



## Forest recovery through applied nucleation: Effects of tree islet size and disperser mobility on tree recruitment in a temperate landscape

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### ABSTRACT

The plantation of tree islets within deforested areas (applied nucleation) has been proposed as a restoration strategy able to catalyze tree colonization in the matrix with reasonable costs and labor compared to traditional restoration methods such as extensive plantations. However, recent work has questioned its effectiveness in comparison to natural forest regeneration, and observational studies have eventually reported a limited expansion of tree islets after years of planting. To infer the processes affecting the effectiveness of applied nucleation, we used a stochastic model able to predict avian movement and fruit consumption, tree seed dispersal and seedling establishment in a fragmented temperate forest landscape of northern Spain. First, we simulated scenarios of natural regeneration and compared them to applied nucleation in terms of tree colonization in the remaining deforested matrix. Subsequently, in applied nucleation scenarios we assessed the effects of islet size and matrix area recovered on tree recruitment into the matrix. Also, we evaluated if such effects were mediated by the scale of movement of frugivores. Our results showed that applied nucleation triggers matrix colonization by trees at higher rates than natural regeneration because it avoids frugivore entrapment within forest edges. Also, that large tree islets can hamper matrix colonization despite being visited more frequently. If large tree islets offer abundant resources, animals do not need to leave their boundaries, concentrating seed deposition within islets. As expected, such effects depended on the scale of movement of frugivores. Our work highlights that in nucleated landscapes, islets harboring fruit-producing trees should attract animal dispersers, and also foster animal inter-islet movement. Both conditions should be met to ensure seed deposition and seedling establishment in the deforested matrix, promoting forest recovery independent of islet expansion through vegetative growth. To achieve these restoration goals, we propose establishing islets whose size and inter-islet distances matches the scale of movement of main seed dispersers present in the area.

### 1. Introduction

Over the last thirty years, an estimated 420 million ha of forest have been lost (FAO, 2020), making deforestation a global change driver (Brondizio et al., 2019). At the same time, the extensive restoration of forests is viewed as a strategy to mitigate against the current climate and biodiversity crisis (Scheidel and Gingrich, 2020). As a result, there is an unprecedented political will to pursue ambitious cross-national

environmental policies aimed at recovering deforested areas (e.g., Aichi targets, Bonn Challenge, Holl et al., 2020). In this context, two mainstream restoration strategies have been applied—passive natural regeneration after land abandonment and active restoration by means of tree plantations (FAO, 2022). When budgets are limited or forest restoration is scaled up over large areas, natural regeneration may represent the only feasible strategy given its reduced economic costs (Chazdon et al., 2020). However, its effectiveness strongly depends on

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the ability of forest systems to overcome disturbed states and tree recruitment bottlenecks, and hence, active intervention is sometimes a requirement (Arroyo-Rodríguez et al., 2017; Holl and Aide, 2011). Here, the most common management action is to establish tree plantations that recuperate forest cover and simultaneously attract seed dispersers to speed up recruitment rates within restoration sites.

An alternative strategy that lies in between natural regeneration and tree plantations is applied nucleation, in which tree islets are planted throughout deforested areas to attract seed dispersers, ameliorate environmental conditions for recruitment and foster seed dispersal into the remaining deforested matrix (Holl et al., 2020; Rey Benayas et al., 2015; Zahawi et al., 2013). Applied nucleation implies an intermediate level of intervention, reducing the costs of restoration plans (Bechara et al., 2021) and favoring a more natural forest recovery (Corbin et al., 2016; Reis et al., 2010). To be an effective restoration strategy, islets first must be colonized by forest species from nearby areas and, second, they must spread and coalesce over time through the vegetative growth of planted trees and, more importantly, by promoting tree recruitment in the deforested matrix remaining between islets (Corbin and Holl, 2012; Rey Benayas et al., 2008). Even though enhanced seed arrival and recruitment inside islets have been repeatedly observed (Holl et al., 2020, 2013; Robinson and Handel, 2000), expansion from islets into the deforested matrix (e.g., Zahawi and Augspurger 2006; Holl et al. 2000) is not always the rule, and some studies evidence severe constraints even after decades of planting (Corbin et al., 2016; Martínez-Baroja et al., 2022). In fact, little is known about the ecological factors affecting the expansion and coalescence of completely functional islets (i.e., those with adult trees producing fruits) (Ursell and Safford, 2022). Hence, evaluating the ecological processes fostering (or hindering) the natural expansion of planted islets towards the deforested matrix seems timely.

To promote the natural expansion of tree islets, frugivorous animals are key allies. In forest systems, they disperse seeds from a high number of species (Herrera, 2002; Rogers et al., 2021) and their foraging and movement decisions set the template on which plant recruitment occurs (Morales and Morán-López, 2021). Tree islets must attract frugivores from nearby forests, but also facilitate their inter-islet movement. In this way, seeds of consumed fruits can be deposited in the deforested matrix while frugivores move throughout the landscape. Increasing islet size seems an effective strategy to attract frugivores (Cook et al., 2005; Fink et al., 2009; Piaia et al., 2020; Zahawi and Augspurger, 2006). However, in large islets frugivores may stay long periods of time and avoid searching for resources in the surrounding areas (see Fedriani et al., 2018; Sasal and Morales, 2013, for similar results in fragmented landscapes). As a result, seed dispersal may be enhanced within planted areas, but sharply decrease outside their boundaries, a pattern consistently found in nature (Cole et al., 2010; Corbin et al., 2016; Rey-Benayas and Bullock, 2015). Therefore, when islets grow and become seed sources, after the development of planted trees to the reproductive adult stage, there may be a fine size balance between being large enough to be attractive for frugivores and visited, but reasonably small to promote their inter-islet movement. Such optimal islet size will not be unequivocal across systems but depend on the scale of movement of main seed dispersers present in the area (i.e., the spatial grain and extent of their movement decisions; Morales and Morán-López, 2021).

In this work, we tested the performance of different restoration strategies (i.e., natural regeneration and applied nucleation) on promoting tree recruitment into a deforested matrix. Also, we evaluated if the size of islets harboring adult trees could modify tree recruitment into the matrix, and if such effects were mediated by the scale of movement of seed dispersers. To this end, we used an agent-based model able to predict frugivory, seed dispersal and seedling establishment (Donoso et al., 2016; Morales et al., 2013) in a fragmented temperate forest of the Cantabrian range (northern Iberian Peninsula). Two characteristics of our study system make it particularly suited to our aims. The landscape is composed of forest patches of contrasting sizes scattered throughout a deforested matrix. Thus, we could parameterize a mechanistic model of

tree seed dispersal and seedling establishment in an environmental context analogous to that expected under applied nucleation. In addition, forest patches are dominated by fleshy-fruited species dispersed by frugivorous birds. Hence, we could explicitly link the effects of islet size on tree recruitment to the movement and foraging activity of seed dispersers.

## 2. Material and methods

### 2.1. Study system

Our research focuses on temperate forests of the Cantabrian range (northern Iberian Peninsula). The landscape is characterized by small forest patches embedded in a deforested matrix of pastures, heathland and rocky outcrops (García et al., 2005b). Secondary forests are dominated by fleshy-fruited trees (ca. 80 % of tree cover), mostly holly *Ilex aquifolium*, hawthorn *Crataegus monogyna*, yew *Taxus baccata*, and rowan *Sorbus aucuparia*. Fleshy-fruited species ripen in autumn (September–November) and their fruits are consumed (and seeds are dispersed) by thrushes (from most to least abundant: *Turdus iliacus*, *T. merula*, *T. viscivorus*, *T. philomelos*, *T. pilaris* and *T. torquatus*, García et al., 2013). Other frugivores in the studied system are carnivorous mammals (e.g., badger *Meles meles*) or small passerines (e.g., Blackcap *Sylvia atricapilla*) but they account for a small fraction of the total amount of dispersed seeds (Rumeu et al., 2020). After dispersal, seeds frequently suffer predation by rodents, especially when deposited under tree canopies (García et al., 2005a). Most surviving seeds germinate after 18 months (i.e., the second spring after dispersal) with small differences between microhabitats (under tree cover vs open areas) (Donoso et al., 2016). After emergence, early seedling survival is strongly constrained by grazing and trampling by ungulates (García and Obeso, 2003; Martínez and García 2017).

We developed this study based on a real landscape consisting on a single plot of 400 × 440 m (17.6 ha), subdivided into 20 × 20 m cells, located in the Sierra de Peña Mayor (1000 m a.s.l.; 43°17'59"N, 5°20'29"W Asturias, Spain; Appendix A, Fig. A2 and Martínez and García 2017 for further details). The study plot represents a spatial gradient of habitat structure, from dense stands of secondary forest to scattered trees isolated within the matrix (Appendix A, Fig. A2).

### 2.2. Summary of model specifications

#### 2.2.1. Landscape properties

Our simulated landscape had the same extension as the study plot. It consisted of a grid of 440 cells (20 × 20 m each) distributed in 22 rows and 20 columns. Each cell was characterized by a total tree cover (m<sup>2</sup>), a cover of each fruiting species (m<sup>2</sup> of *Ilex aquifolium*, *Crataegus monogyna* and *Taxus baccata*) and a species-specific fruit production (number of fruits per cell on species-specific basis). During the simulation set-up, the structural properties of cells (total tree cover and that of fleshy-fruited species) were model inputs from field data. Then cells were classified in two types of habitats—*forest vs matrix*—, considering forest cells those with tree cover value equal or higher than 0.2 (see Appendix A.1, for habitat classification method). To simulate restoration scenarios (i.e., natural regeneration or applied nucleation) we transformed a certain amount of matrix cells into forest habitat (recovered cells hereafter, further details below). Recovered cells aimed to represent forest patches with the potential to operate as seed sources for tree recruitment, i.e., they harbored adult trees mimicking the composition and fruit production of fleshy-fruited species present in the area. See Appendix A.1 for further specifications on landscape simulations and Table A1-2 for a summary of landscape parameters.

#### 2.2.2. Frugivory, seed dispersal and recruitment

We simulated frugivory and seed dispersal using the agent-based model developed by Morales et al. (2013), which was parameterized

with extensive field data in our study site. In our model simulated frugivores move throughout the landscape following species-specific behavioral rules. In particular, they select which cell to land in next based on its distance from the current location and its attractiveness (according to tree cover and fruits available). When arriving to the cell, the microhabitat of landing (*tree cover vs open land*) depends on amount of tree cover present in the cell. If there are fruits available, birds decide how many to consume by drawing a value from a species-specific zero-inflated Poisson distribution. The identity of the species of fruits consumed is assigned based on their relative abundance within the cell (i.e., no *a priori* preference for any fruiting species; Donoso et al., 2017; García et al., 2013). Eaten fruits are then transformed into seeds consumed. After perching, birds decide where to move next. If they move to a new cell, they follow straight lines at a constant speed of 6 m/sec. Seeds in the gut of birds are defecated after a certain amount of time (GPT, i.e., gut passage time), drawn from a gamma distribution fitted to each bird species. If seeds are defecated while the bird is perching, the microhabitat of deposition will depend on where the bird perched; if defecated while in flight, the microhabitat will depend on the amount of tree cover present in the deposition cell. To generate a seed dispersal template, we simulated 5,000 sequences of bird tracks beginning in a random forest habitat cell. During tracks, birds moved and foraged following the rules described above until they left the study plot or performed more than 20 movements. In each track, the identity of birds was assigned proportionally to their relative abundance in the study area. See Appendix A.2 for further details of seed dispersal submodel and Table A3 for a summary of parameters.

After simulated frugivory and seed deposition, dispersed seeds established as one-year old seedlings depending on species- and microhabitat-specific probabilities of post-dispersal predation, germination and one-year survival (based on Donoso et al., 2016; Rodríguez-Pérez et al., 2017). Probabilities of survival during each stage were parameterized with field data from the study area. At the end of our simulations the model tracked per cell and microhabitat, the number of seeds deposited, those surviving predation, as well as early-emerged and one-year old seedlings. See Appendix A.3 for details on post-dispersal submodel and Table A4 for a summary of parameters.

### 2.3. Model validation

We validated our model by simulating tree recruitment in the study plot (real landscape, hereafter) and comparing predicted patterns with field data. In particular, we compared on a species-specific basis the number of seedlings emerging (and surviving) in each habitat (matrix vs forest). Field data corresponded to a survey of early emerged and one-year old seedlings performed in 2011–2012 in 220 cells located in our study plot (Martínez and García, 2017). Model predictions were obtained by running 30 repetitions and calculating mean values (and confidence intervals) of response variables (Appendix A.4).

### 2.4. Simulating forest restoration

To evaluate the performance of different restoration strategies, we compared the effectiveness of applied nucleation to natural regeneration. In particular, the ability of both restoration strategies to promote seed arrival and seedling establishment into the matrix. Subsequently, we analyzed if the size of tree islets affected the effectiveness of applied nucleation and if such effects depended on the scale of movement of frugivores.

#### 2.4.1. Applied nucleation vs natural regeneration

First, we evaluated the effectiveness of applied nucleation as a restoration strategy aimed to enhance forest recovery at higher rates

than natural regeneration. To this end, we compared seed arrival and tree recruitment into the matrix in landscapes where new forest cells created islets, to that expected under the expansion of extant forest patches (Appendix B, Fig. B1). Such growth-from edge pattern has been frequently observed in natural forest regeneration (Martínez-Ruiz et al., 2021; Mouillot et al., 2005) due to a limited seed arrival far from forest patches (Alday and Martínez-Ruiz, 2022; Lorenzon and Massi, 2022).

To simulate natural regeneration, we programmed a growth-from-edge algorithm that iteratively sampled a matrix cell adjacent to a forest and transformed it into new forest habitat. In each step, habitat classification of cells was updated (from matrix to forest) so that new edges emerged, and hence, new matrix cells candidates to become forest appeared. The process of turning matrix cells into forest stopped when the algorithm reached target values of matrix cells transformed into forest (i.e., proportion of recovered cells reaching values from 0.1 to 0.5 of the original matrix area, with 0.05 intervals). To simulate applied nucleation, we created tree islets by randomly choosing a matrix cell and transforming it into forest (initial cell). Then, initial cells expanded orthogonally to create a square tree islet (Fig. B1). Side of islets was 40 m width, which is representative of the scale of movement of thrush species present in the area (Fig. A6A). This leads to an islet area (0.16 ha) within the range of sizes established in different applied nucleation field studies and restoration projects (e.g., Barrera-Cataño et al., 2023; Fernando Campanhã Bechara et al., 2021; but see Zahawi and Augspurger 2006, Holl et al. 2020 for islet size ranges covering smaller extents). Also, such size would be expected after canopy growth due to the development of planted trees to the adult reproductive stage. Tree islets were generated iteratively and stopped when target values of matrix cells transformed into forest were attained (i.e., from 0.1 to 0.5 proportion of matrix cells becoming forest, with 0.05 intervals; Appendix B1).

For each restoration scenario (applied nucleation vs natural regeneration) and proportion of matrix cells transformed into forest (from 0.1 to 0.5) we ran 30 repetitions and obtained mean values and confidence intervals of—(i) total number of seeds arriving at forest restored cells, (ii) proportion of matrix cells receiving seeds, (iii) average number of one-year-old seedlings per matrix cell and (iv) seedling richness. Response variables provided information about the ability of new forest areas to attract frugivores and to promote tree colonization into the remaining deforested matrix.

#### 2.4.2. Effects of islet size

To estimate the effects of islet size on tree recruitment into the matrix, we generated islets of contrasting sizes in scenarios characterized by a certain degree of matrix area recovered (i.e., proportion of matrix transformed into forest). Tree islets were established in the real landscape and in a theoretical landscape, where all cells initially corresponded to matrix habitats (Appendix B, Fig. B2). The former, allowed us to evaluate islet size effects in a real-world setting; the latter, to isolate islet size effects from other variables (e.g., extent and configuration of forest patches already available in the area).

For each type of landscape (real vs theoretical), we combined different levels of forest recovery (from 0.1 to 0.35 proportion of matrix recovered, with 0.05 intervals) and tree islet size (square islets of 20, 40, 60 and 80 m width, with an extension from 0.04 to 0.64 ha). The minimum islet size covered by this gradient was larger than that frequently used in applied nucleation studies (e.g., Zahawi and Augspurger 2006, Holl et al. 2020) but it was imposed by the spatial grain of observational sampling in the real landscape (20 × 20 m cell; Fig. A2). Then, we simulated frugivory and tree recruitment and tracked (i) the proportion of matrix cells recruiting one-year-old seedlings, (ii) the average number of seedlings per matrix cell and (iii) their richness. For each scenario we ran 30 repetitions and calculated mean values of response variables (i–iii) and islet sizes (measured in hectares). To evaluate the effects of tree

islet size, we regressed each response variable against area recovered (proportion of matrix transformed into forest), the size of tree islets (ha) and their interaction. To compare the strength of covariates on response variables, we scaled them previous to analyses. We used generalized linear models with (i) a Beta distribution for the proportion of matrix cells recruiting seedlings, (ii) a Gamma distribution for seedling density in matrix cells and (iii) a Gaussian distribution for mean richness of recruited seedlings. We fitted regressions with JAGS program (Plummer, 2003) using weakly informative priors. We ran 100,000 iterations in three chains and checked for convergence ( $Rhat < 1.1$ ), adequate effective sample sizes of model parameters ( $>1000$ ) and performed a posterior predictive check to evaluate model fit (Appendix B).

2.4.3. Animal movement as a modulator of islet size effects

To make inference about islet size effects somehow independent of the specific values of our gradient, we performed simulations that directly linked the scale of frugivore movement to islet size effects. In this way we could infer the ecological mechanisms behind islet size effects, and hence, facilitated the transferability of our findings to other nucleated landscapes. We simulated tree recruitment in a theoretical landscape with different values of area recovered (from 0.1 to 0.35 of matrix cells transformed into forest, with 0.05 intervals) and islet size (20, 40, 60 and 80 m width) and, additionally, simulated frugivores with contrasting scales of movement (20, 40 and 80 m, by modifying  $a_{ik}$  parameter in eq. A2). To isolate the effects of mobility from other bird characteristics, the rest of behavioral parameters (e.g., GPT, attraction to tree cover) were held as found in the study area. For each combination of area recovered, islet size and bird mobility, we ran 30 repetitions and obtained mean values of (i) the proportion of matrix cells with seedling recruitment, (ii) average number of one-year-old seedlings per matrix cell and (iii) their richness. We regressed responses (i-ii) against islet size as following:  $y_i = a * e^{-b * S_i}$  (the response to recruitment “y” in the i-th scenario exponentially decayed with  $S_i$ , the mean size of the tree islets; a

intercept, b slope). In the case of richness, we applied a linear regression. All statistical and simulation models were built with R-4.3.1 software.

3. Results

3.1. Applied nucleation vs natural regeneration

Overall, our model simulated in a realistic manner the composition of the community of seedlings and their distribution across habitats (i.e., matrix or forest; Appendix C, Fig. C1). As previously observed in the study area, seed arrival and seedling recruitment were tightly linked to tree cover (Fig. C2). Accordingly, under natural regeneration and applied nucleation scenarios, new forest cells attracted frugivores favoring seed arrival within them (Fig. 1A). However, restoration scenarios differed in the degree of seed arrival and seedling recruitment into the matrix. In the case of natural regeneration, higher values of new forest decreased the proportion of matrix cells receiving seeds and recruiting seedlings (Fig. 1B-C, yellow lines). In contrast, applied nucleation enhanced seed arrival into the matrix and maintained high values of seedling establishment (Fig. 1 B-C, blue lines). Regarding the richness of seedlings, values did not differ between restoration scenarios (Fig. 1D).

3.2. Effects of islet size

In the theoretical landscape, we found a negative effect of tree islet size and area recovered on the proportion of matrix cells recruiting seedlings and on the number of seedlings per matrix cell, whereas seedling richness was only affected by tree islet size. We did not find an interactive effect between both covariates. Overall, islet size was the most important driver of matrix recruitment. It was the only factor affecting the richness of seedlings, and its effects were between 1.8 and 2.3 times stronger than area recovered for the rest of response variables

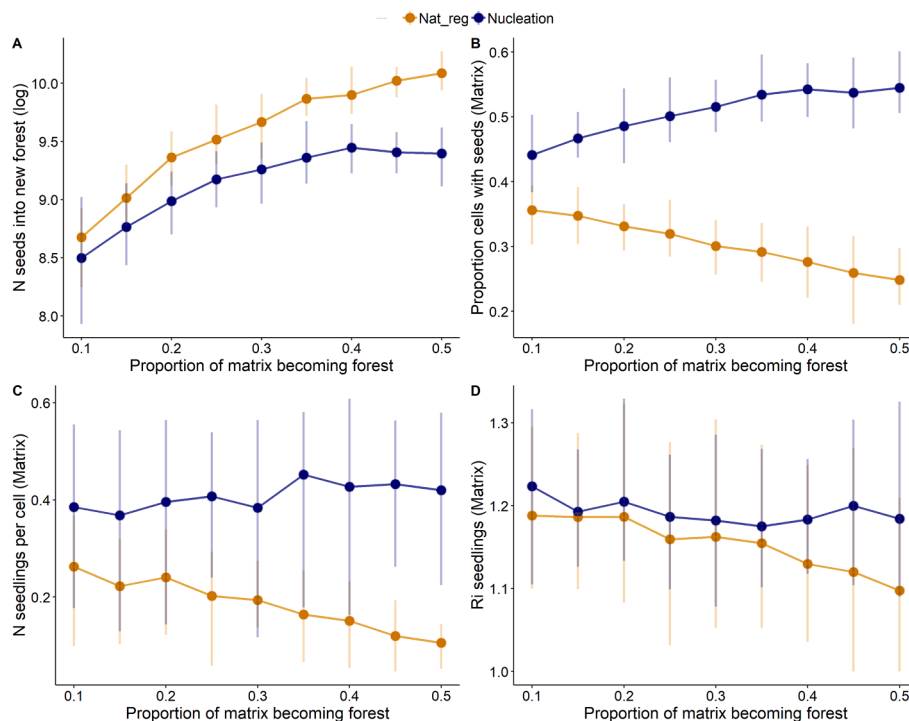


Fig. 1. (A) Total number of seeds arriving at new forest cells (log-transformed), (B) proportion of matrix cells receiving seeds. (C) Average number of one-year-old seedlings recruiting per matrix cell and (D) seedling richness. Colors depict scenarios of natural regeneration (yellow) and applied nucleation (blue). X-axis represents different levels of forest recovered (i.e., proportion of matrix cells transformed into forest). Dots depict mean values and lines 0.95 confidence intervals across 30 repetitions.



**Table 1**

Effects of tree islets size (ha) and area recovered (i.e., the proportion of matrix area transformed into forest) in the (i) proportion of matrix cells recruiting one-year old seedlings, (ii) number of seedlings per matrix cell and (iii) their richness. Mean values of posterior distributions, credibility intervals ( $q_{0.025}$ ,  $q_{0.975}$ ), Rhat, number of effective sample size (Neff) and proportion of the posterior with the same sign as the mean (f). Effects with an f value > 0.95 are in bold.

Response	Covariate	Mean	CI	Rhat	Neff	f
Matrix cells with seedling recruitment	Intercept	-1.76	[-1.82, -1.69]	1	67500	1
	Islet size	<b>-0.19</b>	<b>[-0.25, -0.12]</b>	<b>1</b>	<b>67500</b>	<b>1</b>
	Area recovered	<b>-0.08</b>	<b>[-0.15, -0.02]</b>	<b>1</b>	<b>28275</b>	<b>0.99</b>
	Size*Area	0.03	[-0.04, 0.1]	1	52832	0.84
Number of seedlings per cell	Intercept	4.27	[3.57, 4.85]	1.01	177	1
	Islet size	<b>-0.16</b>	<b>[-0.21, -0.11]</b>	<b>1</b>	<b>42436</b>	<b>1</b>
	Area recovered	<b>-0.09</b>	<b>[-0.14, -0.04]</b>	<b>1</b>	<b>74250</b>	<b>1</b>
	Size*Area	0.03	[-0.03, 0.08]	1	74250	0.85
Seedling richness	Intercept	2.72	[2.68, 2.75]	1	50019	1
	Islet size	<b>-0.07</b>	<b>[-0.1, -0.03]</b>	<b>1</b>	<b>67500</b>	<b>1</b>
	Area recovered	-0.02	[-0.05, 0.02]	1	67500	0.8
	Size*Area	0.01	[-0.03, 0.05]	1	67500	0.75

(Table 1, Fig. 2).

In the real landscape, we found similar patterns (i.e., negative effect of islet size and area recovered). However, both factors reduced similarly matrix recruitment, mainly because the effects islet size were weaker to those found in the theoretical landscape (Appendix C, Table C1, Fig. C4).

### 3.3. Scale of movement of frugivores as a modulator of islet size effects

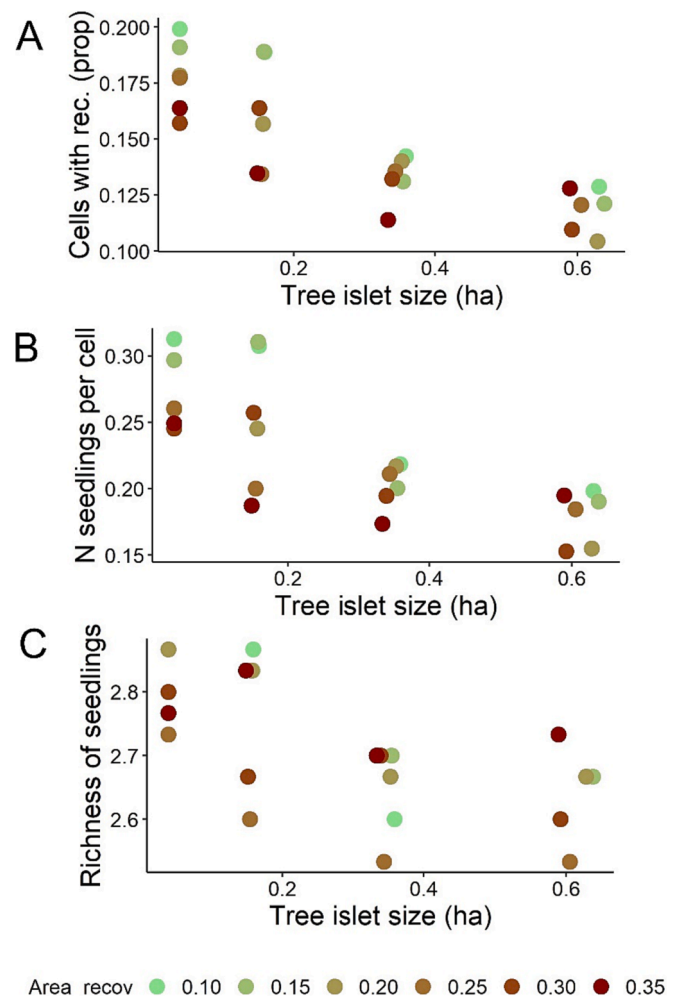
Our results showed that the effects of islet size on tree recruitment into the matrix were tightly linked to the scale of movement of simulated frugivorous birds (Fig. 3). Higher mobility of birds increased average values of all recruitment response variables (Fig. 3, middle panels, intercept). In addition, the scale of bird movement tended to buffer the negative effects of islet size on tree recruitment into the matrix (i.e., tendency towards lower absolute values of regression slopes) (Fig. 3, right panels). In all cases, the proportion of matrix cells restored played a secondary role (Fig. 3, left panels, dot size vs color).

## 4. Discussion

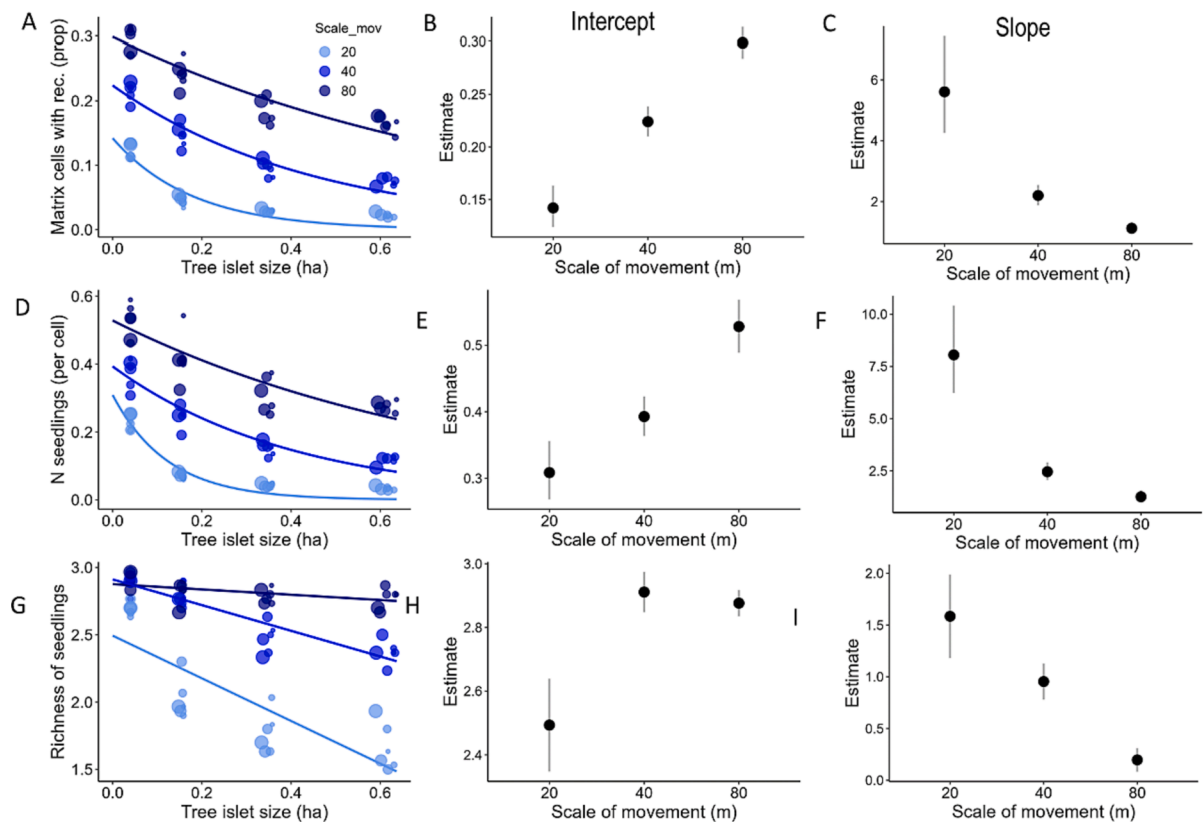
By means of a mechanistic model able to predict tree recruitment, we found that applied nucleation can outperform natural regeneration as a strategy to promote forest recovery in the deforested matrix. Yet, our simulations showed that the effectiveness of tree islets to promote recruitment into the deforested matrix strongly relies on their size. Islets with fruiting trees must attract frugivores, but also foster their movement throughout the landscape so that seeds of consumed fruits can be deposited outside restored areas. Overall, our work provides valuable insights about how frugivores' behavior can affect the colonization of the deforested matrix by tree propagules provided by planted tree islets over time, and hence, the effectiveness of applied nucleation as a restoration strategy.

In our simulations, applied nucleation triggered seed dispersal and seedling establishment into the matrix at higher rates than natural regeneration following an edge-expansion pattern (Fig. 1). In both, natural regeneration and applied nucleation, new forest areas were equally effective in attracting frugivores (Fig. 1A). However, natural regeneration concentrated seed deposition and seedling establishment within forest boundaries, limiting matrix colonization (Fig. 1B-C, orange lines). Entrapment of frugivorous animals within forest patches occurs when the matrix is unattractive (Jones et al., 2017; Levey et al., 2008; Nield et al., 2020), and hence, they are not tempted to leave the forest habitat (Montealegre-Talero et al., 2021; Rodriguez-Perez et al., 2014). In contrast, under applied nucleation, the creation of tree islets scattered throughout the matrix reduced the contrast between forest and matrix habitats and increased their contact area (Fig. B1). As a result, it favored the spillover of birds from forest habitats towards the matrix (Hulvey

et al., 2017), enhancing seed arrival into this habitat and the subsequent seedling establishment (Fig. 1 B-C, blue line). In landscapes where tree islets are planted close to forest patches, the expansion of edges will



**Fig. 2.** Effects of size of tree islets (ha) and matrix area recovered (as proportion of matrix transformed into forest cells) on the (A) proportion of matrix cells recruiting one-year-old seedlings, (B) number of seedlings per matrix cell and (C) their richness. Dots depict mean values of response variables and size of tree islets (ha) across 30 repetitions of scenarios vaying the size of islets (squares from 20 to 80 m width) and the proportion of matrix transformed into forest (color code). Results correspond to simulations in the theoretical landscape. See Appendix C, Fig. C4 for simulations performed in the real landscape.



**Fig. 3.** Effects of tree islet size (ha, x-axis), the scale of movement of frugivorous birds (m, color code) and the proportion of matrix cells transformed into forest through applied nucleation (proportional to dot size) on the establishment of seedlings into the matrix. (Left panels)—(A) proportion of matrix cells recruiting one-year-old seedlings, (D) average number of seedlings per matrix cell and (G) their richness. Lines depict fitted regressions of response variables against tree islet size. (Middle panels)—Intercepts of fitted regressions, and (Right panels)—Absolute values of slopes of fitted regressions. See [Appendix C, Table C2](#) for a summary of estimated parameters.

occur in parallel to tree islet growth. In such case, a mixed response between both scenarios would be expected with some “entrapment” of frugivores within large forest patches and tree islets attracting them towards the matrix. Irrespectively of long-term dynamics, our results support the view that applied nucleation can trigger matrix colonization at higher rates than natural regeneration, at least at the initial stages of forest recovery (Meli et al., 2017; Zahawi et al., 2013).

When evaluating the performance of applied nucleation, our simulations showed that the size of tree islets is a key driver of tree recruitment into deforested areas (Table 1 and Table C1). In both, the theoretical and real landscapes, small tree islets promoted higher rates of tree recruitment into the matrix (Fig. 2, Fig. C4). Small islets were characterized by a higher proportion of edges (Fig. C3, A & C), increasing the contact area between forest and matrix habitats. In addition, they were attractive enough to be visited by frugivores, but too small to offer abundant resources. Consequently, birds left them quickly depositing seeds on their way, favoring a more even distribution of seedlings throughout the matrix (Fig. 2A), a pattern that promotes forest recovery (Robinson and Handel, 2000). In the real landscape, the presence of woodland patches (Appendix B, Fig. B2) attenuated the effects of islet size on matrix recruitment (Fig. C4, Table C1), supporting the view that forest archipelagoes already present in the area can become part of the management plan to attain a more even distribution of seeds and seedling establishment (Wunderle, 1997). In general, the availability of small patches of remnant forest, or even isolated trees, within the matrix enhances a more scattered seed arrival throughout the landscape favoring recruitment (González-Varo et al., 2017; Pizo and dos Santos, 2011).

As expected, our simulations showed that the effects of islet size were not unequivocal, but tightly linked to the scale of movement of seed

dispersers present in the area. Vagile frugivores were less prone to spend long periods of time within large islets and performed inter-islet movements more often. Consequently, they fostered higher rates of matrix recruitment in all landscape configurations (Fig. 3). These results show that matrix permeability is not only a structural property of landscapes but also a functional one, as it depends on the ability of animals to perform inter-patch movements (Zhang et al., 2021). From an applied standpoint, they highlight that the scale of movement of dispersers can affect the performance of applied nucleation restoration strategies. Especially, when islets harbor fruit-bearing trees not only attracting frugivores, but also maintaining them within their boundaries. Thus, animal-centered approaches could complement current designs of applied nucleation plans, which are more focused on selecting plants according to their traits (e.g., growth rates, resistance to harsh conditions, Holl et al., 2020). For instance, if the scale of movement of dispersers is limited, planting a high number of small islets should be more effective than establishing a few large and distant islets. Probably, the optimal design would be establishing islets whose size matches the scale of movement of the most abundant frugivores. If the scale of movement of local dispersers results too restrictive for the restoration plan (e.g., due to increased cost and labor associated to a higher number of small islets), complementing applied nucleation with other interventions intended to attract vagile frugivores would be advisable (e.g., facilitating the availability of nesting sites, as suggested by Martínez-Baroja et al., 2022).

To compare our results with those of previous field studies, several considerations are needed. As previously stated, even though the size of simulated tree islets is within the range of different applied nucleation actions (from 0.04 to 0.64 ha; Barrera-Cataño et al., 2023; Bechara et al., 2021), they were larger than those frequently used in field studies

evaluating islet size effects. Namely, the area of our smallest islet was comparable to the largest islet usually reported (Cook et al., 2005; Holl et al., 2020). Field studies evaluating size effects at smaller spatial extents, have reported better restoration outcomes on large islets (e.g. Zahawi and Augspurger 2006; Fink et al. 2009), a result that seems contradictory to ours. However, based on the parametrized behavioral rules of animal movement (Fig. S6), a similar trend would be expected for an extended gradient including smaller sizes (e.g.,  $2 \times 2$  m, in Zahawi and Augspurger 2006;  $4 \times 4$  m in Holl et al. 2020). Very small islets would be scarcely visited due to limited tree cover (Fig. S6C) and fruit availability (Fig. S6D) in their surroundings, and hence, increasing their size would improve visitation rates (as previously found in experimental approaches, Fink et al. 2009). Integrating findings of field studies and the present modeling approach, we expect a bell-shaped response if islet size effects were tested in a wider gradient (e.g., 0.001—0.50 ha). Very small islands would result unattractive for frugivores and very large ones would “trap” them within their boundaries. Unfortunately, ascertaining such bell-shaped response would require overcoming the technical constraints derived from the spatial grain of our design (the  $20 \times 20$  m cells in the real landscape). This grain facilitated that bird flights were correctly assigned to the corresponding cells within the landscape, but limited our ability to downscale our simulation experiments.

To transfer our findings to other types of forest, several features of our approach must be considered. First, minor effects of recovered area on matrix recruitment may respond to some assumptions of our simulations that reflect specific characteristics of our study system. All simulated scenarios harbored the same community of frugivores (thrushes, which are the dominant frugivore species in the study area). Hence, we did not consider potential declines in frugivores related to habitat loss (McConkey et al., 2012). In addition, though our model accounted for the affinity of frugivores towards tree covered areas (Morales et al., 2013), it did not consider their willingness to cross open areas while moving. Both assumptions are reasonable in our study system, where thrushes are relatively tolerant to moderate degrees of forest fragmentation and, at least some species, frequently fly across the matrix (García et al., 2013; Herrera and García, 2010). In fact, our model could reproduce recruitment patterns in our study plot (Fig. C1). However, these assumptions may not be adequate in fragmented landscapes where frugivores follow edges while moving (Levey et al., 2008) or suffer population declines (Corbin et al., 2016). Under such circumstances we anticipate a more important role of the extension of matrix recovered on tree recruitment. In addition, the negative effects of area recovered on matrix recruitment respond to the fact that inter-islet distances were within the ranges of movement of simulated frugivores (Fig. C3 vs Fig. A6B). Thus, planted areas were not disconnected from each other. As area recovered increased tree islets became closer together (Appendix C, Fig. C3, B & C), frugivores spent less time flying throughout the matrix and the probability of seed deposition in this habitat decreased. In landscapes where the distance between islets represents a barrier for frugivore movement, positive effects of area recovered would be expected.

Finally, we would like to highlight that our predictions are limited to one-year seedling establishment. In our system, early seedling establishment imposes a spatial template of tree sapling occurrence (García et al., 2005a; Martínez and García, 2017). Yet, environmental filters acting at larger timescales can shape the spatial distribution of trees in the deforested matrix (e.g., presence of nurse shrubs) (Martínez and García, 2017). Therefore, it remains an open question if effective tree recruitment will finally lead to complete forest recovery into the matrix. Irrespectively of such caveats, our work provides valuable information from a theoretical and applied point of view. We show that in nucleated landscapes, matrix colonization rates emerge from the interplay between tree islet size, inter-islet distances and animal movement. Thus, explicitly accounting for the scale of movement of most abundant frugivores in the restoration area will be particularly helpful when designing management actions.

## 5. Conclusions

Our work supports the view that applied nucleation is an adequate strategy to promote tree recruitment into the matrix, but questions that large tree islets are better. In particular, when planted islets harbor fruit-producing trees they may offer abundant resources to dispersers, which may concentrate their activities (and seed deposition) within their boundaries. As a result, seed arrival and seedling establishment into the matrix can be insufficient or low. Therefore, when designing nucleated landscapes, accounting for the scale of movements of frugivores present in the area can improve matrix colonization rates, and hence, the performance of management actions. As a rule of thumb, we propose to plant tree islets whose size and inter-islet distances match the scale of movement of most abundant seed dispersers present in the area.

## Authors' contribution

TML and DG conceived the ideas of the work. DG led and organized different field studies used to parameterize our agent-based model and DM led field campaigns. Submodel of frugivore movement and foraging behavior was designed and parameterized by JMM. JRP and ID designed first drafts of the post-dispersal submodel. Final version of the model, merging frugivory and recruitment was designed and implemented by TML. TML and DG designed simulation scenarios and TML analyzed results and wrote the first drafts of this work. All authors revised the work and approved the final version of the article. *Statement of inclusion:* This work involved scientists based in the country where the study was performed.

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## Declaration of Competing Interest

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

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121508>.

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