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Restoration legacy, forest cover and elevation shape frugivory in a tropical landscape

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Abstract

Assisted and passive natural restoration are widely applied strategies for forest restoration, yet their focus on tree recovery makes their effectiveness in restoring broader biodiversity unclear. Assuming that tree recruitment will rebuild whole ecosystems overlooks other taxa and their interactions, and thus underestimates key components of biodiversity like biotic interactions. To address this gap, we assessed how frugivory varied across a restored landscape by assessing how assisted and natural regeneration, together with biotic (fruit size and availability), abiotic (elevation and time), and landscape factors (forest cover and fragmentation) shape frugivore interactions with dummy fruits. We observed that fruit attacks were not driven solely by restoration type but also by a combination of biotic and abiotic factors. Attack rates were higher at greater elevations and in areas with increased old-growth and secondary forest cover. Fruit size also influenced attack rates, particularly in restoration areas, where larger fruits experienced more attacks. Because secondary forest results from both restoration strategies, its spread appears to have helped frugivory recovery and maintenance across the landscape. Yet small, isolated old-growth patches remain crucial as reservoirs of frugivore activity. Our findings indicate that forest recovery efforts should look beyond restoration strategies and explicitly consider how biotic traits, abiotic gradients and landscape structure interact to reestablish frugivory and, by extension, broader ecosystem processes.

Keywords: biotic interactions, dummy fruits, birds, restoration, elevation, landscape analysis

Introduction

In light of the UN Decade on Ecosystem Restoration (2021–2030; UNEP & FAO, 2021), which calls for practical, evidence-based restoration of both species and ecosystem functions, it is vital to assess the performance of different restoration strategies. In this sense, restoring tropical rainforests through effective restoration practices will be essential for safeguarding global biodiversity, as these habitats are increasingly threatened by deforestation, habitat loss, and climate change (Dirzo and Raven, 2003; Pimm et al. 2014). Two common strategies are employed to mitigate these impacts: assisted natural restoration (active restoration) and passive natural restoration (passive restoration) (Holl and Aide, 2011; Chazdon et al. 2021). Although both approaches aim to reverse human-induced degradation and facilitate ecosystem recovery, they differ in their objectives, timelines, and levels of intervention. Each strategy has shown success in restoring forest cover and species diversity (Crouzeilles et al. 2017; Meli et al. 2017; Reid et al. 2018), yet evidence suggests that their outcomes are context-dependent, influenced by various confounding environmental and social factors (Holl and Aide 2011; Chazdon et al. 2021). Moreover, many restoration efforts have traditionally focused on recovering tree species diversity, often overlooking the recovery of ecological processes like biotic interactions (Selwyn et al. 2023; SER, 2021). To better evaluate the success of restoration, it is therefore necessary to assess how different strategies contribute to the recovery of ecosystem functions driven by interacting species. This understanding is critical for guiding restoration actions and meeting global goals in a rapidly changing world.

Evidence on whether assisted or passive natural restoration is more effective for restoring forest cover and biodiversity has yielded mixed results. While some studies indicate that assisted restoration leads to greater diversity recovery (Shoo et al. 2016; Holl et al. 2017; Hua et al. 2022), global meta-analyses indicate that passive natural restoration is more effective (Crouzeilles et al. 2017; Meli et al. 2017). Passive natural restoration is often considered a more efficient approach, as it is the most cost-effective and naturally regenerating forests tend to provide a higher return on investment in terms of biodiversity recovery (Crouzeilles et al. 2017). This conclusion primarily arises from the lower cost of passive natural restoration compared to active restoration, which can be significantly more expensive (Catterall and Harrison 2006). However, when assessing whether assisted or natural regeneration is the more effective strategy, it is crucial to consider the local context (e.g., historical land use, ecosystem resilience, and landscape factors), as these factors strongly influence regeneration success and the interpretation of study results, as evidenced by research supporting assisted regeneration (Shoo et al. 2016; Holl et al. 2017; Hua et al. 2022). Another aspect to consider is that meta-analyses favoring passive natural restoration may be subject to bias and require careful interpretation. For instance, Reid et al. (2018) identified a positive selection bias in meta-analyses: studies on natural regeneration were conducted in more forested regions, inherently

favoring biodiversity measures in those areas. In contrast, assisted restoration was studied under more variable conditions, ranging from highly disturbed habitats to secondary forests, often including landscapes where natural recovery is hindered or stalled by low surrounding forest cover and past land use (Herrera et al. 2011; Laurance et al. 2011a; Reid et al. 2018). For instance, invasive plant species like grasses and ferns can hinder the establishment of dispersed seeds, delaying natural forest regeneration and promoting arrested recovery in these systems. In such degraded habitats, assisted regeneration may be essential to initiate the recovery process (Hartig and Beck, 2003; Roos et al. 2011; Levy-Tacher et al. 2015). Due to site-selection bias and the potential for stalled restoration, Reid et al. (2018) recommended focusing on paired comparisons within a region, ensuring that assisted and natural regeneration are assessed under the same ecological and environmental conditions. Indeed, studies that have conducted such within-region comparisons found no consistent advantage of natural regeneration over assisted restoration (Levy-Tacher et al. 2015; Shoo et al. 2016; Holl et al. 2017).

Frugivory is a key biotic interaction that drives forest regeneration, as frugivores are responsible for most seed dispersal in tropical ecosystems (Jordano, 2000). By dispersing seeds, frugivores facilitate seedling establishment and contribute to vegetation recovery in disturbed areas (Bello et al. 2024; Selwyn et al. 2023). However, many frugivores depend on forested areas for reproduction and foraging (Bonfim et al. 2021; Selwyn et al. 2023). Yet, the widespread loss of native forests has significantly reduced their original cover, threatening not only frugivore species (e.g., birds and mammals) but also their interactions with plants and the ecosystem services they sustain (Fahrig, 2003; Laurance et al. 2012; Fahrig et al. 2019). Evidence shows that in disturbed landscapes, frugivory is limited by forest loss and fragmentation, making restoration efforts crucial for the recovery and maintenance of these keystone interactions (Bonfim et al. 2021; Martínez-Penados et al. 2024). Despite the negative effects of forest loss and fragmentation on frugivores, their persistence and interactions can play a key role in supporting forest regeneration beyond remnant patches by enhancing seed dispersal and contributing to carbon sequestration in regenerating forests (Béllo Carvalho et al. 2023). Frugivore bird spill-over, for example, can occur from secondary and old-growth forest promoting the removal of fruits in disturbed habitats (Béllo Carvalho et al. 2023). However, frugivory dynamics can differ between conserved and disturbed habitats. Because, while some native frugivores facilitate regeneration by dispersing native seeds across both, habitat-generalist species are often linked to the spread of non-native seeds, potentially hindering restoration (Thierry et al. 2022). Moreover, although local frugivore species diversity can be similar across conserved and disturbed habitats, high functional turnover of frugivores and dispersed seeds has been observed which may increase the differences in fruit removal between conserved and degraded habitats (González-Varo et al. 2023). Thus, despite the potential of frugivores to support seed dispersal in regenerating forests, their identity and dynamics can vary with habitat condition. In this context, the extent to which habitat condition

influences frugivory remains poorly understood, particularly regarding how different restoration strategies shape frugivore interactions within recovering areas.

Landscape ecology provide us with tools to understand how the composition (types and amounts of habitats) and configuration (spatial arrangement of habitats) of landscapes influence species and their interactions (Laurance et al. 2011; Haddad et al. 2015; Taubert et al. 2018; Arroyo-Rodríguez et al. 2020) In general, it is recognized that biodiversity is higher in habitats with high forest cover and low fragmentation which promote the dispersal of animals and plants leading to more diverse and healthy environments (Arroyo-Rodríguez et al. 2020; Corro et al. 2019; Bonfim et al. 2021). In the context of frugivory and restoration ecology, integrating landscape and restoration strategies may provide new insights into how restored ecosystems influence biotic interactions, enhancing our understanding of the factors that shape frugivory in disturbed areas. Additionally, elevation related environmental changes and temporal dynamics (i.e., succession and community assembly) may further shape biodiversity and ecosystem functions within restored landscapes (Körner, 2007; Walker et al. 2007; Crouzeilles et al. 2016), making them essential when evaluating restoration success. In this study, we applied a landscape ecology approach and old-growth forest areas as a reference to assess how restoration strategies (assisted vs. natural), biotic factors (fruit size and availability), abiotic factors (elevation and time), and landscape factors (forest cover and fragmentation) shape frugivory dynamics in a tropical cloud forest under restoration in southwest Ecuador. To do so, we conducted a fruit predation experiment using dummy fruits of two sizes (small vs. large), hypothesizing that areas with more recent assisted and natural regeneration, lower forest cover, and greater forest fragmentation should experience lower fruit attack rates. Conversely, we hypothesized that areas with older assisted and natural restoration and greater forest cover with low forest fragmentation should experience higher fruit attack rates (Figure 1a). This expectations are based on the fact that areas with greater forest cover support higher frugivore diversity (Laurance et al. 2011; Reid et al. 2014; Bonfim et al. 2021). Lower forest fragmentation can promote fruit attacks by facilitating frugivore movement within restored landscapes (Figure 1a) (Thierry et al. 2022; González-Varo et al. 2023). Moreover, we expected that over assisted and natural regeneration and old-growth forest areas smaller fruits could experience higher attack rates, as they are accessible to a broader frugivore community (Figure 1b) (Morán-López et al. 2025). Fruit availability was also predicted to affect frugivory, as fluctuations in resource abundance affect frugivory rates in disturbed landscapes (Herrera et al. 2011). Regarding restoration strategies, we hypothesized that assisted restoration areas would result in higher attack rates than naturally regenerating ones due to the targeted planting of fruiting trees in the study area, which may attract frugivores (Figure 1b). For elevation, we predicted greater frugivory in the lowlands, where warm and stable climatic conditions typically support higher frugivore richness and abundance, increasing encounters between frugivores and fruits (Ferger et al.

2016). Time since restoration was used as a proxy for succession and community assembly, with the expectation that older areas would exhibit greater functionality and diversity (Moral et al. 2007; Crouzeilles et al. 2016).

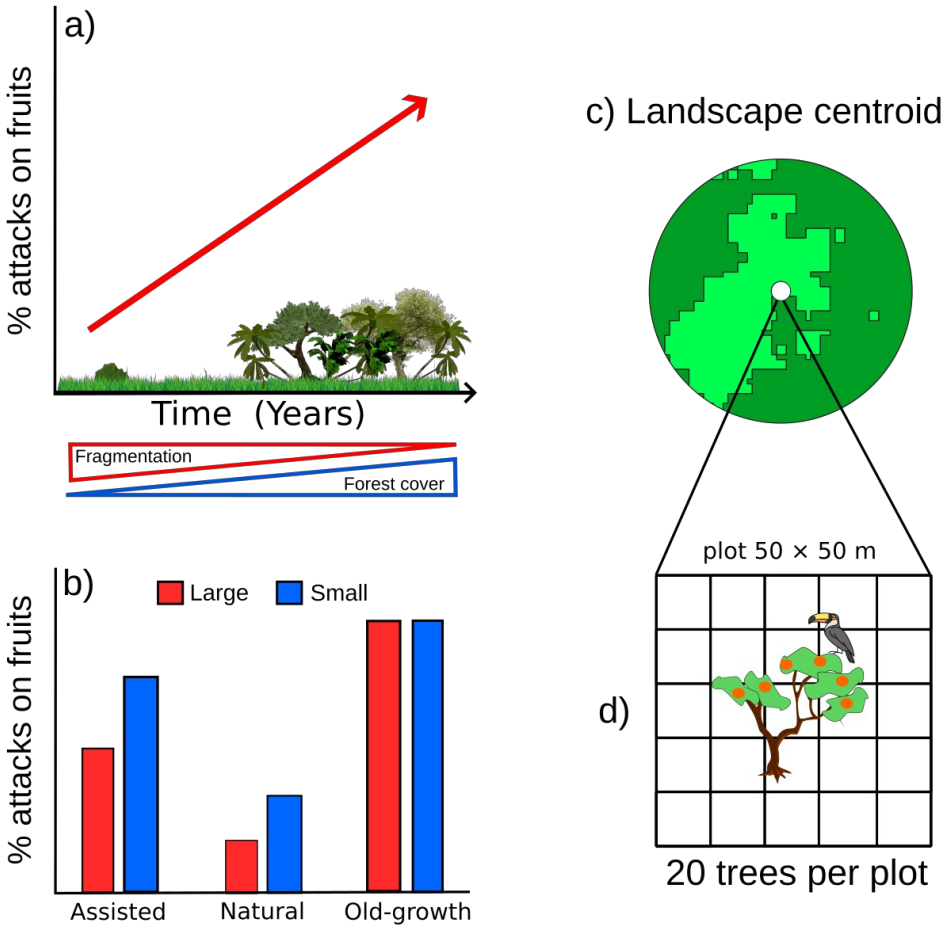

Figure 1. a) Expected proportion of attacks on dummy fruits according to restoration strategy: passive natural regeneration, assisted natural regeneration and reference old-growth forest. b) Expected proportion of attacks on dummy fruits according to landscape composition (forest cover) and configuration (fragmentation). c) Buffer showing the landscape centroid at which each sampling plot was located to assess fruit predation; and d) experimental design at each landscape centroid (n = 21).

Methods

Study site

This study was conducted in the private reserve Buenaventura, located in the province of El Oro in southeastern Ecuador (3°39'13" S, 79°46'4" W). The reserve spans 4,200 hectares and ranges in elevation from 450 to 2,200 meters above sea level. The habitat within Buenaventura reserve is influenced by the Choco biodiversity hotspot and it harbors some of the last remaining and certainly the largest tropical mountain cloud forest of the region, underscoring its high conservation value. However, these forest remnants are surrounded by a highly degraded landscape primarily due to intensive livestock farming (Figure S1). This land use has transformed the natural landscape into a matrix of old-growth forest, restored secondary forest and grasslands dominated by Merker grass (*Pennisetum purpureum*, Poaceae) and the invasive bracken fern (*Pteridium aquilinum*, Dennstaedtiaceae). Merker grass, an invasive species from Africa, grows rapidly—up to 4 meters in height within three months—and out-competes native plants, posing significant challenges for reforestation efforts by impeding the growth of newly planted trees. Bracken fern is a competitive invasive species that produces a dense frond canopy that reduces the amount of light reaching the herbaceous layer of vegetation. It also develops extensive rhizome system that can act as a barrier which prevents the establishment of native plant species. Both Merker grass and Bracken fern represent a challenge for the success of restoration efforts, as they are very hard to control and their presence stalls natural restoration (Hartig and Beck, 2003; Roos et al. 2011; Levy-Tacher et al. 2015et al.).

Restoration strategies in the Buenaventura Reserve are categorized into assisted natural regeneration and passive natural regeneration and have been underway since the reserve's establishment in 1999 (approximately 26 years). Assisted natural regeneration involves planting native tree species (up to 18 different species focusing on fast growing and fruiting trees like *Miconia* sp., *Cecropia* sp., *Ochroma* sp. and *Ficus* sp.) in areas formerly dominated by Merker grass, Bracken fern or a mixture of both. Reforestation teams maintain tree plantations by mowing the surrounding grass and ferns every three months for 3 years (until tree seedlings reach heights that surpass grass and fern cover). Planted trees contribute to forest cover recovery by attracting frugivores and combating the invasive weeds by creating shaded areas that inhibit its spread. Passive natural regeneration involves protecting areas previously used for livestock to allow them to recover autonomously with minimal human intervention beyond ensuring protection. In naturally regenerated areas, isolated trees are present and are expected to perform similar ecological roles as those in actively restored areas, though their abundance is generally lower. Old-growth forests areas are present within the reserve; however, they are highly fragmented, especially near areas previously used for livestock and those currently undergoing restoration.

Landscape selection

In the Buenaventura Reserve, we selected 21 landscapes (mean distance ± SD = 3.52 ± 2.81 km) across three distinct land management types: assisted regeneration, passive natural regeneration, and old-growth forest, with seven landscapes representing each type. Each landscape was established using two different buffer radii: 250 m and 400 m. The selection of these buffer sizes was based on the assumption that species within restored areas respond differently to landscape structure (Crouzeilles and Curran, 2016), with two scenarios: i) restricted bird movement (250 m radius) and ii) less restricted bird movement (400 m radius). Additionally, a distance of 250 m is considered sufficient to achieve statistical independence for bird sampling (Hutto et al. 1986), while both 250 m and 400 m buffers are able to capture the response of frugivore birds to landscape factors (Reid et al. 2014). Sampling was conducted at the centroid of each landscape. Additionally for each landscape centroid we obtained its elevation and plot age (time when regeneration started or forest age). Each landscape centroid is located in well-identified areas of either assisted regeneration, passive natural regeneration, or old-growth forest; however, the surrounding matrix may include a variety of habitat types (e.g., old-growth forest, secondary forests & grasslands).

Landscape level characterization

We categorized forest cover in the landscape using a supervised classification approach with a tree height raster (10 m resolution; Lang et al. 2023) as input. This raster allowed us to categorize forest cover into three distinct classes, verified with tree height data of 50 field points. The resulting map includes three vegetation categories: i) old-growth forest (mean tree height: 29 to 44 m); ii) secondary forest (mean tree height: 20 to 28 m); iii) regenerated areas and grass or fern dominated areas (mean tree height: 0 to 19 m) (Figure S1). After forest cover was categorized the landscape composition and configuration (forest cover and landscape fragmentation) were calculated for each landscape (i.e., buffer). We selected these landscape descriptors because they are considered as main components to describe human-modified landscapes (Arroyo-Rodríguez et al. 2020; Fahrig, 2003). Forest cover (%) for both old-growth and secondary forest was calculated using binary maps (i.e. old-growth forest or non-old-growth forest, or secondary forest or non-secondary forest). We measured landscape fragmentation by measuring the mean patch size (MPS) of the old-growth forest fragments, forest patches where measured in m^2 and further transformed to km^2. Additionally, we measured the distance from the centroids of the assisted and natural regeneration areas to the nearest old-growth forest patch (previously categorized) using the "Shortest line between features" tool in QGIS. Landscape categorization and map manipulation was done with QGIS

version 3.22.4, “landscapemetrics” (Hesselbarth et al. 2019) and “terra” (Hijmans, 2020) in R version 4.4.1 (R Core Team, 2025).

Frugivory experiment

To obtain a consistent proxy of frugivory across the different land management types, we conducted an experiment using artificial fruits of two sizes (small, 10 mm diameter, and large, 20 mm diameter) made from non-toxic red plasticine (Pelikan ®). For this, at the centroid of each landscape, we established a 50 × 50 m plot, where we selected 20 young, fruitless trees (ranging from 1 to 1.8 meters in height) and placed 6 dummy fruits of one size (either small or large) on each tree (Figure 1c). In total, we deployed 120 dummy fruits per landscape (60 small and 60 large), with 2,520 dummy fruits across all landscapes (1,260 small and 1,260 large) (Figure 1c).

After placing the dummy fruits, we left them exposed for 72 hours. After this time, we went back to each landscape centroid and recorded whether each fruit had been attacked (registered as 1) or not (registered as 0) to determine the proportion of attacked fruits of each size at each landscape. We also documented the type of marks on each fruit, identifying whether they were made by birds, mammals, or arthropods (Figure S2). If a fruit disappeared from a focal tree, we searched the surrounding area to determine the type of mark it had; if we could not find the fruit, it was classified only as attacked without recording the type of attack it had. After recording the attacks, we collected the remaining fruits. Note that plasticine dummy fruits offer a standardized, durable, and non-toxic tool for controlled ecological experiments, enabling a consistent measure of frugivore attacks.

Fruit availability

In order to have a measure of fruit availability at each site we made a sampling by counting and estimating all the fruits that where observed within the 50 × 50 m plot. This was made by the same observer in all landscapes using binoculars and a hand tally counter. This was done to asses if fruit availability influences attack rates on dummy fruits.

Data analysis

As a first step in understanding how fruit attacks vary across the Buenaventura Reserve, we examined the different types of markings observed on dummy fruits. Specifically, we assessed whether markings caused by birds, arthropods, or mammals differed between fruit sizes (small and large) and across restoration strategies. We used a Generalized linear model (GLM) with binomial error distribution with link *logit* with the proportion of attacked fruits as dependent factor with type of marking (bird, arthropod, mammal or other), fruit size (small and large) and restoration strategy (assisted, natural restoration and old-growth forest) as independent factors. Unidentified markings were excluded from this analysis.

After examining the variation in attack markings, we assessed which set of landscape factors, derived from either a 250 m or 400 m buffer, better explained attacks on dummy fruits. To do this, we first excluded all attacks made by arthropods, as well as markings of unidentified origin form our data, to avoid any potential confounding effects. This decision was based on our goal of specifically assessing frugivory, either by birds or mammals. We then fitted two generalized linear models (GLMs) with binomial error distribution and *log* link. In the first model, the proportion of attacked fruits was included as the dependent variable, with old-growth forest cover, secondary forest cover, and mean patch size measured within the 250 m buffer as predictors. The second model had the same dependent variable but included landscape metrics measured within the 400 m buffer. We then compared the models using the corrected Akaike Information Criterion (AICc), selecting the buffer size associated with the lowest AICc value. The 250 m buffer yielded a lower AICc (374.83, R^2=0.11) compared to the 400 m buffer (378.64, R^2=0.09), indicating that landscape factors at the smaller scale provided a better fit for explaining attack patterns on dummy fruits.

After determining the spatial scale at which fruit attacks (either by birds or mammals) were best explained, we assessed how restoration strategy (assisted, natural restoration and old-growth forest), fruit size (large vs. small), landscape metrics within a 250 m buffer (old-growth forest cover, secondary forest cover, and mean patch size), elevation, fruit availability, and plot age (time since restoration and forest age) influenced the proportion of attacks on dummy fruits. First, we standardized all numerical variables (landscape metrics, elevation, fruit availability and plot age) to improve model comparisons. Then, we fitted a global model (i.e., including all factors) using a GLM with binomial error distribution and *logit* link: $Y = \beta 0 + Restoration\ strategy + Fruit\ size + Forest\ cover + Secondary\ forest\ cover + Mean\ patch\ size + Elevation + Fruit\ availability + Plot\ age + \epsilon$ where Y represents the the proportion of attacked fruits, $\beta 0$ is the intercept and ϵ the model residuals. Next, we assessed multicollinearity within the global model by calculating the Variance Inflation Factor (VIF) for each predictor. We found that plot age had a VIF of 4.16, indicating high collinearity. We then fitted a new model excluding plot age and introduced an interaction between restoration strategy and fruit size to further examine how attack rates on dummy fruits varied across sites and fruit sizes. The final model was: $Y = \beta 0 + Restoration\ strategy + Fruit\ size + Forest\ cover + Secondary\ forest\ cover + Mean\ patch\ size + Elevation + Fruit\ availability + (Restoration\ strategy \times Fruit\ size) + \epsilon$ where Y represents the proportion of attacked fruits, $\beta 0$ is the intercept and ϵ the model residuals. All models were implemented in R version 4.4.1 (R Core Team, 2025) and post-hoc comparisons were made using the “emmeans” package (Lenth, 2025). Additionally, we assessed the role of spatial autocorrelation in the proportion of attacked fruits by using Moran’s I and correlograms. For this, we first grouped all pairwise plot distances into 12 bins of equal sample size (centroids: 410 m to 10 500 m). Distance bins were built so that each bin contained approximately the same number of

pairwise distances. This ensures equal statistical power across bins, even though the distance ranges vary in order to achieve equal counts. For each bin, we ran 999 permutations to obtain the observed Moran's I, its expected value under randomness, 95 % confidence limits, and a p-value. This was done with the package "letsR" (Vilela and Villalobos, 2015) in R version 4.4.1 (R Core Team, 2025).

Moreover, although plot age was the only factor with high collinearity, we assessed the correlations among landscape metrics (old-growth forest cover, secondary forest cover, and mean patch size), elevation, fruit availability, and plot age with Spearman correlation tests. We also evaluated differences in primary and secondary forest cover and mean patch size (MPS) across restoration strategies, for this we fitted two models. First, we used a binomial generalized linear model (GLM) with a *logit* link function, where forest cover was the dependent variable, and forest cover type (primary or secondary) and restoration strategy were the independent variables. Second, we fitted an ANOVA, with MPS as the dependent variable and restoration strategy as the independent variable. Additionally, we assessed whether the distance from the centroids of assisted and natural regeneration areas to the nearest old-growth forest patch differed using a two-tailed t-test. These analyses were conducted to better describe and understand the spatial arrangement of the studied landscape.

Results

A total of 803 fruits (31% of all dummy fruits) were attacked, including 373 small fruits (15%) and 430 large fruits (16%). Among the attacked fruits, 669 (83%) were marked by birds (361 large, 308 small), 30 (3.7%) by mammals (23 large, 7 small) and 51 (6.3%) by arthropods (37 large, 14 small). Additionally, 53 fruits (6.6%) were either lost or had unidentified markings (9 large, 44 small) (Figure S2). Bird markings were the most frequent type of attack across both fruit sizes (χ^2=1349, df = 3, P = 0.0001). Larger fruits were more frequently attacked than smaller ones across all marking types (χ^2=5.23, df = 1, P = 0.02) (Figure 2a). Marking type either made by birds, mammals or arthropods were similar among assisted, natural regeneration areas and old-growth forest (χ^2 = 2.87, df = 2, P = 0.23) (Figure 2b).

When assessing which factors best explained the proportion of fruit attacks, we found that elevation, old-growth forest cover, secondary forest cover, and the interaction between fruit size and restoration strategy explained the variation in attack rates (Table 1, Figure 3). Specifically, fruit attacks increased with elevation, forest cover and secondary forest cover. Contrary to our prediction, larger fruits experienced higher attack rates in both assisted (mean ± SE = 0.32 ± 0.76) and natural restoration areas (0.34 ± 0.66) compared to old-growth forest (0.22 ± 0.65). In contrast, small fruits were attacked at similar proportions across assisted (0.25 ± 0.75), natural (0.24 ± 0.65), and old-growth (0.27 ± 0.65) areas. Notably, in natural restoration sites, larger fruits (0.34 ± 0.66) were attacked more frequently than smaller ones (0.24 ± 0.65), whereas

in assisted and old-growth forests, attack rates were similar for both fruit sizes. Beyond restoration strategies and fruit size, elevation and forest cover were identified as the main factors explaining attacks rates on dummy fruits followed by secondary forest cover. The Moran's I spatial autocorrelation analysis did not show significant clustering on the frequency of attacks on fruits across different distances (up to 6 km). At longer distances (around 8 kilometers), landscapes showed signs of dissimilarity (Moran's I = -0.35, P = 0.0001). These results suggest a shift from no spatial autocorrelation at shorter distances to dispersion at greater distances (Figure S3).

Regarding the correlation between landscape metrics (forest cover, secondary forest cover, and mean patch size), elevation, fruit availability, and plot age, we observed several significant relationships. Plot age showed a positive correlation with old growth forest cover (r = 0.57, P = 0.0001) and mean patch size (MPS) (r = 0.44, P = 0.01). Additionally, old-growth forest cover was positively correlated with MPS (r = 0.89, P = 0.0001), indicating that older sampling plots tend to have greater and more continuous forest cover in their surroundings. Conversely, plot age was negatively correlated with elevation (r = −0.36, P = 0.01), suggesting that older plots are more common at lower elevations. Forest cover was also negatively correlated with elevation (r = −0.33, P = 0.03) and secondary forest cover (r = −0.44, P = 0.003). Moreover, MPS was negatively correlated with secondary forest cover (r = −0.62, P = 0.0001), indicating that plots with less old-growth forest cover tend to be located at higher elevations, have greater secondary forest cover, and are more fragmented (Figure S4). When assessing how forest cover (%) varied among land use-types, we observed that secondary forest cover across assisted, natural and old-growth forest (assisted: 0.52 ± 0.2, natural: 0.56 ± 0.15, old-growth forest: 0.5 ± 0.28) was higher than old-growth forest cover (assisted: 0.21 ± 0.24, natural: 0.25 ± 0.15, old-growth forest: 0.42 ± 0.29) (χ^2 = 4.66, df = 1, P = 0.03). However, we did not observe differences in old-growth v.s. secondary forest cover among restoration strategies (χ2 = 0.56, df = 2, P = 0.75) (Figure 4a). Regarding mean patch size (MPS), we found that both assisted (0.016 ± 0.005 km²) and natural (0.015 ± 0.003 km²) restoration areas exhibited higher forest fragmentation compared to old-growth forest areas (0.065 ± 0.015 km²) (F = 7.07, df = 2, P = 0.002) (Figure 4b). Distance to the nearest old-growth forest were similar between assisted (mean ± SD= 140.77 ± 87.16 m) and natural regeneration areas (68.64 ± 87 m) (t = 1.14, df = 10.25, P = 0.28)

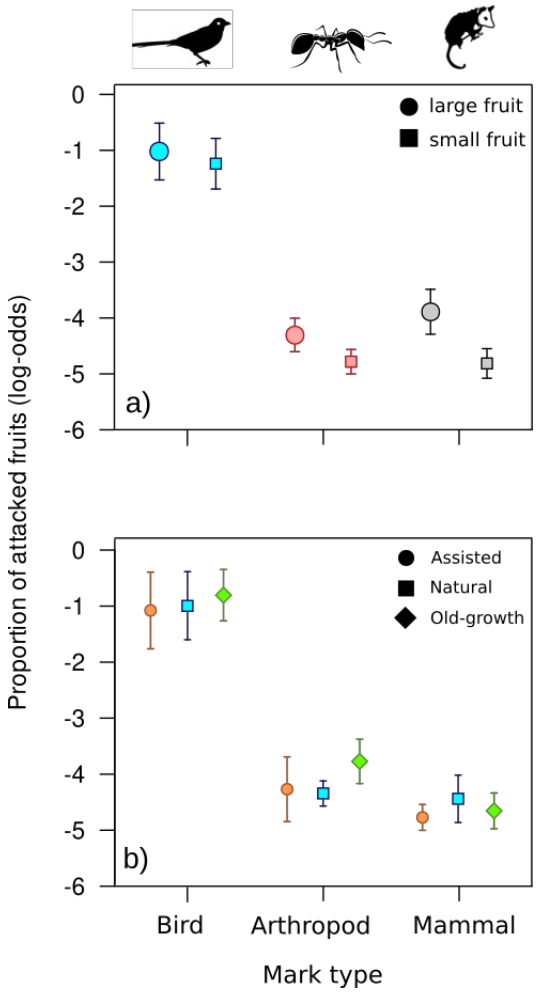

Figure 2. Proportion of attacks on dummy fruits a) by fruit size and type of mark and b) by restoration strategy and type of mark. Circles and squares represent mean values, and error bars indicate standard errors for all treatment combinations. Proportions are presented as log-odds, transformed using the *logit* link function from the statistical model. Unidentified markings were excluded from this analysis.

Table 1. Deviance table showing the contribution of each predictor to the likelihood of fruit attacks. The explained deviance represents each factor's proportion of the total likelihood ratio χ^2. Bold values indicate statistical significance ($P < 0.05$).

Factor	LR χ^2	df	Contribution to LR χ^2 (%)	P
Restoration strategy (R)	4.38	2	6.19	0.12
Fruit size (S)	9.62	1	**13.6**	**0.001**
Forest cover	18.06	1	**25.53**	**0.0001**
Secondary forest cover	5.81	1	**8.21**	**0.004**
Mean patch size	0.44	1	0.62	0.422
Elevation	23.46	1	**33.17**	**0.0001**
Fruit availability	0.91	1	1.3	0.19
R × S	8.04	2	**11.37**	**0.005**
Total	70.75			

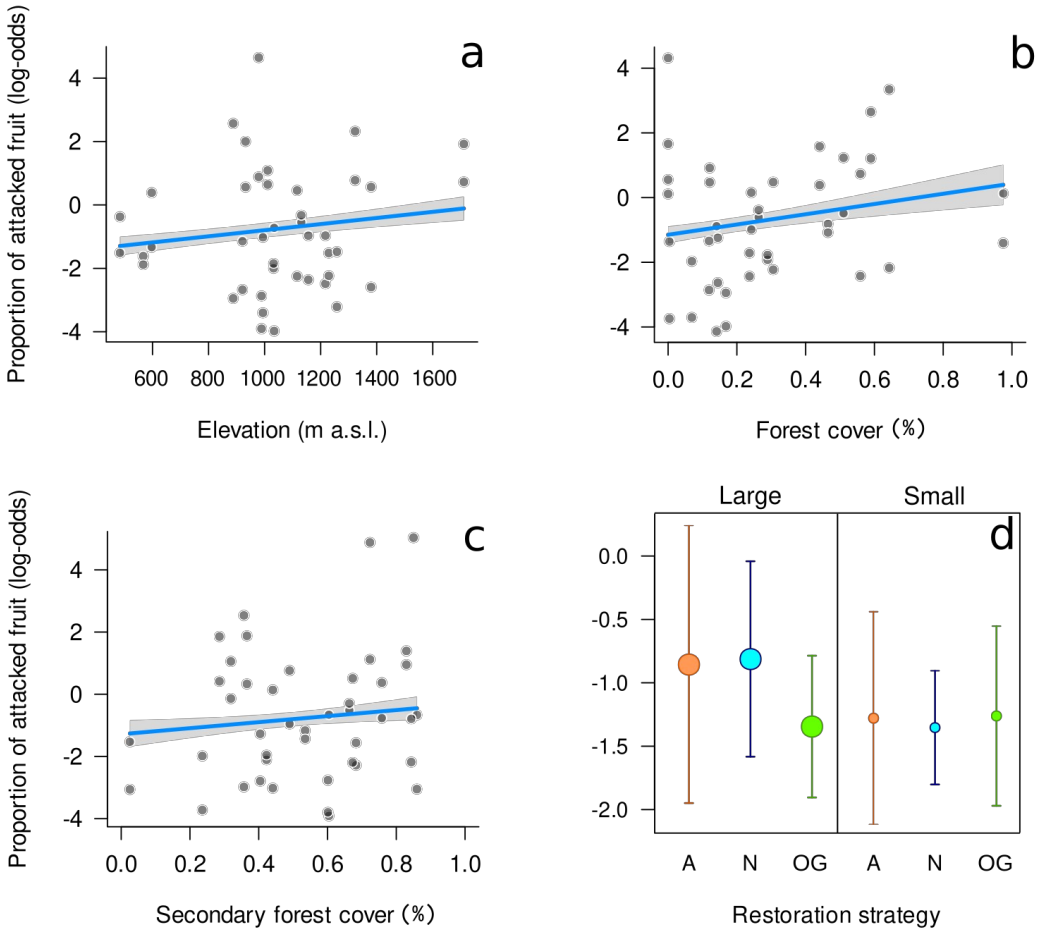

Figure 3. a) Relationship between elevation and the proportion of bird and mammal attacks on dummy fruits. b) Relationship between forest cover and the proportion of attacks on dummy fruits. c) Relationship between secondary forest cover and the proportion of attacks on dummy fruits. d) Variation in the proportion of attacks on dummy fruits across restoration strategies and fruit sizes: “A” denote assisted restoration, “N” natural regeneration and “OG” old-growth forest data respectively. The left panel represents attacks on large fruits, while the right panel represents attacks on small fruits. Points indicate mean values, and error bars represent standard errors for all treatment combinations.

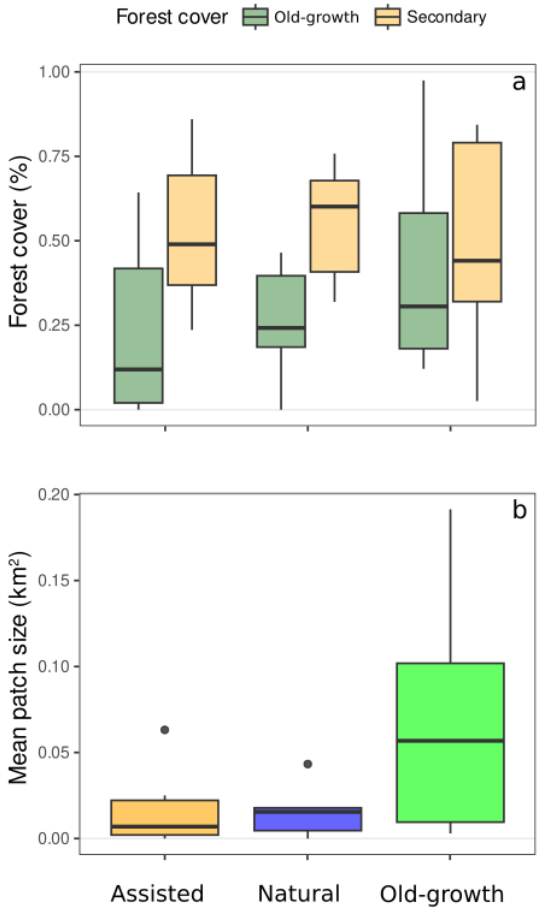

Figure 4. a) Variation of old-growth and secondary forest cover (measured in 250m buffers) across assisted, natural restoration areas and old-growth forest areas. b) Variation of forest fragmentation (mean patch size, measured in 250m buffers) across assisted, natural restoration areas and old-growth forest areas. The lines represent the first and four quartiles, the box represents the second and first quartiles and the line within the box represents the median for each category.

Discussion

Identifying where and how animals interact with plants remains a major challenge in restoration ecology, as much of the theoretical and empirical work has focused on species gains and losses rather than on the recovery or disruption of biotic interactions. In this study, using a controlled experiment within a landscape under restoration, frugivore activity was recorded in both assisted and natural regeneration areas mainly driven by birds and likely supported by the presence of small old-growth forest patches and surrounding secondary growth. Along with forest cover, fruit size explained differences in fruit attack rates, particularly when comparing restoration areas with old-growth forests. Elevation also influenced attack rates, possibly reflecting changes in frugivore abundance across the elevational gradient. These findings indicate that both old and regenerating forests play a role in sustaining frugivory, and that neither assisted nor natural regeneration appears to be clearly more effective in restoring this interaction in degraded habitats. These observations contribute to a better understanding of frugivory dynamics in disturbed tropical forests and show the potential outcomes of different restoration approaches in restoring biotic interactions.

Attacks on fruits where recorded at similar rates between assisted and natural restoration areas, indicating that active reforestation is not necessarily more effective than passive natural regeneration in restoring frugivory to disturbed habitats. This result is particularly clear when comparing attack rates between small and large fruits as both assisted and natural restoration areas showed similar trends, with large fruits experiencing higher predation, while small fruits, though similarly targeted, were attacked less frequently. In old-growth forest, and contrary to our predictions, overall attack rates were lower than in restored areas, especially for large fruits. Despite the similar trends observed between assisted and natural restoration, the contribution of assisted restoration to frugivory in the Buenaventura Reserve should not be overlooked, particularly considering that natural regeneration in some areas is stalled due to the presence of invasive herbs. Without human intervention, many of these areas (dominated by invasive grasses and ferns) would likely not have recovered to the point of supporting frugivory dynamics comparable to those seen in naturally regenerating sites (Hartig and Beck, 2003; Roos et al. 2011; Levy-Tacher et al. 2015). Rather than being discouraging, our results show that assisted restoration can provide suitable habitat for frugivores in areas where natural regeneration can be stalled. Therefore, planted trees in assisted regeneration areas, may help kickstart secondary growth by enabling seed consumption and dispersal similar to that expected in naturally regenerating areas. Since birds were the main frugivores and targeted larger fruits in restoration areas, our findings might reflect a spill-over effect, where large frugivores from old-growth forests move into disturbed habitats and interact with large fruits. Previous evidence has shown that birds move more often from secondary and old-growth forests into degraded areas than the reverse, visiting and removing fruits consistently and promoting seed

dispersal in these areas (Béllo Carvalho et al. 2023). In this case, spill-over effects are evident. For example, one of the largest and most conspicuous frugivorous birds in the studied landscape, the yellow-throated toucan (*Ramphastos ambiguus*) can be observed foraging in assisted, natural regeneration areas and in old-growth forest. Toucans have documented movement capabilities of up to 2 km (Holbrook & Loiselle 2007; Holbrook 2011), and in the studied landscape, the centroids of assisted and natural restoration areas are, on average, no more than 170 m from old-growth forest. These short distances, combined with the high mobility of birds, suggest that large frugivores like toucans can easily move between old-growth forest, secondary forest, and restoration areas. In fact, large birds like toucans (*R. ambiguus*, *R. brevis* and *Pteroglossus torquatus*), guans (*Ortalis erythroptera*, *Penelope purpurascens* and *Chamaepetes goudotti*) and trogons (*Trogon collaris* and *Pharomachrus auriceps*) can be seen foraging in small trees within areas under restoration, though they also occur in old-growth forest. Higher attack rates on larger fruits in restoration areas can also be explained by the optimal foraging framework (MacArthur and Pianka, 1966). Because larger fruits represent a resource of higher nutritional value, making them a more profitable choice than small fruits, especially under harsher conditions like those found in restored habitats. In the case of smaller fruits, we observed that across all the studied areas they were less frequently attacked, despite being accessible to a more frugivore species (e.g., birds of various sizes) which is not consistent with our predictions (Dáttilo et al. 2023; Morán-López et al. 2025). A factor potentially explaining low attack rates on smaller fruits within old-growth forest is the vertical stratification of frugivores. This is because we limited our experiment to assessing understory frugivory, which is typically dominated by small birds, while larger birds and primates capable of consuming large fruits are more often found in the canopy layers of old-growth forests (Thiel et al. 2021). This methodological limitation might have hindered our results and could underestimate large fruit consumption within forested areas. The reduced consumption of smaller fruits in both restoration and old-growth forests, along with the reduced consumption of large fruits in old-growth forests, could limit dispersal opportunities for small-fruited and large-fruited plants respectively. Reduced dispersal of small-fruited plants could slow forest regeneration and hinder the establishment of early-successional species, while limited dispersal of large-fruited plants may impair the persistence and regeneration of late-successional tree species (Galetti & Dirzo 2013; Bello et al. 2015), ultimately impacting the structure and species diversity and functional traits of these forest ecosystems (Galetti et al. 2013).

Despite the many structural and ecological differences between old-growth and secondary forests (Chazdon, 2014), we observed that increasing the area of both forest types promote fruit attack rates. Congruent with our results, higher attack rates on fruits in old-growth forest areas were expected, as these forests are older and have a higher structural complexity, providing habitat for a larger number of frugivorous birds and increasing opportunities for interactions to occur (Guariguata

and Ostertag, 2001; Chazdon, 2014; Bonfim et al. 2021). However, despite their higher suitability for maintaining frugivores, old-growth forests surrounding the studied restoration areas are highly fragmented and embedded within a matrix of secondary forest. While in this study fragmentation does not appear to influence frugivory, the role of small old-growth forest patches should not be overlooked, as they could be acting as reservoirs for frugivorous birds and sources of propagules, helping to sustain frugivory in restored areas (Herrera et al. 2011; Reid et al. 2014; Bello et al. 2024). This is because, old-growth forest patches in the Buenaventura Reserve are closely spaced and embedded within a secondary forest matrix, which likely facilitates frugivore movement and feeding among the different areas of the reserve (Savary et al. 2024). Although secondary forest are recognized for harboring diverse animal and plant communities and play an important role in sustaining frugivores (Acevedo-Charry and Aide 2019), it recovers slowly and cannot fully replace old-growth areas, as it often lacks forest specialists and key functional groups (Letcher et al. 2015; Rozendaal et al. 2019). Therefore, conserving frugivory in the landscape requires a dual strategy that protects both secondary and old-growth forest, as previously proposed for tree species diversity (Rozendaal et al. 2019). Secondary forests have been recognized as crucial for future biodiversity conservation, as their distribution is expected to expand, potentially mitigating pressures on primary old-growth forests (Guariguata and Ostertag, 2001; Chazdon, 2014). However, despite their ecological value, it remains uncertain whether secondary forests will ever fully resemble old-growth forests (Frick et al. 2014) or if forest restoration is sufficient for long-term biodiversity conservation. Forest age (or time since restoration) should also be taken into account, since older sites tended to have greater old-growth forest cover. This correlation implies that mere passage of time has helped rebuild frugivore-plant interactions. As restored areas mature, they develop more complex structure (taller canopy, understory layers) and richer fruit resources (Guariguata and Ostertag, 2001; Lebrija-Trejos et al. 2008; Escobar et al. 2025), both of which attract a wider range of frugivores. In short, maintaining frugivory in Buenaventura reserve hinges on safeguarding both old-growth fragments and expanding secondary forest, while ensuring protection in restored sites over time in order to allow them to mature.

In lowlands, species richness and abundance tend to be higher due to warm, stable climates (McCain & Grytnes 2010; Rahbek et al. 2019), which generally promotes more interactions (Roslin et al. 2017; Hargreaves et al. 2019). Contrary to this expectation, fruit attack rates increased with elevation across our 400–1 700 m a.s.l. gradient, an effect that held regardless of forest cover or restoration strategy. We measured fruit availability along this gradient but found no significant correlation with elevation, indicating that higher attack rates at greater heights are not simply explained by differences in fruit abundance. In this sense we could argue that the higher markings of fruits may reflect higher frugivore abundance, as interaction frequencies are largely driven by species abundance (Krishna et al. 2008). Although we did not directly sample

frugivore communities, our results are consistent with previous studies reporting non-linear elevational patterns in frugivory. For example, Terborgh (1977) found that frugivorous bird diversity in the Andes peaked between 1 400 and 1 600 m, likely due to the local abundance of fruiting species in families such as Ericaceae, Rubiaceae, and Melastomataceae. The observed mismatch between fruit availability and attack rates suggests that other factors, such as frugivore community composition, foraging behavior, or microclimatic conditions, may explain the pattern. To better understand these dynamics, future research should combine elevation surveys of frugivores with detailed fruit trait data and microclimate measurements to evaluate their combined influence on frugivory across the elevation gradient studied.

In conclusion, our study shows that frugivory is a resilient and dynamic interaction that persists in both assisted and natural regeneration areas. Its recovery in restored sites appears to depend on the presence of remnant old-growth patches and the surrounding secondary-forest matrix, which together facilitate the movement and feeding of frugivores. To sustain these interactions, conservation efforts should focus on protecting and connecting remaining old-growth fragments and promoting secondary-forest expansion around them. Long-term protection of restored areas will then allow them to develop the structural complexity and fruit resources needed to attract frugivores and drive natural regeneration.

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Statements & Declarations

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Competing Interests

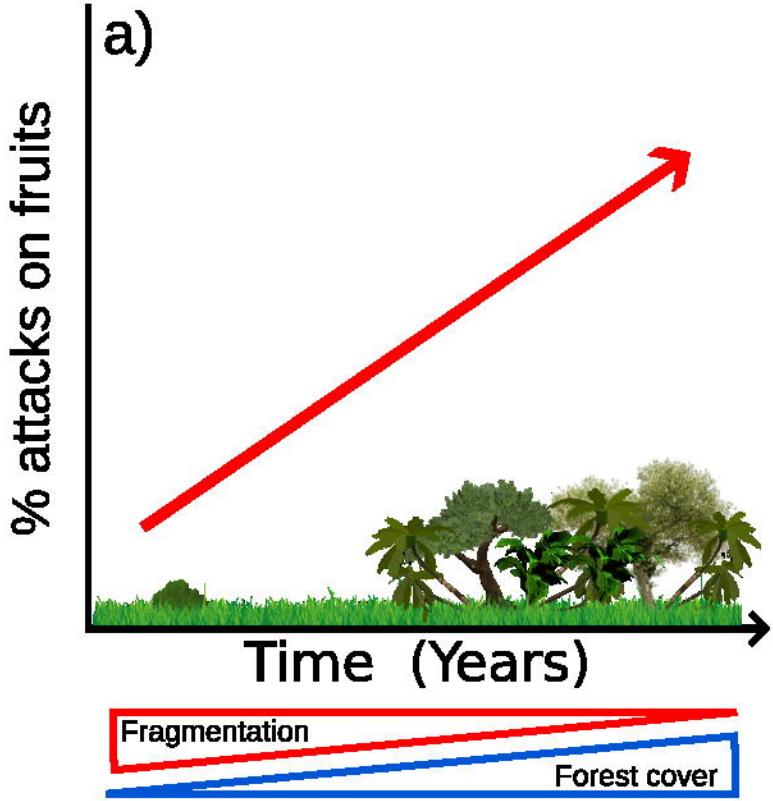
The authors have no relevant financial or non-financial interests to disclose.

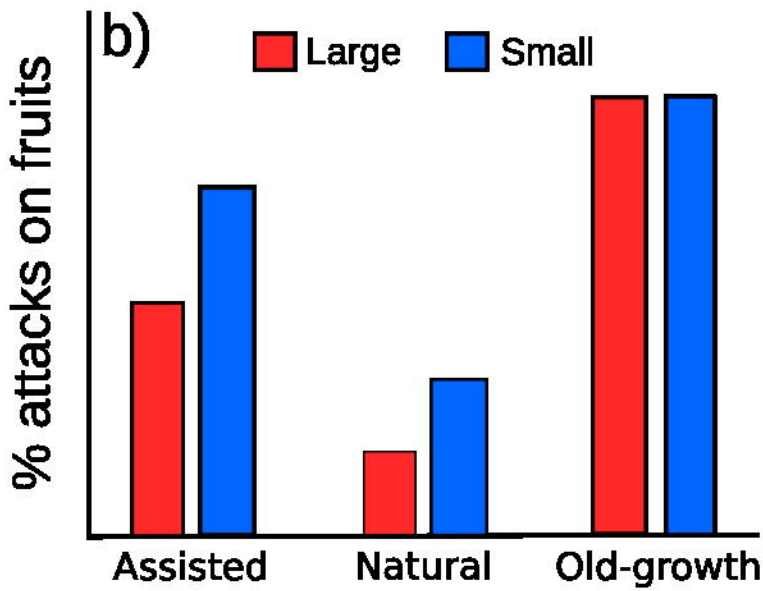
Author Contributions

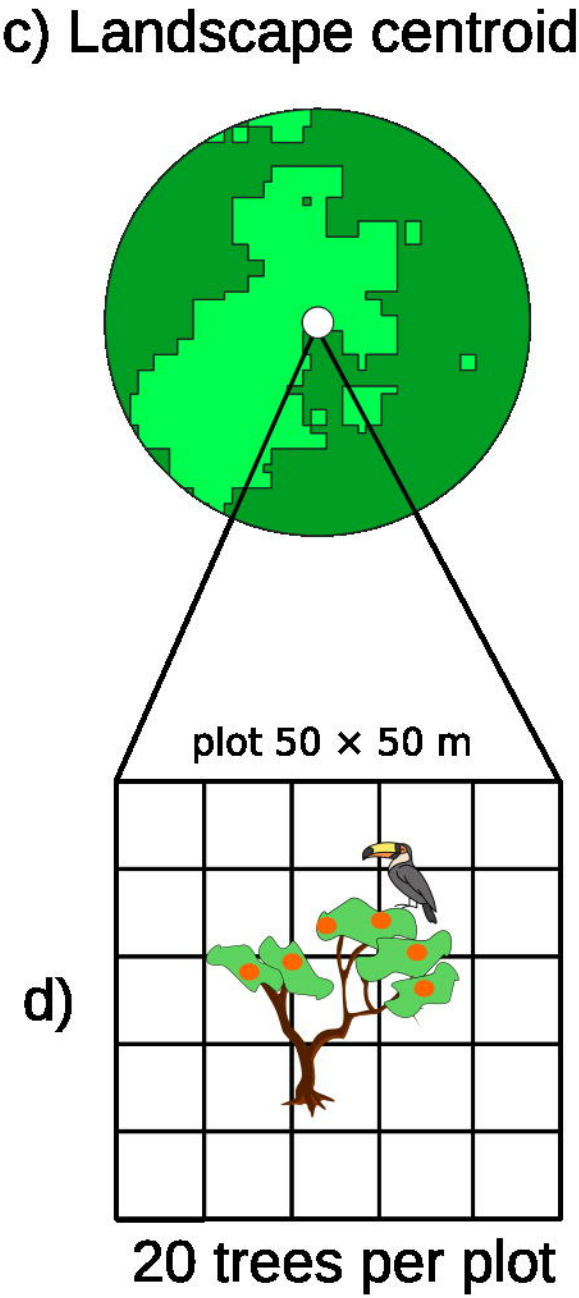
Original idea was developed by Pedro Luna, with input from Juan E. Guevara-Andino, H. Martin Schaefer and Nico Blüthgen. Pedro Luna, Betzabet Obando-Tello and Leonela E. Dávila-Narváez carried out field work. Pedro Luna carried out map manipulation and data analysis. The first draft of the manuscript was written by Pedro Luna and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

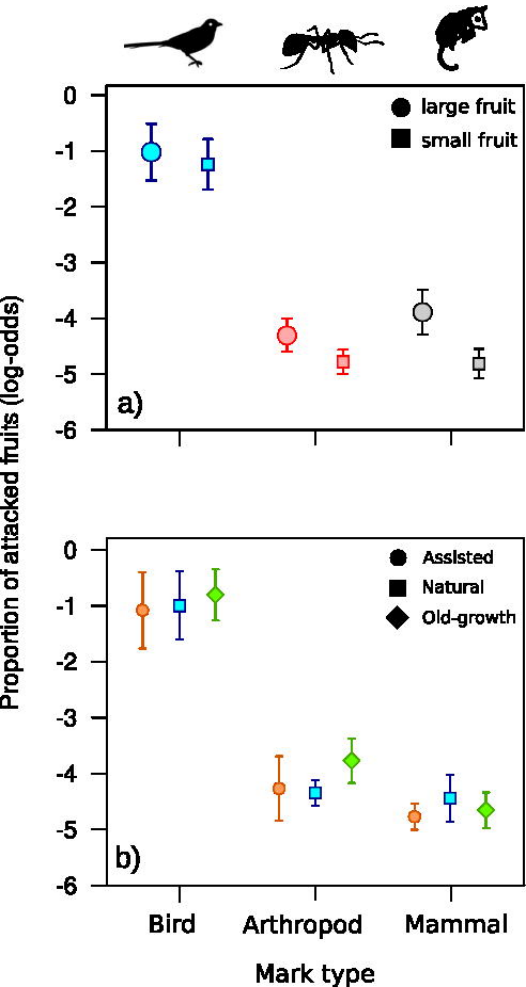
Data availability

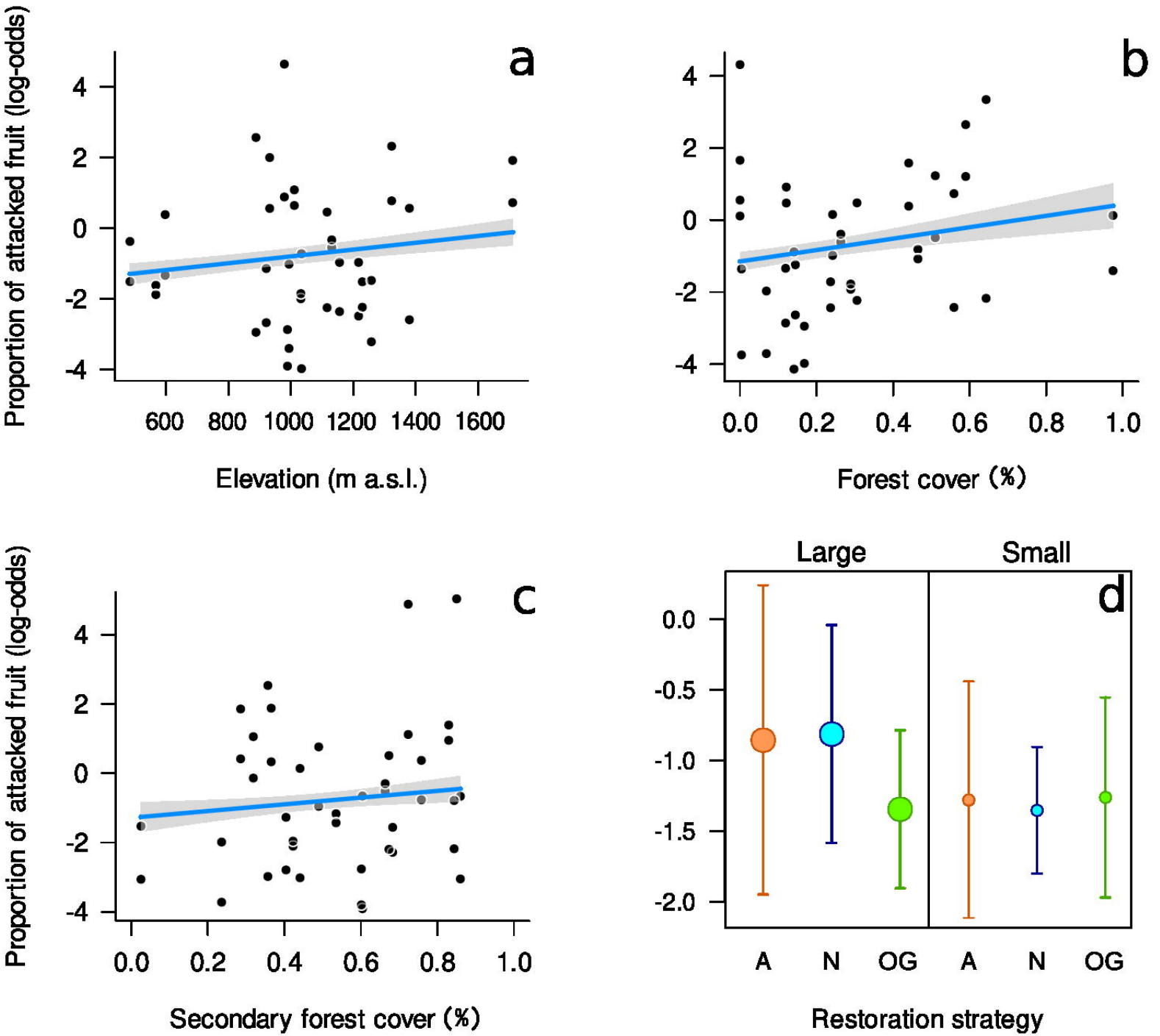
The datasets and maps generated during and/or analysed during the current study are available from the corresponding author on request.

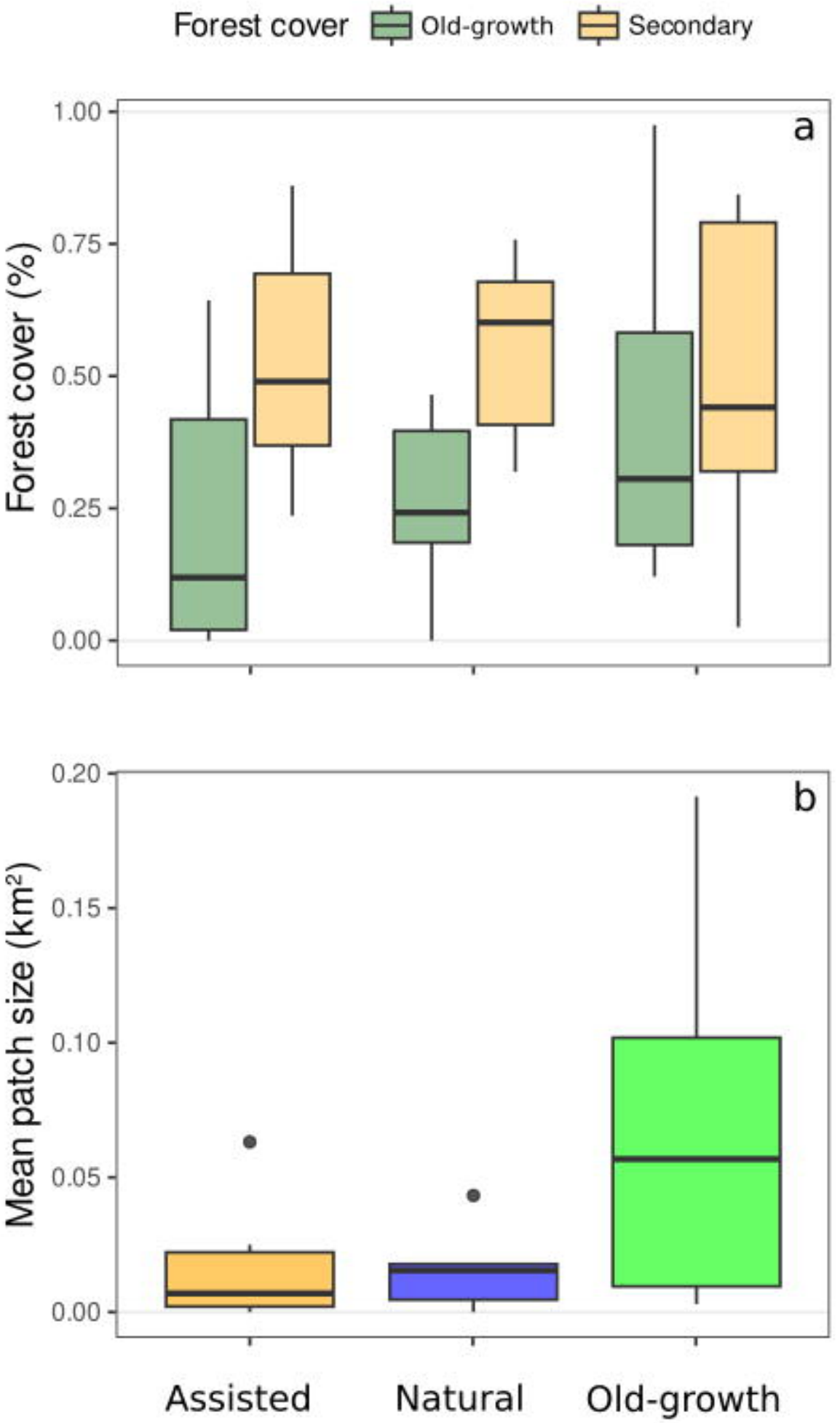

a)
% attacks on fruits
Time (Years)
Fragmentation
Forest cover


b)
Large
Small
% attacks on fruits
Assisted
Natural
Old-growth


c) Landscape centroid
plot 50 × 50 m
d)
20 trees per plot


large fruit
small fruit
a)
Assisted
Natural
Old-growth
b)
Proportion of attacked fruits (log-odds)
0
-1
-2
-3
-4
-5
-6
Bird
Arthropod
Mammal
Mark type


a
Proportion of attacked fruit (log-odds)
4
2
0
-2
-4
600
800
1000
1200
1400
1600
Elevation (m a.s.l.)
b
4
2
0
-2
-4
0.0
0.2
0.4
0.6
0.8
1.0
Forest cover (%)
c
Proportion of attacked fruit (log-odds)
4
2
0
-2
-4
0.0
0.2
0.4
0.6
0.8
1.0
Secondary forest cover (%)
Large
Small
d
0.0
-0.5
-1.0
-1.5
-2.0
A
N
OG
A
N
OG
Restoration strategy


Forest cover
Old-growth
Secondary
a
Forest cover (%)
1.00
0.75
0.50
0.25
0.00
b
Mean patch size (km²)
0.20
0.15
0.10
0.05
0.00
Assisted
Natural
Old-growth