habitat if its density there is high, and that the degree of specialization is a better measure of biodiversity change (Devictor et al., 2008). To assess specialization for each vegetation type, we looked at bird species' diet categories, following dos Anjos et al. (2019) approach. 'Specialists' in that study were understood to be species that feed on a single food type that represents more than 70% of their entire diet, while generalists were birds feeding on various types of foods.

The term 'indicator species' itself, meanwhile, could also have different interpretations (Butler et al., 2010; Lindenmayer et al., 2000). Indicator species are most often defined as individuals specific to a particular habitat type and sensitive to changes in their environment. Simultaneously looking at ecological attributes, we looked for potential indicator species, focusing on dominant species, as well as both individual species and groups of species that could act as indicators. We also considered 'management indicator species', species that indicate specific environmental conditions or illustrate disturbance regimes in the vegetation.

To look for potential individual or group indicator species, we computed the indicator value by combining specificity A (the positive predictive value of a species as an indicator of the target site) and fidelity B (the sensitivity of a species as an indicator of the target site) (De Cáceres and Legendre, 2009; Dufrene and Legendre, 1997). For each species i in each site group j, we multiplied the product of A*ij* (which is the mean abundance of species *i* in the sites of group *j* compared with all groups in the study) by B*ij* (which is the relative frequency of occurrence of species *i* at the sites of group *j*), as follows:

$$A_{ij} = Nindividuals_{ij}/Nindividuals_{i.}$$

$$B_{ij} = Nsites_{ij}/Nsites_{.j}$$

$$INDVAL_{ij} = A_{ij} \times B_{ij} \times 100$$

The maximum of A*ij* is A = 1, which is when species *i* is only present in cluster *j*; while the maximum of B*ij* is B = 1, which is when species *i* is present in all transect replications in each vegetation class. A and B values were tested for significance ($p < 0.05$) (De Cáceres et al., 2012). In this analysis, 'site group' is the vegetation class (i.e., young fallow, old fallow, forest), and 'cluster' means the replication of transect data for 5 days in each vegetation class. To look into potential indicator species for each vegetation type, we emphasized the value of specificity (A) over fidelity; thus, species having significant A > 0.8 and B > 0.1 values were considered to be potential indicator species (Hansen et al., 2016).

Following Chytrý et al. (2002), and in addition to the IndVal result, we calculated the Pearson's phi coefficient of association, to determine the ecological preferences of bird species among a set of site group combinations (the replication of the same sampling points). The correlation index values express the fact that a species tends to 'avoid' or 'look for' particular vegetation types. Bird species having a correlation value in the range of 0.5–1 are specific to the habitat in question (Gogtay and Thatte, 2017; Schober and Schwarte, 2018).

The use of the IndVal index and the correlation analysis have been proven effective for bioindicators (Bakker, 2008; Cheng et al., 2012; McGeoch et al., 2002), having outperformed 'simple' species richness count calculations, as this approach is robust to variation in the presence of rare species (Basset et al., 2004). Identified indicators comply with both habitat specificity and fidelity tests (Gardner, 2010). Both the indicator value (IndVal) and Pearson's phi coefficient were assessed using the Indicspecies package (De Cáceres et al., 2020) in R version 4.0.2 (R Core Team, 2020).

3. Results

In a sampled lowland region of ca. 90,000 km^2 in West Kalimantan, we recorded a total of 10,519 individuals for 214 bird species from 60 families, almost 90% of the 241 known lowland forest species for Borneo Island (Gill et al., 2020). About 80% of the 214 bird species recorded prefer an intact mixed dipterocarp forest environment, as shown by the higher correlation value percentage (Fig. 2). The industrial oil palm sites were the most 'avoided' vegetation for all bird species, with only 6% of birds adapting to this land use.

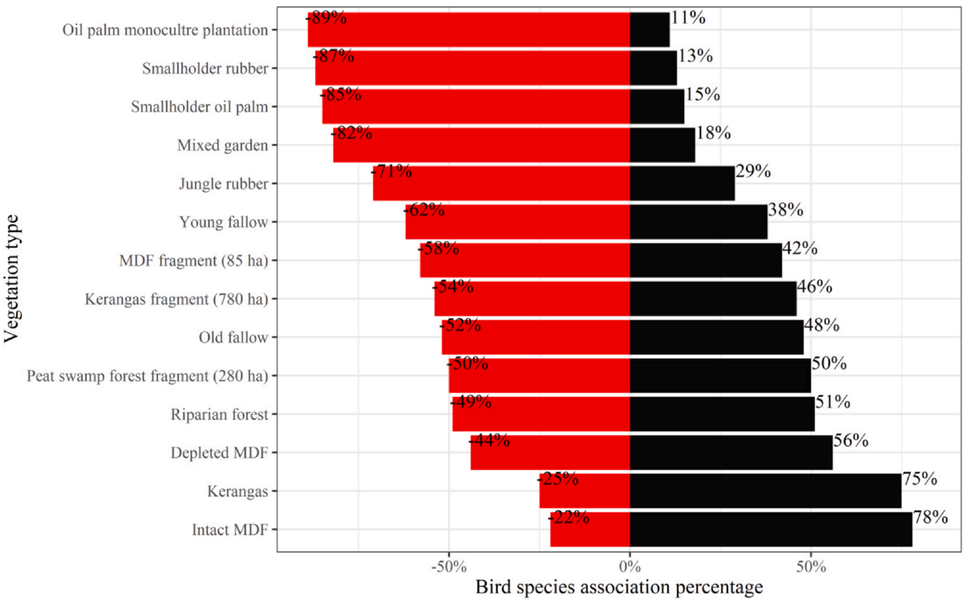

Fig. 2. Percentage of Pearson's phi coefficient of association: Black bars show the positive percentage and red bars show the negative percentage of birds' preference (association) for a particular vegetation type. Intact mixed dipterocarp forest is favored by 78% of the birds, in contrast to oil palm plantations, which were the least favored vegetation (11% of all bird species). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

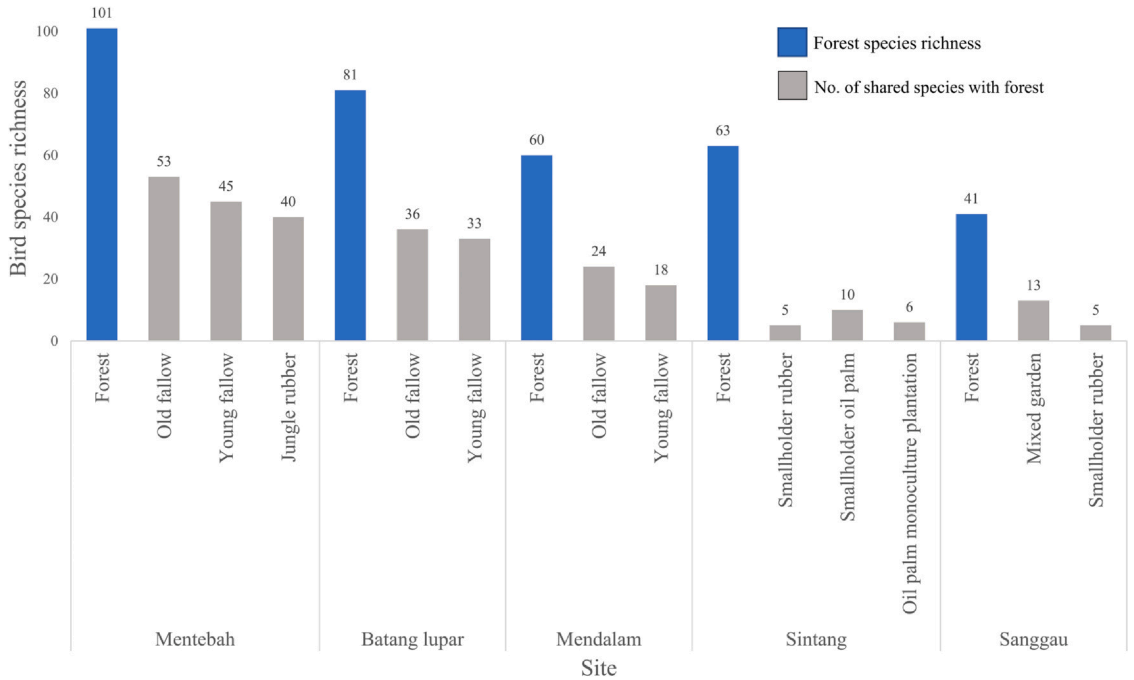

Fig. 3. Among sites, the bird species richness gradually decreased from the continuous forest areas of Mentebah and Batang Lupar to the more fragmented Sintang and Sanggau landscape mosaics. The percentage of shared species between forest and nearby vegetation type in Mentebah and Batang Lupar was still high. It dropped drastically in Sintang and Sanggau, indicating increased fragmentation and loss of connectivity with continuous forest.

3.1. Sørensen dissimilarity index and beta diversity of sites

At landscape level, along the east–west gradient of fragmentation and isolation, the forest species richness in the agricultural matrix decreased from the highly forested Kapuas Hulu Regency (Mentebah, Batang Lupar, Mendalam) landscape to the more depleted forest-agriculture mosaics of Sintang and Sanggau (see Figs. 1 and 3).

The total dissimilarity (β_{SOR}) between sites indicates that overall bird species composition differs in the more fragmented landscape of Sanggau and Sintang, compared to sites closer to the vast contiguous forest of Kapuas Hulu Regency (Batang Lupar, Mentebah, Mendalam, Semitau). Batang Lupar, Sintang, and Sanggau share just nine species of birds. In addition, the Sørensen nestedness-resultant dissimilarity (β_{SNE}) shows that intact mixed dipterocarp forest, *kerangas* forest, and old fallow are related in their composition. On the contrary, the young fallow species composition is very different from that of intact forest, showing the importance of maintaining late-successional stages to support forest species. Further, species composition of respective successional stages (young and old fallow) is rather distinct between sites, while species composition in jungle rubber gardens is dissimilar to that of the mixed gardens known as *parua* and *tembawang*.

3.2. Diversity indices and rarefaction

The values of diversity indices for each vegetation type are shown in Table 2, and rarefaction curves are seen in Fig. 4. The rarefaction curves flattened, indicating that the sampling effort was adequate for each vegetation type's bird assemblage. Not surprisingly, the highest species richness was found in intact mixed dipterocarp forest (n = 146), as well as in old fallow (n = 119) and *kerangas* forest (n = 102), and young fallows when in proximity to contiguous forest (n = 94). The three lowest species richness values were for: forest fragments within an oil palm concession (mixed dipterocarp forest fragment 85 ha in size, n = 38); smallholder rubber plantations (n = 30); and industrial oil palm plantations (n = 27).

Together with species richness, Shannon-Weiner (H) and Fisher alpha indices showed consistent decline from the intact mixed dipterocarp forests to the industrial oil palm plantations and gave similar habitat ranking results, confirming that the sampling was adequate. They showed slightly different ranking when representing bird diversity in agriculture or disturbed vegetation, while Berger-Parker index confirmed the bird diversity deterioration, homogenization of the composition by few dominant species in agriculture habitat.

Table 2
Value of bird diversity indices for each vegetation type. The conversion of forest to fallow stages reduced bird species richness by 18%, while forest conversion to smallholder oil palm reduced bird species richness by 73%, and conversion from forest to a monoculture industrial oil palm landscape reduced richness by 82%. The mixed dipterocarp forest fragment of 85 ha inside an oil palm concession, 10 years after its isolation, showed a lower species richness when compared with successional stages (young and old fallows) that were close to intact forest.

Land use	Diversity indices				
	Species richness	Shannon-Weiner	Berger–Parker	Fisher's alpha	PD[a]
Mixed dipterocarp forest (MDF)	146	4.45	0.05	42.69	–
Old fallow	119	4.32	0.05	37.77	18%
Kerangas forest	102	4.08	0.07	28.68	30%
Young fallow	94	3.95	0.07	26.86	36%
Peat swamp forest (280 ha) fragment	61	3.77	0.09	19.58	58%
Kerangas fragment (780 ha)	54	3.70	0.06	16.55	63%
Riparian forest	60	3.58	0.11	17.44	59%
Depleted MDF	73	3.49	0.13	16.59	50%
Jungle rubber	49	3.43	0.11	17.51	66%
MDF fragment (85 ha)	38	3.34	0.10	11.21	74%
Mixed garden	44	2.96	0.13	8.89	70%
Smallholder rubber	30	2.90	0.12	6.07	79%
Smallholder oil palm	39	2.87	0.17	8.69	73%
Industrial oil palm plantation	27	2.84	0.12	6.40	82%

[a] PD: species richness percentage difference, with intact forest as the baseline.

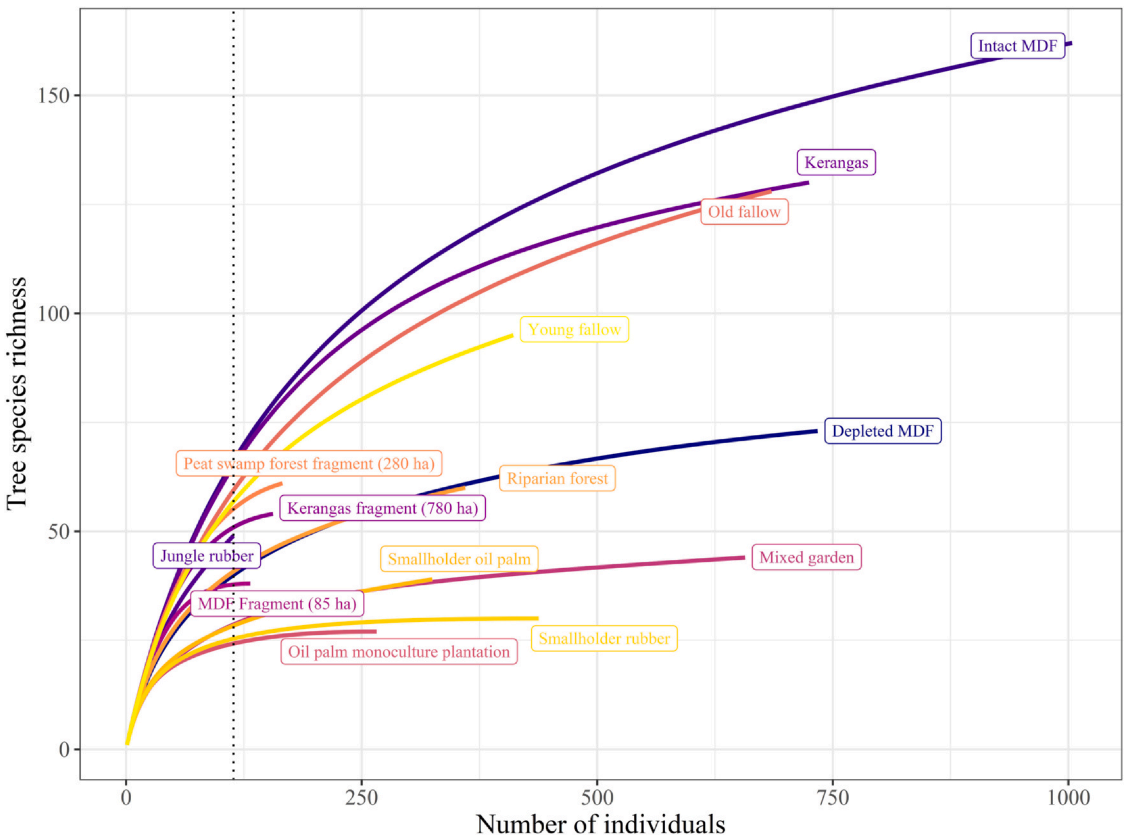

Fig. 4. Individual-based rarefaction of bird species for 14 vegetation types. The species richness of intact mixed dipterocarp forest consistently exceeds that of other vegetation types. The richness of *kerangas* and old fallows significantly exceeds that of young fallows, forest fragments, depleted forest, and riparian forest by as much as 400 and 500 individuals, based on non-overlapping confidence intervals. The bird richness of smallholder rubber, mixed garden, and oil palm plantations is the lowest.

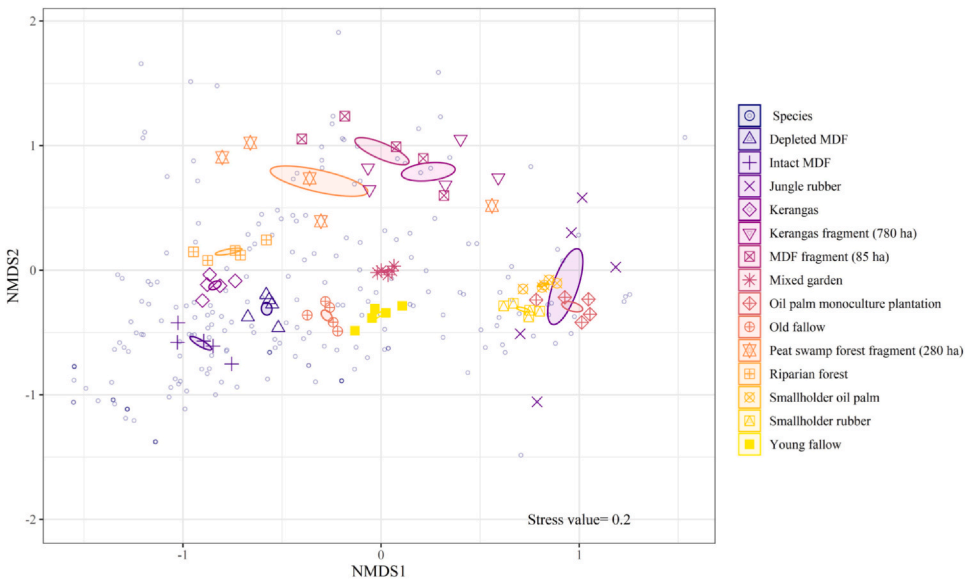

Fig. 5. Ordination of bird communities in nonmetric multidimensional scaling (NMDS) space, using Bray–Curtis dissimilarity as coded by vegetation type.

3.3. Non-metric multidimensional scaling

Based on ecological distance, NMDS ordination shows similarity-dissimilarity of bird species assemblages when coded into the 14 vegetation types surveyed, differentiating intact forest, fragments, and diverse agricultural uses (Fig. 5). We can see from Fig. 5 that intact mixed dipterocarp forest is individualized on the left part of the graph. *Kerangas* and riparian forests are close to each other, while depleted forest and old fallows have similar compositions, with young fallows somewhat adjacent. Mixed gardens are separate from other vegetation types. All forest fragments (peat swamp, *kerangas*, and mixed dipterocarp forest) are grouped, while at the far-right part of the graph, jungle rubber, smallholder rubber, and smallholder oil palm form a cluster. Industrial oil palm species composition is farthest from the intact Mixed Dipterocarp forest species composition. The ANOSIM analysis of similarity among vegetation types ($R = 0.85$, sig. p-value = 0.001), also confirmed that species association is significantly different for each vegetation type.

3.4. Abundance

The five most abundant species for each vegetation type are listed in Table 3. At all forest sites, including forest fragments, the little spiderhunter (*Arachnothera longirostra*), a generalist, and the black-and-yellow broadbill (*Eurylaimus ochromalus*), an invertebrate specialist, were the most abundant birds, but neither were ever observed on farmland. These two could be selected as 'general' indicators of good forest condition. However, these species did not appear as significant potential indicators based on IndVal analysis (see Section 3.5.).

In land uses with higher disturbance levels, including forest fragments, traditional jungle rubber, and mixed garden agro-forestry, a very abundant bird is the bold-striped babbler (*Mixornis bornensis*), an insectivore specialist from the lowlands to the hills of Borneo. This species is common in all disturbed secondary forest and more open areas such as smallholder rubber and oil palm farms or even industrial oil palm plantations. This species could be considered as a 'general' indicator of disturbed sites.

3.5. Single-species indicators

Using IndVal, we found six indicator species that were significantly associated to forest; some of these were quite abundant while others were rare species. Of the six species, five are specialists that feed on insects only (Table 4). The most significant indicators for the intact mixed dipterocarp forest sites were the near-threatened great argus (*Argusianus argus*), the cinnamon-rumped trogon (*Harpactes orrhophaeus*), and the vulnerable rhinoceros hornbill *(Buceros rhinoceros)*. *Argusianus argus* is also very sensitive to disturbance. *Harpactes orrhophaeus* is widespread throughout Borneo, exclusive to undisturbed forest and nowadays holds near-threatened status. *Buceros rhinoceros* is locally common in primary forest, but is now endangered because of its highly prized feathers and casque.

In the *kerangas* forest, potential indicator birds were the lesser cuckoo shrike (*Lalage fimbriata*) which has least-concerned status, the near-threatened rufous-tailed shama (*Copsychus pyrropygus*), and the near-threatened gray-breasted babbler (*Malacopteron albogulare*). These birds, which are indicators of nutrient-poor environments, were also found in peat swamps.

Table 3
The five most abundant bird species for each vegetation type.

Feeding guild and species	Forest				Forest fragments			Fallow forest and traditional agroforestry				Plantation		
	Intact MDF	Kerangas	Rip.	Dep. MDF	Kerangas	MDF	PS	Old fallow	Young fallow	Mixed garden	Jungle rubber	SH Rubber	SH OP	OP
FruitNect														
Brachypodius atriceps	x	–	–	–	–	–	–	x	–	x	–	–	–	–
Gracula religiosa	–	–	–	–	x	–	–	–	–	–	–	–	–	–
Psilopogon chrysopogon	–	–	–	x	–	–	–	–	–	–	–	–	–	–
Psilopogon duvaucelii	–	x	–	x	–	–	–	x	–	x	–	–	–	–
Psilopogon mystacophanos ***NT***	–	–	–	x	–	–	–	–	–	x	–	–	–	–
Psilopogon rafflesii ***NT***	–	x	–	–	–	–	–	–	–	–	–	–	–	–
Pycnonotus goiavier	–	–	–	–	–	–	–	–	–	–	x	–	x	x
Pycnonotus plumosus	–	–	–	–	–	–	–	–	–	–	–	x	–	–
Invertebrate														
Anthreptes rhodolaemus ***NT***	–	–	–	–	–	–	–	–	–	–	x	–	–	–
Collocalia esculenta	–	–	–	–	x	–	–	–	–	–	–	–	–	–
Cyanoderma erythropterum	x	–	x	–	–	–	–	–	x	–	–	–	–	–
Dicrurus paradiseus	–	–	–	–	–	–	x	–	–	–	–	–	–	–
Eurylaimus ochromalus ***NT***	x	x	–	x	–	x	x	–	–	–	–	–	–	–
Hypothymis azurea	–	–	x	–	–	–	x	–	–	–	–	–	–	–
Malacopteron magnum ***NT***	–	x	–	–	–	–	–	–	–	–	–	–	–	–
Micropternus brachyurus	–	–	–	–	–	x	–	–	–	–	–	–	–	–
Mixornis bornensis	–	–	–	–	–	x	–	–	x	–	x	x	x	x
Orthotomus sericeus	–	–	–	–	–	–	–	–	x	x	–	x	–	–
Pellorneum capistratum	–	–	–	–	–	–	x	–	–	–	–	–	–	–
Prinia flaviventris	–	–	–	–	–	–	–	–	–	–	–	–	x	x
Rhipidura javanica	–	–	–	–	–	–	–	–	x	–	x	x	x	x
Trichastoma rostratum ***NT***	–	–	–	–	–	x	–	–	–	–	–	–	–	–
Omnivores														
Amaurornis phoenicurus	–	–	–	–	x	–	–	–	–	–	–	–	–	–
Arachnothera longirostra	x	x	x	x	x	x	x	x	x	x	–	–	–	–
Corvus enca	–	–	–	–	–	–	–	x	–	–	–	–	–	–
Pycnonotus brunneus	–	–	–	–	–	–	–	x	–	–	–	–	–	–
Pycnonotus erythropthalmos	x	–	x	–	–	–	–	–	–	–	–	–	–	–
PlantSeed														
Lonchura fuscans	–	–	–	–	–	–	–	–	–	–	x	x	x	–
Spilopelia chinensis	–	–	–	–	x	–	–	–	–	–	–	x	–	x

Vegetation type abbreviation—MDF: Mixed Dipterocarp Forest; Rip.: Riparian; Dep. MDF; Depleted MDF; PS: Peat swamp; SH: Smallholder; OP: Oil palm; Conservation status—NT: near-threatened species; no symbol: least concern species.

Table 4
IndVal potential indicator species for each vegetation type, and their diet.

Vegetation type	Species	A	B	p-value	IUCN	Diet guild
Intact MDF	*Argusianus argus*	1	0.8	0.001 ***	*NT*	*FruiNect*
	Harpactes orrhophaeus	0.9	0.8	0.001 ***	*NT*	*Invertebrate*^{S}
	Buceros rhinoceros	1	0.6	0.003 **	*V*	*FruiNect*^{S}
Kerangas	*Lalage fimbriata*	1	1	0.001 ***	LC	*Invertebrate*^{S}
	Copsychus pyrropygus	0.9	1	0.001 ***	NT	*Invertebrate*^{S}
	Malacopteron albogulare	0.8	0.8	0.001 ***	NT	*Invertebrate*^{S}
Depleted MDF	*Malacopteron magnirostre*	0.9	1	0.001 ***	*LC*	*Invertebrate*^{S}
	Alophoixus bres	1	0.8	0.001 ***	*LC*	*Omnivore*
	Pomatorhinus montanus	1	0.8	0.001 ***	*LC*	*Invertebrate*^{S}
Mixed garden	*Erpornis zantholeuca*	0.9	0.8	0.001 ***	*LC*	*Invertebrate*^{S}
Smallholder oil palm	*Treron vernans*	1	0.8	0.001 ***	*LC*	*FruiNect*
	Ixobrychus cinnamomeus	1	0.6	0.001 ***	*LC*	*VertFishScav*

VertFishScav: vertebrates, fish, and scavengers; FruiNect: fruit and nectar; S: specialist. IndVal result—A: specificity value, B: fidelity value. IUCN conservation status—NT: near threatened, V: vulnerable, LC: least concern. Significant p-value codes: $p < 0.001$ '***', $p < 0.01$ '**', $p < 0.05$ '*'.

Table 5
The 10 only significant species combinations as indicators for each vegetation type.

No.	Site	Species combination	A	B	p-value
1	Intact MDF	*Alophoixus phaeocephalus*^{O} + *Cyornis umbratilis*$^{NT/I}$	1.0	1.0	0.001 ***
2	Old fallow	*Cymbirhynchus macrorhynchos*^{I} + *Gracula religiosa*^{F}	0.9	1.0	0.001 ***
3	Young fallow	*Macronus ptilosus*^{NT} + *Pycnonotus goiavier*^{LC}	0.9	1	0.001 ***
4	Depleted MDF	*Calyptomena viridis*$^{NT/F}$ + *Psilopogon mystacophanos*^{F}	1.0	1.0	0.001 ****
5	Peat swamp fragment	*Amaurornis phoenicurus*^{O} + *Malacopteron cinereum*^{I}	1.0	0.6	0.003 **
6	*Kerangas* forest	*Aegithina tiphia*^{I} + *Nyctyornis amictus*^{I}	1.0	1.0	0.001 ***
7	Mixed garden	*Abroscopus superciliaris*^{I} + *Brachypodius atriceps*^{F}	1.0	1.0	0.001 ***
8	Smallholder oil palm	*Aegithina tiphia*^{I} + *Treron vernans*^{F}	1.0	0.8	0.001 ***
9	MDF fragment	*Lanius tigrinus*^{I} + *Trichastoma rostratum*$^{NT/I}$	1.0	0.6	0.003 **
10	Smallholder rubber	*Abroscopus superciliaris*^{I} + *Aegithina tiphia*^{I}	1.0	1.0	0.001 ***

IUCN conservation status—NT: near threatened, V: vulnerable, no sign: least concern. Feeding guild—I: Invertebrate; F: FruiNect; O: Omnivore; PS: PlantSeed. IndVal result—A: specificity value, B: fidelity value. Significant p-value codes: $p < 0.001$ '****', $p < 0.01$ '**', $p < 0.05$ '*'.

The best indicators for Sanggau's isolated and depleted forest were the mustached babbler (*Malacopteron magnirostre*), the gray-cheeked bulbul (*Alophoixus bres*), and the chestnut-backed scimitar babbler (*Pomatorhinus montanus*), the latter two both holding least-concerned status.

The white-bellied erpornis (*Erpornis zantholeuca*), a least-concern status species, appeared as a potential indicator in the mixed gardens of Sanggau, while in the smallholder oil palm mosaic landscape, two conspicuous indicator species were the pink-necked green pigeon (*Treron vernans*) and the cinnamon bittern (*Ixobrychus cinnamomeus*), both least-concern species. No single potential indicator species was spotted for the smallholder rubber plantations or industrial oil palm plantations, where mostly low-conservation status and generalist birds feeding on multiple food types were present.

3.6. Species combinations

We did not find any significant species combinations for four vegetation types: riparian forest, *kerangas* fragment, jungle rubber, and oil palm plantation. Significant species combinations as indicators for the other ten vegetation types are given in Table 5; all these species had high specificity (A) and fidelity (B) for specific vegetation. The presence of one species increased the predictive value for the other in targeted vegetation types.

3.7. Forest-dependent and farm-dependent species

Table 6 shows the 28 bird species that had a high positive correlation with forest habitat. Among these 28 bird species, 54% are listed as having vulnerable or near-threatened status, and 74% are specialists with single item diet, emphasizing their vulnerability to habitat disturbance. Among these forest-dependent species, about half were also occasionally spotted in old fallows and nearby mixed gardens that resemble old secondary forest in structure.

In contrast to the high abundance and richness of forest sites, forest fragments within RSPO-certified oil palm plantations had much lower numbers of bird species. The number of shared species between nearby forest, forest fragments inside a concession, and monocultural industrial oil palm stands, is shown in Fig. 6. The five vegetation categories shared just seven species (4%) of the total 180 bird species. The small number of species shared between forest and forest fragments indicates that the fragments inside concessions, although relatively large in size (ca. 85 ha mixed dipterocarp forest, 280 ha peat swamp forest, 780 ha *kerangas* forest) clearly had a greatly-reduced number of bird species, when compared with the large contiguous natural forest species pool.

Table 6
Bird species identified as 'forest-dependent' in this study, cross-checked with IUCN and HBW databases.

Species	Corr*	Habitat				IUCN	MGO
		NF	DF	SF	PSF		
Argusianus argus[F/-]	1	X	X	–	X	NT	–
Cuculus micropterus[I/S]	1	X	X	X	X	LC	X
Alcippe brunneicauda[I/S]	0.83	X	X	X	–	NT	–
Malacopteron magnirostre[I/S]	0.83	X	X	X	X	LC	X
Tricholestes criniger[O/-]	0.83	X	–	X	–	LC	–
Chloropsis cochinchinensis[F/-]	0.78	X	–	–	X	NT	–
Cyornis banyumas[I/S]	0.76	X	X	–	–	LC	X
Mulleripicus pulverulentus[I/S]	0.76	X	X	–	X	VU	X
Nyctyornis amictus[I/S]	0.76	X	–	X	–	LC	X
Pomatorhinus montanus[I/S]	0.76	X	–	–	–	LC	–
Calyptomena viridis[F/S]	0.65	X	X	–	X	NT	–
Eurylaimus javanicus[I/S]	0.65	X	X	X	X	NT	X
Harpactes orrhophaeus[I/S]	0.65	X	–	–	–	NT	–
Hemiprocne comata[I/S]	0.65	X	X	X	–	LC	–
Iole olivacea[O/-]	0.65	X	–	X	X	NT	X
Anthracoceros albirostris[F/-]	0.62	X	X	X	–	LC	X
Buceros rhinoceros[F/S]	0.62	X	X	–	X	VU	–
Erythropitta granatina[I/S]	0.62	X	–	X	X	NT	X
Malacocincla abboti[I/S]	0.62	X	–	–	X	LC	–
Ptilocichla leucogrammica[I/S]	0.62	X	X	–	X	VU	–
Psilopogon chrysopogon[F/-]	0.61	X	X	X	–	LC	X
Copsychus malabaricus[I/S]	0.60	X	–	X	X	LC	–
Harpactes duvaucelii[I/S]	0.60	X	–	–	X	NT	–
Criniger bres[O/-]	0.57	X	X	–	–	LC	X
Phaenicophaeus sumatranus[I/S]	0.57	X	–	X	X	NT	X
Stachyris maculata[I/S]	0.56	X	–	X	X	NT	X
Psilopogon mystacophanos[F/-]	0.55	X	X	X	X	NT	–
Terpsiphone paradisi[I/S]	0.52	X	–	X	X	LC	X

Feeding guild—I: Invertebrate; F: FruiNect; O: Omnivore; PS: PlantSeed; S: Specialist; -: Generalist; Vegetation—NF: natural forest, DF: depleted (lightly logged) forest; SF: secondary regrowth forest; PSF: peat swamp forest; MGO: occasionally spotted in mixed garden and orchards; IUCN conservation status—LC: least concern; NT: near threatened; VU: vulnerable.

* These asterisks are the usual representation of statistical significance.

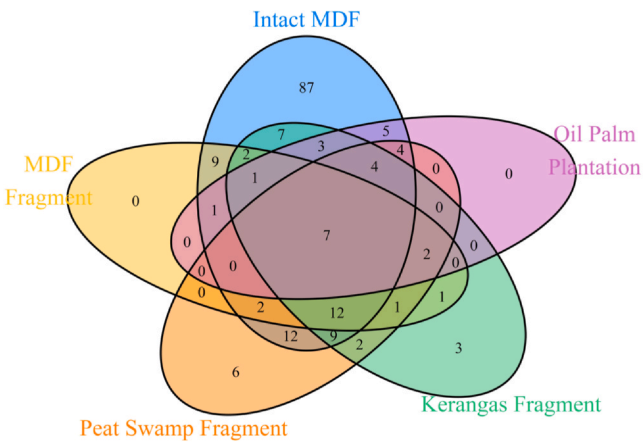

Fig. 6. Venn diagram showing numbers of shared and unique bird species in intact MDF and forest fragments within oil palm concessions. Just 7 species (generalists) are shared across intact MDF, forest fragments and oil palm plantation. MDF sites have the highest number of unique bird species (n = 87), *kerangas* forest fragments and peat swamp have just six and three respectively, while MDF fragments and oil palm plantations have no unique species.

Table 7 shows the results of the Pearson's phi correlation value for the four farming system categories: industrial plantation, smallholder plantation, traditional agroforestry, and swidden agriculture fallows.

For the industrial oil palm estate sample, the range of Pearson's correlation varied between −0.40 and 0.27, meaning that no bird species could be considered specific to that habitat, confirming the results shown in Table 4. For smallholder oil palm, the correlation ranged between −0.28 and 0.618, and just two species had strong correlation values. For smallholder rubber, the correlation ranged between −0.26 and 0.42, while for the jungle rubber habitat, the correlation ranged between −0.262 and

Table 7
Bird species identified as farm-dependent using Pearson's phi correlation.

No.	Farming system	Veg	Species name	Corr*	Recorded habitat*				IUCN
					MDF	PSF	SF	Farm*	
1	Smallholder plantation	OP	*Treron vernans*	0.89	X	–	X	X	LC
			Ixobrychus cinnamomeus	0.62	X	–	X	X	LC
2	Traditional agroforestry system	MG	*Erpornis zantholeuca*	0.71	X	–	X	–	LC
			Abroscopus superciliaris	0.68	X	–	–	–	LC
			Prionochilus xanthopygius	0.61	X	X	–	X	LC
			Psilopogon mystacophanos	0.51	X	X	–	–	NT
3	Fallow forest	OF	*Treron fulvicollis*	0.62	–	X	–	–	NT
			Cymbirhynchus macrorhynchos	0.56	X	–	X	X	LC
			Macropygia emiliana	0.51	X	–	X	–	LC
		YF	*Microtarsus melanoleucos*	0.79	X	–	X	X	NT
			Rhyticeros undulatus	0.65	X	–	X	–	V
			Ducula aenea	0.62	X	–	X	X	LC
			Macronus ptilosus	0.51	X	–	–	–	NT

Vegetation code—OP: oil palm, MG: mixed garden, OF: old fallow, YF: young fallow. Corr*: correlation value. Recorded habitat—MDF: forest; PSF: peat swamp forest; SF: secondary forest; Farm: orchards, mixed gardens, smallholder rubber, also disturbed areas that include cleared areas with scattered trees; IUCN conservation status—LC: lower concern; NT: near threatened; VU: vulnerable.

0.43. No bird species were found strongly correlating to these habitats. The correlations for mixed garden ranged between –0.21 and 0.9, and only four species of 47 were highly correlated to this environment.

The general bird species composition for the swidden agriculture landscape mosaics of food crop fields and fallows of different ages was different depending on the proximity to mature forest. The correlation was between –0.1 and 0.6 for old fallows and –0.19 0–0.65 for young fallows. Of the 151 bird species, only three species in old fallows and four species in young fallows were highly associated to these successional stages.

4. Discussion

Across a forest fragmentation gradient in Borneo, we sampled various landscape configurations at increasing distances from the continuous intact forest. This allowed us to examine how bird communities change with the increased isolation of forest patches, investigating at the same time the relative conservation value of various land uses within the agricultural matrix. We searched for potential ecological indicators with the aim of setting a baseline for future monitoring of ecosystem and environmental covariates using bird species.

Many studies on birds in Southeast Asia have shown a decrease in species richness and abundance of birds in response to land use changes (SI 2). Our results endorse this trend for West Kalimantan, showing a significant reduction of bird species richness, from the more complex, natural, old secondary and fallow-swidden forest landscape mosaic to the simplified habitat of industrial oil palm plantations. In light of our results, some unique characteristics of West Kalimantan's agricultural matrix, and the pros and cons of our approach, are worth discussing.

4.1. Agricultural matrix as habitat contribution to forest-dependent species

Amid the general fragmentation of natural habitats and homogenization of landscapes into large monoculture areas, evidence on how the agricultural matrix contributes to biodiversity conservation and functional connectivity has often been put forward (Franklin and Lindenmayer, 2009; Harvey et al., 2008; Kremen and Merenlender, 2018; Mendenhall et al., 2016; Prugh et al., 2008). A farmland bird category, defined as bird species that feed on farmlands during the breeding season (RSBP, 2020), is used in European bird monitoring (Wild Bird Index monitoring program; see Sheehan et al., 2010). This category has been successfully tested in Canada (Kirk et al., 2020), but rarely in the tropics, and the concept is difficult to apply to the traditional swidden agriculture landscapes we surveyed, where farming plots are embedded into a mosaic of fallows and forest patches. At our farmland sites in West Kalimantan, the numbers of specialist and endangered species seen in the swidden landscape decreased when we looked at smallholder and monoculture industrial plantations. From a total of 214 recorded species, just 11% were seen only on farmland and never in the forest. These all were generalists with least concern conservation status.

How the agricultural matrix contributes to the preservation of forest-dependent species in West Kalimantan landscapes was also part of our enquiries. This is contextually discussed below for each agriculture land use.

4.1.1. Fallows in forest swidden agriculture landscape mosaics

Fallows are known to hold high bird species richness, because they meet all the factors that increase biodiversity and have 'keystone structures' that provide shelter and vital services not only for birds, but also other species in the landscape (Tews et al., 2004). These keystone structures are related to the reestablishment of the vegetation's structural complexity through successional processes, thereby providing new habitat niches. However, some authors have shown that the age of a secondary forest may not necessarily be the main predictor of high numbers of forest bird species, rather its connectivity to nearby primary forest (Mayhew et al., 2019).

In West Kalimantan, oil palm and other cash crop plantations tend to replace the fallows, which are often regarded as an 'unproductive land use' linked to under-developed areas. At our sites, the fallows of the more forested landscape mosaic of the Batang Lupar and Mendalam sites harbored a higher diversity than the fallows of Sintang and Sanggau, which were far from large forest blocks. It was clear that some cross-over spillover from the forest – the movement of organisms between habitats, including dispersal and foraging activity (Blitzer et al., 2012; Tscharntke et al., 2012) – occurred in areas where the fallows were close to large continuous forest areas. This species movement from forest into neighboring agriculture land has often been reported from other landscapes in the region (Boesing et al., 2018; Tscharntke et al., 2011; Zhijun and Young, 2003).

For young and old fallow vegetation, we did not find single indicator species, rather potential combinations of species. In young fallows, the fluffy-backed tit-babbler (*Macronus ptilosus*), a conspicuous species in early successional stages of vegetation after slash and burn, was indeed very abundant in the shrub-fern savannahs common in our Batang Lupar and Mendalam sites, always in association with the yellow-vented bulbul (*Pycnonotus goiavier*), a successful opportunist (Phillipps and Phillipps, 2016). In old fallows, the black-and-red broadbill (*Cymbirhynchus macrorhynchos*), a forest-edge specialist, often spotted along the banks of rivers and in our depleted forests, was frequently associated with the common hill myna (*Gracula religiosa*).

4.1.2. Complex vs. simplified agroforestry systems

Complex agroforests are a special type of agroforestry system characterized by a forest-like multi-strata structure, in which useful tree crop species attain substantially greater density than that seen in natural forest, through planting, selection, and management (De Foresta and Michon, 1997; Schroth et al., 2004). Forest-dependent bird species have often been recorded in areas under this land use (Bhagwat et al., 2008; Oke and Odebiyi, 2007).

In our sites, conspicuous complex agroforestry systems were the local mixed tree gardens known as "*tembawang*" (Astiani and Ripin, 2016; Marjokorpi and Ruokolainen, 2003), jungle rubber—replaced nowadays by clonal varieties in monoculture plantations (Joshi et al., 2002; Wulan et al., 2006)—and "*tengkawang*" (*Shorea* spp. producing the *tallow nut*) seminatural forest gardens (Dudot, 2014; Suzuki et al., 1997; Winarni et al., 2017). These habitats are structurally similar to old secondary forests, or even natural forest in the case of *tengkawang* forest gardens (Astiani and Ripin, 2016).

Potential indicator species for these mixed gardens were all least concern forest species (IUCN, 2019), the most abundant being the white-bellied erpornis (*Erpornis zantholeuca*) and the yellow-bellied warbler (*Abroscopus superciliaris*). These are recorded as rare residents of forests throughout Borneo, but in our study, they were abundantly found in the mixed gardens of fragmented landscapes, that may act as refuges for these species. It was remarkable that the most isolated sites (Sanggau and Sintang) maintained such a high number of forest bird species, with Sanggau having a greater abundance. For Sanggau, this is without doubt due to the presence of the rather exceptional *parua* communal forest gardens, in addition to the *tembawang* mixed gardens – farming systems that did not exist in Sintang. Even without considering the *parua*, the *tembawang* traditional mixed garden contributed 19% of the overall bird species richness at the Sanggau site, remarkably the highest contribution after natural forest in that area. These *tembawang* became refuges for many forest bird species, sometimes even harboring more forest birds than the nearby depleted forest.

Although the jungle rubber areas we studied were less rich in bird species than fallows and mixed gardens in the same area, they still harbored high species richness and abundance. In Sumatra, the bird species richness of jungle rubber was once found to be similar to that of primary forest and old secondary forest (Beukema et al., 2007; Joshi et al., 2002; Thiollay, 1995). Strikingly, while the survey done in 1992–1993 (Thiollay, 1995) indicated a very similar bird species richness compared to nearby primary forest and jungle rubber (sr: 180 and sr: 105), the replicated survey at the same location 22 years later resulted in a greatly reduced number of bird species recorded in both forest (then heavily disturbed) and jungle rubber (sr: 26, sr: 17) (Prabowo et al., 2016). This shows how quickly the general habitat became degraded and how imperative long-term studies and monitoring programs are, because of the time lag issues in ecological impact assessment.

Other agroforestry systems exist in Indonesia that are almost absent from West Kalimantan. Cocoa and coffee could be important land uses for birds. Our mixed garden species richness was similar to that found in cocoa agroforestry near the Lore Lindu National Park (Clough et al., 2009; Waltert et al., 2004). Those authors showed that one-fourth of the forest specialists detected in cocoa agroforestry could not exist without the direct presence of natural forest. A high density of multi-strata shade trees plays an important role in supporting bird diversity across all functional groups, as was also demonstrated for coffee plantations (O'Connor, 2005; Siebert, 2002).

4.1.3. Smallholder vs. industrial (rubber and oil palm) plantations

It is a well-known fact that bird species richness decreases dramatically after forest conversion to monoculture plantations (Aratrakorn et al., 2006; Danielsen and Heegaard, 1995; Peh et al., 2006), and our study supports these findings. However, we did notice some differences between smallholder and industrial plantations.

Smallholder oil palm fields were always part of a mosaic of various land uses and successional stages that influenced overall biodiversity level. Bird abundance in smallholder oil palm fields was fivefold higher than that of industrial plantations, in line with studies on Peninsular Malaysia (Azhar et al., 2013; Yahya et al., 2017), and all species were of least concern status, confirming the results of other studies in the region (Aratrakorn et al., 2006; Fujita et al., 2016). The only identified potential indicator of the smallholder oil palm landscape, *Cinnamon bittern*, is also commonly recorded in irrigated paddy fields and grasslands near settlements (HWB, 2019). This bird seems to have adapted to the smallholder oil palm mosaic landscape as well.

This species can be used as an indicator of the health of the smallholder plantation, for instance, by checking its population trend after insecticide utilization.

We found no potential indicator species for environmental quality in either industrial oil palm or rubber plantations, and no bird species were significantly associated to these land uses. Contrary to our findings for oil palm sites, some of the species recorded in the monoculture rubber plantations were also observed in the forest, although at a very low abundance level. These were mostly generalists of least concern conservation status.

As for other land uses, the proximity of forest affects the number of birds present at oil palm and rubber plantations, facilitating a daily arrival of commuters from forest to plantation to seek food (Sheldon et al., 2009). At our oil palm concession sites, far from continuous intact forest, half of the 28 species were never seen in the closest forest, while the others were occasionally spotted at a low abundance level.

Not surveyed in our landscape, because this land use represented very small surfaces, tree (pulp and paper) plantations are also known to affect bird species richness. The *Paraserianthes falcataria* stand structure appeals to certain groups of birds, thereby maintaining some level of biodiversity inside the plantation (Hanowski et al., 1997; MacArthur and MacArthur, 1961; Mitra and Sheldon, 1993; Rotenberg, 2007).

4.2. Concepts and methodological considerations

The concepts of ‘specialization’ and ‘indicator species’ are both often perceived or understood differently. This can make comparisons with other works difficult, and impact the choice of methods to identify meaningful indicators for baseline monitoring of populations. These aspects are discussed below in line with our results, together with identified shortcomings.

It is often argued that the more specialized a species is, the more sensitive it is to fragmentation and degradation, and that measuring specialization may thus be helpful in predicting which species are likely to thrive in degraded landscapes (Devictor et al., 2010; Kirk et al., 2020, for a review on the issue). However, criteria used for specialist identification vary, with different definitions for forest dependency leading to potentially different results. For instance, following Bennun et al. (1996) classification of forest specialists (undisturbed forest), forest generalists (forest strips and edges, breeding in the forest), and forest visitors (sometimes in the forest, not dependent, familiar and breeding in non-forest habitats), Douglas et al. (2014) list forest-dependent specialists but also introduce a forest-dependent generalist category. These authors found that ‘forest-dependent generalists’ were positively related to and benefitted from the presence of native tree species on agricultural land. Our definition of specialist was more circumscribed, based on diet, and in our records in West Kalimantan, no species appeared as forest-dependent ‘generalists’. Forest specialists were never spotted inside plantations, but some of the generalists observed in farmland were occasionally recorded inside the forest.

Other authors suggest using the occurrence or dominance of species to characterize specialization (Devictor et al., 2008; Hutto, 1998). Testing this idea, we used Pearson’s phi coefficient, and found that taking only dominance or occurrence into account did not sufficiently define the ecological specialization besides elementary information on the “preference” for a particular habitat. Besides, frequency and abundance measurements are also known to be potentially affected by many factors at the time of the survey (Lõhmus et al., 2018; Morrison, 1986; Steele et al., 1984), and we do not recommend using only occurrence or dominance to define specialization.

It is also commonly understood that specialists, as they use a restricted range of resources, must automatically qualify as good indicator species. That is questionable since it is difficult to use rare specialist species as indicators, for instance, as some level of density and size of population are required for meaningful monitoring. While we acknowledge that the indicator concept itself has several limitations, notably that no single biological indicator can provide all the information needed to interpret the response of an entire ecosystem (Carignan and Villard, 2002; Rapport, 1990), and that a single population may not reflect the complexity of the environment (Lindenmayer and Fischer, 2003; Lindenmayer and Likens, 2011; Simberloff, 1998), we found that the use of the IndVal index, as a proxy to measure individual indicator species or potential associations between species groups, proved to be very valuable. The advantage of the IndVal index is its nonhierarchical design, so it can be generalized to any site arrangement, compute the value of species presence–absence, systematically cluster site groups, and calculate the value of specificity (A) and fidelity (B).

For the data collection process, sampling intensity was our first concern. The computed rarefaction curves leveled off, and although some rare bird species may not have been assessed because of detectability issues, our data should be considered fairly representative of the Borneo lowland forest and agriculture matrix landscape.

Secondly, we did not use distance sampling while recording bird presence and abundance. We were, therefore not able to assess detection function models (Buckland et al., 2015) in determining abundance. Our naïve estimates of abundance were, therefore, probably an underestimate of the actual abundance values (Bailey et al., 2004). However, in their studies on long-term variation of abundance or occupancy of species, many authors show how the two types of estimates are highly correlated (Blake et al., 2017; Hegerl et al., 2017; Rovero et al., 2014). Since the purpose of our survey was to compare various land use and vegetation types, a naïve estimate of abundance provides a satisfying alternative for assessing patterns of change over time, while still recognizing that our estimates are likely lower than real abundance.

Lastly, we did not collect data on hunting practices in our sites. Helmeted hornbill hunting in West Kalimantan is a well-known threat to the species (Beastall et al., 2016), and the songbird trade is still at its highest level in Kalimantan (see Rentschlar et al., 2018). Future research should include this data when monitoring the population trends of our identified indicator species.

4.3. Landscape management, monitoring and the way forward

It has been argued that landscape structure modification and habitat loss will have many negative consequences for ecosystems, to the point they may collapse (Chapin et al., 1997; Ellison et al., 2005). Notably, the loss of keystone species linked to particular ecosystem functions will hamper ecological processes and the production of services (Díaz and Cabido, 2001; Ellison et al., 2005). Some keystone species functions directly affect other species, and their loss will result in cascading alterations leading to more severe habitat fragmentation and degradation, and further species loss (Terborgh et al., 2010). It is therefore crucial to be able to monitor ecosystem health and long-term trends in wildlife population and diversity, including keystone species, to determine the impact of this generalized fragmentation, habitat quality degradation, and monoculture agricultural transformation on species. Monitoring the status of some well identified groups may allow us to determine critical thresholds, such as forest fragment patch size, shape or isolation status, beyond which the original landscape structure and ecosystem state will be irretrievably lost, unless enormous and costly efforts are made around restoration and enhancement of the connectivity between vegetation fragments.

Our results highlight the relative impacts of different agricultural practices and land uses on the potential conservation outcomes of forest birds, notably the need to consider the integration of fragmented habitats into landscape management schemes to maintain a certain level of forest bird diversity in the agricultural matrix.

In the present configuration of this agricultural matrix in West Kalimantan, species in smallholder and monoculture plantations mostly appeared to be generalists, and the abundance and diversity of birds was, as expected, clearly inferior to that seen in natural forest, as well as in fallows and agroforestry. Farm species were strikingly low in abundance and had little conservation value as per IUCN standards, industrial oil palm plantations being the worst in this respect. Notable exceptions were traditional mixed gardens associated with old fallows. In line with other studies (De Foresta and Michon, 1997; Padoch and Peters, 1993), we found that these traditional agroforestry plots linked to swidden agriculture systems have higher conservation value when compared with industrial and smallholder plantations, as they harbor highly associated and forest-dependent, often endangered, bird species. They have high potential as shelters for biodiversity conservation, and for contributing to forest connectivity and restoration initiatives. However, their resilience in the long run is uncertain. It is noteworthy that bird and other species occurring in such isolated forest patches embedded within a non-forest matrix may be more sensitive to sudden environmental stressors, or may experience “ecological trapping” phenomenon (Pärt et al., 2007). How long these habitats can maintain species composition, population viability, and ecosystem functions similar to that of intact forest is unknown, due to the lack of monitoring programs. This is also the case for the retention of forest patches and riparian strips within oil palm estates observed in our study; these areas could support bird diversity, but long-term data are needed.

For the development of such monitoring programs, much more understanding on the behavior, reproductive rate and long-term population dynamics of bird species will be needed. In particular, understanding of the thresholds for minimum viable population size (Bolger et al., 1991; Ryan and Siegfried, 1994; Soulé, 1987) is both critical and lacking. In addition, and since species richness and composition can hide important information about the impacts of land-use change on species traits and functional ecology, parallel studies devoted to functional diversity as an indicator of ecological conditions should be conducted. These will provide additional information and understanding of how diet guilds, not just species richness or abundance, respond to landscape fragmentation, the isolation of forest patches and conversion, shedding further light on the bird population dynamics of endangered forest gardens and traditional complex agroforestry ecosystems in Borneo.

5. Conclusion

In the context of drastic landscape changes in Borneo, we assessed the relative contribution that forest habitat fragmentation, and various land uses make to the original forest bird diversity, with the ultimate goal of setting a baseline for future monitoring of the impact of changes on landscape structure using bird species, and assessing how different agricultural options affect environmental and habitat quality in West Kalimantan.

We provided new data on the impacts of these land-use changes on Bornean birds, confirming a significant reduction in bird species richness from complex forest structures to simplified monoculture habitats. We used three complementary approaches, specialization-dominant species, single species, and groups of species as indicators, and found several indicator species significantly associated to forest, depleted or old secondary forest, and mixed gardens. These species can contribute to future conservation and agricultural management decisions.

While the area devoted to industrial agriculture keeps expanding, our results emphasize that in the agricultural matrix, farm-dependent species show strikingly low species richness and have little conservation value. Notable exceptions were the traditional mixed gardens and old fallows associated with swidden agriculture, when in proximity to forest, confirming the importance of such habitats to forest bird species conservation. However, the long-term preservation of such mosaic landscapes is uncertain, and there is a lack of monitoring programs that can contribute to long-term biodiversity conservation and ecosystem service maintenance.

Keeping in mind the contextual nature of the indicator concept, our list of potential bird indicator species sets a baseline for such monitoring programs. This list can help in the monitoring of habitat quality and the health of forest agriculture landscape mosaics, as well as improve the effectiveness of management, conservation and monitoring in future. In addition to existing lists of threatened species (IUCN), knowing population trends and dynamics for selected indicator bird species will increase the effectiveness of landscape management and monitoring, ensuring the sustainability of forests and tree-based agriculture land mosaics; it will also boost the future monitoring of restoration designs reconnecting degraded and fragmented forest landscapes. Maintaining such landscape features will require the strengthening of current landscape management, through strategies to promote the sustainable use of bird-friendly habitats.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01610.

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