Bottom-up cascading effects of quarry revegetation deplete bird-mediated seed dispersal services

Ana D. Sampaio[ab], Pedro F. Pereira[b], Alice Nunes[c], Adelaide Clemente[c], Vânia Salgueiro[a], Carmo Silva[ab], António Mira[ab], Cristina Branquinho[c], Pedro A. Salgueiro[ab]

[a]UBC- Unidade de Biologia da Conservação,
Universidade de Évora, Pólo da Mitra, Ap. 94,
7006-554 Évora, Portugal
[b]MED – Mediterranean Institute for Agriculture, Environment and Development.
University of Évora. Pólo da Mitra, Apartado 94, 7006-554 Évora, Portugal
[c] cE3c - Centre for Ecology, Evolution and Environmental Changes, Faculdade de
Ciências, Universidade de Lisboa, C2, Campo Grande, 1749-016 Lisboa, Portugal.

Corresponding Author

anadsampaio@gmail.com
UBC - Unidade de Biologia da Conservação,
Universidade de Évora, Pólo da Mitra, Ap. 94,
7006-554 Évora, Portugal
MED – Mediterranean Institute for Agriculture, Environment and Development.
University of Évora. Pólo da Mitra, Apartado 94, 7006-554 Évora, Portugal

Abstract

Quarrying activities cause profound modifications on ecosystems, such as removal of vegetation cover, biodiversity loss and depletion of ecosystem services. Ecological restoration stands as a solution to revert such effects. Concomitantly, awareness is currently being given on ecosystem services and ecological processes to evaluate restoration efficiency.

The objective of the study was to access restoration success in a quarry subjected to restoration practices for the last 40 years involving the plantation of native Mediterranean vegetation and the non-native Aleppo pine *Pinus halepensis*. The study was carried out by assessing the effectiveness of seed dispersal service provided by birds in the restored quarry by comparing this service to neighbouring natural (shrubland) and other semi-natural areas (oak-pine mixed open and Aleppo pine forest) present at the landscape. For this purpose, we explored bird composition structure and seed dispersal networks using point counts and faecal samples of mist-netted birds. We also collected vegetation structure data and explored its effect on bird community composition.

Our results showed that bird abundance in the restored quarry was significantly lower, and its bird community was compositionally different than natural shrubland and semi-natural areas. For instance, seed-dispersing birds, woody and shrub/ground foragers and partially migrators were the most affected groups at the restored area. Bird composition and their traits were likely driven by vegetation characteristics, such as native vegetation cover, fruit richness and Aleppo pine cover. Concurrently, seed dispersal network in the restored quarry was less complex than in other areas.

Seed dispersal services in the restored quarry were below the reported values of neighbouring natural and semi-natural areas and likely driven by the low abundances of seed-dispersing birds. We consider that the causes affecting this group’s low abundance can be related to revegetation measures favouring Aleppo pine, combined with a shallow soil depth and poor soil quality, which may have constrained native vegetation development.

We conclude that seed dispersal services at the quarry are depleted, which may suggest a low ecological restoration success. We highlight that quarry revegetation with non-native species must be avoided, since it may alter bird composition structure and hence, the seed dispersal service.

Keywords: birds; ecological network; ecological traits; ecosystem services; habitat restoration; Mediterranean

1. Introduction

As global Human population increases, the demand for infrastructures fuels the need to deliver mineral resources, thus sustaining the growth of extractive industries (Kesler et al., 2015; Carvalho 2017). Notwithstanding their socio-economic value, quarrying activities cause profound modifications on ecosystems, such as removal of vegetation cover, biodiversity loss and the depletion of ecosystem services (Akanwa et al., 2017; Fugiel et al., 2017). Therefore, there is an urging need to employ effective restoration practices in post-extraction areas to accelerate ecosystem recovery (Salgueiro et al., 2020a). Traditionally, restoration practices largely relied on soil formation and revegetation, however, awareness on the restoration of ecological processes and the services they provide is currently increasing (e.g., Dmitrakova et al., 2018; Salgueiro et al., 2020b).

Addressing ecological processes at restored sites, namely how species within a community interact, is considered an important tool to assess the effectiveness of restoration practices (Cadotte et al., 2011) and to understand the condition and self-sustainability of disturbed ecosystems (Bacles et al., 2006; Larsen et al., 2010). Seed dispersal, for instance, plays an essential role in plant population spread, colonisation and community dynamics (Nathan, 2006) enforcing ecosystem resilience (Spiegel & Nathan, 2007; Rey & Alcántara, 2000). Many plants often rely on seed dispersal services provided by frugivorous animals to colonise new areas (Herrera, 2002). Consequently, seed dispersal mediated by animals (i.e., zoochory) can contribute to further assist ecosystem restoration by promoting revegetation of vacant unrestored areas (Salgueiro et al., 2020b), if suitable conditions for their establishment are granted. Birds are among the most important seed dispersal service providers (Whelan et al., 2008) and often considered good indicators of their provision (García et al., 2010). Moreover, birds are also considered as highly sensitive to ecosystem disturbances as they embrace a wide range of ecological traits, namely considering the way they interact with plants, their feeding behaviour and spatio-temporal distribution (i.e. phenology) (Drapeau et al., 2000; Brotons et al., 2018). Consequently, declines of bird populations or changes in avian communities are expected to disrupt plant-animal interactions (Inger et al., 2015). The potential of seed-dispersing birds to assist revegetation of degraded areas by mining or quarrying activities remains overlooked, since interactions between bird and plant communites in restored areas are poorly understood (Šálek, 2012 ;Makoto & Wilson, 2018). Seed dispersal services are highly sensitive to human disturbance (Neuschulz et al., 2016), and the evaluation of such services offers evidence on ecosystem integrity as an indicator of suitable restoration practices (García et al., 2010; Zhang et al., 2018).

The aim of this study was to assess the restoration success by comparing the effectiveness of seed dispersal services provided by birds in a restored quarry area with other three locally representative habitats: one natural (shrubland) and two semi-natural habitats (mixed open oak-pine and pine forests). In each area, we assess bird community and trait composition (based on ecological function towards seeds of fleshy fruited species, feeding behaviour and phenology) in addition to plant-disperser interactions to investigate how potential changes in the community driven by habitat attributes mediate seed dispersal provision. Considering that revegetation practices are aimed to accelerate the process of habitat restoration in quarries, we hypothesize that seed dispersal services are being provided at similar levels in the restored area as in nearby natural and semi-natural areas.

2. Materials and Methods

2.1. Study Area

This study was conducted at Arrábida's Natural Park (classified in 1976), a calcareous mountain chain at southwest Portugal (38°29'24.51"N, 8°59'43.60"W) influenced by a dry Mediterranean climate. Landscape is dominated by the Mediterranean *maquis* characterised by dense semi-deciduous and evergreen sclerophyllous vegetation (Portuguese oak *Quercus faginea*; kermes oak *Quercus coccifera*; strawberry tree *Arbutus unedo;* wild Mediterranean olive *Olea europaea* var. *sylvestris;* juniper *Juniperus phoenicea;* Mediterranean mastic tree *Pistacia lentiscus*; and Narrow-leaved mock privet *Phillyrea angustifolia*; Catarino, 1982). In addition, the study region comprises non-native Aleppo pinewood *Pinus halepensis* and mixed oak-pine forest patches.

In this area, extraction industries explore limestone as a natural resource. The largest and oldest active limestone and marl quarries at Arrábida (SECIL-Outão) were founded in 1904. Limestone/marl exploitation was carried out from top to bottom of a hill, forming benches spaced by 10/20 m slopes. Revegetation practices were carried out since 1983 with soil landfilling (≃1 meter) on exposed rock and through the planting of native sclerophyllous vegetation and with Aleppo pine trees, which were traditionally used in reforestation. Quarry revegetation plans started in a period when Aleppo Pine species was commonly planted in the Iberian Peninsula to reduce soil erosion (Pausas et al., 2004). The main purpose of planting this non-native species was to decrease soil loss by erosion, to enhance seedling establishment of native species and, ultimately, to rapidly reduce the visual impact of the exposed rock slopes in the landscape. In 2001, a local study showed that the artificial revegetation favoured a quicker establishment of species and reduced the visual impact (Werner et al., 2001). The *restored quarry area* (*Res*) where sampling took place, was located at the center of the restored quarry and was revegetated in the 1990's. We further selected three different areas depicting from the most representative natural and semi-natural areas within the natural park (Fig.1): 1) a *natural shrubland* (*Shr*) dominated by Mediterranean *maquis*; 2) a *mixed open forest (Mix*) with semi-deciduous and evergreen sclerophyllous shrubs, and low densities of oak pine, planted Stone Pine *Pinus pinea* and Aleppo Pine trees, and 3) a dense mature *Aleppo pine forest* area (*Pin*) planted more than 60 years ago (Ruiz-Peinado et al., 2001), with trees reaching twice the height of *Res* pines and natural encroachment of native understorey of evergreen sclerophyllous vegetation.

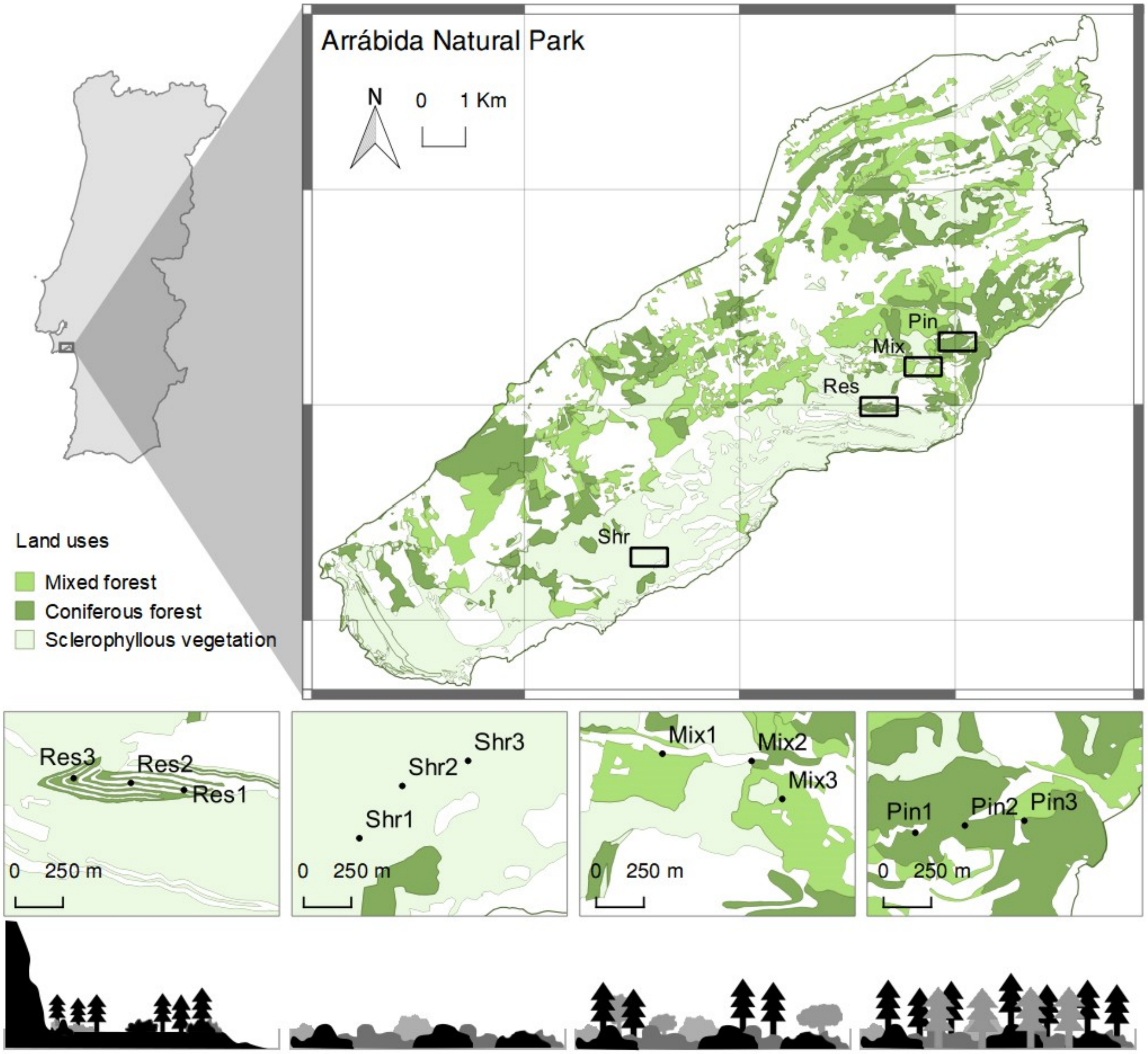

Figure 1. Land uses of Arrábida Natural Park and the four sampling areas: *Res* (restored quarry), *Shr* (natural shrubland), *Mix* (mixed open forest) and *Pin* (Aleppo pine forest). Sampling was replicated in three plots per area.

2.2. Sampling data

We set three plots in each sampling area (*Res*, *Shr*, *Mix* and *Pin*) located at a minimum distance of 250 meters to ensure spatial independency of surveyed birds. Sampling was performed monthly (September 2018-February 2019) in all plots, summing up a total of six sessions performed during autumn/winter fructification season.

Bird communities and seed dispersal services were assessed using two methodologies in each session: (1) point counts and (2) mist-net captures, respectively. We performed 10-minute point counts at the centroid of each plot to assess bird community by counting all individuals detected within a radius of 50 meters. This procedure was conducted by the same observer at dawn before mist-net set up, thus accounting for the period of highest bird detectability (Bibby et al., 2000). Seed dispersal service was determined by collecting faecal samples of captured birds. For this purpose, in each plot, we place 36 meters long mist-nets, open from dawn to dusk (≈8 hours and 25 minutes ± 35 minutes) with a verification periodicity of 30 minutes. All birds were ringed with a permit by Portuguese National Institute for Nature Conservation and Forests attributed to PFP (187/2018) and left in cotton bags for 30 minutes to obtain faecal samples. Each sample was stored in individual containers for posterior seed identification with silica pellets (to avoid seed deterioration by moulds). In laboratory, faeces were examined under a binocular magnifying glass (10x). Intact seeds were identified by experts to the lowest taxonomic level possible based on a local reference collection.

Regarding fruit availability, we recorded only plant species that were producing ripe fleshy fruits during sampling period in each plot and at the beginning of each session (*R_fruits*) (along both sides of the mist-nets). Although we captured the period of fructification of most autumn/winter Mediterranean fleshy fruited species (Herrera, 1984), we were unsuccessful to detect ripe fruits of Arrábida local species asparagus *Asparagus* spp., jasmine *Jasminum fruticans,* white osyris *Osyris alba,* mock privet *Phillyrea latifolia,* black hawthorn *Rhamnus lycioides and* Mediterranean buckthorn *Rhamnus alaternus* (Catarino, 1982).

In relation to vegetation structure, we assessed native and non-native vegetation cover and height once in each plot using the line-intercept method (Elzinga et al., 1998) with two parallel transects of 12.5 m. Woody plants that intercepted the line were identified to the species level. For statistical analysis, we grouped all native species into two canopy-height categories: ≥5 m and <5 m to discriminate native tree layer (*c_nat_trees*) from native understorey layer (*c_nat_shrubs*) (Gschwantner et al., 2009). Cover measures from all species within each of these categories were summed. Likewise, vegetation height was also averaged per each category (*h_nat_shrubs*; *h_nat_trees*). Regarding non-native pines, the canopy cover from all pines was summed up (*c_pine*) and heights were averaged (*h_pine*) per plot (Table S1, Supporting information).

2.3. Statistical analysis

2.3.1. Bird community composition

To reduce autoreplication between sessions, species and abundances of all sessions were pooled and averaged for each plot. Each sampling plot was considered a spatial replicate.

An univariate Analysis of Variance (ANOVA) was applied to compare bird abundance between areas followed by pairwise Tuckey's post-hoc tests. A Permutational Analysis of Variance (PERMANOVA) was conducted with Bray–Curtis dissimilarity scores to test for differences in community composition between areas. Pairwise PERMANOVA tests were carried out based on 999 Monte Carlo (MC) permutations due to the low number of possible permutations between pairs of replicate plots. PERMANOVA was performed using the software PRIMER-E (PRIMER-E, Version 6; Clarke & Gorley, 2005).

An RLQ analysis was performed on point count data followed by a fourth-corner analysis to explore and test the relationship between vegetation structure and bird trait composition in each area (Dolédec et al., 1996). As stated by RLQ procedures (Dray et al., 2014), a Correspondence Analysis (CA) was initially carried out on bird composition data (table L: species abundance x plots) linking vegetation variables table (table R: vegetation variables x areas) to bird traits table (table Q: traits x species). A Principal Component Analysis (PCA) was performed on vegetation variables table (table R: vegetation variables x areas) with seven continuous vegetation variables: *R_fruits; c_nat_shrubs*; *c_nat_trees; c_pine; h_nat_shrubs*; *h_nat_trees, h_pine* (Table S1, Supporting information). A Hill-Smith PCA was carried out on a bird trait table accounting for three categorical variables considering bird phenology (exclusively migratory species – *migr*; partially migratory species – *partial_migr*; exclusively resident species – *resid*), feeding behaviour (forages in woody plant species – *woody*; forages in the open ground – *ground_o*; forages in the ground near vegetation – *ground_v*) and ecological function towards seeds of fleshy fruited species (does not interact with fleshy fruited species – *no_int*; disperses fleshy fruited seeds – *seed_disp*; predates on fleshy fruited seeds – *seed_pred*) (Table S2, Supporting information). We classified species traits according to literature (Cramp & Perrins, 1994; Herrera, 1998; Table S3, Supporting information). RLQ function combines the previous analyses and generates a cross-covariance matrix bettween vegetation variables and bird traits mediated by bird abundance.

The fourth-corner analysis tested the significance between correlations of the bivariate vegetation variables and bird traits by a randomization procedure with 49,999 permutations through random permutations of table L or R rows following with permutations of table Q rows or table L columns and p-value = 0.05. RLQ and fourth-corner procedures were carried out with ADE4 package of R-Statistics (Dray & Dufour, 2007) in R-Statistics (R Core Team, 2018).

2.3.2. Effectiveness of seed dispersal service

Plant-disperser interactions were analysed to assess seed dispersal service and to compare seed dispersal networks between areas. Plant-disperser pairwise interactions were defined as the total number of faeces of a bird species that contained at least one intact seed of one plant taxa. For each plot we pooled samples from all sessions and calculated the following network metrics (Dormann et al., 2009) to compare seed dispersal networks between areas: bird richness; seed richness; interaction evenness, *web asymmetry* (ratio between the number of disperser species and dispersed species), *Linkage density* (proportion of links per species), *weighted NODF* (the degree to which the interactions of the poorly connected species are a subset of the highly connected species), *high-level niche overlap (HL)* (index of similarity based on the overlap of disperser species interactions), *low-level niche overlap (LL)* (index of similarity based on the overlap of dispersed species). Univariate ANOVAs were performed to compare metrics between areas followed by Tuckey's tests once significant effect of area on bipartite metrics was found. Bipartite networks and extraction of network indices were carried out with Bipartite package in R-Statistics (R Core Team, 2018).

3. Results

3.1. Bird community composition

We found significant differences in bird abundances between areas (F(3,8) = 8.29, p-value = 0.0078). Tukey post-hoc tests revealed significantly lower bird abundances in *Res* (5.9 ± 1.26 birds per plot/session, totalling 107 birds of 17 species) compared to *Mix* (12.9 ± 2.9 birds per plot/session, 232 individuals of 21 species) and to *Pin* (11.1 ± 1.3 birds per plot/session, 199 birds of 19 species). No differences were detected between *Shr* bird abundances (10.1 ± 0.7 birds per plot/session, 182 birds of 15 species) and the remaining areas.

When considering bird groups based on ecological function towards seeds of fleshy fruited species, seed dispersers were most abundant in *Mix*: 8.88 ± 1.58 birds per plot/ session; *Shr*: 8.33 ± 0.76 birds per plot/ session and *Pin*: 7.39 ± 0.63 birds per plot/ session) (Fig. 2). In *Res* the most abundant group was the seed predators (Fig. 2). Furthermore, this area showed the lowest number of seed dispersers of all areas (2.72 ± 0.63 birds per plot/ session). However, for seed predators and birds that do not interact with fleshy fruited seeds, the differences between their abundances in *Res* and in the other areas were less divergent (Fig. 2).

Regarding phenology traits, the average abundance of resident birds (*resid*) was similar between *Res* (3.61 ± 1.42 birds per plot/ session) and *Pin* (3.89 ± 0.42 birds per plot/ session), but lower than *Shr* (6.39 ± 0.51 birds per plot/session) and *Mix* (6.00 ± 1.70 birds per plot/session; Fig. 2). Partial migrators (*partial_migr*) were less abundant in *Res* (1.50 ± 0.17 birds per plot/session) and *Shr* (3.00 ± 0.10 birds per plot/session) than in the remaining areas. The average abundance of migratory birds (*migr*) was lower than the other two phenologies but similar among the four areas.

Considering feeding behaviour, open-ground foragers (*ground_o*) were less abundant in all areas equitably, reaching the lowest values in *Shr* (0.5 ± 0.33 birds per plot/session) and higher abundances in *Pin* (1.50 ± 0.60 birds per plot/session) followed by *Res* (1.44 ± 0.51 birds per plot/session) and *Mix* (1.33 ± 0.50 birds per plot/session). Woody foragers (*woody*) were generally higher than the other groups, being less abundant in *Res* (2.89 ± 0.86 birds per plot/session) than *Mix* (6.83 ± 1.92 birds per plot/session), *Shr* (5.46 ± 0.42 birds per plot/session) and *Pin* (4.56 ± 0.25 birds per plot/session). The pattern is similar when comparing with near vegetation ground foragers (*ground_v*), as *Res* recorded the lowest abundance values (1.44 ± 0.51 birds per plot/ session) and *Pin* showed the highest abundances (4.94 ± 0.59 birds per plot/session; Fig. 2).

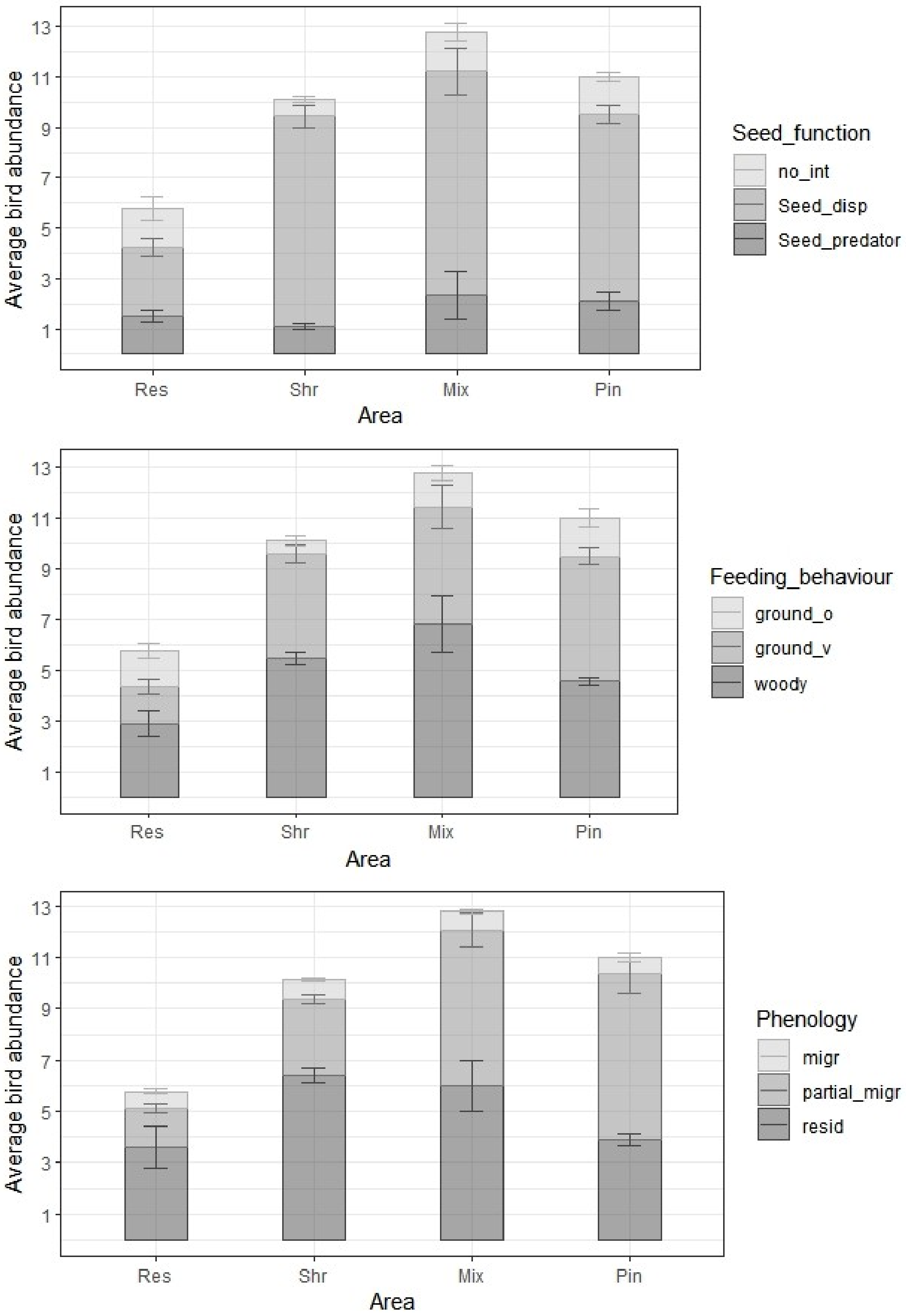

Figure 2. Bird abundances in each area partialled out by ecological function towards seeds of fleshy fruited species, feeding behaviour and phenology (bars). Whiskers represent ± standard deviation. For traits abbreviations see Table S2, Supporting

information. *Res* (restored quarry area), *Shr* (natural shrubland), *Mix* (mixed open forest) and *Pin* (Aleppo pine forest).

We found significant differences regarding bird community composition between areas (F(3,8) = 6.99, P-value <0.001). Pairwise comparison revealed significant compositional differences between bird communities for all areas (p-value <0.05) except between *Pin* and *Mix* (p-value = 0.27; Table 1; Fig. 3).

Table 1. Pairwise comparisons performed using 999 Monte-Carlo permutations, after a permutational analysis of variance (PERMANOVA) on bird community composition. *Res* (restored quarry area), *Shr* (natural shrubland), *Mix* (mixed open forest) and *Pin* (Aleppo pine forest).

Pairwise comparisons	p-value
Res x Mix	0.013
Res x Shr	0.013
Res x Pin	0.008
Shr x Pin	0.013
Shr x Mix	0.03
Pin x Mix	0.27

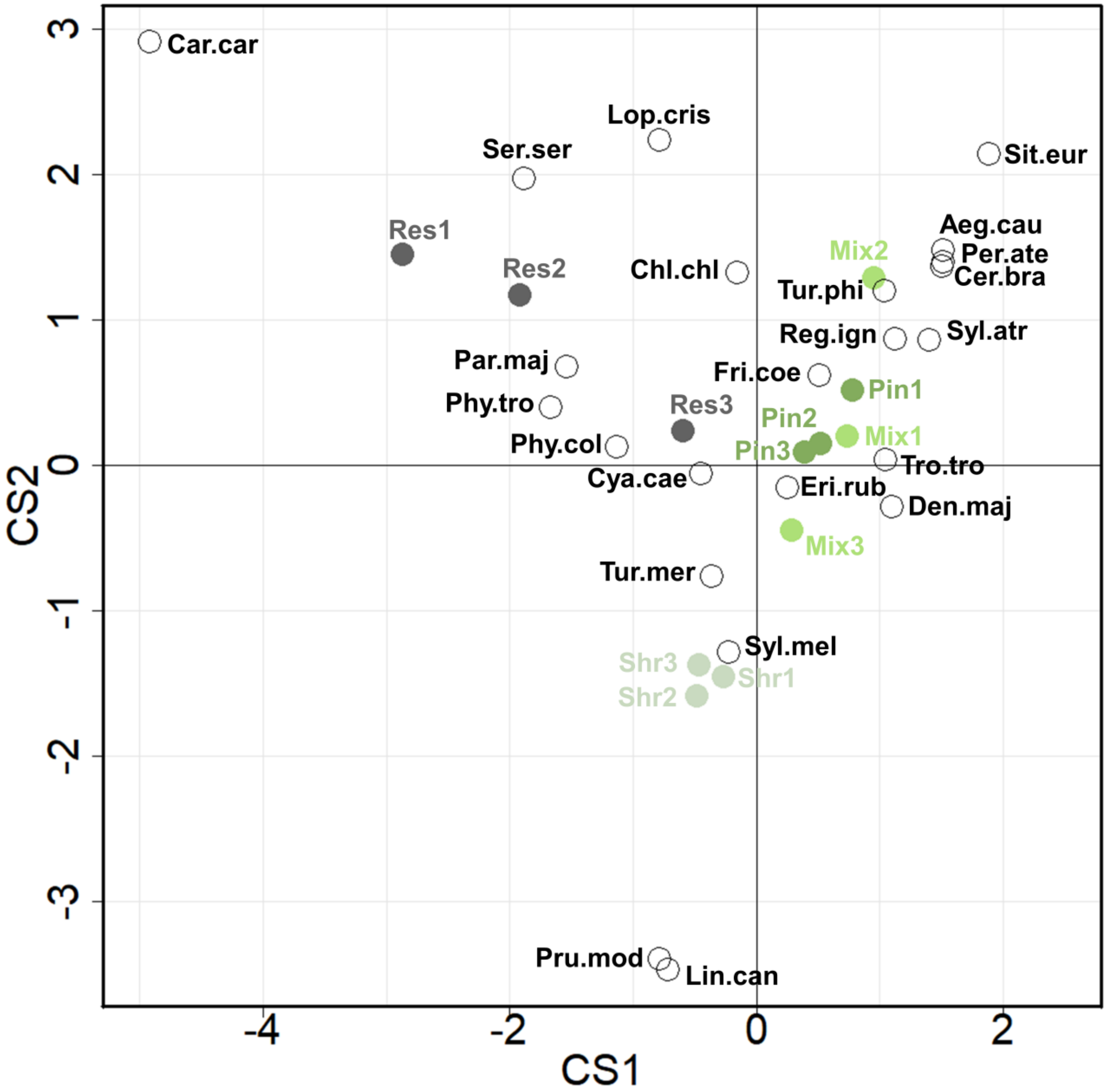

Figure 3. Correspondence analysis of bird communities: species scores are represented as empty circles and plot scores as filled circles. *Res* (restored quarry area), *Shr* (natural shrubland), *Mix* (mixed open forest) and *Pin* (Aleppo pine forest). For species abbreviations: Table S3, Supporting information.

The first two axes of the RLQ analysis explained 64.55% and 32.30% of the total projected inertia, respectively (Table S4, Supporting information). The first axis represents a gradient of increasing vertical complexity of vegetation, with a positive contribution of pine tree height and cover (*h_pine*: r = 0.19, p-value = 0.008; *c_pine*: r = 0.19, p-value = 0.025) and native shrubs height and native tree cover (*h_nat_trees*: r = 0.18, p-value = 0.051; *c_nat_trees*: r = 0.18, p-value = 0.054; Fig. 4; Tables S5; S6, Supporting information). *Mix* and *Pin* areas were proximate to each other and positively related to the first axis (Fig. 4). The second axis correlates positively with plant species with fleshy ripe fruits (*r_fruits*: r = 0.17, p-value = 0.048; Fig. 4). *Res* and *Shr* were located on opposite ends of the second axis, with Res in the bottom. In fact, *Res* showed the lowest number of plant species with ripe fruits (Fig. 4; Table S6, Supporting information for values).

In terms of bird traits, the first axis was positively related with partially migratory birds (*part_migr*: r = 0.22, p-value = 0.015) and negatively related with resident birds (*resid*: r = -0.21; p-value = 0.042). Partially migratory birds were associated to *Mix* and *Pin*, whereas resident birds occurred more abundantly in *Shr*. The second axis showed a positive correlation with seed dispersers (*seed_disp*: r = 0.20; p-value = 0.004) and was negatively associated with open-ground foragers and birds that do not interact with seeds (*ground_o*: r = -0.18; p-value = 0.011, no_int: r = -0.16; p-value = 0.031, respectively) (Table S7, Supporting information). Seed dispersers tended to occur more abundantly in *Mix* and *Pin*, while they were less related to *Res* that shows lower cover of native shrubs and trees (Fig. 4; Table S6, Supporting information for values).

Fourth-corner analysis revealed a significant positive effect of four variables on partially migratory bird abundance: number of plant species with fleshy ripe fruits (*r_fruit*: r = 0.19; p-value = 0.025), native shrubs cover (*c_nat_shrubs*: r = 0.21; p-value = 0.021), height of native trees (*h_nat_trees*: r = 0.22; p-value = 0.011) and pine height *(h_pine*: r = 0.18; p-value = 0.017) (Fig. 4). On the other hand, resident bird abundance was negatively affected by pine height (*h_pine*; r = -0.18; p-value = 0.022) and less affected by cover and height of native trees (*c_nat_trees*: r = -0.19; p-value = 0.044*, h_nat_trees*: r = -0.19, p-value = 0.050) (Fig. 4). Pine cover had a marginally negative effect on seed-dispersing birds (c_pine: r = -0.17; p-value = 0.050) (Fig. 4; Table S8, Supporting information).

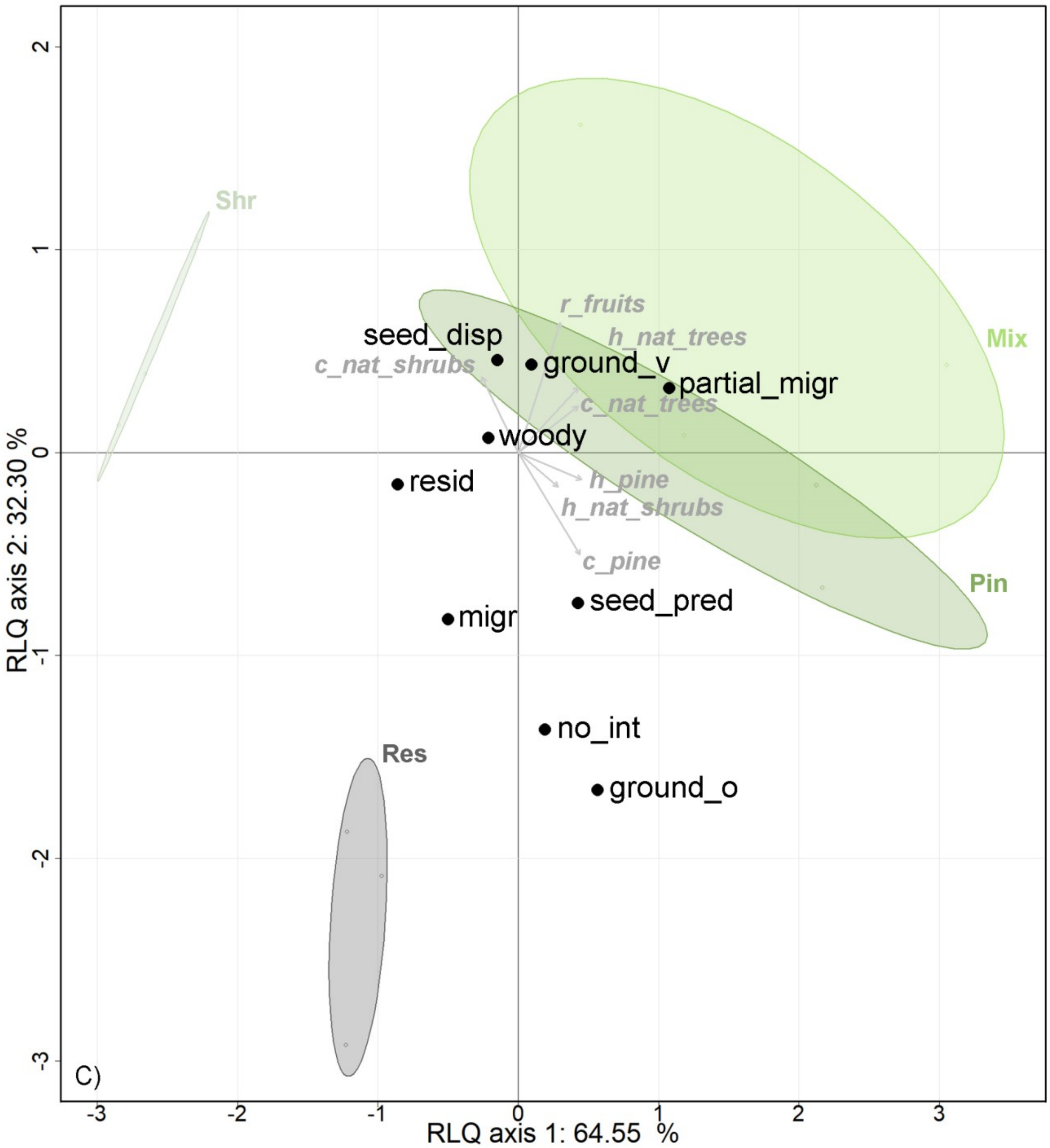

Figure 4. RLQ showing vegetation and trait vectors. Ellipses represent 50% of the total variation of vegetation scores per area. *Res* (restored quarry area), *Shr* (natural shrubland), *Mix* (mixed open forest) and *Pin* (Aleppo pine forest). For vegetation and trait abbreviations: Tables S1 and S2, Supporting information.

3.2. Effectiveness of seed dispersal service

Regarding mist-netted birds, a total of 567 faeces were collected, of which 158 (27.9%) contained at least one seed. We captured a total of nine potential seed disperser species of which seven species defecated at least one seed: European robin *Erithacus rubecula*, blackbird *Turdus merula*, song thrush*Turdus philomelos*, Sardinian warbler *Sylvia melanocephala,* Eurasian blackcap *Sylvia atricapilla*, garden warbler *Sylvia borin*, blue tit *Cyanistes caeruleus* (Fig. 5). *E. rubecula*, *S. atricapilla* and *S. melanocephala* were the main dispersers captured. The average number of captured dispersers was much lower in the *Res* (3.67 ± 0.58 individuals) than in all other areas: 14.33 ± 7.57 individuals in *Shr*, 17 ± 1.73 in *Pin* and 18.33 ± 2.52 in *Mix*. Defecated seeds obtained in this study corresponded to 25 plant taxa. The number of plant species was much lower in *Res* (6 species), being two to three times higher in *Mix* (12 species), *Pin* (13 species) and *Shr* (19 species). *Res* also exhibited the lowest number of bird/plant interactions with 12 interactions (8 ± 7 interactions/plot; Fig. 5). The remaining areas showed a similar number of interactions in *Mix* (69 interactions; 23 ± 2.65 interactions/plot), followed by *Pin* and *Shr* with 66 and 61 interactions (22 ± 5.29; 20.33 ± 11.15 interactions/plot), respectively (Fig. 5). *S. atricapilla* was the main disperser in *Mix, Shr*, and *Pin* representing 70% (48 interactions), 61% (37 interactions), and 52% (34 interactions) of the total interactions of each area. At *Res*, *S. atricapilla*, totalized only 17% of all interactions (2 interactions), being overtaken by *E. rubecula* and *Sylvia melanocephala*, which dispersed approximately 50% (6 interactions) and 25% (3 interactions), respectively.

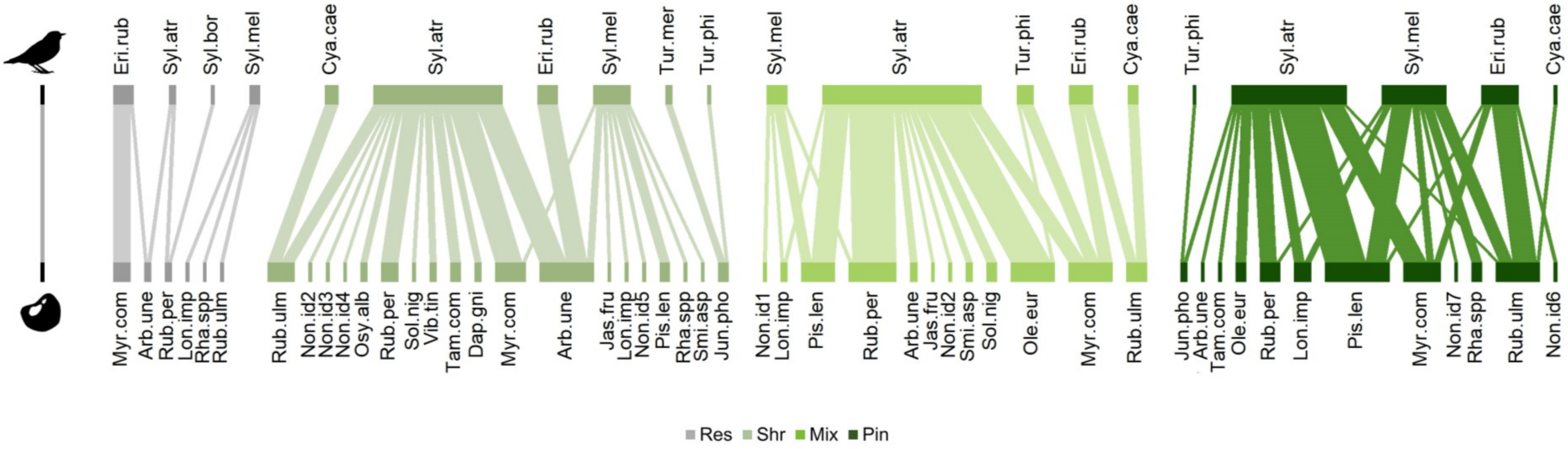

Figure 5. Seed dispersal networks of the four sampling areas. Seed-dispersing birds are shown in the upper level of the network and dispersed plant species in the lower level. All networks are shown in the same scale. A single interaction is represented by the line thickness of the example on the left side of the image. Bird species abbreviations: Cya.cae (blue tit *Cyanistes caeruleus*), Eri.rub (European robin *Erithacus rubecula*), Syl.atr (Eurasian blackcap *Sylvia atricapilla*), Syl.bor (garden warbler *Sylvia borin*), Syl.mel (Sardinian warbler *Sylvia melanocephala*), Tur.mer (blackbird *Turdus merula*), Tur.phi (song Thrush *Turdus philomelos*). *Res* (restored quarry area), *Shr* (natural shrubland), *Mix* (mixed open forest) and *Pin* (Aleppo pine forest). For plant species abbreviations: Table S9, Supporting information.

ANOVA tests revealed significant differences in several metrics, such as plant species (F(3,8) = 5.48, p-value = 0.024), linkage density (F(3,8) = 6.98, p-value = 0.013), interaction evenness (F(3,8) = 10.24, p-value = 0.041), niche overlap (HL) (F(3,8) = 5.42, p-value = 0.025), niche overlap (LL) (F(3,8) = 4.91, p-value = 0.032) and web assymetry (F(3,8) = 7.50, p-value = 0.010) metrics. Tukey tests revealed that *Res* showed the most differences when compared to the remaining areas. Overall, *Res* exhibited significantly lower network metric values than the other areas, with an exception of web assymetry metric, which displayed a higher value in this area (Fig. 6). Nonetheless, network metrics did not show significant differences between *Shr*, *Mix* and *Pin*. *Res* area recorded significantly lower values for plant species and linkage density when compered with *Shr* and *Mix*. Regarding interaction eveness, *Res* showed significantly lower values than *Shr* and *Pin*. In the case of bird niche overlap (HL) differences were found between *Res* and both *Mix* and *Pin*. *Res* showed the lowest value of bird niche overlap. *Res* plant niche overlap (LL) was only significantly lower when compared with *Mix*.

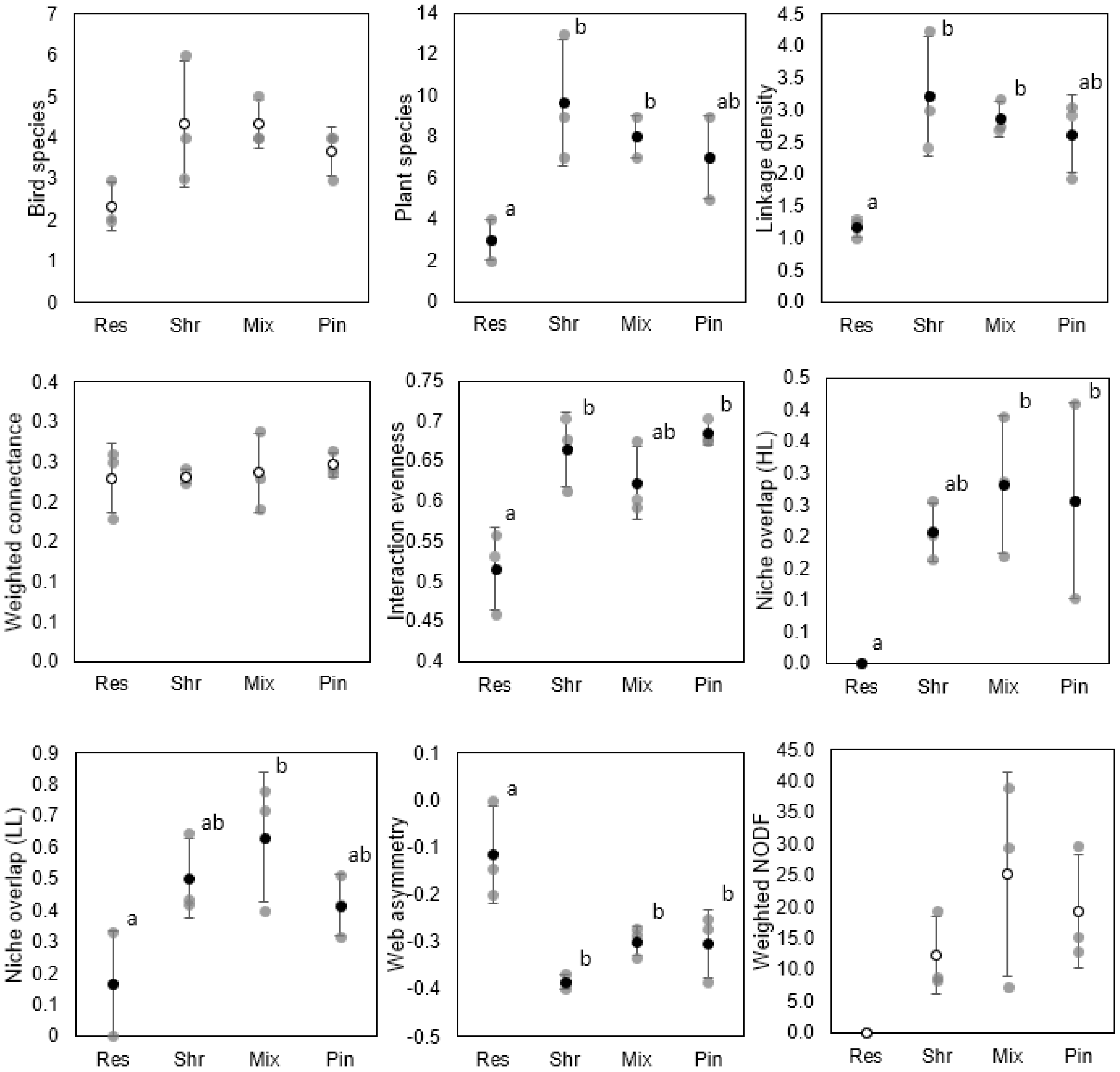

Figure 6. Mean and standard deviations of network metrics for each area. Black filled dots represent average values of the metrics with significant differences between areas. Grey dots represent metric values per plot. *Res* (restored quarry area), *Shr* (natural shrubland), *Mix* (mixed open forest) and *Pin* (Aleppo pine forest).

4. Discussion

Contrarily to our expectations, our results showed that seed dispersal services at restored quarry area were being provided below the levels of natural and semi-natural neighbouring areas. Mediterranean bird communities are known to be rich in generalist species (with broad ecological niche occurring in a wide range of successional stages), in edge species (preferring intermediate successional stages) and in species that are well adapted to respond to habitat restoration (Santos et al., 2002; Brotons et al., 2018). However, despite the effort employed in restoration, most of the interaction network metrics analysed for the quarry area showed significant deviations from the metrics obtained for the natural (shrubland) and semi-natural habitats (mixed open oak-pine and Aleppo pine forests). On the other hand, both natural and semi-natural areas performed similarly, which suggests that this service is provisioned independently from habitat type. Overall, network interactions in the restored area were simple and asymmetric, showing a much lower linkage density. The dissimilarity of interaction evenness values between the restored and the reference areas indicate that the revegetated quarry services are depleted (Kaiser-Bunbury & Blüthgen, 2015). Seed dispersal services in the restored area are thus more susceptible to disruption, most likely because they are sustained by a low number of interacting birds and plants, and small sized networks may suffer from increased vulnerability (Power & Stout, 2011; González-Castro et al., 2012).

The small network size of the restored quarry relates to low seed disperser abundance, pinpointed by a significant compositional change in the bird community when compared with the other areas. Specifically, the abundances of non-interacting and seed predator species are similar to seed dispersers in the restored area, whereas in the other areas seed dispersers represent the dominant group. Forest resident birds such as European goldfinch *Carduelis carduelis*, European serin *Serinus serinus* or great tit *Parus major* (non-seed dispersers) were more correlated with the restored area. These species are known forest generalists with large habitat breadths (Rey-Benayas et al., 2010), for this reason they can successfully occupy the non-mature Aleppo pine stands of the restored area. Regarding seed-dispersing species, which occurred mostly in mixed open forest and natural shrubland areas, *E. rubecula*, *S. atricapilla* and *S. melanocephala* were the key in providing these services, otherwise compromised if these species were absent from an area. For example, although *S. atricapilla* was one of the most abundant species in mixed open and Aleppo pine forests, it was scarce in the restored area. Apart from preventing further complex interaction networks, the scarcity of *S. atricapilla* is a potential indicator of low fruit availability (Herrera, 1998; Tellería et al., 2008). *S. atricapilla* and *E. rubecula* were the most abundant partially migratory species thus contributing to the significant positive relationship with native tree cover and height and richness of plants that produced ripe fleshy fruits. Whereas *S. melanocephala* and *T. merula* which were abundant resident species in our study may benefit from habitats with lower trees during winter to improve their breeding success in the following spring (Wysocki et al., 2004; Mettke-Hofmann & Gwinner, 2004).

Low abundances of seed dispersers in the restored area may be related with vegetation structure and feeding resources availability, considered a key features in determining bird assemblages (Bohada-Murillo et al., 2019; García et al., 2011). In fact, RLQ analysis clearly segregated the areas based on vegetation structure, namely along a gradient of tree height and tree cover and, to a lower extent, on the availability of plants with ripe fleshy fruits. The number of species that produced ripe fleshy fruits was low in the restored area, even though revegetation measures included several native fleshy fruited species usually consumed by birds.

RLQ results suggested that Aleppo pine cover negatively influenced the abundance of seed-dispersing birds. This effect may be accurate for the restored area, whose seed disperser abundances were very low, but not for Aleppo pine forest area where abundances were not distinct from shrubland and mixed open forest (Fig. 2). Although our results showed that native shrub cover (*c_nat_shrubs*) did not significantly affected bird composition and bird trait assemblages, it is known to be a more critical factor determining bird species establishment than Aleppo pine cover (Lopez & More, 1997). In the case of our restored area characterised by low soil quality and shallow depth (Correia et al., 2001), native vegetation may undergo a more intense negative interaction (i.e., competition) with Aleppo pine than in Aleppo pine forest resulting in a less dense understorey cover (Bellot et al., 2004; Nunes et al., 2014). On the other hand, the high understorey cover in Aleppo pine forest area may have buffered against the unsuitability of pine cover for bird species, thus contributing to higher seed disperser abundances as the density of shrubs are generally higher in older than in young pine plantations (Rodríguez-Pérez et al., 2018).

In conclusion, our results suggest a bottom-up cascading effect of revegetation practices in seed dispersal service provided by birds. Overall, Aleppo pine cover associated with poor soil quality and shallow soil depth in the restored area might be constraining the development of native vegetation and, consequently, plant species with ripe fleshy fruits. Sparce native vegetation cover and reduced food resources induced changes in bird communities by hindering habitat suitability for seed-dispersing species. Consequently, the number of birds able to provide seed dispersal services were below the expected numbers reported in neighbouring areas, leading to the depletion of this service in the restored area.

4.1 Implications for restoration practices

One of the final goals of restoration is to achieve a self-regulated ecosystem state through the recovery of ecological functions (Gann et al., 2019). A depleted seed dispersal service will be susceptible to disruption and will cause a profound negative effect on plant regeneration (Rey & Alcántara, 2014), therefore, compromising logistic and financial efforts invested on restoration.

Quarries in Mediterranean environments are challenging to restore given the shortage of water during dry seasons (Nunes et al., 2016). Given the scarce available information on quarry restoration techniques, Aleppo pine plantation seemed the best strategy to employ at the time. Proper assessments of the effects of such early strategies are now a current demand from companies that have invested on restoration prior to the overwhelming information that is now becoming available. Our study innovates by reporting cascading effects from these early restoration strategies on ecosystem services, a concept present for decades in the scientific background, but only in recent years became widely acknowledgeable by other circles of the society, including restoration ecology (see Young et al. 2005, Roberts et al., 2009).

Assessing seed dispersal interactions revealed to be an effective indicator of restoration success by unravelling the provision of ecosystem services by birds. Further, addressing bird community composition based on biological traits of birds provided an insight on ecosystem functioning by detailing how species and traits are distributed within four areas. The complementarity of both approaches (seed dispersal interactions and bird community composition) allowed us to understand the drivers of ecosystem functioning and how they entangle with restoration practices. In our study we concluded that a 40-years old restored quarry is not yet functioning as the neighbouring natural or semi-natural habitats.

Our findings allow us to recommend: (1) the avoidance of non-native species inclusion since it may have a negative effect on native fruit-bearing vegetation reestablishment, particularly in areas with low soil depth and nutrient depleted, and (2) the use of native plants should be favoured assuring the development of suitable habitats to attract native fauna to take advantage of the ecological services it provides.

Author contributions

PAS and CS conceived the idea; PAS, PFP and ADS designed the methodology; ADS, PAS, PFP, VS and AN collected the data; ADS and AC identified seeds; ADS analysed the data with major contributions of PAS and PFP; ADS led the writing of the manuscript with major contributions of PAS and PFP; AN, AC, VS, CS, AM and CB reviewed the manuscript; AM and CB supported the financial costs of field and laboratory work. All authors contributed to the drafts and gave final approval for publication.

Research data for this article

Data will be available upon request.

Acknowledgments

We acknowledge SECIL-Outão for funding this study and granting access to the quarry, Carolina Carvalho for the help provided during fieldwork, Alexandra Silva for logistical support, and LabOr - Laboratory of Ornithology (MED) for the support on bird trapping material and discussion of the manuscript.

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