Tree and bird functional groups as indicators of recovery of regenerating subtropical coastal dune forests

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Running head: Monitoring tree and bird recovery

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Abstract

Functional diversity indicators are increasingly used to monitor forest function recovery because they connect biodiversity to ecosystem functions. However, identifying which functions deviate from a reference forest has not received much attention, despite its potential to inform restoration interventions. In this study, we used functional groups to assess the recovery of ecosystem functions in regenerating coastal dune forests. We surveyed birds and trees in forest of different ages and a reference old-growth forest in KwaZulu-Natal, South Africa. We classified species into functional groups for each taxa based on functional traits or *a priori* defined categories (i.e. guilds) and quantified the number of species within functional groups as a proxy of function stability. Bird species density followed an asymptotic trajectory, reaching old-growth forest values after 25 years. Insectivores and granivores showed saturating trajectories, whereas small frugivores and generalists increased linearly. With the exception of large frugivores, relative abundances of bird functional groups progressed towards old-growth forest values as the forest aged. Tree species density increased linearly with forest age. In contrast to old-growth forests, large canopy trees and understory shrubs were under-represented, while mid-canopy trees dominated regenerating forests. Our result suggests that most bird, but not tree functions, may have been restored. The trend in large frugivore numbers may warrant further investigation, as their low numbers may have hampered the recovery of tree functions. We conclude that functional group trajectories can track functions that deviate from a benchmark, and may therefore direct adaptive actions to recover the stability of regenerating forest.

Keywords: Bird guilds; functional diversity; functional redundancy; monitoring; plant-animal links

Implications for practice

- Because functional diversity links biodiversity and ecosystem functions, functional groups based on effect traits can be used as a proxy to track ecosystem functions' recovery.
- Functional group trajectories may potentially direct restoration efforts by indicating the ecosystem functions that deviate from a reference forest.
- Monitoring functional groups of one taxon (e.g. plants) only offers a partial view of the recovery process. It is important to monitor different taxa that are related to different ecological processes to better assess the recovery of ecosystem functions.

Introduction

Restoration success is typically evaluated against reference sites that resemble pre-disturbance conditions (Hallett et al. 2013). Yet, there is little consensus on what should be monitored to assess restoration success (Brancalion & Holl 2016), particularly when restoration aims at restoring ecosystem functions (Kollmann et al. 2016). Most monitoring protocols, especially those focused on plants, rely on taxonomically based indicators, such as diversity and abundance (Wortley et al. 2013). However, taxonomic indicators do not offer mechanistic insights into restoration processes and functions (Engst et al. 2016). Functional diversity indicators have been proposed as an alternative to taxonomic indicators (Brancalion & Holl 2016). Functional diversity indicators are easy to measure, tend to follow predictable trajectories (Bu et al. 2014) and reflect on ecosystem functions and ecological processes that structure restored communities (Mouillot et al. 2013). However, functional indicators provide little information on target species, or groups of species, that may be of conservation concern or provide key ecological functions (e.g. large frugivores, Galetti et al 2013; Jaunatre et al. 2013). Moreover, in a successional context, functional indicators do not provide information on when a particular species, or species group, is over-represented, which could indicate a potential shift in the successional pathway (Suding & Hobbs 2009).

The monitoring of functional groups over time as indicators of restoration success could overcome the shortcomings of functional and taxonomic indicators. Functional groups can reduce the complexity of species-rich systems to a few categories that represent key ecological functions (Chazdon et al. 2010). Restoration efforts can then be focused on groups that are under-represented in the restored forest compared to the reference forest. Classifying species into functional groups based on shared functional trait values is not a new idea (e.g. Chazdon et al. 2010). However, previous efforts have been based on traits that are affected by environmental filters (i.e. response traits; e.g. Verheyen et al. 2003; Swaine & Whitmore 1988), rather than those that affect ecosystem functions (i.e. effect traits; Lavorel & Garnier 2002). Functional groups based on response traits can help to understand how species composition will respond to resource availability or disturbances, but they offer little information on how they will affect ecosystem functions. For instance, species can be classified into groups with different regenerating capacities based on their seed mass to anticipate their response to disturbances (i.e. in terms of dispersal or seedling establishment and survival). Yet, it would be difficult to grasp how these groups will affect ecosystem functions (e.g. net primary productivity). Classifying species into functional groups based on effect traits assumes that all species that belong to a group will have similar effects on an ecosystem function (i.e. many species within a particular group will indicate high levels of redundancy). Thus, an ecosystem function may be "insured" against single species declines (i.e. 'insurance hypothesis'; Yachi & Loreau 1999), as a number of species perform a similar function. Following this approach, monitoring functional effect groups can reflect on the resilience of restored forests compared to reference benchmarks. Efforts that asses how species losses affect ecosystem stability are common (Mori et al. 2013), but few studies investigate how a regenerating forest builds up functional resilience by adding new species to different functional groups.

Evaluating restoration success does not only depend on choosing an appropriate ecological indicator, but also on the taxonomic group considered (Crouzeilles et al. 2016). For instance, compared to other taxonomic groups, birds may show earlier signs of recovery because they are able to make use of young new-growth forests (Crouzeilles et al. 2016). Conversely, a much longer time period must elapse before vegetation structure of a new-growth forest resemble that of old-growth forests, if it is achieved at all (Wassenaar et al. 2005; Poorter et al. 2016).

The monitoring of different taxonomic groups may therefore provide a more integrative view of restoration success or failure. However, compared to studies that analyse plants or animals separately, studies that combine information on plants and animals are scarce (McAlpine et al. 2016), even though restoration actions that integrate plant and animal perspectives have been shown to accelerate forest recovery (Zahawi et al. 2013).

In this study, we assess functional group trajectories of two taxa (birds and trees) in regenerating coastal dune forest that are developing in response to post-mining rehabilitation initiatives in KwaZulu-Natal, South Africa. We surveyed plant and bird species in forests of different ages (12 to 38 years) and a reference old-growth forest, and assigned each species to a functional group based on effect traits. Previous studies on these forests have shown that succession is driving regeneration trajectories towards a reference forest (Grainger & van Aarde 2012; Wassenaar et al. 2005; Rolo et al. 2016a). However, it is uncertain if these patterns, based mostly on taxonomic indicators, relate to a similar increase in the stability of functions across groups and among taxa. We specifically aim to assess: i) if regeneration patterns derived from functional groups offer a similar notion of success than those derived from common taxonomic indicators, ii) if the addition of species over time is equally distributed across functional groups and progress towards the reference forest or iii) if there are functions that are under- or over-represented. We hypothesized that functional groups can offer more insight than common taxonomic indicators on assessing restoration success by pointing out which functions deviate from the reference forest. Nevertheless, regardless of the indicator, we expect that the outcomes can differ widely depending on the taxa monitored.

Methods

Study area

The study area is located approximately 20 km north of Richards Bay (28°43'S, 32°12'E) in

KwaZulu-Natal, South Africa. We studied a set of rehabilitating coastal dune forests and a reference, old-growth forest. Coastal dune forest belongs to the Indian Ocean Coastal Belt (IOCB) forests of southern Africa (Mucina & Rutherford 2006). The IOCB covers a strip less than ~35 km wide along 800 km of the eastern coastline of South Africa and represents the southern tip of East African Coastal Forest that extends until Somalia (Burgess & Clarke 2000). In South Africa, an estimated 82% of coastal forests have been lost due to subsistence farming, unregulated burning, commercial logging, agricultural plantations, and urban developments (see Olivier et al. 2013 and references therein). Remaining fragments are now small, isolated, and surrounded by a matrix of natural and human land-use types and likely harbour an extinction debt (Olivier et al. 2013). Although dune forests are sensitive to disturbance, their relatively high ecological resilience provides the potential to recover following the withdrawal of these stressors (van Aarde et al. 2014). The climate of the study area is humid and sub-tropical (van Aarde et al. 2014). Long-term mean annual rainfall (1976-2015) was 1336 ± 117 mm year^{-1} since rehabilitation.

Sand dunes mining started in 1976 (van Aarde et al. 1996). After mining, dunes were reshaped and covered with the pre-mined harvested topsoil. Then, they were seeded with a mixture of annuals, grasses and *Acacia karroo* seeds, a pioneer tree species that naturally occurs in coastal dune forest (Ward 2011). Afterwards, the vegetation developed on its own accord (van Aarde et al. 1996). As a result, the study area comprises a set of rehabilitating known-aged sites. The unmined old-growth forest included in this study (Sokhulu forest, 28°27′S, 32°25′E) was the closest relatively large patch of undisturbed forest to the mining lease area. This forest is part of the dune forest of the Mapelane Nature Reserve (~1500 ha), which belongs to the iSimangaliso Wetland Park.

Sampling scheme and data collection

Nine sites (eight new-growth forest sites and an old-growth forest) were sampled in 2015. The age of new-growth forest sites ranged between 12 and 38 years in 2015. New-growth forests covered an area of ~ 600 ha (77.3 ± 8.2 ha stand^{-1}) and were adjacent to each other, stretching parallel to the coastline along a distance of ~15 km. The reference old-growth forest was located ~ 14 km northwards of the new-growth forests and covered an area of ~ 500 ha. Aerial photographs of the old-growth forest show that this forest patch has been intact since at least 1937 (Wassenaar et al. 2005). Plant surveys were conducted in 15 randomly located quadrats of 16 x 16 m for each site. All woody plants (hereafter trees for simplicity) taller than 0.2 m were identified at the species level and counted. The diameter at breast height (DBH) was measured in all individuals taller than 1.7 m.

Birds were surveyed using point counts (Bibby et al. 2000). Ten survey points were randomly located within each of the eight new-growth, and one old-growth forest sites and were at least 178m apart. Each point was surveyed six times; as sampling saturation was most likely to occur after six survey visits (CERU unpublished data). Six trained observers surveyed points between 0400 h and 0900 h from December 2014 to January 2015. At each point, birds were allowed two minutes to resettle after the arrival of the observer. Thereafter, all birds seen or judged to be heard within a 60 m radius were recorded for a period of 10 minutes. For each bird seen, estimated distances from the observer to the bird were recorded by a digital rangefinder (Nikon Laser 550As). Birds seen flying over the canopy were not recorded. No surveys were conducted in rainy or windy weather conditions.

Classification of species into functional groups

Plant functional groups were defined following Laliberté et al. (2010). Briefly, we computed a matrix of species trait dissimilarities using Euclidean distances. We then used Ward's clustering on the dissimilarities matrix to classify each species into functional effect groups. We used functional trait data presented in Rolo et al. (2016b), namely specific leaf area (SLA, cm^2/g), wood density (WD, g/cc) and maximum plant height (m), but including C:N ratio, that was analysed in a stable isotope ratio mass spectrometer (Thermoquest EA 1110 elemental analyser), instead of δ13C as reported in Rolo et al. (2016b). SLA, and C:N relates to growth rate. They have been linked to ecosystem functions such as decomposition rate or net primary productivity (Lavorel & Garnier 2002; Lavorel et al. 2007). WD relates also to growth rate as well as survival. WD and plant height have been linked to ecosystem functions such as carbon stocks or standing biomass (Lavorel & Garnier 2002; Lavorel et al. 2007). We only included effect traits, those that influence ecosystem processes, following the recommendations of Cornelissen et al. (2003) and Díaz et al. (2007). The final classification of each species was based on visual inspection of the cluster dendrogram (Fig. S1). Mean values of each trait for each functional group are shown in Table 1.

Bird species were placed into *a priori* defined functional groups following the classification of Cumming and Child (2009). The authors classified South African bird species into nine functional groups based on their foraging behaviour, following the general categories provided by Sekercioglu (2006). When a bird species forages on different sources, Cumming and Child (2009) assigned it to multiple groups. However, to be consistent with the plant functional group definition, where we assigned each species to a unique group, species with multiple foraging behaviours were classified in a newly created category (i.e. generalist feeders). We assigned species to seven functional groups (small (<200 g) and large (>200 g) frugivores, generalist

Table 1. Mean values (± S.E.) of effect traits (maximum plant height (m), specific leaf area (cm^2/g; SLA), wood density (g/cc; WD) and carbon:nitrogen ratio (C:N)) for each tree functional group (tall trees with intermediate values of SLA (T.M) and tree or shrubs species that occupy the mid- and under-story with high (TS.H), medium (TS.M) or low (TS.L) SLA). Different letters within trait depict significant differences at $p < 0.05$ among groups.

Group Name	Plant Height	SLA	WD	C:N
TS.H	6.67 ± 0.69a	218.05 ± 13.88c	0.60 ± 0.02ab	15.59 ± 0.96a
TS.M	7.27 ± 0.84a	140.38 ± 8.07ab	0.66 ± 0.01b	21.49 ± 0.99b
TS.L	8.25 ± 1.93a	88.07 ± 8.54a	0.64 ± 0.02ab	37.59 ± 2.31c
T.M	19.82 ± 1.07b	141.22 ± 10.59b	0.56 ± 0.03a	21.46 ± 1.34b

feeders, granivores, insectivores, pollinators and raptors). We used a 200 g threshold because there was not any frugivore with body weight between 60 and 200 g. We gathered bird foraging behaviour and body weight from Roberts' Birds of Southern Africa (Hockey et al. 2005). Using foraging behaviour to classify bird species has been shown to be an informative approach to study the stability of bird communities (Karp et al. 2011; Luck et al. 2013) and to track their contribution to different ecosystem services and functions (Sekercioglu 2006).

Data analysis

To assess if tree and bird functional groups differed among sites across the chronosequence we first computed relative abundances and species densities (i.e. number of species for each quadrat / point; Chazdon 2011) for each functional group. Relative abundances for each functional group were computed as the number of individuals belonging to a particular group out of the total number of individuals in each quadrat / point. We then fitted generalised linear models with relative abundance as the dependent variable and site as the independent variable using a binomial distribution. We fitted separate models for each functional group and taxa and included the independent variable of site as a categorical factor.

To assess the relationship between site age and species density, we fitted generalised linear models with species density as the response variable and time as a predictor. We also fitted generalized additive models (GAM; Wood 2006) for groups that during exploratory graphical analysis showed non-linear trends. As species numbers are counts, we fitted a Poisson distribution and checked for overdispersion. Most models did not show signs of overdispersion. Only one functional group of trees and one of birds were significantly overdispersed. We used a negative binomial distribution in these two models (Zuur et al. 2009). To assess if species density of trees and birds were similar between the rehabilitating stands and the old-growth forest we computed 95 % confidence intervals of species density of the old-growth forest by bootstrapping (Smith & van Belle 1984). We assumed that species density of rehabilitating stands had reached old-growth forest levels when confidence intervals overlapped.

Mean species density values within functional groups can be considered as an index of functional redundancy (FR; Bruno et al. 2016). Assuming functional groups as a set of species that have traits with similar effects on ecosystem function, an increase in mean species density values across functional groups will represent a higher number of species contributing similarly to an ecosystem function and thus higher FR. In addition, to take into account how the abundance of individuals varies between functional groups, we computed Shannon diversity for each taxa using relative abundances. We used one-factor ANOVA with FR and Shannon diversity as dependent variables and site as an independent variable, to assess the differences between sites on FR and Shannon diversity. We did not include *A. karroo* in any analysis because it was seeded in the regenerating stands. All analysis were conducted in R v3.2.5 (R Core Team 2016).

Results

Tree species density followed a significant linear pattern with increasing values as the forest age, but without overlapping with old-growth forest values (Fig.1). Bird species density showed a significant non-linear trend across the chronosequence. The non-linear trend followed an asymptotic pattern, with a consistent increase during the first 25 years of forest regeneration, plateauing thereafter at values similar to those recorded for the old-growth forest. Site age explained a larger amount of variation for bird than for tree species density (Fig.1).

We identified four tree functional groups based on specific leaf area, maximum height, wood

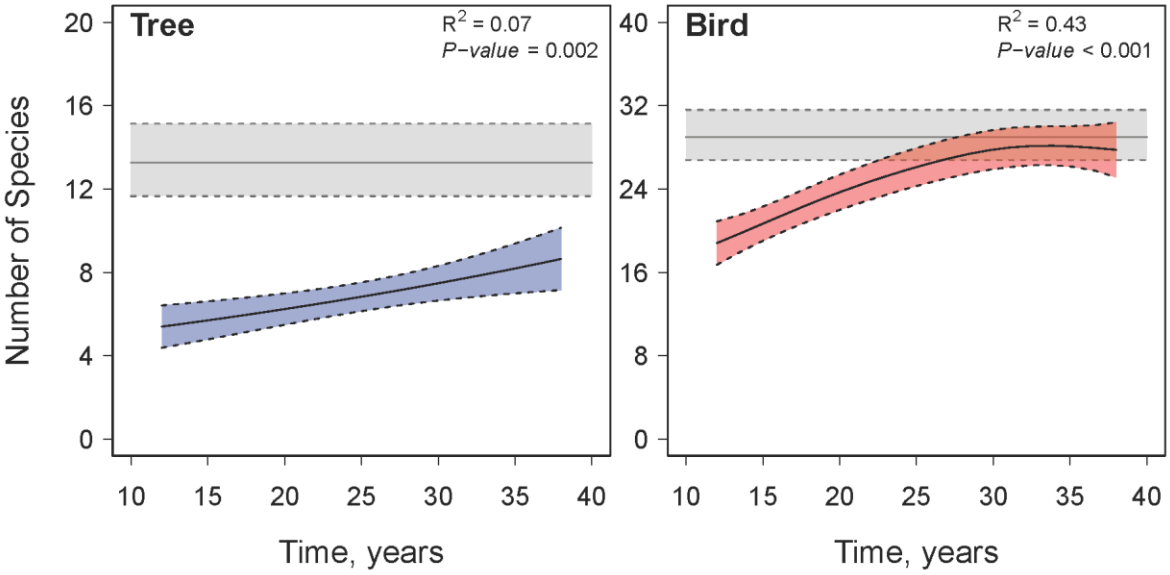

Figure 1. Modelled number of tree and bird species (solid line) and 95% CI (dashed line) across sites of different age since mining. Horizontal grey lines depict average number of tree and bird species (solid) and 95% CI (dashed) in the old-growth forest.

density and C:N ratio (Fig. S1). Specific leaf area and height differed the most among groups (Table 1). Based on these two traits, functional groups can be distinguished as tall trees with intermediate values of specific leaf area (T.M; n = 17), and tree or shrubs species that occupy the mid- and understory with high (TS.H; n = 12), medium (TS.M; n = 15) or low (TS.L; n = 6) specific leaf area (Table 1; Fig. S1).

Trees and birds showed different species density patterns among functional groups (Fig. 2 & 3). For trees, TS.M, TS.L, and T.M functional groups increased significantly as the forest aged and showed similar trends to overall tree species density (Fig. 1 & 2). Conversely, TS.H decreased linearly as the forest aged. T.M and TS.H functional groups had lower species density values than the old-growth forest for all sites, whereas both TS.M and TS.L functional groups reached old-growth forest values early in the chronosequence (Fig. 2).

Most functional groups of birds reached similar species density values to those of the old growth forest. Insectivores (n = 55) and pollinators (n = 4) showed asymptotic patterns, similar to overall bird species density (Fig. 1 & 3), which plateaued around 20 years of age. However, small frugivores (n = 8) and generalists (n = 25) increased consistently across the chronosequence, reaching similar levels of species density to the old-growth forest in older rehabilitating stands. Raptors (n = 9), large frugivores (n = 5) and granivores (n = 8) did not follow significant patterns. Raptors and granivores had similar species density values to the old-growth forest, while large frugivores had lower species density values than the old-growth forest for all sites.

Relative abundances of tree functional groups were, in general, significantly different between regenerating sites and the old-growth forest (Fig. 4). Most individuals in regenerating sites

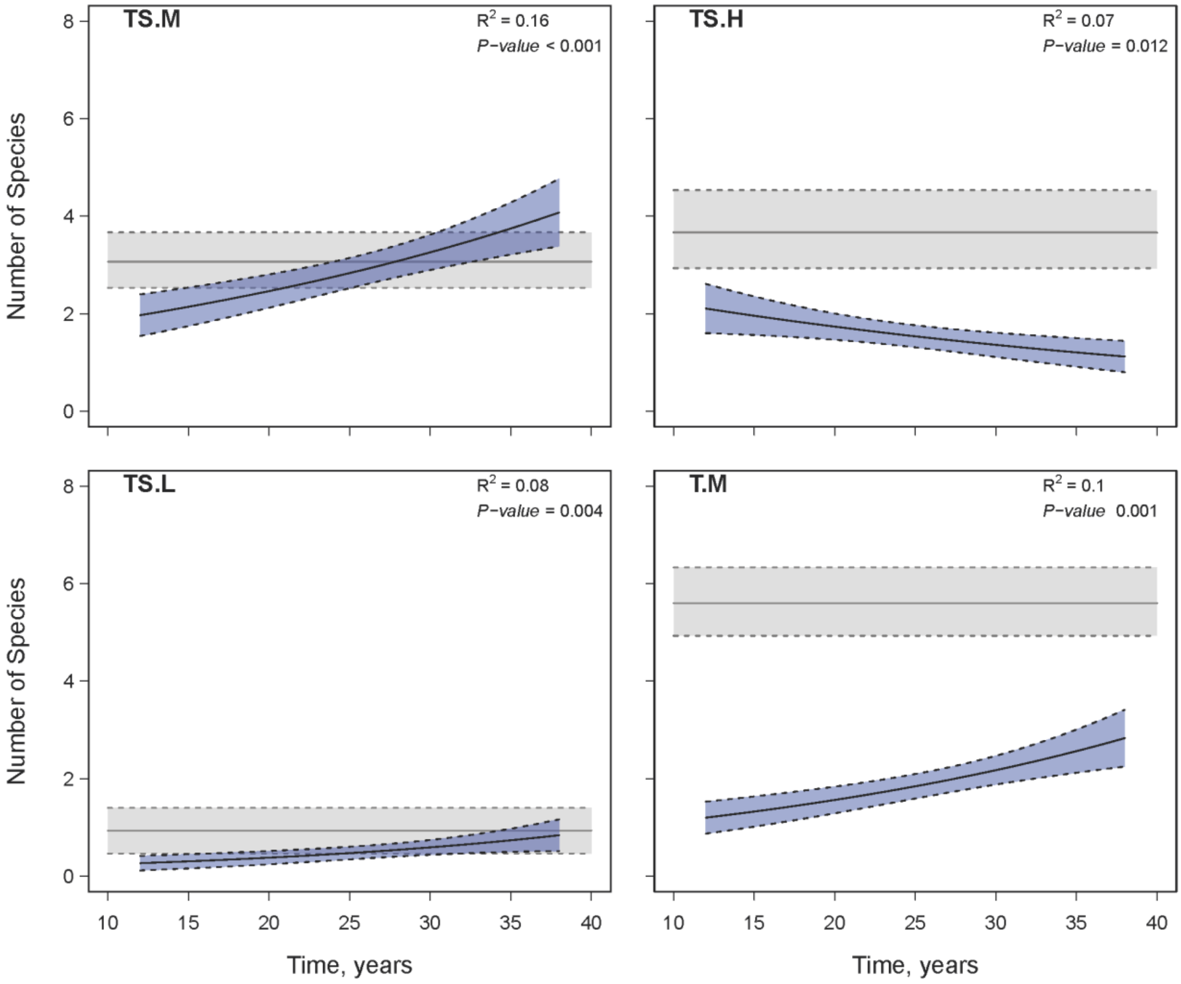

Figure 2. Modelled number of species (solid line) and 95% CI (dashed line) for each tree functional group across sites of different age since mining. Horizontal grey lines depict average number of tree species (solid) and 95% CI (dashed) in the old-growth forest.

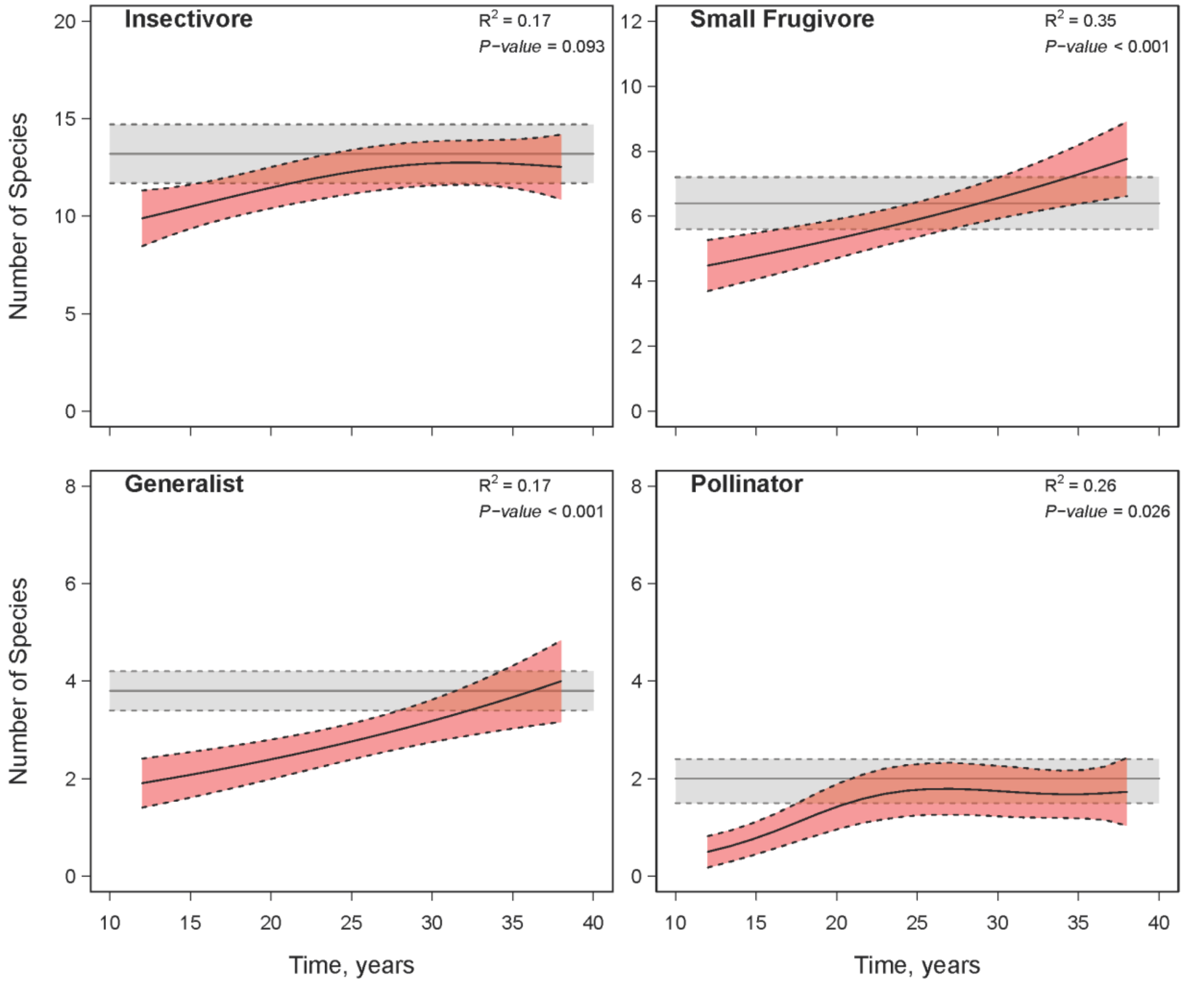

Figure 3. Modelled species density (solid line) and 95% CI (dashed line) for each bird functional group across sites of different age since mining. Horizontal grey lines depict average number of bird species (solid) and 95% CI (dashed) in the old-growth forest. Note that raptor, large frugivore and granivore groups are not shown because models were not significant.

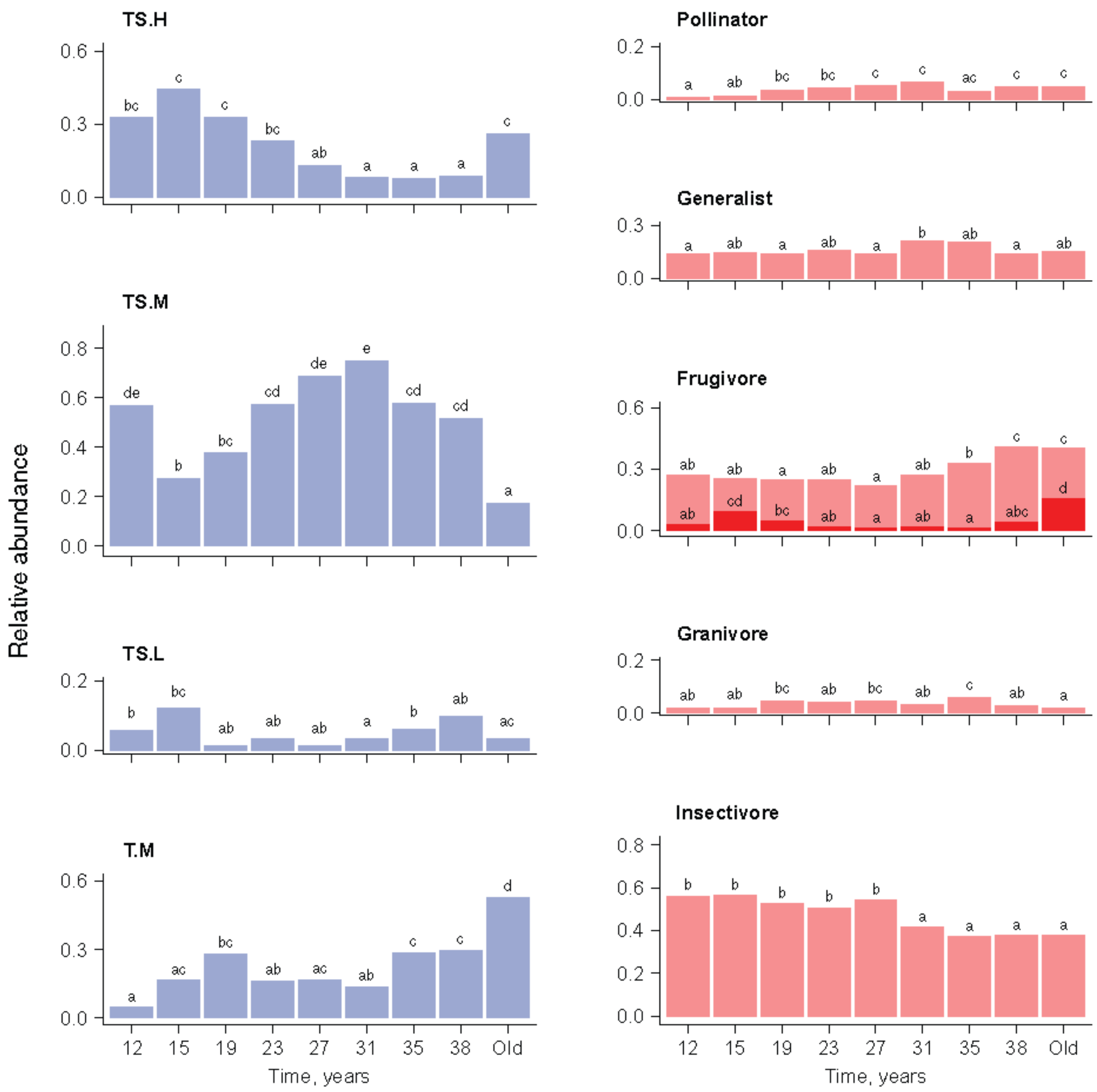

Figure 4. Relative abundance of tree (left) and bird (right) functional groups for each site. Different letters depict significant differences at $p < 0.05$ among sites within functional group. Note that Raptors are not included because of their low abundances. Large frugivores abundances are depicted in dark red.

belonged to the TS.M functional group, whereas this functional group was among the least represented in the old growth forest. Moreover, relative abundance values of the TS.H functional group, had significantly lower values at older than at younger regenerating sites. For birds, most relative abundances values progressed towards old-growth forest values as the forest aged with the exception of large frugivores, whose abundances did not progress towards old-growth forest levels -the oldest rehabilitating site had significantly lower abundances of large frugivores than the old-growth forest. For the other functional groups, the oldest rehabilitating site and the old-growth forest did not show significant differences. In regenerating forest, the oldest sites had higher values of pollinators and small frugivores and lower values of insectivores and large frugivores when compared to younger sites. The absolute number of individuals for each functional group and taxa followed a similar pattern to that of relative abundances (Fig. S2)

Functional redundancy and Shannon diversity for trees and for birds differed among sites (F=6.6 $p < 0.001$, F=6.7 $p < 0.001$ FR of trees and birds; and F=5.1 $p < 0.001$, F=8.6 $p < 0.001$ Shannon diversity of trees and birds). For trees, all sites had significantly different FR values than the reference forest, with the exception of the oldest rehabilitating site. For birds there were no differences to the reference site from the three oldest regenerating forest.

Discussion

Our results confirmed the expectation that classifying species into functional groups can provide more insights than only monitoring species density patterns. This was especially evident for trees as functional group patterns deviated from the overall pattern. For instance, the species density of the TS.H tree group decreased as the forest aged, whereas overall species density increased linearly as the forest aged. Moreover, regenerating forests were dominated by TS.M individuals, whereas this group was not abundant in the old-growth forest.

Conversely, most birds soon reached old-growth forest levels, both in terms of species density and relative abundances. These findings suggest that bird, but not tree functions, may have been restored in the rehabilitating forest. However, given the low numbers of large frugivores, and their importance for dispersal (Galetti et al. 2013), the apparent recovery of bird functions should be taken with care. Highlighting which functions deviate from the reference forest is one advantage of assessing functional groups trajectories, because it offers the opportunity of guiding restoration efforts.

Limitations of functional groups

Classifying species into functional groups can augment the information provided by common diversity measures. An advantage of this approach is that the functions that deviate from a benchmark can be identified and tracked over time. It may therefore direct restoration actions to focus on specific under-represented groups. In addition, it can illustrate the functional redundancy of a regenerating forest, which in turn provides insight into the stability of ecosystem functions if species losses occur (Mori et al 2013). When implementing this approach, it is important to consider how species are assigned to functional groups. The functional identity of a species may depend on which functional traits are selected and how the classification is performed. We classified bird and tree species based on functional effects traits or *a priori* categories that have been shown to relate to different ecosystem services and functions (Cumming & Child 2009; Sekercioglu 2006; Díaz et al. 2007), and to be important in a restoration context (Gustafsson et al. 2016; Lindenmayer et al. 2016). Thus, we are confident that our approach can offer insights on the studied restoration effort as well as other species-rich systems. Nevertheless, similarly to functional diversity indices, functional traits should be carefully selected to characterize the functional strategy of each species (e.g. fast or slow-growing for plants) as well as ecosystem functions important to the restoration activity

(Mouillot et al. 2013).

Functional groups as indicators of recovery

Evaluating to what extent pioneer tree species are replaced by late-successional species is commonly used to assess successional pathways of regenerating tropical and sub-tropical forest (Chazdon et al. 2010; Lebrija-Trejos et al. 2010). The assumption is that the replacement of species is followed by an increase in complexity and heterogeneity, both in terms of tree cohorts and vertical structure, eventually resembling an "old-growth" forest (Chazdon 2011). Our results suggest that the studied rehabilitating forests were located at an intermediate state along this gradient (i.e. pioneers vs late-successional). Tree species that occupied a middle stratum in the forest vertical structure with average values of specific leaf area (TS.M) were over-represented in the rehabilitating forests, both in terms of number of species and abundance of individuals, as compared to the reference forest. On the other hand, plants that add structural complexity to a forest, such as large canopy trees (T.M) or understory shrubby species (TS.H), were rare in the rehabilitating forest, but abundant in the reference forest. Moreover, the species density of this latter group decreased as the forest aged.

Previous studies on these forests have shown that the seeded pioneer *A. karroo* start to be senescent at later regeneration stages, opening canopy gaps that can act as an environmental filter (Grainger & van Aarde 2013, Rolo et al. 2016b). High values of specific leaf area have been related to understory environments where light availability is a limiting factor (Poorter 2001). Indeed, there was a relatively high number of individuals of TS.H group both at early regeneration stages and in the old-growth forest, where canopy openness is low (Rolo et al. 2016b). These results suggest that the increase in light availability following the demise of *A. karroo* may limit the recruitment, or even jeopardize the survival of this functional group.

Large frugivore and TS.H abundances followed similar patterns in regenerating forest. This result suggests that the slow recovery of the TS.H and T.M could be the indirect effect of large canopy gaps on large frugivores occurrence. The TS.H and T.M groups were the most abundant in the old growth forest and both groups have mostly large fleshy fruits. In each group, 83% and 70 % of the species have fleshy fruits, and on average, their fruit diameter is 12.3 ± 2.6 and 12.4 ± 1.9 mm, respectively. In addition, large frugivores can potentially feed on plants of both groups, such as the Purple Crested Turaco that has been describe to feed on *Antidesma venosum* (i.e. TS.H) and *Celtis africana* (i.e. T.M) (Hockey et al. 2005). Large frugivores are crucial for dispersal, especially for large seeded plants, and are sensitive to changes in forest structure (Galetti et al. 2013; Senior et al. 2013). For instance, young regenerating plantations could be unsuitable for large frugivores as compared to forest patches (Styring et al. 2011). As a result, changes in forest structure may have led to a limited presence of large frugivores and TS.H and T.M groups in late regenerating forests because of a negative feedback between biotic (reduced effective dispersal) and abiotic (presence of gaps) filters. The low numbers of plant groups that provide complexity to regenerating forest could result in a reduction in the provision of other ecosystem functions (e.g. carbon storage; Bastin et al. 2015) and habitat opportunities at other trophic levels (Lindenmayer et al. 2012; Brady & Noske 2010).

Despite the low numbers of large-canopy trees, our results showed that as new-growth forests aged the number of species and the abundance of individuals of the rest of bird functional groups progressed towards the reference level. This result accords with the findings of others, which suggest that birds can make use of immature forest and, therefore, show signs of recovery sooner than trees (Crouzeilles et al. 2016).

The different trajectories among bird functional groups and the larger variability explained by site age for birds than for trees accords with the notion that subtle changes in vegetation over time affect bird functional group composition. For instance, the number of insectivore species seemed to saturate as the forest aged, while the relative abundance of individuals decreased. In contrast, small frugivores showed a consistent increase both in number of species and abundance of individuals. Young regenerating forests are dominated by *A. karroo* (Rolo et al. 2016b), resembling a monospecific plantation. *Acacia karroo* are principally insect-pollinated (Barnes et al. 1996). Young stands may therefore provide more foraging opportunities for a few species of insectivores for which plantations can be a suitable habitat (Sheldon et al. 2010). However, for small frugivores or other functional groups foraging opportunities increase as the forest age (Lindenmayer et al. 2016).

Overall, these results suggest that it is important to monitor mutiple taxonomic groups to evaluate the success of a restoration action. The ability of birds to make use of young regenerating forests and the linkages between functional groups of both taxa provide an opportunity to plan holistic restoration actions. However, to take advantage of this approach it is important to fully understand plant-bird interactions, particularly between large frugivores and TS.H and T.M groups.

Functional redundancy as a tool to plan the recovery of degraded systems

Restoration in a changing environment requires the ability to assist the recovery of the resilience of degraded forest (Suding 2011; Nimmo et al. 2015). Predicted increases in the incidence of extreme climatic events or the intensification of anthropogenic pressures could have devastating effects on young regenerating forests (Laliberté et al. 2010; Jentsch & Beierkuhnlein 2008). Focusing on functional redundancy to plan restoration actions may increase the chances of recovering functionally resilient forests (Suding 2011). For instance, given the likely ability of birds to make use of young forests, the inclusion of other mid-canopy tree species with known plant-disperser relationships in the plant selection process of restoration projects could accelerate the recovery of degraded systems (Zahawi et al. 2013). Although large canopy trees and shrubs can add niche opportunities, mid-canopy trees may provide foraging opportunities for a large number of birds from different groups at an early regenerating stage. In addition, the early presence of fruiting plants may limit the negative feedback between changes in structure due to senescent pioneers, large frugivores, and forest plants. Alternatively, at late regenerating stages, planting under-represented groups with known linkages to large frugivores may also improve the chances of successful restoration (Reid et al. 2015). For instance, promoting the presence of plants of the TS.H and T.M functional groups in small canopy gaps by enrichment planting could favour the presence of large frugivores.

Overall, restoration initiatives that comply with an adaptive management strategy may benefit from monitoring changes of functional groups over time. It can help to track changes of groups that provide key ecological functions (i.e. large frugivores) or of under-represented groups of conservation concern. It also highlights linkages with functional redundancy and could inform initiatives to improve the stability of regenerating forests.

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Supplementary Information

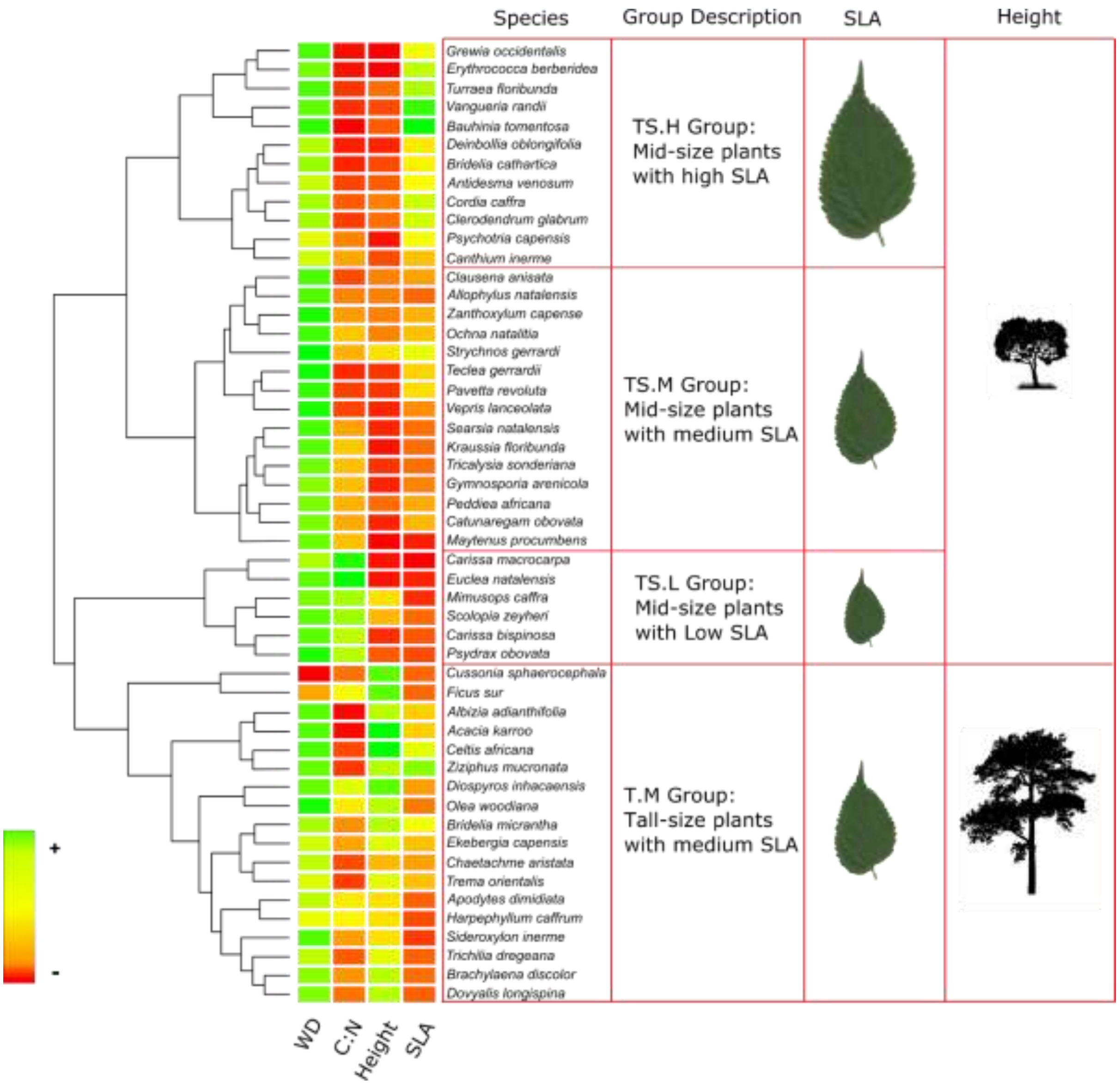

Figure S1 Dendrogram based on maximum plant height (m), specific leaf area (cm^2/g; SLA), wood density (g/cc; WD) and carbon nitrogen ratio(C:N) used to classified tree species into functional groups. The heatmap depicts trait values of each species.

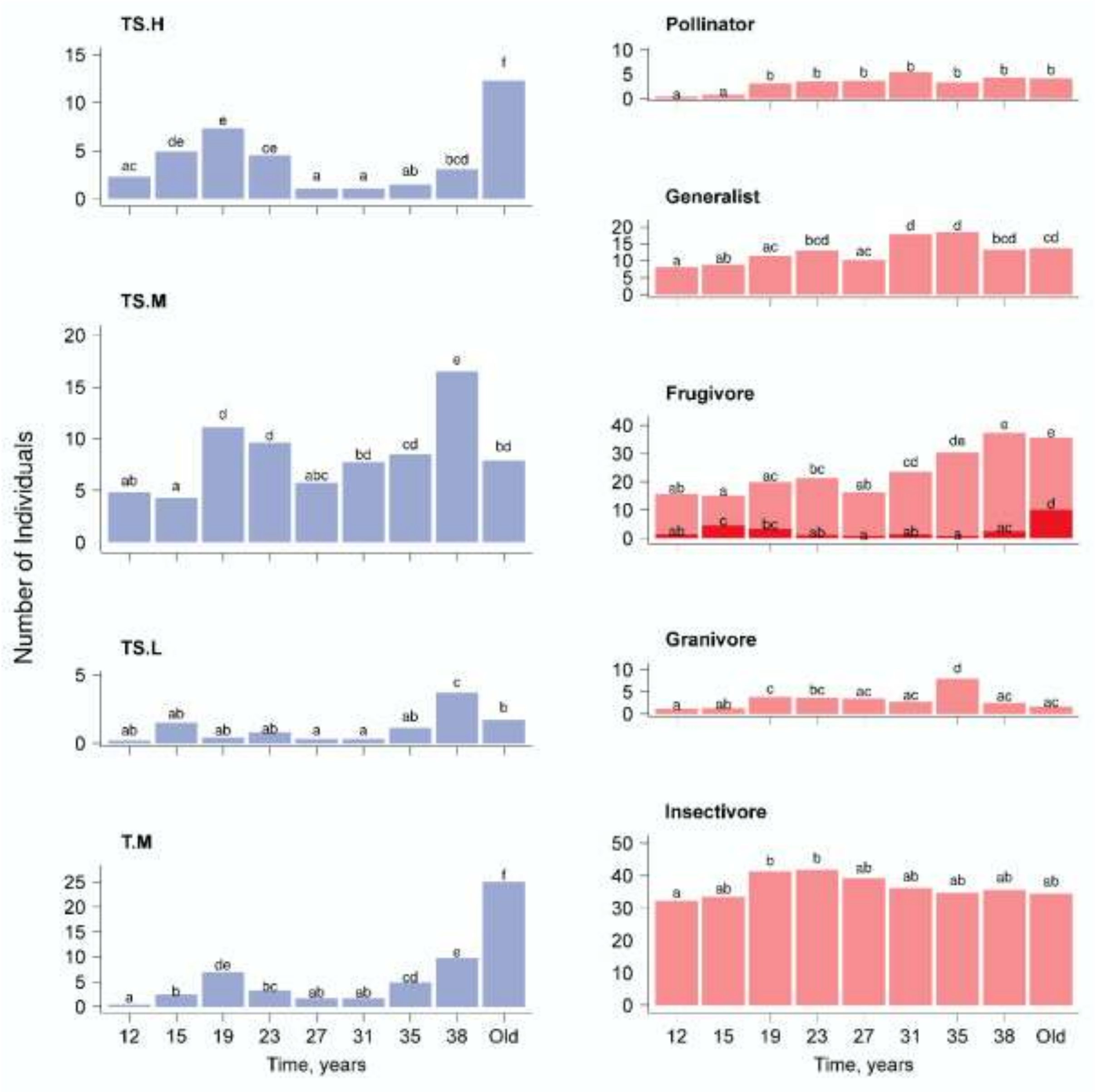

Figure S2. Absolute abundance of tree (left) and bird (right) functional groups for each site. Different letters depict significant differences at $p < 0.05$ among sites within functional group. Note that Raptors are not included because of their low abundances. Large frugivores abundances are depicted in dark red.