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RESEARCH ARTICLE

Understorey bird responses to the abandonment of artisanal gold mining in Guyana

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Abstract

1. Artisanal small-scale gold mining (ASGM) is linked to deforestation across Amazonia. In the Guiana Shield region, ASGM is responsible for around 90% of deforestation and forest degradation, making it the largest threat to species richness in this biodiverse region.
2. In Guyana, ASGM sites typically remain surrounded by intact forest, creating an 'enclosed edge' ecosystem. We currently have a poor understanding of the biodiversity value of these areas, or the capacity for ecological recovery once mining activity has ceased.
3. We surveyed 16 ASGMs of differing mine sizes and years since abandonment, sampling bird community and vegetation structure in the centre of each mine, the immediate mine edge, 100 m from the mine edge and in five control forest sites.
4. Mines and their immediate edges supported unique bird assemblages, with few forest-dependent species and many generalists. However, species composition in the forest 100 m from mine edges remained similar to control forest, implying that any edge effects radiating from mines were minimal. Forest-dependent species numbers were positively related to time since mine abandonment, yet full recovery of the bird community was not observed, even in mines that ceased activity 20 years previously.
5. We found a positive relationship between the number of forest-dependent bird species and canopy cover, suggesting that as vegetation regrows and canopy cover increases, the forest avifauna is able to recover.
6. *Policy implications.* Whilst many forest-dependent birds will avoid the exposed mine centre, diversity at the immediate edge has the potential to recover, particularly in smaller and older mines. As we have found that natural vegetation recovery occurs at the mine edges and not within the centre, targeted restoration efforts might focus on mine edges to enhance recovery rates, whilst ensuring that populations in nearby forest remain viable sources to repopulate these degraded habitats.

KEYWORDS
Amazonia, avian, Guiana Shield, Guyana, rainforest, recovery, restoration

1 | INTRODUCTION

Tropical forests play a critical role in climate regulation and are among Earth's most ecologically complex ecosystems (Lewis et al., 2015; Pillay et al., 2022). More than 90% of all global deforestation occurs in the tropics (UN FAO, 2020), resulting in edge effects that impact remaining forest habitat (Bourgoin et al., 2024). Over the last 30 years, the world's largest and most biodiverse tropical forest, the Amazon, has lost 20% of its areal extent, primarily due to agricultural expansion, logging, urbanisation and mining (Bourgoin et al., 2024; Kuschnig et al., 2019).

Forests of the Guiana Shield cover 26% of the Amazon (2.3 million km^2 of Guyana, Suriname, French Guiana, Brazil, Venezuela and Colombia) and are rich in biodiversity and carbon (Baccini et al., 2012; Grenyer et al., 2006). Since the early 2000s, the primary drivers of deforestation and forest degradation in this region have shifted from agricultural conversion to artisanal small-scale gold mining (ASGM) (Alarcón-Aguirre et al., 2023; Kalamandeen et al., 2018). More recently, increasing gold prices have led to a 'gold rush', with ASGM now accounting for approximately 90% of deforestation within the Guiana Shield (Kalamandeen et al., 2020). In Amazonia, artisanal small-scale gold mines vary in size, shape and physical features, including extensive areas of barren mud or sand, mine pits (where the soil or sand is extracted), 'overburden' (removed and deposited soil or sand) and tailing ponds (where water collects after being filtered for gold) (Figure 1). These features tend to inhibit the regrowth of plants by removing nutrients and the seed bank. Indeed, studies of abandoned gold mines in this region have documented some of the slowest rates of forest recovery globally (Alarcón-Aguirre et al., 2023; Kalamandeen et al., 2020), although vegetation specifically in overburden areas has a reasonable recovery rate comparable to that of land converted to pasture (Kalamandeen et al., 2020).

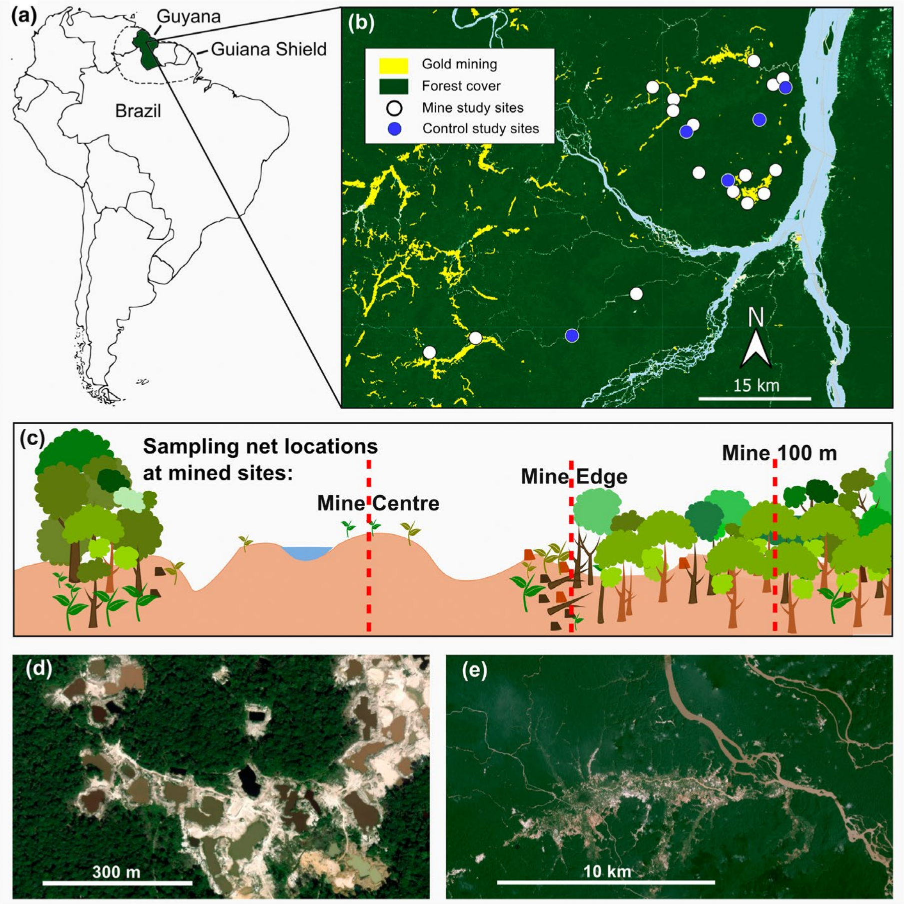

FIGURE 1 Locations of mine survey sites in Guyana. (a) Location of Guyana and the Guiana Shield (dashed line) in South America, (b) study area showing survey sites, forest cover and the distribution of gold mining activity, (c) the layout of the three net locations in and around gold mines, (d and e) satellite imagery showing examples of gold mines of varying sizes/shapes from Bing Maps (2024) and PBC and Planet (2024).

The current literature on forest loss and degradation within Amazonia has focused heavily on conversion to agriculture, forest fragmentation and associated edge effects (Barlow et al., 2006; Birch et al., 2024; Stouffer, 2020). It is widely accepted that declining fragment size has a negative influence on biodiversity, to the point where small fragments are often unable to sustain the populations of many species (Laurance et al., 2018; Lees & Peres, 2008; Stouffer & Bierregaard Jr., 1995). In contrast, ASGM creates 'enclosed edges', which are pockets of deforestation surrounded by continuous forest (Figure 1), representing an ecological system that is not well understood. We expect abandoned mines to alter local ecological communities by changing the microclimatic and structural characteristics of the habitat in the immediate area, as well as causing edge effects that penetrate surrounding forest (Bourgoin et al., 2024; Pfeifer et al., 2017). This impact may also depend on the surrounding landscape context. Larger blocks of continuous forest can buffer edge effects and facilitate recolonisation compared to mines located near forest fragments. To date, little is known about the biodiversity of artisanal small-scale gold mines after the cessation of activity, as research has mainly focused on mapping the extent of the mining problem and the potential for mercury contamination (Kalamandeen et al., 2018; Pisconte et al., 2024; Schwartz et al., 2023).

Birds are valuable bio-indicators of environmental change, responding predictably to disturbances (Barlow et al., 2006; Powell, Wolfe, et al., 2015). Birds are also key seed dispersers and play a vital role in forest regeneration (Gardner et al., 2019). In Amazonia, studies have indicated that forest specialist bird guilds, such as ant following and understorey insectivores, are less adaptable to anthropogenic change and canopy openings than others (Barlow et al., 2006; Harris et al., 2024; Laurance & Gomez, 2005; Powell, Cordeiro, & Stratford, 2015). Furthermore, many understorey species are averse to gap-crossing, making them particularly vulnerable to isolation within fragments by limiting their dispersal ability (Claramunt et al., 2022; Laurance et al., 2004; Laurance & Gomez, 2005). In contrast, more mobile canopy-dwelling birds typically traverse large areas of unsuitable habitat, making them less directly affected by the small-scale disturbances created by abandoned gold mines, as demonstrated by Barros et al. (2022) and Bradfer-Lawrence et al. (2018). The sensitivity and greater breadth of specialisation in understorey birds, compared to canopy birds, make them an ideal study system to examine the impacts of small-scale gold mining on biodiversity in tropical forests (Bradfer-Lawrence et al., 2018).

Here, we use understorey birds as ecological indicators in and around abandoned artisanal small-scale gold mines to understand the biodiversity value, edge effects and capacity for recovery of these 'enclosed edge' ecosystems. We undertake our research in Guyana, where historically low deforestation rates have recently escalated due to the expansion of ASGM (Benn et al., 2020). Predictions of gold mining expansion in Guyana suggest that up to 9% of total forest cover could be lost by 2043 without intervention (Hayes et al., 2023). We address three research questions: (i) how do bird communities vary from the centre of the mine to the surrounding forest?; (ii) does canopy cover influence the species richness of forest-dependent bird species?; and (iii) is there evidence of bird community recovery within mined sites?

2 | METHODS

2.1 | Quantifying bird and landscape covariates

We based our study on artisanal small-scale gold mines where mining activity had ceased ('abandoned'), to the west of the Essequibo River in Guyana (Figure 1) during the dry seasons between February 2022 and May 2023. This region is predominantly lowland moist tropical forest (Espinosa et al., 2022). We surveyed 21 sites: 16 artisanal small-scale gold mines (hereafter referred to as 'Mines') of varying sizes and years since abandonment and five forest control sites (Table 1). All sampled sites were separated by at least 1 km to maintain spatial independence, avoiding forest fragments. Sites were selected randomly from the subset of mining areas that were accessible and met these criteria. Information on the year of abandonment was obtained from local miners/workers who had existing knowledge of the sites and their history. All mines in this study were located within a largely intact forest landscape embedded with patches of deforestation from gold mining (Figure 1b). The mines varied in their stage of ecological recovery; some supported only sparse vegetation such as grasses, whilst others had developed patches of shrubs and small trees. Several sites also contained standing water or small streams running through the centre or along the edge. Photographic examples of these varied mine conditions are provided in Figure S1. At each site, we classified the soil type following Espinosa et al. (2022) according to whether it was sandy (>85% sand) or loam (mostly clay or silt with <50% sand) (Table 1). Permission to undertake research was obtained from the Guyana Environmental Protection Agency (EPA) and the Ministry of Amerindian Affairs (MOAA) to undertake research on indigenous lands (Karrau Region 7) under the permit reference number: 20211209 BR023.

We surveyed understorey birds at each site using 12 mist nets (12 × 2.6 m, mesh size 36 mm). We used four nets at each of three net locations within each mine: Mine Centre (within or alongside regrowing vegetation in the centre of the mine), Mine Edge (running perpendicular along the edge vegetation), and 100 m perpendicular from the edge of the mine within surrounding forest (Mine 100 m; Figure 1c). The choice to sample at 100 m followed earlier studies (e.g. Laurance et al., 2002) that found edge effects on birds to subside by 100 m from a forest edge. At the control sites, all 12 mist nets were placed together in a line. Mist nets were opened at 06:00 and closed at 18:00 (although they were also closed during periods of heavy rain) for 4 days, equating to a total of ~576 mist net hours per site (12 nets × 12 h × 4 days = 576 h). Nets were checked every 30 min (except for the Mine Centre nets, which were checked every 15 min between the hours of 11 AM and 3 PM due to extreme heat). The decision to set nets for several days was based on optimising the number of hours that nets were operational since moving nets would reduce sampling time (Marques et al., 2013), especially for smaller

TABLE 1 Years since mine abandonment, soil type (following Espinosa et al., 2022), mine area (m^2) and the percentage of mining-associated deforestation within buffers of 100 m, 500 m 1 km for each of the 16 mines and five controls (C1-5) surveyed. Buffers were generated from the Mine Centre.

Site	Years since abandonment	Soil type	Mine area (m^2)	Mining in 100 m buffer (%)	Mining in 500 m buffer (%)	Mining in 1 km buffer (%)
1	7	White sand	27,000	68.2	7.4	2.4
2	5.5	Loam	123,000	90.9	28.6	26.3
3	10	White sand	251,000	99.9	39.8	27.3
4	7	White sand	7000	19.3	9.0	20.9
5	3	White sand	41,000	97.5	21.5	17.8
6	4	Loam	12,000	49.5	15.3	33.1
7	15	Loam	356,000	55.8	28.7	32.3
8	15	Loam	51,000	68.6	13.2	13.1
9	20	Brown sand	19,000	48.3	3.0	0.8
10	12	Loam	226,000	97.3	20.3	12.8
11	9	Loam	90,000	86.4	26.3	14.6
12	20	White sand	436,000	79.4	33.8	13.1
13	15	White sand	19,000	68.5	5.0	1.2
14	4	White sand	16,000	42.3	1.9	0.5
15	10	White sand	566,000	53.1	20.8	16.9
16	5	Loam	25,000	70.6	6.9	1.8
C1	—	White sand	—	—	—	—
C2	—	White sand	—	—	—	—
C3	—	Loam	—	—	—	—
C4	—	White sand	—	—	—	—
C5	—	Loam	—	—	—	—

mine sites where options were limited. We identified recaptures through a small clip on one tail feather to reduce handling time and excess stress on birds. Birds were identified to species level using a regional field guide (Ascanio et al., 2017) and categorised into three primary feeding guilds: frugivores, insectivores and nectarivores. We also classified species as forest-dependent or not forest-dependent (hereafter referred to as 'generalists'), based on whether species are known only from forested habitats, or also occur widely in disturbed landscapes in the Guianas (Table S1). This was done by B. J. O'Shea who has more than 20 years of experience surveying birds in the Guianas. Ethical approval was obtained from the University of Kent (application ref.: 01-PGR-21/22.).

Adjacent to each net location, canopy height was visually estimated to the nearest 5 m by an experienced observer. Canopy cover was measured using an iPhone 10 photograph taken at a height of 1.5 m above the ground at the centre of the plot, before calculating the canopy cover percentage in ImageJ (Version 1.49b) following Xiong et al. (2019). At control sites these were carried out at the first net, the 6th net and the 12th net and then averaged between the three measurements. To understand the impact of mining activity at local and landscape levels, we also determined the percentage of mining-associated deforestation within three radii from the Mine Centre net location using Sentinel-2 data (10 m resolution): 100 m, 500 m and 1 km (Table 1). We did this by drawing polygons around all of the mining areas within the maximum buffer in QGIS Development Team (2025). The package 'sf' (Pebesma, 2022; R-spatial community, 2024), with functions 'st_buffer' and 'st_intersection', was used to calculate the percentage cover values. This method was also used to calculate the area of the study mines to the nearest m^2.

2.2 | Data analysis

All bird recaptures and species recorded only once across the entire dataset were excluded from analyses. To examine the influence of mining on birds across the landscape, our analyses were undertaken at two levels—firstly the 'site' level where we compared Mines versus controls and secondly by disaggregating the Mine data into the 'net location' level, where we compared Mine Centre versus Mine Edge versus Mine 100 m versus control. All analyses were undertaken in R (R Core Team, 2024).

We explored the variation in bird community structure between sites and net locations using non-metric multi-dimensional scaling (NMDS). To account for minor deviations from the standard sampling effort due to weather, survey effort was standardised to capture rates per 100 mist net hours. The ordinations were based on

Bray–Curtis dissimilarity coefficients of species-level bird capture rates and calculated using the function 'vegdist' in the R package 'Vegan' (Oksanen et al., 2022). We used permutational multivariate analysis of variance (ADONIS) and pairwise ADONIS (Oksanen et al., 2022) to test for differences in bird community structure between sites and net locations, with Bonferroni corrections applied to adjust for Type I error rates. To ensure that assumptions of ADONIS were met, we also tested for homogeneity of dispersion using the betadisper function in Vegan. The dispersion test evaluates whether the variability in community composition differs significantly among groups, which is a key assumption for interpreting ADONIS results.

To identify species driving the bird communities at different net locations, we conducted indicator value analysis (IndVal) in 'Vegan' (Table 2; Dufrêne & Legendre, 1997; Oksanen et al., 2022) also using the data standardised to 100 net hours. IndVal assesses the degree to which a species exhibits specificity (uniqueness to a particular habitat) and fidelity (frequency of occurrence in a particular habitat) to identify indicator species.

To estimate species richness, we used the 'iNEXT' package in R (Hsieh et al., 2019). We generated species accumulation curves at the level of all sites pooled (separately for Mine and control) and all net locations pooled (Mine Edge, Mine Centre, control). We also estimated richness for each site and net location level individually. We rarefied from 100 iterations and extrapolated from a standard sample size of 50 individuals for the site level and 30 for the net location level to account for differences in sampling effort. These were repeated for forest-dependent and generalist species and for each feeding guild separately (whereby estimates were derived at different numbers of individuals for each grouping depending on the number of individuals at each site within each grouping—shown in Table S4). Our accumulation curves allowed for visual comparison of pooled species richness representing landscape scale (gamma) diversity, whilst our estimated richness at the site level allowed us to explore potential relationships with covariates (see GLMs below) and to test for differences in point level (beta) diversity. We employed independent *t*-tests to compare estimated richness and capture rates between the Mine and control sites at the site level. Additionally, paired *t*-tests were conducted to compare these metrics between net locations (Mine Centre vs. Mine Edge; Table S5) estimated richness and capture rates. Due to multiple comparisons, Bonferroni corrections were applied to adjust for potential Type I errors.

Generalised linear models (GLMs) were used to investigate potential relationships between estimated bird species richness at each Mine, with years since mine abandonment, mine area (m^2), deforestation from mining in three different buffer distances around mines, canopy cover and canopy height. To ensure comparability and improve the interpretability of the model coefficients, all continuous potential predictor variables were standardised to the same scale (by subtracting the mean and dividing by the standard deviation resulting in a mean of zero and standard deviation of one). To account for potential collinearity, any variables with a variance inflation factor score >5 were removed from the model. We evaluated all possible combinations of predictor variables using the dredge function from the R 'MuMin' package and retained models with ΔAICc <2 for further inspection. Although multiple top models were identified, we did not perform model averaging. Instead, we report the single best model, the one with the lowest AICc as our final model.

3 | RESULTS

A total of 1758 birds were captured from 134 species across the 21 sites. Three species dominated: *Ramphocelus carbo* (silver-beaked tanager; $n=193$), *Pseudopipra pipra* (white-crowned manakin; $n=119$) and *Campylopterus largipennis* (grey-breasted sabrewing; $n=103$). Of the 505 individual forest-dependent birds captured during this study, only 75 were in the Mine Centre, most of which were either *C. largipennis* or *Thalurania furcata* (fork-tailed woodnymph) (55% and 20%, respectively, both hummingbird species). In contrast, a higher number of forest-dependent bird species, totalling 188 individuals, were captured at the Mine Edge (Figure 3). Median canopy height and canopy cover increased sequentially from the Mine Centre to the Mine Edge, to Mine 100 m and on to the control sites (Figure S2).

NMDS ordinations and ADONIS tests at the site level showed that bird community composition within the mines differed significantly from controls (ADONIS $F=7.6$, $p=0.001$; Figure 2a). At the net location level, the Mine 100 m and control bird communities were indistinguishable. Mine Centre, Mine Edge and control net locations each had distinct bird community structure (pairwise ADONIS Bonferroni corrected $p=0.006$ for all three combinations; Figure 2b; Table S3).

At the site level, the betadisper test was not statistically significant ($p=0.077$), indicating that the variability in bird community composition did not differ significantly between the mine and control sites. This suggests that at the site level, the observed differences in community composition (as indicated by the ADONIS test) are not due to differences in variability between the groups. However, at the net location level, the test was statistically significant ($p=0.001$), indicating that dispersion did vary among habitat types. Pairwise comparisons (Table S4) showed that Mine Edge had significantly higher within-group dispersion than Control sites (Bonferroni-adjusted $p<0.001$), and marginally higher than Mine Centre ($p=0.075$). These results suggest that increased ecological heterogeneity at the Mine Edge may contribute to observed differences in bird community composition, particularly at finer spatial scales.

This initial analysis revealed that the avifauna sampled in the forest near mine edges (i.e. Mine 100 m) was indistinguishable from that of the controls (Bonferroni corrected $p=0.978$, Table S3, Figure 2). Therefore, for subsequent analyses we removed the Mine 100 m net location data as our objective was to assess the impact of mines on the birds, and this initial analysis showed that edge effects were not impacting bird community structure at that distance from mines. Consequently, apart from our initial ordinations where all net locations are included, the sampling effort in all subsequent analyses is higher in the controls than the Mines, because the Mine data had the 100 net location removed.

TABLE 2 Indicator species for the Mine Centre, Mine Edge and control net locations determined using IndVal (Dufrêne & Legendre, 1997).

Scientific name	Common name	Feeding guild	IndVal stat	p
Mine Centre				
Ramphocelus carbo	Silver-beaked tanager	Frugivore	0.938	0.001***
Tyrannus melancholicus	Tropical kingbird	Insectivore	0.901	0.001***
Sporophila castaneiventris	Chestnut-bellied seedeater	Granivore	0.875	0.001***
Chloroceryle americana	Green kingfisher	Piscivore	0.829	0.001***
Columbina passerina	Common ground dove	Granivore	0.817	0.001***
Coerba flaveola	Bananaquit	Nectarivore	0.715	0.005**
Myiozetetes cayanensis	Rusty-margined flycatcher	Insectivore	0.707	0.001***
Chlorestes notata	Blue-chinned sapphire	Nectarivore	0.652	0.006**
Synallaxis gujanensis	Plain-crowned spinetail	Insectivore	0.641	0.009**
Euphonia violacea	Violaceous euphonia	Frugivore	0.591	0.018*
Myiarchus tuberculifer	Dusky-capped flycatcher	Insectivore	0.559	0.028*
Myrmotherula surinamensis	Guianan streaked antwren	Insectivore	0.559	0.027*
Thraupis episcopus	Blue-grey tanager	Frugivore	0.559	0.046*
Saltator maximus	Buff-throated saltador	Frugivore	0.557	0.033*
Mine Edge				
Pseudopipra pipra	White-crowned manakin	Frugivore	0.762	0.005**
Cercomacroides tyrannina	Dusky antbird	Insectivore	0.75	0.002**
Thamnophilus murinus	Mouse-coloured antshrike	Insectivore	0.625	0.011*
Xiphorhynchus pardalotus	Chestnut-rumped woodcreeper	Insectivore	0.594	0.047*
Lophotriccus galeatus	Helmeted pygmy tyrant	Insectivore	0.548	0.038*
Control				
Isleria guttata	Rufous-bellied antwren	Insectivore	0.894	0.001***
Willisornis poecilinotus	Scale-backed antbird	Insectivore	0.871	0.001***
Myiobius barbatus	Whiskered myiobius	Insectivore	0.863	0.001***
Pithys albifrons	White-plumed antbird	Insectivore	0.849	0.001***
Gymnopythis rufigula	Roufus-throated antbird	Insectivore	0.841	0.001***
Epinecrophylla gutturalis	Brown-bellied stipplethroat	Insectivore	0.775	0.001***
Geotrygon montana	Ruddy quail-dove	Omnivore	0.775	0.001***
Glyphorynchus spirurus	Wedge-billed woodcreeper	Insectivore	0.709	0.003**
Thamnomanes ardesiacus	Dusky-throated antshrike	Insectivore	0.676	0.001***
Myrmotherula longipennis	Long-winged antwren	Insectivore	0.65	0.002**
Bucco capensis	Collared puffbird	Insectivore	0.632	0.010**
Formicarius analis	Black-faced antthrush	Insectivore	0.632	0.020*
Tunchiornis ochraceiceps	Tawny-crowned greenlet	Insectivore	0.632	0.010**
Xenops minutus	Plain xenops	Insectivore	0.632	0.010**
Thamnomanes caesius	Cinerous antshrike	Insectivore	0.629	0.002**
Platyrinchus saturatus	Cinnamon-crested spadebill	Insectivore	0.605	0.012*
Schiffornis olivacea	Guianan schiffornis	Insectivore	0.558	0.007**
Myrmotherula menetriesii	Grey antwren	Insectivore	0.553	0.004**

Note: IndVal stat values indicate the strength of a species to the habitat with higher values indicating a strong affiliation. IndVal stats are ordered from largest to smallest within each section.

***$p < 0.001$, **$p < 0.005$, and *$p < 0.05$.

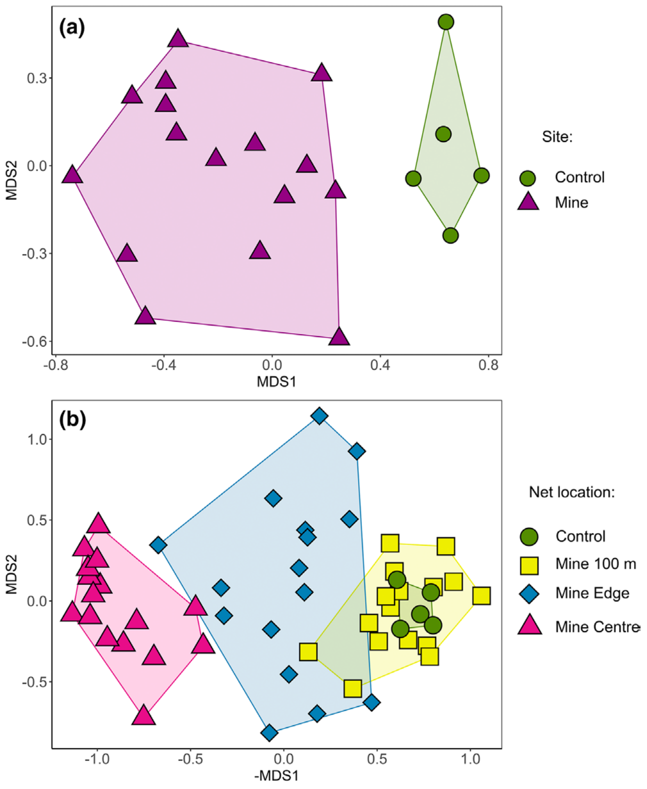

FIGURE 2 Non-metric multi-dimensional scaling (NMDS) ordinations of the bird communities at (a) the site level (Mine equates to the three mine net locations combined) (stress = 0.148) and (b) the net location level (without the Mine 100 m data, which was excluded) (stress = 0.186). All differences are significantly different (*$p < 0.05$) apart from Control vs. Mine 100 m (b). Full ADONIS tests of the comparisons are provided in Table S1.

Indicator species analysis showed that each net location (Mine Centre, Mine Edge and control) had a distinct suite of indicators. Eighteen species were associated with the controls, five with the Mine Edge and 14 with the Mine Centre (Table 2). Indicators of control sites were mostly forest-dependent insectivorous species, such as *Isleria guttata* (rufous-bellied antwren), *Willisornis poecilinotus* (scale-backed antbird), *Myiobius barbatus* (whiskered myiobius), *Pithys albifrons* (white-plumed antbird) and *Gymnopythis rufigula* (rufous-throated antbird). In the Mine Edge, the two species with the highest indicator scores were *Pseudopipra pipra* (white-crowned manakin) and *Cercomacroides tyrannina* (dusky antbird). Whilst a greater number of indicator species were associated with the centre of mines, all were habitat generalists, including *Ramphocelus carbo* (silver-beaked tanager), *Tyrannus melancholicus* (tropical kingbird), *Sporophila castaneiventris* (chestnut-bellied seedeater) and *Chloroceryle americana* (green kingfisher).

Species accumulation curves showed that overall pooled species richness was higher in the Mine than control sites (Figure S3a). However, when we consider forest-dependent and generalist species separately, the controls had greater species richness (Figure S3b), whilst the mines contained more generalist species (which were almost absent in the controls; Figure S3c). At the net location level, species richness was highest in the Mine Edge, followed by the Mine Centre and then the control net locations (Figure S3d).

Comparing point level estimated species richness for each Mine and control shows that median estimated richness was similar between mines and controls (Figure 3a, Table S5). When these same analyses were restricted to forest-dependent birds only (Figure 3b), there was higher richness in the controls, but the difference was not significant (Table S5). Comparing median estimated richness in the Mine Centre and Mine Edge net locations revealed that there were more forest-dependent bird species at the Mine Edge (Figure 3e), and this was additionally supported by the species accumulation curves (Figure S2d). Capture rates did not significantly differ between any of the comparisons ($p > 0.05$ in all cases; Table S5).

Generalised linear models revealed that estimated species richness of the different bird groupings was influenced by different predictors. Years since abandonment positively predicted estimated richness of the forest-dependent birds ($\beta = 0.37$, CI = 0.07–0.67) and both frugivores and insectivores ($\beta = 0.38$, CI = 0.03–0.72 and $\beta = 0.70$, CI = 0.43–0.98, respectively, Figure 4). However, none of the potential predictors influenced estimated richness for the overall community, nectarivores or generalists. The best model for insectivores explained 87% of the variability in estimated richness and included years since abandonment ($\beta = 0.70$, CI = 0.43–0.98), canopy height at the Mine Edge ($\beta = -0.51$, CI = -0.81 to −0.22) and mine size ($\beta = -0.56$, CI = −0.85 to −0.29; see Table S6). Of the three buffers of deforestation (from mining) around mines, none were identified as potential predictors for any of the estimated species richness groups.

At the net location level, canopy cover was positively linked to higher species richness for forest-dependent species ($\beta = 0.75$, CI = 0.47–1.04) explaining 68% of the variability. However, no relationship was found for all species, explaining 9% of the variability, and generalist species had a negative correlation with canopy cover ($\beta = -0.39$, CI = −0.61 to −0.18) explaining 36% of the variability.

4 | DISCUSSION

We found that gold mining in Guyana alters the species composition of understory bird assemblages, leading to an impoverishment at the mine centre. The overall number of species at mines is actually higher than in control forest sites due to an influx of generalist species; yet, fewer forest-dependent species are detected at the mine centre, up to two decades after abandonment. However, with increasing time since mine abandonment, there are signs of recovery in the understorey avifauna with a greater number of forest-dependent species at the edges of mines that have been abandoned for longer periods. Indeed, we observed the establishment of some low-level bushy regrowth within mines, although this did not represent a canopy per se. Nonetheless, our findings demonstrate that canopy cover is a key predictor of bird species diversity, but its effects differ across species groups. Forest-dependent species and insectivores were positively associated with higher canopy cover, highlighting their

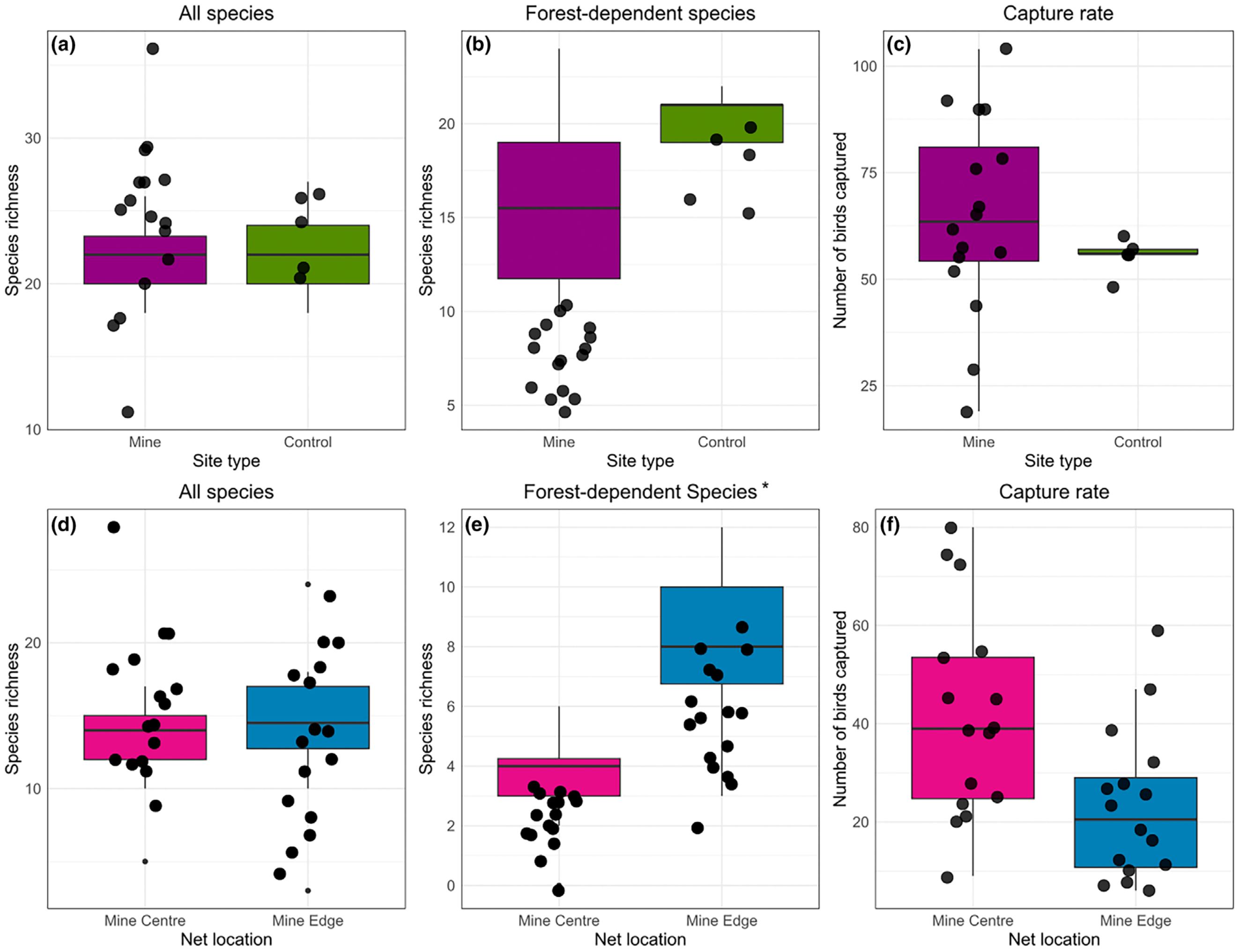

FIGURE 3 Boxplots of bird estimated species richness for all taxa (a and d), forest-dependent species (b and e) and capture rates for all species (c and f) for all mine ($n = 16$) and control ($n = 5$) sites. Mine in (a–c) equates to the data from the Mine Centre and Mine Edge combined. Vertical line indicates the median value, the box indicates the upper and lower quartiles, points indicate outliers. An asterisk next to the panel title indicates a statistical significant difference (*t*-test). Black dots represent the raw data (unadjusted) points.

reliance on structurally intact forest. In contrast, generalist species exhibited a negative relationship with canopy cover, suggesting a preference for more open or edge-like environments. These opposing responses help explain the overall lack of a strong canopy–richness relationship across all species and underscore the importance of disaggregating responses by ecological group. This finding is in line with previous studies that have demonstrated some species are vulnerable to canopy thinning or removal (Jirinec et al., 2022).

Our study focused specifically on understorey bird communities using mist nets. Whilst this method underrepresents canopy-dwelling and highly mobile species, it is well suited for detecting smaller, less mobile birds that we expected to be particularly sensitive to this kind of habitat degradation and microhabitat changes. Consequently, our findings primarily reflect patterns in this sensitive component of the avifauna and should be interpreted within that context. Further studies incorporating complementary techniques such as point counts or acoustic monitoring would be valuable for assessing responses of the broader bird community.

At the landscape scale, species accumulation curves revealed greater overall estimated species richness in mined areas compared to control sites. However, site-level analyses of estimated species richness did not always reflect this trend, highlighting discrepancies between beta (local scale) and gamma (landscape scale) diversity.

The slow recovery rates of woody biomass in artisanal small-scale gold mines found by Kalamandeen et al. (2020) were also observed in our study. Mines that have had less time to recover harboured a distinct bird community, characterised by higher numbers of generalist species and lower numbers of forest-dependent taxa. Most of the forest-dependent species detected at control sites were only captured in mines that had been abandoned for at least 10 years, and these were detected almost exclusively at the edge of the mine (except for *C largipennis*). This implies that after such time, the mine edge is beginning to become usable habitat for understorey forest-dependent birds, consistent with the findings of Mestre et al. (2013) in Brazil, where bird recovery following fire was noticeable after a decade. However, our findings contrast with those of Barros

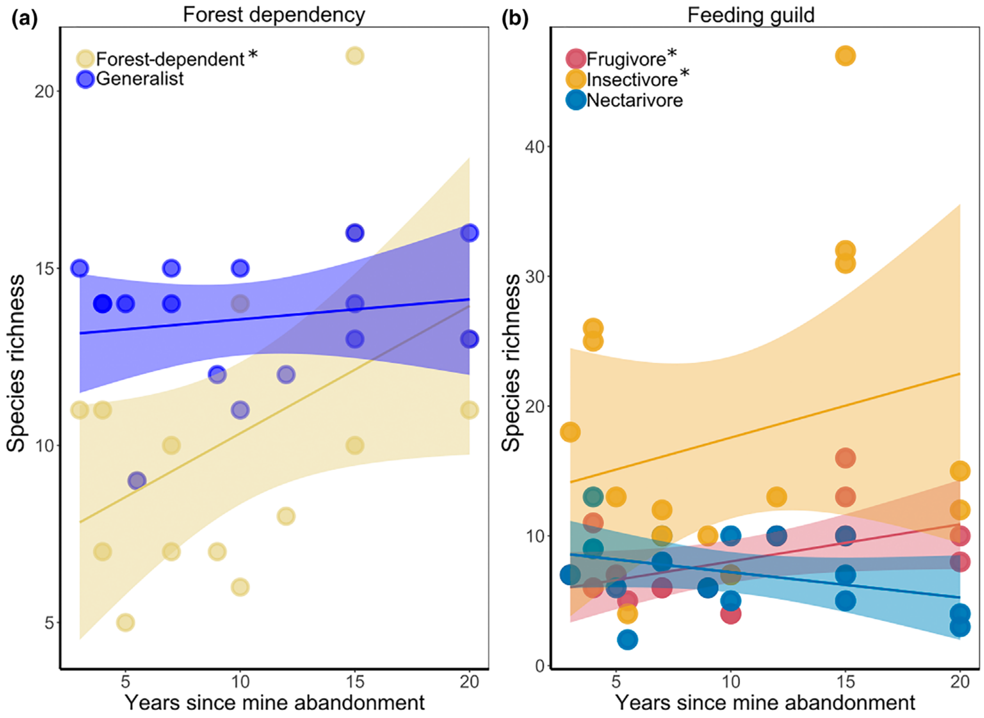

FIGURE 4 Relationship between estimated species richness and years since mine abandonment for (a) forest-dependent vs. generalist and (b) across feeding guilds. Bold lines indicate the linear line of best fit and shaded areas show 95% confidence intervals. An asterisk next to the dataset name title indicates a statistically significant *t*-test.

et al. (2022), who found no improvement in species numbers with time since abandonment of mines in the Eastern Amazon; this difference may reflect the use of different sampling methods, with mist nets focusing on a more sensitive subset of the avian community, whilst point counts sample a broader portion of the bird community, potentially making subtle differences less detectable. Furthermore, Barros et al. (2022) only investigated mines up to 8 years post-abandonment, a relatively short period in which to identify recovery in bird community structure.

Our results indicate that nectarivores (primarily hummingbirds) were more associated with mines that had only recently been abandoned since capture rates and species richness decreased with years since abandonment, likely due to a change in plant species within the mine centre and mine edge (as also observed by Alarcón-Aguirre et al., 2023; Kalamandeen et al., 2020). For example, *Heliconia* flowering plants are known to thrive in forest gaps (Felton et al., 2006; Rundel et al., 1998) and were found at many of the mines that had been abandoned for less than 5 years. However, as all the mines are embedded within a large contiguous forest (albeit somewhat degraded by mining activity), the presence of these forest-dwelling hummingbird species is most likely due to the surrounding habitat, rather than reflecting direct or sustained use of the disturbed mine environment. These records may represent transient foraging visits or crossings. In contrast, forest-dependent bird species, such as ant-following specialists, were typically restricted to mines where activity had stopped more than a decade before and exclusively at the edges of the mines. Similarly, the numbers of insectivore species were positively associated with years since abandonment. However, we did not observe a decline in the richness of generalist species, only capture rates, possibly related to a lack of vegetation regrowth within the mine centre.

The biodiversity impacts documented in this study reflect the responses of understorey bird communities to small-scale mining in tropical forest in Guyana and may be representative of broader patterns across similar artisanal mining contexts elsewhere in Amazonia. However, as this study focused exclusively on understorey species sampled using mist nets, the findings should be interpreted with caution when generalising to other components of the avifauna or to the full vertical structure of bird communities. Despite these limitations, our findings provide valuable insights into how sensitive understorey species respond to the habitat changes associated with abandoned mines. In contrast, the influence of industrial mining is likely to be greater in magnitude. Larger industrial mines often cause more concentrated disturbances over wider areas, also with the addition of high levels of traffic and noise pollution due to associated road infrastructure (Duarte et al., 2015). Our results suggest that the enclosed edge nature of ASGM creates pockets of deforestation resulting in unsuitable habitats for understorey birds, but at a highly localised scale with negligible permeation of disturbance into neighbouring forest. Indeed, the effects of mining appear limited to the immediate vicinity of the mine, with the avifauna observed 100 m into adjacent forest being similar in composition to that observed in control forest sites. This supports previous findings from Amazonia where edge effects tend to be most pronounced within 100m from edges, depending on structure and cause of edge (Harper et al., 2005; Patten & Smith-Patten, 2012). Despite these findings, it must also be acknowledged that surrounding the study mines was mostly an intact forest landscape, which likely buffered the effects of localised disturbances from mining. Given the known impacts of forest fragmentation on bird communities in Amazonia, we would expect different results in landscapes already impacted by forest degradation and removal.

We found that individual species responses to mining varied and may be related, at least in part, to feeding ecology. The insectivores *Willisornis poecilinotus* (scale-backed antbird) and *Myiobius barbatus* (whiskered myiobius) were each only captured once at the edge of a mined site, whereas both species were caught at all control sites, indicating a sensitivity to any level of mining. Other insectivores such as *Thamnomanes ardesiacus and T. caesius* were only found at mine edges that had been abandoned over a decade previously, and all but one of the control sites supported *T. ardesiacus*. *Thamnomanes* antshrikes are known to be nuclear species in mixed species foraging flocks (Munn & Terborgh, 1979), one of the groups most impacted by forest loss and fragmentation (Powell, Wolfe, et al., 2015). The presence of *T. ardesiacus* at mines which have been abandoned for over a decade indicates the suitability of habitat at the edges of mines that are beginning to recover. This trend among forest-dependent species indicates that mining influences behaviour and habitat use, as very few of these species were detected at the centre of mines. This is supported in our results with a strong affiliation for higher levels of canopy cover and canopy height, especially among insectivores. Disturbance-sensitive species such as *Epinecrophylla guttaralis* (brown-bellied stipplethroat) and *Formicarius analis* (black-faced antthrush) were only captured at control sites, implying that even after 20 years of recovery some species still avoid mined areas. *R. carbo*, a generalist omnivore representative of disturbed habitats throughout Amazonia, was present at all mined sites and had the highest indicator value for the Mine Centre. It was often captured in high numbers in mines but was not recorded at any of the control sites, indicating that this species will readily and potentially quickly colonise sites following habitat degradation. We also found that mist nets placed within the Mine Centre had higher capture rates than those at edges, likely due to their position close to the sparse regrowing vegetation often used to roost or feed by many of the birds captured. These vegetation patches might also be used as cover from predators or stop-off points for birds seeking to cross open areas, which could also explain the higher capture rate. However, these results may be a reflection of the use of mist nets for sampling, highlighting the need for further investigation to determine whether these patterns reflect true ecological use or methodological artefacts. Artisanal small-scale gold mining is predominantly alluvial, with sites typically located near water sources and many mines containing small streams (Figure S1). This may help explain why species such as *Myrmotherula surinamensis* (guianan streaked antwren) and *Chloroceryle americana* (green kingfisher), both commonly associated with riparian/aquatic habitats, were identified as indicators of the Mine Centre (Ascanio et al., 2017).

Artisanal small-scale gold mines and their enclosed edges in tropical forest are a poorly understood ecological system. In this context, our study focuses on biodiversity impacts associated with potential edge effects, and the recovery of bird communities following mine abandonment. We find that edge effects do not appear to extend as far as 100m from the edge of mines for bird species. In contrast, the lack of canopy within mines represents an unsuitable habitat for forest-dependent birds, supporting other research indicating the reluctance of some species to cross open areas (Laurance et al., 2004). Even after 20 years of mine abandonment, the Mine Centre appears to remain an unfavourable habitat for forest-dependent birds, whilst generalist species can be found in reasonable numbers. However, our work shows that there is some recovery of bird communities at the edges of mines, albeit slow, with some forest-dependent species found a decade after the cessation of mining activity. With little to no canopy and very few forest-dependent species in the centre of mines, active restoration may be required to speed up recovery processes. However, active restoration methods need to be explored to understand their effectiveness. As we indicate that some natural vegetation regrowth appears to be occurring at mine edges, any active restoration methods might be more effective in these areas compared to the mine centre. Nonetheless, it is encouraging that forests immediately surrounding mines contain more-or-less complete bird communities, providing opportunities for a quick recovery once mines are rehabilitated.

AUTHOR CONTRIBUTIONS

Sean J. Glynn, Jake E. Bicknell, Matthew J. Struebig and Zoe G. Davies conceived the ideas and designed methodology; Sean J. Glynn, Breon Allicock, Jean Herce and Lara Hall collected the data; Sean J. Glynn and Jake E. Bicknell analysed the data; Sean J. Glynn and Jake E. Bicknell led the writing of the manuscript with input from Zoe G. Davies, Matthew J. Struebig, Brian J. O'Shea and Arianne E. Harris. All authors contributed critically to the drafts and gave final approval for publication, which Sean J. Glynn led.

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CONFLICT OF INTEREST STATEMENT

We the authors verify no affiliations with or involvement in any organisation, nor are there any competing interests with any financial interest (such as honoraria; participation in speakers' bureaus; membership, employment, consultancies, stock ownership or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript. Matthew J. Struebig is an Associate Editor of *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo Repository: https://doi.org/10.5281/zenodo.16748216 (Glynn et al., 2025).

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SUPPORTING INFORMATION

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

Table S1. List of species, their feeding guild and the forest dependent/generalist classification for all bird species in this study. Definitions of forest dependent or generalist are provided in the Methods.

Table S2. Bird groups and the number of individuals at which species richness was estimated from using species accumulation curves in iNEXT.

Table S3. Pairwise ADONIS tests comparing bird community dissimilarity between Net locations.

Table S4. Pairwise Comparisons of Homogeneity of Multivariate Dispersion (betadisper) for Bird Community Composition.

Table S5. *T*-test results with Bonferroni corrected *p* values for species richness differences for all species, forest dependent species and capture rates at the site level and at the net locations. Mine refers to the combined Mine Edge and Mine Centre net locations. Significant *p* values are indicated in bold.

Table S6. Generalised linear model (GLM) outputs as chosen by the best model with the lowest AIC for each of the different groups of species richness for mines only compared to the site variables of: mine size, years since abandonment, canopy cover at the Mine Edge and canopy height at the Mine Edge. The control data was removed from these analyses as they lack mine size or years since abandonment.

Table S7. Generalised Linear Model (GLM) outputs as chosen by the best model with the lowest AIC for each of the different groups of species richness for each of the net locations (Mine centre, Mine Edge and Control) compared to the variables of number of saplings, number of large trees and canopy cover at each of the locations.

Figure S1. Examples of mines within this study at various stages of recovery, (a) 20 years, 19,000 m^2 in area, (b) 15 years, 19,000 m^2 in area, (c) 10 years, 566,000 m^2 in area and (d) 5 years, 123,000 m^2 in area.

Figure S2. Boxplots of (a) Canopy height (m), and (b) Canopy cover (%) at each of the net locations for all mines ($n=16$) and Controls ($n=5$).

Figure S3. Species accumulation curves calculated in iNEXT for (a) Site all species (Control vs. Mine); (b) Site forest-dependent species (Control vs. Mine); (c) Site generalist species (Control vs. Mine); and (d) Net Location all species (Control vs Mine Centre vs. Mine Edge) level with 95% confidence intervals displayed by the shaded areas. Solid lines show rarefied values, dashed lines show extrapolated estimates.

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