Morán Ordóñez, Alejandra; Hermoso, Virgilio; Martínez-Salinas, Alejandra. «Multi-objective forest restoration planning in Costa Rica : balancing landscape connectivity and ecosystem service provisioning with sustainable development». Journal of environmental management, Vol. 310 (May 2022), art. 114717. DOI 10.1016/j.jenvman.2022.114717

Journal of Environmental Management

Multi-objective forest restoration planning in Costa Rica: balancing landscape connectivity and ecosystem service provisioning with sustainable development

--Manuscript Draft--

Manuscript Number:	
Article Type:	Research Article
Keywords:	Nature-Based Solutions; Neotropical Birds; Spatial Conservation Planning Tools; Species Distribution Models; Secondary Forest; Tropical forests
Corresponding Author:	Alejandra Morán-Ordóñez Center for Ecological Research and Forestry Applications: Centre de Recerca Ecologica i Aplicacions Forestals SPAIN
First Author:	Alejandra Morán-Ordóñez
Order of Authors:	Alejandra Morán-Ordóñez
	Virgilio Hermoso
	Alejandra Martínez Salinas
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Title page

Title: Multi-objective forest restoration planning in Costa Rica: balancing landscape connectivity and ecosystem service provisioning with sustainable development

Authors: Alejandra Morán-Ordóñez[1,2,] , Virgilio Hermoso[2], Alejandra Martínez-Salinas[3]

Affiliations:

[1] Ecological and Forestry Applications Research Centre (CREAF), Edifici C Campus de Bellaterra, 08193, Cerdanyola del Valles, Spain

[2] Consorci Centre de Ciència i Tecnologia Forestal de Catalunya (CTFC), Ctra. St. Llorenç de Morunys, km. 2, 25280, Solsona, Spain.

[3] CATIE – Centro Agronómico Tropical de Investigación y Enseñanza, 30501, Turrialba, Cartago, Costa Rica.

Corresponding author:

Alejandra Morán-Ordóñez

Ecological and Forestry Applications Research Centre (CREAF)

Address: Edifici C Campus de Bellaterra, 08193, Cerdanyola del Vallés (Spain)

Phone: (+34) 973 48 17 52 (Ext. 330); Email: alejandra.moran@ctfc.cat
/a.moran@creaf.uab.cat

ACKWNOLEDGMENTS

This research was supported by the European Union's H2020 research and innovation program under the Marie Sklodowska-Curie grant agreement No. 691149 (SuFoRun). A.M.O and V.H. were supported by the Spanish Government through the Juan de la Cierva and Ramón y Cajal fellowship programs (IJCI-2016-30349 and RYC-2013–13979 respectively) and the CERCA Programme/Generalitat de Catalunya. A.M.S. was supported by the US Fish and Wildlife Service (USFWS) through the Neotropical Migratory Bird Conservation Act (NMBCA, grant F18AP00472). We thank Lindsay Canet for facilitating the official land cover map developed for the Volcanica Central Talamanca Biological Corridor (VCTBC) Strategic Plan (2016-2021).

CREDIT AUTHOR STATEMENT

Alejandra Morán-Ordóñez: Conceptualization, Methodology, Formal Analyses, Writing-Original draft preparation; **Virgilio Hermoso**, Methodology, Writing- Original draft preparation; **Alejandra Martínez Salinas**: Conceptualization, Original draft preparation.

Alejandra Morán Ordóñez
Senior PostDoctoral Fellow
Ecological and Forestry Applications Research Centre
a.moran@creaf.uab.cat

Dear Editor,

We would be grateful if you would consider our manuscript entitled "Multi-objective forest restoration planning in Costa Rica: balancing landscape connectivity and ecosystem service provisioning with sustainable development" for publication in *Journal of Environmental Management*.

A fundamental problem of landscape-scale restoration approaches is to balance conservation goals (e.g. biodiversity and ecosystem services recovery) and economic interests. Forests are one of the main Costa Rican' environmental and economic assets. Forest conservation is promoted through a series of mechanisms i.e. Payment for Ecosystem Services schemes, and establishment of biological corridors to restore or increase landscape connectivity. The recently launched Costa Rican National Decarbonization program targeting net-zero emissions for 2050 emphasizes the need to promote both forest restoration for services like carbon sequestration and storage, and economic activities associated with biodiversity-friendly land management.

In this study, we planned a spatially optimal, multi-objective forest restoration across the Volcanica Central Talamanca Biological Corridor in central Costa Rica. The Corridor plays a key biological role at the national and continental scale, increasing forest connectivity across Central America to facilitate dispersal of emblematic species such as the Jaguar. However, only 57% of the corridor is currently forested, and further forest restoration will conflict with other land uses (e.g. cattle grazing, coffee and sugar cane production), some of them of high economic importance (30% of milk and meat national production comes from this area). Restoration efforts must consider the potential impacts on local income. Our optimal planning approach found the key areas within the Corridor where forest restoration increases forest connectivity and ecosystem services (e.g. carbon sequestration, recreation opportunities), with minimum impact on current co-existing land uses. In other words, we identified areas suitable for forest restoration while accounting for land opportunity costs.

Our results will inform restoration efforts within the Corridor, highlighting synergies and potential conflicts between conservation (e.g. forest connectivity), sustainable development (e.g. ecotourism) and maintenance of traditional uses (e.g. cattle grazing). More broadly, our optimal planning approach will be of interest to a wide audience of ecologists and practitioners. This combination of relevant results and demonstration of a rigorous planning approach integrating multiple ecosystem services and stakeholders interests fits ideally within the scope of *Journal of Environmental Managemen*t, particularly since we use a publicly available tool for multi-objective forest restoration that can be easily applied in other regions.

Thank you in advance for your consideration and I look forward to your correspondence.

Kind regards,

Alejandra Morán-Ordóñez (on behalf of all authors)

CREAF. Campus UAB. Edifici C 08193 Cerdanyola del Vallès (Barcelona)
Tel. + **34 93 581 13 12** contacte@creaf.uab.cat **www.creaf.cat** | **blog.creaf.cat**

- We used spatial planning tools to design a forest restoration plan across a biological corridor in Costa Rica
- Restoration sought to maximize provision of forest-related ecosystem services and forest connectivity
- We evaluated the role of land opportunity costs of current uses on identifying potential areas for restoration
- Accounting for land opportunity costs changed the most the spatial design of forest restoration plans
- We discussed the opportunities (e.g. PES) and challenges in implementing forest restoration in the study area

Abstract

Degradation, fragmentation and loss of tropical forests has exponentially increased in the last decades leading to unprecedented rates of species extinctions and loss of ecosystems functions and services. Forest restoration is key to recover ecosystems health and achieve Sustainable Development Goals. However, restoring forests at the landscape scale presents many challenges, since it requires balancing conservation goals and economic development. In this study, we used a spatial planning tool (Marxan) to identify priority areas for restoration satisfying multiple objectives across a biological corridor in Costa Rica. Biological corridors are critical conservation instruments promoting forest connectivity while acknowledging human presence. Increasing forest connectivity requires restoration initiatives that will likely conflict with other land uses, some of them of high national economic importance. Our restoration plan sought to maximize the provision of forest-related services (i.e., seed dispersal, tourism and carbon storage) while minimizing the impact on current land uses and thus avoiding potential conflicts. We quantified seed dispersal and tourism services (birdwatching potential) using species distribution models. We used the carbon sequestration model of InVEST to quantify carbon storage potential. We tested different restoration scenarios that differed in whether land opportunity costs of current uses were considered or not when identifying potential areas for restoration, or how these costs were estimated. We showed how a landscape-scale forest restoration plan accounting for only forest connectivity and ecosystem service provision capacity can greatly differ from a plan that considers the potential impacts on local livelihoods (through the loss of land opportunity costs). Spatial planning tools can assist at designing cost-effective landscape-scale forest restoration plans, identifying priority areas where forest restoration can maximize ecosystem provision and increase forest connectivity. Special care must be paid to the use of adequate estimates of opportunity cost, to avoid potential conflicts between restoration goals and other legitimate land uses.

Keywords: Nature-Based Solutions; Neotropical Birds; Spatial Conservation Planning Tools; Species Distribution Models; Secondary Forest; Tropical forests

INTRODUCTION

Forest conservation and restoration at the global scale is key to recovering ecosystems health, and achieving Aichi Biodiversity Targets and Sustainable Development Goals (Chazdon, 2019; Griscom et al., 2017). This is especially relevant in tropical biodiversity hotspots where forest degradation, fragmentation and loss has exponentially increased in the last decades leading to unprecedented impacts on biodiversity, biogeochemical cycles, climate change and ecosystems integrity (Alroy, 2017; Davidson et al., 2012; Lovejoy and Nobre, 2019). In middle-to-lower income countries restoration of forest ecological integrity is critical to maintaining cultural identities and greatly contributes to the sustainable development of local communities and their health (Bullock et al., 2011; Fisher et al., 2019; Zhang et al., 2019). Forest biodiversity supports the livelihoods of these communities directly, through the provision of goods (e.g., food, wood products, medicines), and indirectly by generating income opportunities (e.g., ecotourism), and more generally, providing many other valuable non-material services such as pollination, pest and disease control, regulation of climatic conditions, soil loss mitigation and risk disaster reduction (e.g., landslides, floods) (Brandon, 2014).

Forest restoration targets can be achieved by combining passive and active interventions, focusing respectively on either minimizing human disturbances to allow for unassisted recovery or actively intervening to accelerate restoration (Holl and Aide, 2011). Natural regeneration following land sparing and abandonment (i.e., regrowth of secondary forests) represents one of the most cost-effective forest restoration strategies (Brancalion et al., 2019; Chazdon et al., 2020), potentially allowing to achieve a faster and cheaper recovery of forest biodiversity and ecosystem functions (e.g., increased functional connectivity, carbon sequestration, energy fluxes) than actively increasing forest extent using for example monoculture plantations (Seddon et al., 2019; Zhang et al., 2021). However, a fundamental problem of forest restoration approaches regardless of whether they are active or passive, is to upscale them across large territories (i.e., achieve landscape-scale restoration) since this requires balancing restoration and economic development, the factor responsible for forest degradation in the first place (Chazdon et al., 2017; Holl, 2017).

Integrating spatially-explicit planning tools and forest conservation policies and incentives can prove key to plan landscape-scale forest restoration across areas where conflicts between ecosystem recovery and socioeconomic development might arise (Chazdon et al., 2020; Strassburg et al., 2019). Costa Rica represents a unique setting to demonstrate the advantages of these planning exercises provided its internationally recognized efforts to increase forest extent and connectivity via several policies, laws and conservation instruments (Sánchez-Azofeifa et al., 2007). Besides its formal network of national protected areas, Costa Rica has also incorporated the figure of *biological corridors* into its conservation toolkit (DeClerck et al., 2010). These biological corridors are multifunctional landscapes, seeking to promote biodiversity conservation and increasing forest connectivity between national protected areas - and broadly across Central America -, while pursuing sustainable socio-economic development and human well-being. Adequate planning of landscape-scale forest restoration in biological corridors is key to ensure the achievement of nation-wide conservation objectives and minimize conflicts with other legitimate traditional land uses and sources of livelihood for local populations (Powlen and Jones, 2019).

In this study, we demonstrated the feasibility of using conservation planning tools to identify priority areas for forest restoration satisfying multiple objectives across a biological corridor in Costa Rica. We sought to identify priority areas for restoration to increase forest connectivity across the corridor, maximizing the provision of other forest-related services such as seed dispersal, tourist opportunities and carbon storage, while minimizing the impact on existing socio-economic activities. We explicitly evaluated the differences between a landscape-scale forest restoration plan accounting for only forest connectivity and ecosystem service provisioning from a scenario that considers the potential impacts on local livelihoods through the loss of land opportunity costs. We discuss our results in terms of the potential on-the-ground implementation of this approach to contribute to forest restoration targets across Costa Rica and elsewhere.

METHODS

Study area

The study area is the Volcanica Central Talamanca Biological Corridor (VCTBC; area approx. 115,000 ha), located on the Caribbean slopes of the Volcanica Central mountain range of Costa Rica (Fig. 1). It was designated in 2003 with the main goal of restoring and/or increasing the functional connectivity between the Volcanica Central and the Talamanca mountain ranges, located in the north and south central regions of Costa Rica respectively (Fig. 1), focusing at the local scale on increasing connectivity between protected areas surrounding the VCTBC (e.g., Turrialba, Barbilla and Tapantí National Parks), and at a broader scale, on increasing connectivity of the forested areas across Central America to facilitate dispersal of emblematic species such as the Jaguar (*Panthera onca*). Forests cover 57% of the total area of the corridor, where the second dominant land use is pastures (30%) and other agricultural uses (10 %), such as coffee plantations (4%) and annual crops (2%). Besides its ecological goals, the VCTBC pursues the sustainable development of local economies by the involvement of stakeholders in achieving sustainable management of natural resources (Canet-Desanti, 2016).

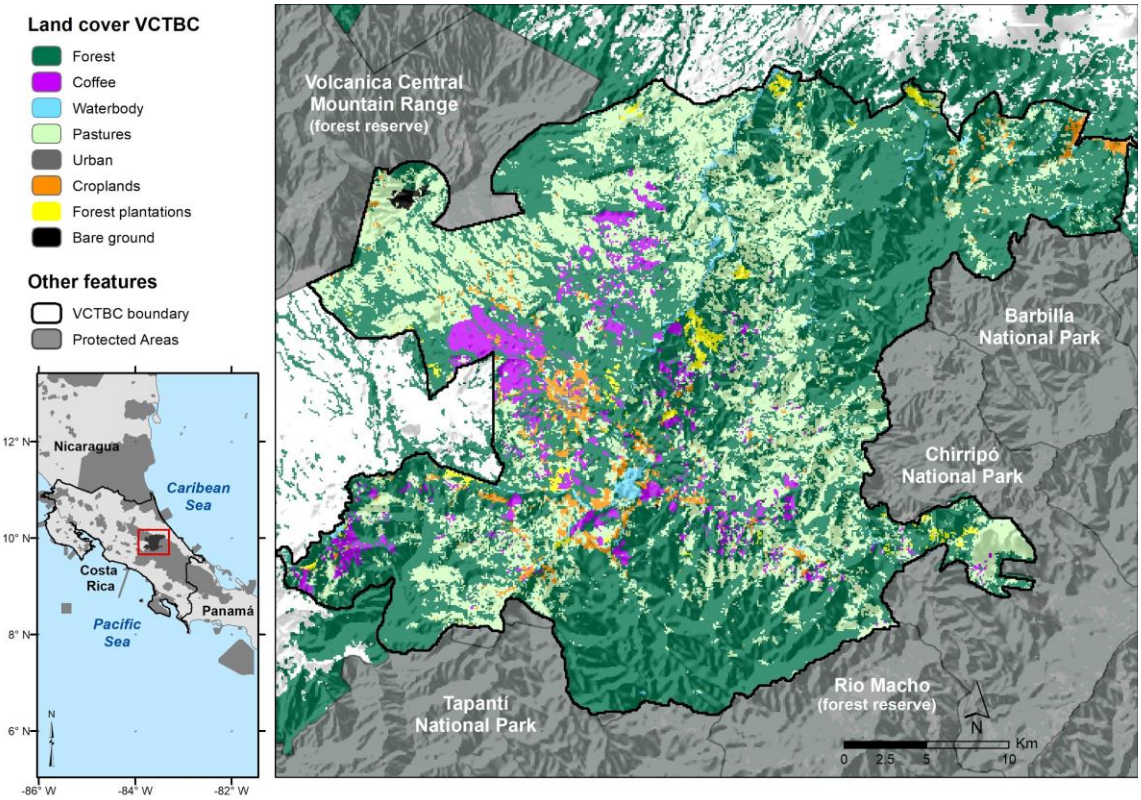


Figure 1*. Study area. The map shows the dominant land cover types in the Volcanica Central Talamanca Biological Corridor (VCTBC; source: Canet-Desanti, 2016). The inset map on the bottom left shows the location of the biological corridor in the context of the network of protected areas in Costa Rica and across Central America.*

Mapping ecosystem services values

We mapped three forest-related ecosystem services (ESS) of high relevance for the goals of the biological corridor: 1) Seed dispersal (supporting service): frugivorous birds are important seed dispersal agents and actively promote natural regeneration and plant diversity (Harms et al., 2000; Morrison and Lindell, 2011), providing with effective means of forest restoration in human-disturbed landscapes (Crouzeilles et al., 2017); 2) Ecotourism linked to birdwatching (cultural service): Costa Rica is one of the top destinations for birdwatchers in Latin America (Echeverri et al., 2019), contributing to the development of ecotourism businesses and the sustainable development of local communities (Sekercioglu, 2002); and 3) Carbon sequestration (regulation service): low-cost natural regeneration or assisted forest regeneration of tropical forest has a large potential for contributing to climate change mitigation via carbon sequestration and storage (Chazdon et al., 2016), making forest restoration one of the main axes of the recently launched Costa Rican National Decarbonization program to 2050 (Costa Rica Government, 2019).

To map the seed dispersal and the potential ecotourism services across the biological corridor, we developed species distribution models using Maxent (Phillips et al., 2006; Phillips and Dudík, 2008) for 62 frugivorous bird species with known presence in the VCTBC, also culturally valued by birdwatchers and locals because of multiple reasons (e.g., their esthetic and acoustic beauty, identity values, etc.) (Echeverri et al., 2019) such as the Resplendent Quetzal *(Pharomachrus mocinno*), the Red-capped Manakin (*Ceratopipra mentalis*) or the Collared Aracari (*Pteroglossus torquatus*). Current predictions of habitat suitability for selected bird species were used as a subrogate of the seed dispersal service, assuming seed rain and forest recovery can be potentially higher in areas closer to or within locations with higher suitable conditions for the service-provider species. The projected habitat suitability of the species across the biological corridor assuming all current non-forest areas were restored to forest was used as a subrogate of the ecotourism service potential. For both the seed dispersal and the ecotourism service, we only retained species for which we could generate reliable models in terms of predictive performance (47 species with Area Under the Curve > 0.7; Hanley and McNeil, 1982) (Appendix S1). We used the distribution of each species as an individual subrogate for the ecosystem service. Although the service could be provided by a reduced number of abundant species, we aimed to maximize the number of species that would both benefit from restoration and naturally promote it and, therefore, contribute to the resilience of the overall ESS provision (Chain-Guadarrama et al., 2019; Mouillot et al., 2013). Carbon sequestration potential was mapped using the InVEST Carbon Storage and Sequestration model (version 3.7.0) developed by the Natural Capital Project (Sharp et al., 2018). Using the VCTBC official land cover map as a reference (Canet-Desanti, 2016), the model estimated the potential change in carbon sequestration per hectare if all current non-forested areas in the biological corridor were restored to forest. For parameterizing the model, each land cover (i.e., forest, coffee plantations, crops, pastures, forest plantations, bare ground) was associated with a total carbon storage capacity per ha following values from Vallet et al. (2016). For this analysis, we assumed improvement in carbon sequestration across the corridor could only be achieved through the conversion of coffee plantations, crops, and pastures to forests. All the three ESS were mapped at 1 ha spatial resolution. The spatial predictions of current and future habitat suitability of the 47 frugivorous birds (subrogates of seed dispersal and ecotourism ESS, respectively) along with predictions of the carbon sequestration potential from the InVEST model constituted the 95 ESS features that input the prioritization analyses. See Appendix S1 for full details of data sources and handling, the species and carbon modelling parametrization, fit and validation and mapping methods.

Spatial prioritization of forest restoration

We used the spatial prioritization tool Marxan (Ball et al., 2009) to identify priority areas for forest restoration across the biological corridor to maximize provision of the three ESS (i.e., seed dispersal, ecotourism and carbon storage) while increasing spatial forest connectivity. Marxan uses an optimization algorithm that seeks to minimize an Objective Function (Eq. 1) across I restoration units and J ESS features:

$$OF = \sum_i^I Cost_i + \sum_j^J SPF * Feature\ Penalty_j + CSM \sum_i^I Connectivity\ Penalty_i \qquad \text{Eq. 1}$$

We only considered pastures, annual crops and coffee plantations as land covers with potential to be restored to forest, totaling 51852 ha, each hectare representing an individual restoration unit. The selected land covers represent the only ones that could potentially benefit from economic incentives associated to climate mitigation targets – Payments for Environmental Services) (Sánchez-Azofeifa et al., 2007).

We ran different restoration scenarios that differed in the assumptions of the opportunity costs of each restoration unit (i.e., the revenues per ha that could be potentially lost when restoring forest over the current land uses) (first element of Eq. 1): 1) an *Equal opportunity cost* (**Equal**) that assumed all restoration units had equal opportunity costs, regardless their current land use; 2) a *Homogeneous opportunity cost scenario* (**Homog**) that assumed the opportunity costs of each restoration unit only depended on its current land use, regardless of its spatial location across the corridor. The opportunity costs of restoring forest over pastures, annual crops and coffee plantations across the biological corridor were sourced from the Total Added Values per ha of each of these land uses reported for the study area in Vallet et al. (2016) (Appendix S2); 3) a *Heterogeneous opportunity cost* scenario (**Heter**), where the opportunity cost of each restoration unit for each land use varied across the biological corridor to account for differences in productivity across environmental gradients. In this case, depending on the replaced land use and its elevation. The most productive lands for annual crops and coffee in the VCTBC are above the 1000 m.a.s.l, whereas the most productive pastures for dairy farming (one of the main economic activities in the VCTBC) are those above the 800 m.a.s.l (C.V. and F.C. Unit of Livestock and Environmental Management, CATIE, personal communication). Since the actual difference in revenues per ha depending on land use and elevation was unknown, we tested three variations of this scenario in which the opportunity costs of restoration units over current land uses were 30%, 50% or 100% higher in lands above the before mentioned elevational thresholds than below (**Heter30**, **Heter50** and **Heter100**, respectively). The opportunity costs below those thresholds were assumed the same as in the **Homog** scenario. The use of these scenarios sought to evaluate how accounting for land opportunity costs could influence the optimal spatial design of landscape-scale forest restoration plans across the corridor.

We ran a sensitivity analyses over a range of targets, to evaluate how much forest restoration would be needed if we sought to increase the ESS provision between 0.01 to 20% compared to current levels. For reference, a 0.01% increase in carbon sequestration compared to current levels would require the restoration of an approximately minimum of 15, 25 or 29 ha of croplands, pastures and coffee plantations, respectively, to forest (being connectivity and other ecosystems features not considered). Marxan applies a Feature Penalty for not achieving a target set for each ESS feature (second element in Eq. 1). The contribution of this Feature Penalty to the overall Marxan solution is weighted by the Species Penalty Factor coefficient (SPF). To ensure that targets for all ESS features were achieved across solutions, we set a high SPF (SPF=10). This SPF brought the weight of the Feature Penalty into line with that of the Costs in Eq. 1.

Finally, the Connectivity Penalty in Eq. 1 is a penalty for not selecting restoration units spatially aggregated. We derived connectivity penalties from the geographic distance d*ij* to the nearest 8-neighbours of each restoration unit (penalty = d_{ij}-2). The Connectivity Penalty is weighted within the objective function by a Connectivity Strength Modifier (CSM). Higher CSM values result in solutions where restoration units are more spatially clumped, but it comes to higher costs. For this reason, it is necessary to calibrate the CSM value. We calibrated the CSM (Eq. 1) for each scenario and target following Ardron et al. (2010). However, and given the large amount of forest already existing in the biological corridor (approx. 57% of the total area), small CSM values led Marxan solutions to select all the available areas for restoration, even at low targets (Appendix S3). To avoid the connectivity constraint to override Marxan´s solutions, we selected a CSM value over the calibration curves that allow us to balance both objectives as well as to allow fair comparison of achieved connectivity values across scenarios (Appendix S3).

For each scenario, we run Marxan 100 times, using standard annealing parameters. In all runs and scenarios, current forest cover was locked-in, while water bodies, bare ground and urban areas were always locked-out (i.e., not considered for their potential to achieve targets). All scenarios were run both using the calibrated CSM value (Appendix S3) and considering a CSM = 0, to assess the impact of connectivity constraints in spatial prioritization outputs. In each scenario, we selected the best solution out of the 100 independent runs (Marxan best solution from here on) and use it to make comparisons across all scenarios using three metrics: (1) the number of restoration units required by the best solution (reflecting total restoration efforts); within each set of restoration units we calculated the percentage of each current land use selected for restoration in each combination of scenario-target; (2) total restoration opportunity cost (in Colons, Costa Rican currency) calculated for each best solution based on the same opportunity cost (**Homog**) so values could be compared across scenarios, and (3) the overall forest connectivity achieved. Connectivity achieved in each scenario was calculated using a connectivity index that measures the relative connectivity achieved in the solution compared to the maximum connectivity that could have been achieved if all restoration units in the solution were fully connected. This connectivity index is independent of the number of restoration units in the solution and, therefore, comparable across scenarios and targets (Hermoso et al., 2020). We also measured the selection frequency of restoration units in best solutions across all targets for each scenario.

RESULTS

Restoration targets were achieved for all 95 ESS across all scenarios and tested targets (Appendix S4). For a given target, the number of hectares selected for forest restoration (restoration units) was slightly smaller in the **Equal** scenario than in those considering opportunity costs (**Homog**, **Heter30**, **Heter50** and **Heter100**; Fig. 2, Appendix S5). The selection frequency of different land uses across Marxan's best solutions also markedly differed between scenarios (Fig. 2). The **Equal** scenario identified pasturelands as the most suitable land cover to promote forest restoration (accounting for more than 80% of restoration units selected in best solutions, regardless the target considered). Approximately 10% of selected restoration units in this scenario corresponded to croplands < 1000m (in targets from 1 - 20). On the contrary, scenarios considering opportunity costs prioritized the selection of restoration units in lowlands, where the total opportunity cost was smaller (e.g., selection of restoration units over pastures at < 800 m were prioritized over selection of pastures > 800m; Fig. 2; Appendix S5, S6). As a result, the **Homog** and **Heter** scenarios selected a larger proportion of restoration units across current coffee plantations (15%; the land use with the smallest total added value) and forest plantations and did not select restoration units in current croplands - except when large targets were considered (target values 18 – 20). For example, for a target of 1% increase in service provision, Marxan best solutions suggest forest restoration of 10%, 8.4% and 7.1% of current pastures, croplands, and coffee plantations respectively in the **Equal** scenario (approx. 2400 ha). Alternatively, best solutions of the **Homog** scenario suggest forest restoration of 12.6% and 20.6% of current pastures and coffee plantations (approx. 3200 ha) (**Homog** and **Heter30**, **Heter50** and **Heter100** best solutions were similar; Appendix S5, S6).

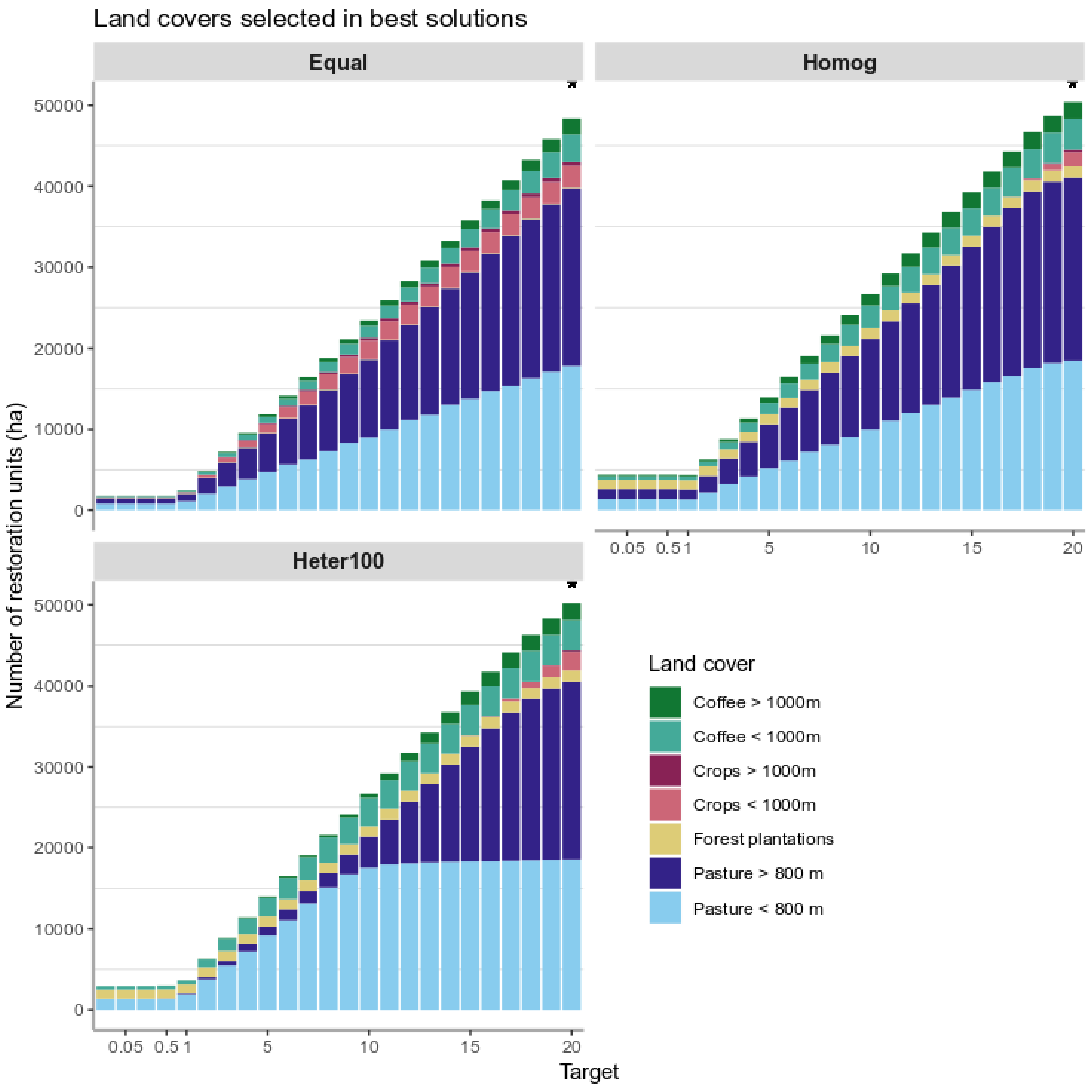


Figure 2. *Number of units (hectares) selected for forest restoration across the biological corridor, under each combination of scenario (Equal Opportunity Cost, Homogeneous Opportunity Cost, Heterogeneous Opportunity Cost 100%) and target. Colors within each bar reflect the proportion of each land use (coffee plantations, crops, pastures, and forest plantations) selected within the set of restoration units in each of the Marxan's best solutions. The asterisk on top of the bar of the target 20 marks the total number of hectares available for restoration across the biological corridor. See Appendix S5 for results of the Heter30 and Heter50 (not shown here because of their resemblance with the Heter100 solution).*

Although the total number of restoration units selected for any given target was smaller under the **Equal** scenario, the total opportunity costs of this scenario were much higher than those of best solutions of scenarios accounting for opportunity costs (Fig. 3). The **Homog.** scenario and all versions of the *Heterogeneous Opportunity Cost* scenarios (**Heter30**, **Heter50** and **Heter100**) showed similar costs, only that starting to diverge for targets over 15%, being the **Heter100** scenario the most expensive.

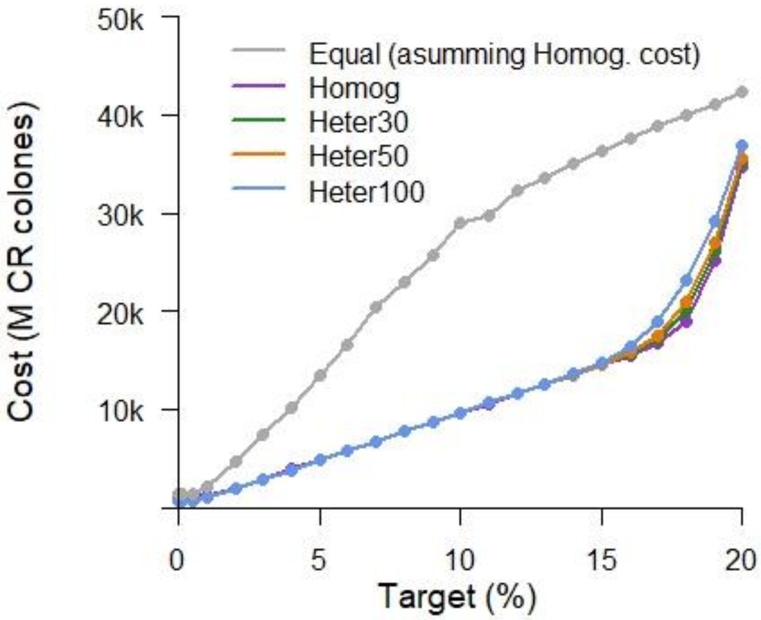


Figure 3. *Estimated forest restoration costs in Millions of Colons (Costa Rican currency) across scenarios and targets. To ease comparison between scenarios, costs were calculated by summing up the current land opportunity costs of the selected restoration units in the Marxan's best solutions for each scenario (i.e., taking the costs of the* ***Homog*** *scenario as reference to compare opportunity costs across all scenarios).*

Marxan best solutions across all scenarios markedly increase forest structural connectivity compared to current connectivity across all targets (Fig. 4a) but especially compared to reforestation scenarios that sought to achieve ESS targets without accounting for connectivity (CSM==0; Fig. 4b). We found small differences in connectivity achievement across all tested scenarios, with the **Equal** scenario attaining a slightly lower structural connectivity than the other scenarios, especially at small targets. The spatial outputs of the best solutions differed mostly between the **Equal** and other scenarios (Fig. 5; Appendix S7, S8). The **Equal** scenario identified as best areas for forest restoration those units on the edges of already existing forest patches, regardless of the current land use and following a scattered pattern across the corridor. The **Homog**, **Heter30**, **Heter50** and **Heter100** scenarios identified key areas for forest restoration those placed across the central parts of the biological corridor, connecting already existing forest patches from North to South; these include already existing forest plantations that did not contribute to the overall achievement of ESS targets but mostly to increasing forest connectivity but also, and most importantly, coffee plantations and pastures in lowlands in the northcentral parts of the corridor (Fig. 1).

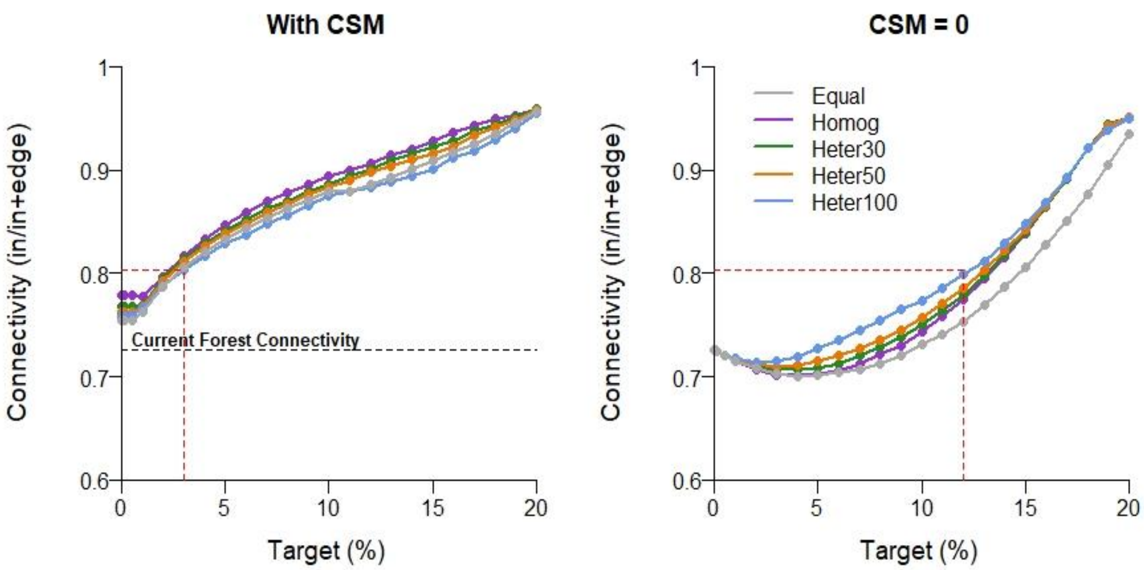
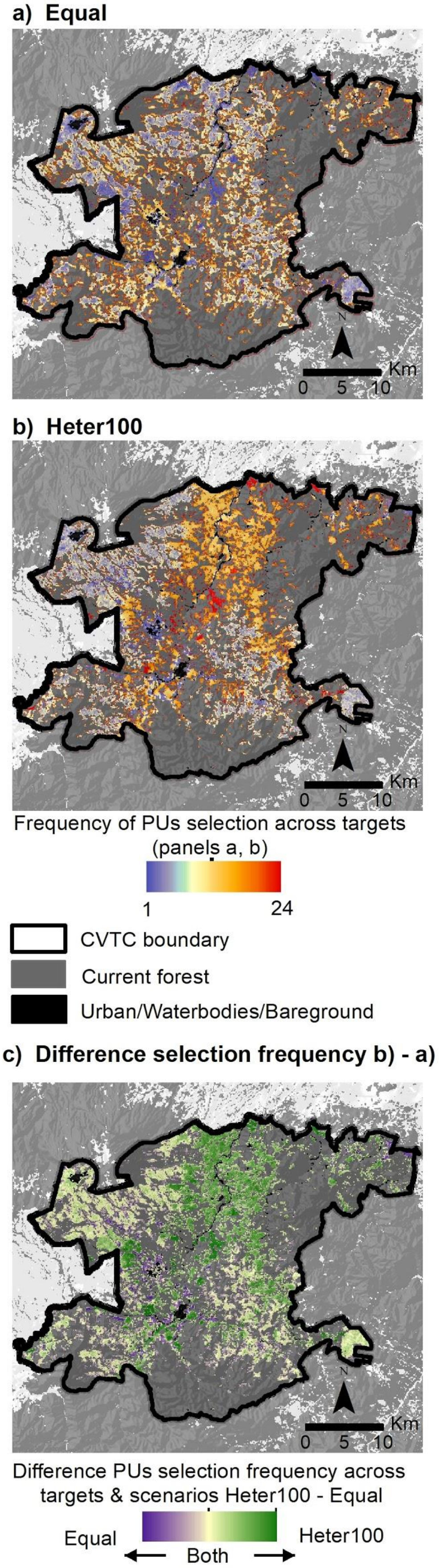


Figure 4. *Overall forest structural connectivity achieved across scenarios and targets when connectivity is considered in the planning process along with ESS targets (left panel 'With CSM') or when increasing connectivity is not considered in the planning process (right panel 'CSM=0'). The intersection between the dashed red lines points to an increase in connectivity of 10% regarding current levels and how it is achieved at much higher costs when CSM=0. For example, to achieve that increase in connectivity under the Heter100 scenario (see intersection between dashed red lines in both plots), the number of hectares to restore (as identified in Marxan best solution) was of 8,877 when connectivity was considered along ESS targets in the spatial prioritization (with CSM) and of 30,368 when CSM=0.*

__Figure 5__ Frequency of selection of restoration units in best solutions across all tested targets (24) in the two most contrasting planning scenarios __a)__ Equal Opportunity Cost (__Equal__) and __b)__ Heterogeneous Opportunity Costs (__Heter100__). The map in panel __c)__ highlights the differences in frequency of selection of restoration units between the Heter100 and the Equal scenario, with areas in yellow indicating restoration units that are selected with the same frequency in both scenarios. See Appendix S7 for comparative results for the Homog., Heter30 and Heter50 scenarios. See Appendix S8 for best solutions for targets 1, 5 and 10.



DISCUSSION

We have demonstrated how to identify priority areas for forest restoration for multiple objectives, by using a freely available spatial planning tool. Our results showed that a landscape-scale forest restoration plan only considering forest connectivity and the increase of ESS provision capacity greatly differed from a plan also considering potential impacts on local livelihoods, i.e., accounting for opportunity costs associated with forest restoration. When planning blindly to opportunity costs (**Equal** scenario), our results suggest that landscape-scale forest restoration plans could lead to potential socio-economic impacts and management conflicts (selection for restoration units with the highest opportunity costs). Careful consideration of potential constraints to the implementation of restoration is, therefore, crucial to ensure that restoration recommendations arising from planning exercises will encounter less local opposition. We also showed that the reduction in opportunity cost can be achieved at no expenses of other objectives, such as increasing ESS provision or connectivity. Our approach to restoration planning is suitable for other landscape-scale restoration plans elsewhere (and regardless of the ecosystem aiming to restore), where multiple-objectives are pursued and where potential conflicts between these could arise, being a useful and reality-grounded tool to foster optimal restoration interventions.

Our restoration planning approach addresses recent calls for increasing the cost-efficiency of forest restoration programs by using spatially-explicit systematic planning approaches (Gourevitch et al., 2016; Strassburg et al., 2019); these allow to identify areas where restoration programs have the potential to maximize benefits in terms of biodiversity recovery and ESS provision at minimum costs. They could also be used to evaluate trade-offs between potentially competing objectives (e.g. maximizing ecosystem service provision and biodiversity; Ramel et al., 2020). One of the main differences between solutions across scenarios considering opportunity costs and those of the **Equal** scenario were that the later suggested the restoration of croplands and pasturelands in the highest parts of the corridor as the most efficient way to achieve the ESS targets (lower number of restoration units needed), whereas the former did not select those areas as a priority. However, the croplands in the highest parts of the corridor are highly productive compared to those in the lowlands, being the type of crops grown in those areas (e.g., potatoes and onions) strongly demanded at the national and international level (Vallet et al., 2016). The productivity of dairy pasturelands at higher altitudes is also higher and it is mostly oriented to the production of Turrialba cheese which has a *Protected Designation of Origin* by the World Trade Organization since 2012, recognizing cheese characteristics linked to this specific geographical location and its artisanal way of production. This makes the **Equal** scenario not only the most expensive in terms of total opportunity cost (Fig. 3) but also, the scenario in which forest restoration would be less feasible to achieved in real life , having the largest consequences in terms of loss of cultural heritage of the VCTBC among all tested scenarios (i.e. loss of cultural services and relational values; Chapman et al., 2020; Daniel et al., 2012). On the other hand, our results also showed that accounting for opportunity costs (scenarios **Homog**, **Heter30**, **Heter50** and **Heter100)** did not translate into loss of connectivity or service provision values, as the later scenarios were equally effective at achieving targets. Therefore, we found little trade-offs between avoiding socio-economic conflicts and promoting restoration for increasing ESS provision and connectivity across the corridor, the two main objectives pursued here.

Accounting for opportunity costs when designing landscape-scale forest restoration plans is critical to design reality-grounded interventions. The estimates of opportunity costs that we used were based only on the current revenues the farmers get from the goods they produce, without considering any potential changes in market demands and product prices or accounting for other intangible benefits (e.g., biodiversity conservation value of certain land uses). Given the relevance that the use of opportunity cost had on the selection of priority areas for restoration, the selection of adequate estimates of these opportunity costs, including consideration of temporal dynamics, deserves special attention. For example, Marxan best solutions of the **Homog**, **Heter30**, **Heter50** and **Heter100** scenarios selected current coffee plantations more frequently over croplands for restoration (Fig. 2), because currently, the yield of coffee plantation per ha at the VCTBC is 25 times lower than from croplands (Appendix S2; Vallet et al. 2016). However, these opportunity costs are temporally dynamic (e.g., dependent on market prices fluctuations) and can be estimated in different ways (i.e., using current land prices, using historical changes in land prices to estimate future value, using productivity values per ha, etc.), which would translate into changes in the spatial distribution of priority areas for restoration. Ideally, opportunity costs should also account for the intangible contributions of land uses; for example, coffee agroforestry systems (where coffee plants interact with a diverse set of perennial woody species) have been shown to support greater levels of native biodiversity compared to other crops and other coffee management systems (e.g., coffee monocultures) and to contribute to functional connectivity of forest-dependent bird species which in turn provide supporting and regulating services such as seed dispersal and pest control (Chain-Guadarrama et al., 2019; De Leijster et al., 2021). Sustainable certified production in agroforestry systems is also eligible for incentives for premium products. If all these ecological benefits and the potential premium prices over sustainable certification were considered, opportunity costs of coffee agroforestry plantations across the VCTBC would probably exceed by large those of pastures or vegetable crops, completely changing the forest restoration solutions presented here. Similarly, if potential revenues from ecotourism development after forest restoration could be estimated, they would probably exceed the land opportunity costs of any of the current uses in the biological corridor and change the spatial solutions of the landscape-scale forest restoration plan.

Implementing any of the landscape-scale forest restoration solutions identified by the most cost-efficient scenarios will inevitably require the involvement of the people living in the landscape (Chazdon et al., 2017; Holl, 2017) as well as finding adequate financial incentives to landowners (Brancalion et al., 2012). In this regard, forest restoration actions across the VCTBC could benefit from the Payments for Environmental Services (PES) scheme of Costa Rica directed to promote forest protection and recovery across the country (GGGI, 2016). This scheme, mainly financed through the national fuel tax and operationalized through the National Forestry Financial Fund (FONAFIFO), pays private landowners who own forests or who promote forest recovery in their land, in recognition of the ESS provided (Liagre et al., 2021; Sánchez-Azofeifa et al., 2007). It subsidizes land-use management practices leading to forest protection, forest management in primary and secondary forest, and sustainable management of agroforestry systems among other interventions (Sánchez and

Navarrete, 2017). The scheme gives a strong emphasis on the potential social impact of those interventions (e.g., prioritizing subsidies to small landholders and to indigenous lands; Molina Murillo et al., 2014) and facilitates private investments when possible. Forest restoration across the corridor could benefit from a combination of PES options depending on the location and current use of the land. For example, both low- and highland pastures located in steep slopes have already been subsidized in different pilot projects across the corridor to spare land and promote regrowth of secondary forests with the ultimate goal of reducing soil loss and sediment transport and prevent negative impacts on hydroelectrical plants (under the "water resource protection" PES scheme; Estrada-Carmona and DeClerck, 2012).

Passive restoration following natural regeneration of secondary forest could represent an interesting cost-effective landscape-scale forest restoration measure to apply across the corridor (especially across pasturelands and croplands, although the success of natural regeneration will strongly depend on past land use practices; Holl and Aide 2011). In this regard, all Marxan solutions presented here suggest areas where this restoration option could be facilitated to a great extent by the presence of seed dispersers (i.e., frugivorous birds). However, in Costa Rica, forest expansion due to the regrowth of secondary forests has been hampered by several factors including the existence of a strong forest law that bans land use change over forested land, the lack of knowledge by landowners of financial mechanisms to support the management of secondary forests (option only contemplated and fully developed in Costa Rica legislation in 2016 Decreto 399952 - MINAE) as well as the lengthy and complex bureaucracy and administration processes to access them (e.g., an officially approved forest management plan is mandatory to access incentives for forest management; Reyes et al., 2018). In fact, the PES funds directed to natural afforestation and forest management during the period 2006-2017 represented less than 4% and 0.5% of PES funds granted to forest protection, respectively (FONAFIFO stats 2018; www.fonafifo.go.cr). Forest plantations can also be contemplated as an option to increase forest extent and structural connectivity across the corridor and, as such, have been recurrently selected in the best solutions of scenarios accounting for land opportunity costs (Fig. 2, Fig. 5; Appendix S7). Forest plantations are eligible for financial mechanisms besides the PES scheme (e.g., the carbon credits market through the UN REDD+ program), making them currently attractive for owners of marginal land. They can be used as a pathway to forest recovery (Alexander et al., 2016) and have proven useful to trigger ecosystem recovery in other areas of Costa Rica (e.g., Guanacaste; Pringle, 2017). However, they do not represent a universal solution: monoculture plantations can maximize carbon sequestration at high costs to the provision of other services and ecological functions (FONAFIFO et al., 2012; Zhang et al., 2021). In this regard, private companies in the carbon market are increasingly interested in paying for carbon sequestration which is ‘bundled’ to other ecosystem and social benefits (Estrada-Carmona and DeClerck, 2012; FONAFIFO et al., 2012; GGGI, 2016) and thus, a multi-objective spatial prioritization protocol as the one presented in this study can prove key to identify areas where to maximize such investments.

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Appendix S1. Species distribution models (subrogates of ESS provision)

1.1. Species data

We accessed occurrence data of neotropical birds in Costa Rica for the period 1990-2019 from the Global Biodiversity Information Facility (https://www.gbif.org/; eBird Observational Dataset: 10 June 2019). We filtered this dataset (4,164,402 records) to retain only frugivorous birds with presence in the biological corridor, and one record per ha (100 m^2; finest spatial resolution of environmental predictors). We kept only species with at least 30 records in order to minimize the possible negative influence of small samples sizes in modelling outputs (Hernandez et al., 2006; Wisz et al., 2008), ending up with a list of 62 bird species to model and 100,429 occurrence records.

1.2. Environmental predictors

We sourced long-term average climatic data for Costa Rica from the WorldClim database (version 2.0; 1 km – spatial resolution). From the 19 bioclimatic variables available in WorldClim, we retained a subset of four variables with maximum Pearson's pairwise correlation of 0.55 (Dormann et al., 2013; Tabachnick and Fidell, 1996): average mean temperature (Bio 1), Temperature annual range (Bio 7), Annual precipitation (Bio 12) and precipitation of the wettest month (Bio 13). Correlations between variables were calculated across all occurrence records of the filtered data set (also called target-group background points; Phillips et al., 2009) (see mode details in the "Habitat Suitability Section"). Additionally, and because we were interested in understanding the response of species to forest restoration, we used a predictor accounting for the percentage of forest cover in each hectare. Forest cover data from Costa Rica was derived from the 2012 forest map of Costa Rica (SIREFOR www.sirefor.go.cr; vector format). This map had clouds covering large parts of the forest areas. We filled the clouds' gaps in the forested areas using the 2005 forest map of Costa Rica (SIREFOR). Costa Rica has a strong conservationist forest law that does not allow forest harvest in national reserves and state forests, nor the conversion of forest on private land to other uses. Thus, we assumed that if a given pixel was covered with forest in 2005 it would keep the same cover in 2012. The forest cover predictor was not correlated with the climatic variables (Pearson´s $R < 0.1$). We found some discrepancies between the national forest map of Costa Rica and a land cover map expressly developed in 2012 for the VCTBC (the amount of forest cover in the VCTBC map was higher than the national forest map; Canet-Desanti, L. 2016). Thus, while the model predictor derived from the national forest map (% of forest per ha) was used to train the models at the Costa Rica level, the 2012 forest cover map of the VCTBC was used to make predictions at the VCTBC level (the scale at which conservation planning analyses were carried out).

1.3. Habitat suitability maps

We modelled the distribution of 62 bird species using MaxEnt(version 3.3.3k; Phillips et al., 2006; Phillips and Dudík, 2008), a machine learning method designed for dealing with presence-only data (Elith et al., 2011) while taking into account the distribution of environmental predictors in the background area of analysis. Exploratory analyses showed that species records were biased towards areas of high accessibility (e.g. roads and urban areas). Biased survey data can lead to environmentally and geographic biased predictions that might reflect the sampling effort rather than the species' true distributions across the study area (Fithian et al., 2015; Kramer-Schadt et al., 2013; Phillips et al., 2009). To reduce the possible effect of geographical bias in presence data on SDM predictive performance, we provided background points to MaxEnt in such a way as to copy the geographic and environmental bias of the occurrence records by using as background all available records for birds over Costa Rica. This approach, known as "target-group background" approach (Phillips et al., 2009), has been shown to perform well in dealing with bias (Fithian et al., 2015; Kramer-Schadt et al., 2013; Phillips et al., 2009). Same background points were used in all species models.

MaxEnt models were run with default settings except we controlled the complexity of the response shapes by allowing only linear, quadratic and product features in the model. These are similar to linear, quadratic and interaction terms in regression models, and their simplicity guards against models being overfitted to samples, making them more general for prediction (Elith et al., 2011; Merow et al., 2014). Predictive performance (in terms of discrimination ability; Guillera-Arroita et al., 2015) and uncertainty of the fitted responses was assessed using the area under the area under the receiver-operator characteristic curve (AUC; Hanley and McNeil, 1982) adapted for use with presence - background samples (Phillips et al., 2006). We estimated AUC using the ten-fold cross-validation provided in Maxent.

We evaluated bias reduction effectiveness (i.e., whether modelling the species using a ‘target-group background’ was better than considering a random background over Costa Rica), by asking experts on birds in the study area to compare model outputs (map predictions) and predictive performance values of models based on those two background selection methods (target-group vs random background). Models fit using the target-group background approach were validated by experts as better reflecting the habitat suitability of the species in the study area than the models assuming random background.

From the initial list of species with enough records available to run MaxEnt models (62 species), we retained for the subsequent MARXAN analysis only those whose species whose models’ predictive performance was moderate to high (cross-validated AUC > 0.7; Swets, 1988) (47 species; Table S1). We re-fitted the model of each species using all presence records, to take advantage of the full amount of information for each species (cross-validated models used only 9/10 parts of the data in each iteration). These are called ‘full’ models; outputs of ‘full’ models were used as inputs for the spatial prioritization analyses (*Spatial prioritization of forest restoration* section in main text).

1.4. Habitat suitability maps to mapped ecosystem services

To map the seed dispersal service for each species across the biological corridor, we made predictions of the models over the current land cover map of the VCTBC. These inform about the areas with current higher habitat suitability for the species and where we could expect seed dispersal (seed rain) to be higher, contributing naturally to forest restoration (Crouzeilles et al., 2017). To map the ecotourism service for each species across the biological corridor, we made spatial predictions of the models assuming all current non-forested areas in the VCTBC were covered in forests. This predicts how the habitat suitability of the species with touristic value will change across the biological corridor if forest restoration would take place.

Table S1. List of bird frugivorous species considered for the analyses (scientific and common name), the predictive performance for the Maxent models following 10-fold cross validation (mean AUC test± SD) and the number of samples available to fit the models (n samples). Species with low predictive performance (test AUC < 0.7) were not considered for the spatial prioritization analysis (15/62 species).

Scientific name	Common name	AUC$_{TEST \pm SD}$	N samples
Attila spadiceus	Bright-rumped Attila	0.673 ± 0.018	2095
Aulacorhynchus prasinus	Emerald Toucanet	0.893 ± 0.010	1211
Baryphthengus martii	Rufous Motmot	0.868 ± 0.014	566
Caryothraustes poliogaster	Black-faced Grosbeak	0.875 ± 0.013	562
Catharus frantzii	Ruddy-capped Nightingale-Thrush	0.941 ± 0.009	513
Ceratopipra mentalis	Red-capped Manakin	0.829 ± 0.023	730
Chlorophanes spiza	Green Honeycreeper	0.747 ± 0.015	2061
Chlorothraupis carmioli	Carmiol´s Tanager	0.913 ± 0.013	422
Corapipo altera	White-ruffed Manakin	0.800 ± 0.023	732
Cotinga amabilis	Lovely Cotinga	0.897 ± 0.028	43
Cyanerpes lucidus	Shining Honeycreeper	0.781 ± 0.020	999
Cyanoloxia cyanoides	Blue-black Grosbeak	0.721 ± 0.022	1138
Dacnis cayana	Blue Dacnis	0.747 ± 0.021	1130
Dacnis venusta	Scarlet-thighed Dacnis	0.775 ± 0.018	1136
Dives dives	Melodious Blackbird	0.558 ± 0.014	3957
Elaenia flavogaster	Yellow-bellied Elaenia	0.613 ± 0.014	3253
Elaenia frantzii	Mountain Elaenia	0.896 ± 0.009	1142
Eubucco bourcierii	Red-headed Barbet	0.880 ± 0.017	412
Habia fuscicauda	Red-throated Ant-Tanager	0.864 ± 0.013	721
Ixothraupis guttata	Speckled Tanager	0.850 ± 0.021	592
Lipaugus unirufus	Rufous Piha	0.789 ± 0.034	511
Manacus candei	White-collared Manakin	0.855 ± 0.009	1407
Mionectes oleagineus	Ochre-bellied Flycatcher	0.703 ± 0.023	1132
Mionectes olivaceus	Olive-striped Flycatcher	0.826 ± 0.025	542
Mitrospingus cassinii	Dusky-faced Tanager	0.920 ± 0.017	195

Scientific name	Common name	AUC_{TEST} ±SD	N samples
Monasa morphoeus	White-fronted Nunbird	0.910 ± 0.018	211
Myadestes melanops	Black-faced Solitaire	0.898 ± 0.010	1011
Myiopagis viridicata	Greenish Elaenia	0.742 ± 0.030	482
Oncostoma cinereigulare	Northern Bentbill	0.742 ± 0.030	556
Ortalis cinereiceps	Gray-headed Chachalaca	0.674 ± 0.014	2646
Phainoptila melanoxantha	Black-and-yellow Silky-flycatcher	0.945 ± 0.010	453
Pharomachrus mocinno	Resplendent Quetzal	0.932 ± 0.009	750
Piranga bidentata	Flame-colored Tanager	0.922 ± 0.010	794
Piranga leucoptera	White-winged Tanager	0.867 ± 0.023	267
Procnias tricarunculatus	Three-wattled Bellbird	0.820 ± 0.030	578
Psarocolius montezuma	Montezuma Oropendola	0.719 ± 0.010	4550
Psilorhinus morio	Brown Jay	0.701 ± 0.012	3932
Pteroglossus torquatus	Collared Aracari	0.794 ± 0.015	2060
Querula purpurata	Purple-throated Fruitcrow	0.948 ± 0.015	247
Ramphastos ambiguus	Yellow-throated Toucan	0.733 ± 0.011	3894
Ramphastos sulfuratus	Keel-billed Toucan	0.755 ± 0.011	3318
Ramphocelus passerinii	Scarlet-rumped Tanager	0.676 ± 0.009	6137
Ramphocelus sanguinolentus	Crimson-collared Tanager	0.854 ± 0.012	814
Saltator atriceps	Black-headed Saltator	0.781 ± 0.015	1163
Saltator maximus	Buffed-throated Saltator	0.640 ± 0.012	4127
Semnornis frantzii	Prong-billed Barbet	0.926 ± 0.011	568
Stilpnia larvata	Golden-hooded Tanager	0.696 ± 0.011	3780
Tachyphonus delatrii	Tawny-crested Tanager	0.916 ± 0.017	294
Tachyphonus luctuosus	White-shouldered Tanager	0.760 ± 0.024	898
Tachyphonus rufus	White-lined Tanager	0.740 ± 0.024	766
Tangara gyrola	Bay-headed Tanager	0.756 ± 0.019	1376
Tangara icterocephala	Silver-throated Tanager	0.811 ± 0.013	1723
Tangara lavinia	Rufous-winged Tanager	0.930 ± 0.019	155
Thraupis episcopus	Blue-gray Tanager	0.577 ± 0.010	8361

Scientific name	Common name	AUC$_{TEST}$ ±SD	N samples
Thraupis palmarum	Palm Tanager	0.637 ± 0.012	4643
Trogon caligatus	Gartered Trogon	0.672 ± 0.017	2096
Trogon collaris	Collared Trogon	0.880 ± 0.014	600
Trogon massena	Slaty-tailed Trogon	0.790 ± 0.016	1526
Trogon rufus	Black-throated Trogon	0.783 ± 0.021	1107
Turdus assimilis	White-throated Thrush	0.826 ± 0.022	726
Turdus grayi	Clay-colored Thrush	0.564 ± 0.010	8871
Zimmerius parvus	Mistletoe Tyrannulet	0.667 ± 0.016	2519

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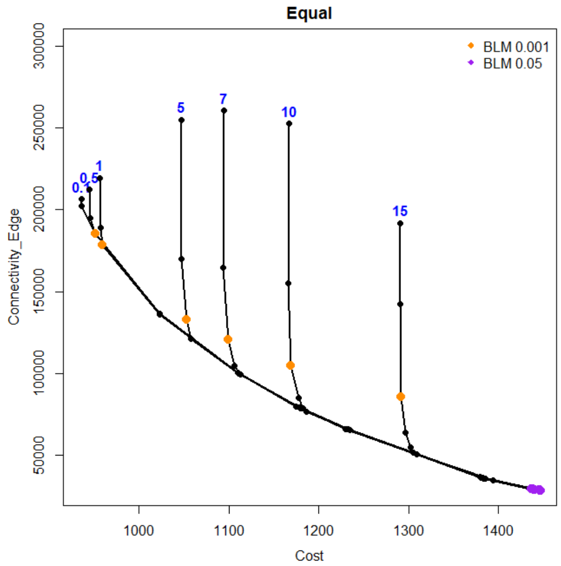
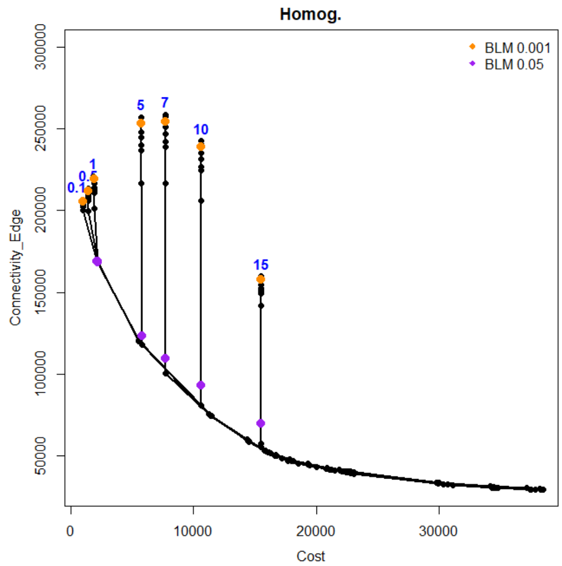
Appendix S2. Estimated total added value in Colons (Costa Rican currency) per ha of goods produced in agricultural land across the corridor (source: Vallet et al., 2016)

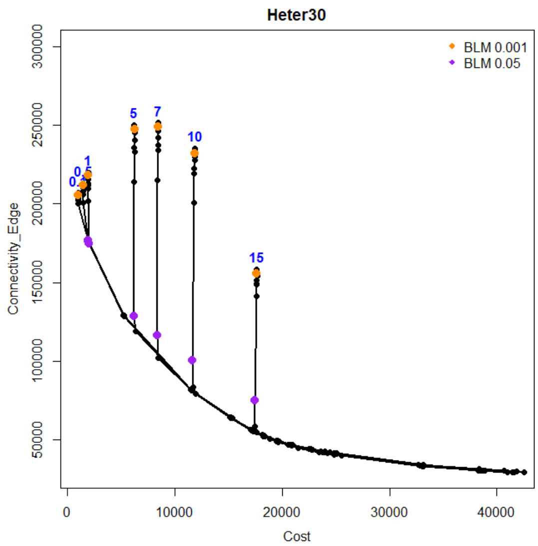
Agricultural land uses (Figure 1 main text)	Added value
Coffee plantations	297,663
Pastures	396,668
Crops	7,882,732

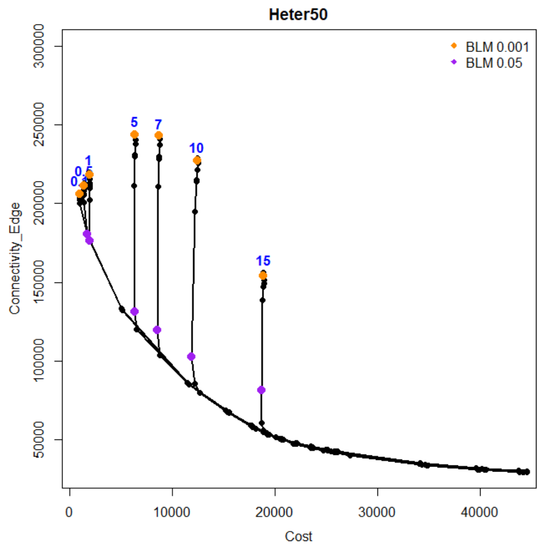
Ref. Vallet, A., Locatelli, B., Levrel, H., Pérez, C.B., Imbach, P., Carmona, N.E., Manlay, R., Oszwald, J., 2016. Dynamics of ecosystem services during forest transitions in Reventazón, Costa Rica. PLoS One 11, 1–18. https://doi.org/10.1371/journal.pone.0158615

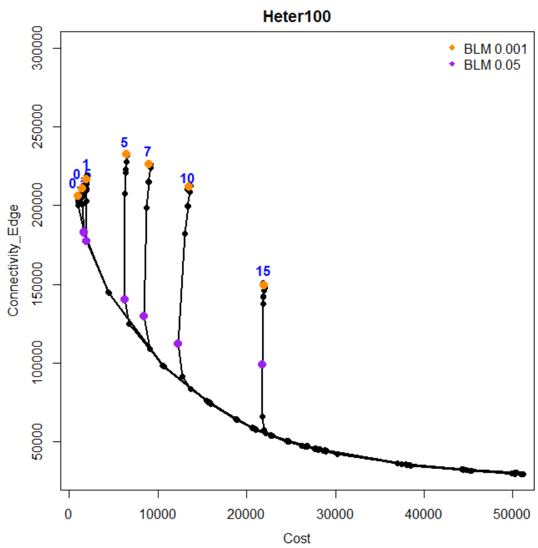
Appendix S3 CSM calibration curves





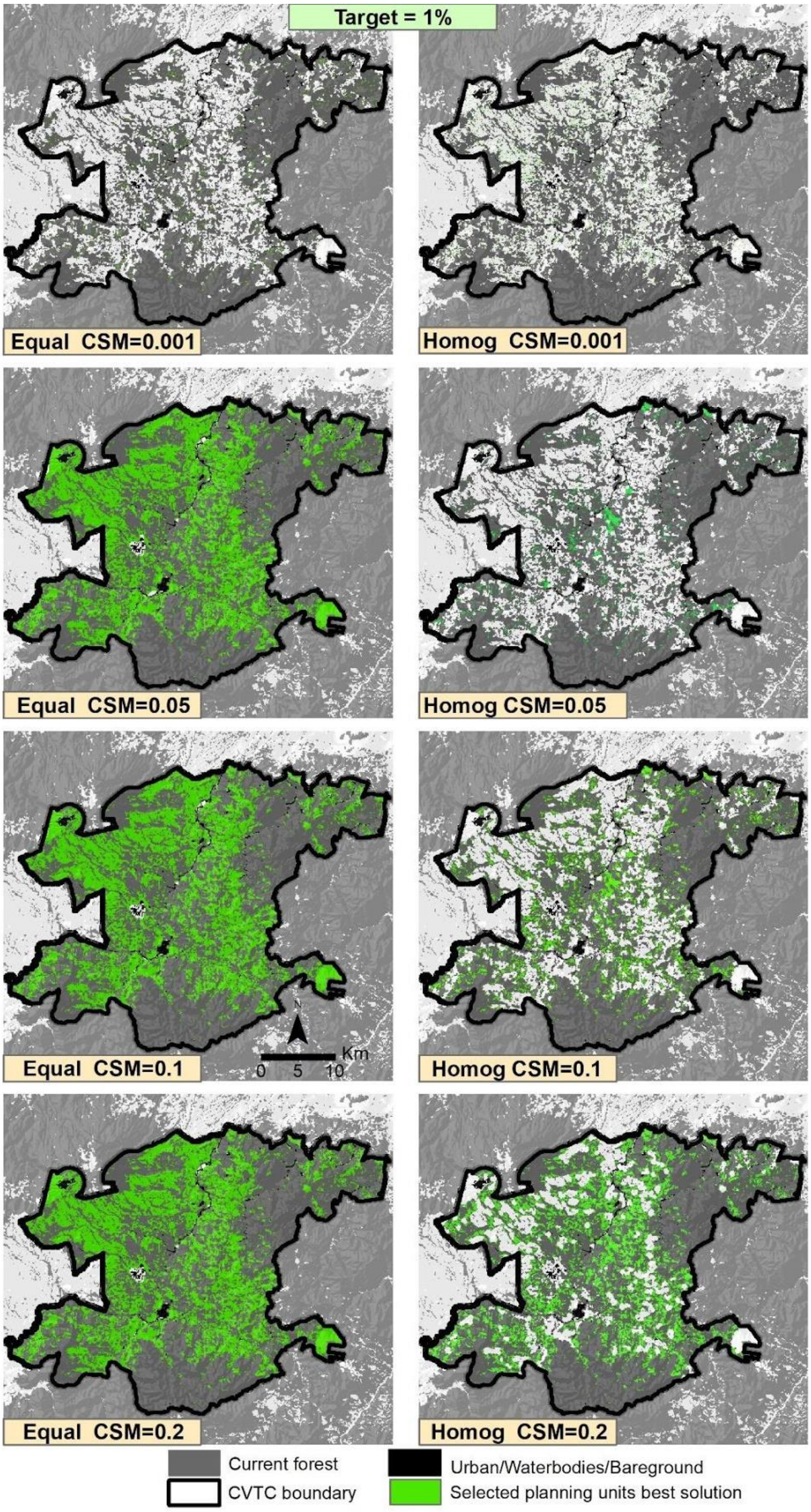






CSM calibration curves considering different cost layers at targets 0.1, 0.5,1,5,10, and 20. The orange points in each graph represent the intersection between Cost and Connectivity for a CSM=0.001 (value selected for running the **Equal scenario** prioritization) and the purple ones, the intersection at CSM=0.05. (value selected for running the **Homog**, **Heter30**, **Heter50** and **Heter100** scenarios). The selection of CSM values over the calibration curves allowed us to balance the achievement of ecosystem services targets and the connectivity objectives (see maps below).

Best solutions for Equal and Homog scenario when target=1% and at different CSM values



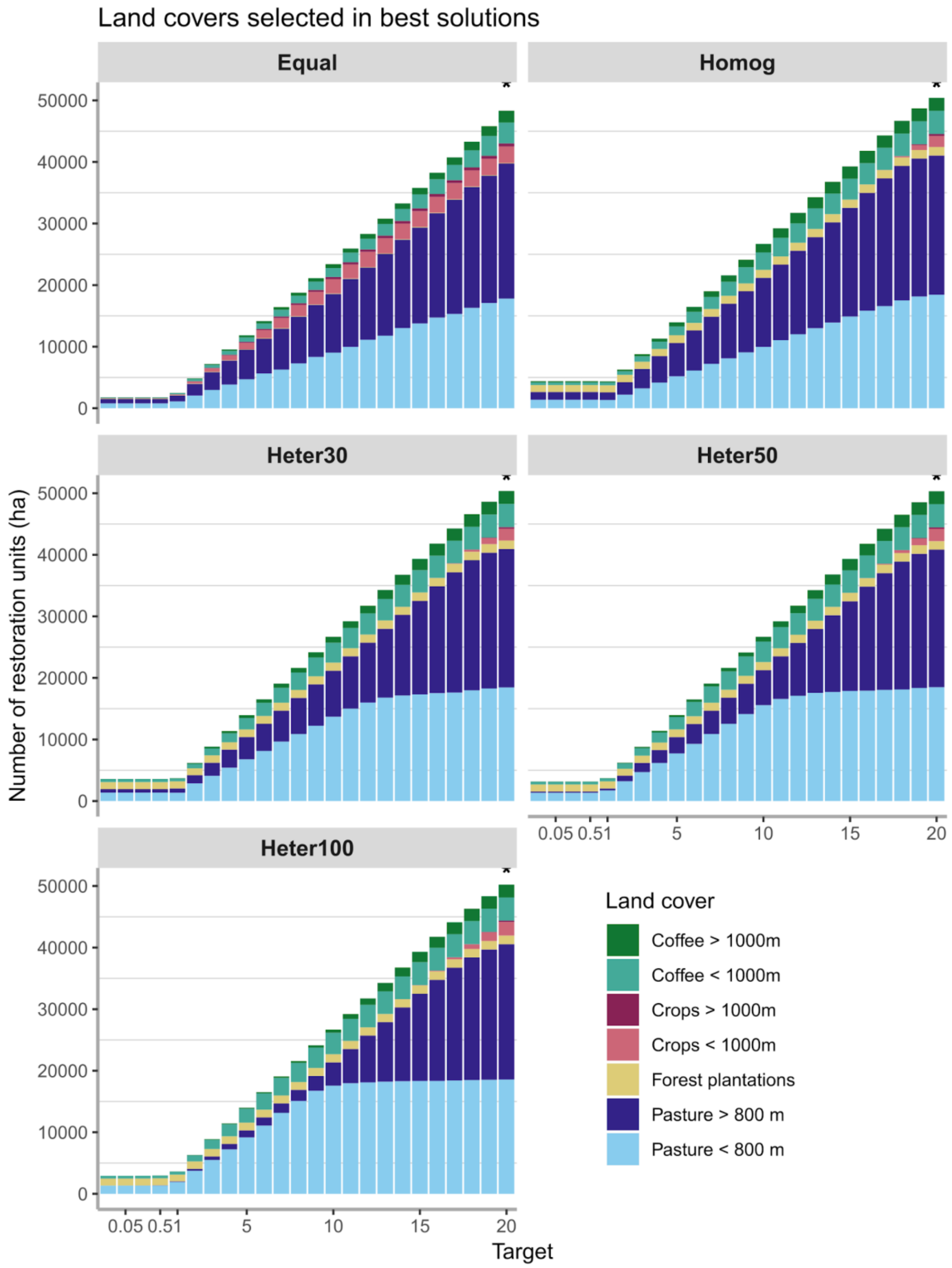
Appendix S4. Percentage of target achievement across tested scenarios and targets (median, minimum, and maximum values across the 95 ES features). A value of 100% indicates the full target achievement. Note that for small targets (those < 1) there is an extremely large overall target achievement that results from connectivity constraints. This reflects the fact that the selection of restoration units does not only seek to achieve targets across the 95 ES features but also to increase forest connectivity (i.e. many restoration units are selected in best solution because connectivity constraints overinflating the overall target achievement for each of the 95 ES features).

		Target achievement %		
Scenario	Target	Median	Max.	Min.
Equal Opportunity Cost (**Equal**)	0.01	36934.2	174564.2	6988.8
	0.05	7386.8	34912.7	1397.8
	0.1	3693.4	17456.4	698.9
	0.5	738.7	3491.3	139.8
	1	518.2	2250.0	100
	2	503.2	1791.4	100
	3	495.7	1499.6	100
	4	485.8	1300.4	100
	5	484.0	1177.4	100
	6	480.5	1081.9	100
	7	478.6	999.9	100
	8	476.8	914.2	100
	9	474.3	877.1	100
	10	476.2	799.1	100
	11	474.1	752.0	100
	12	475.0	720.8	100
	13	475.6	671.7	100
	14	474.7	635.7	100
	15	479.2	603.4	100
	16	476.7	566.4	100
	17	479.0	548.6	100
	18	479.4	515.3	100
	19	480.4	499.2	100
	20	479.1	484.9	100
Homogeneous Opportunity cost (**Homog**)	0.01	67895.3	249221.0	12814.9
	0.05	13579.1	49844.1	2563.0
	0.1	6789.5	24922.0	1281.5
	0.5	1357.9	4984.4	256.3
	1	677.5	2522.9	128.4
	2	527.8	1748.9	100
	3	523.2	1469.8	100
	4	521.3	1325.4	100
	5	517.3	1167.4	100

	6	516.6	1056.6	100
	7	515.5	938.6	100
	8	513.5	887.3	100
	9	513.9	824.6	100
	10	513.8	750.7	100
	11	511.7	718.6	100
	12	510.2	676.3	100
	13	513.0	642.0	100
	14	510.3	597.6	100
	15	511.3	561.7	100
	16	509.4	543.1	100
	17	504.9	532.1	100
	18	503.3	528.3	100
	19	496.0	511.2	100
	20	486.8	493.5	100
Heterogeneous Opportunity Cost 30% (**Heter30**)	0.01	51256.5	247207.0	9171.3
	0.05	10251.3	49441.2	1834.3
	0.1	5125.6	24720.6	917.1
	0.5	1025.1	4944.1	183.4
	1	549.9	2500.2	100
	2	547.6	2105.7	100
	3	545.9	1733.4	100
	4	544.6	1493.7	100
	5	545.2	1336.7	100
	6	545.6	1194.7	100
	7	542.5	1084.4	100
	8	538.5	984.5	100
	9	538.1	915.8	100
	10	536.7	832.1	100
	11	534.5	781.4	100
	12	533.0	725.0	100
	13	528.6	673.4	100
	14	521.3	636.0	100
	15	517.0	601.7	100
	16	511.8	567.1	100
	17	506.3	543.4	100
	18	502.6	524.2	100
	19	494.8	506.5	100
	20	486.2	490.7	100
Heterogeneous Opportunity Cost 50% (**Heter50**)	0.01	46103.9	250934.2	5932.8
	0.05	9220.8	50186.7	1186.6
	0.1	4610.4	25093.3	593.3
	0.5	922.1	5018.7	118.7
	1	575.6	3044.6	100
	2	564.8	2241.6	100

	3	560.9	1823.3	100
	4	557.0	1553.3	100
	5	554.0	1389.1	100
	6	552.1	1248.6	100
	7	551.3	1122.6	100
	8	552.4	1024.6	100
	9	549.6	936.6	100
	10	543.1	856.9	100
	11	539.0	793.6	100
	12	533.5	740.5	100
	13	528.8	700.3	100
	14	522.8	652.8	100
	15	520.0	613.3	100
	16	512.2	578.4	100
	17	507.2	547.7	100
	18	500.9	526.4	100
	19	493.5	507.1	100
	20	485.7	490.8	100
Hetrerogeneous Opportunity Costs 100% (**Heter100**)	0.01	40799.4	247030.0	245.2
	0.05	8159.9	49405.8	108.1
	0.1	4084.4	24702.9	101.1
	0.5	824.3	4940.6	100
	1	577.3	3269.7	100
	2	571.0	2397.1	100
	3	569.7	1983.2	100
	4	569.5	1702.7	100
	5	562.0	1501.0	100
	6	560.6	1319.4	100
	7	561.8	1179.6	100
	8	559.4	1063.5	100
	9	556.6	976.3	100
	10	551.0	893.7	100
	11	544.1	828.4	100
	12	537.0	767.1	100
	13	530.8	711.8	100
	14	524.0	663.7	100
	15	519.2	622.3	100
	16	512.8	586.2	100
	17	506.4	554.9	100
	18	499.2	531.0	100
	19	493.1	511.7	100
	20	485.6	494.1	100

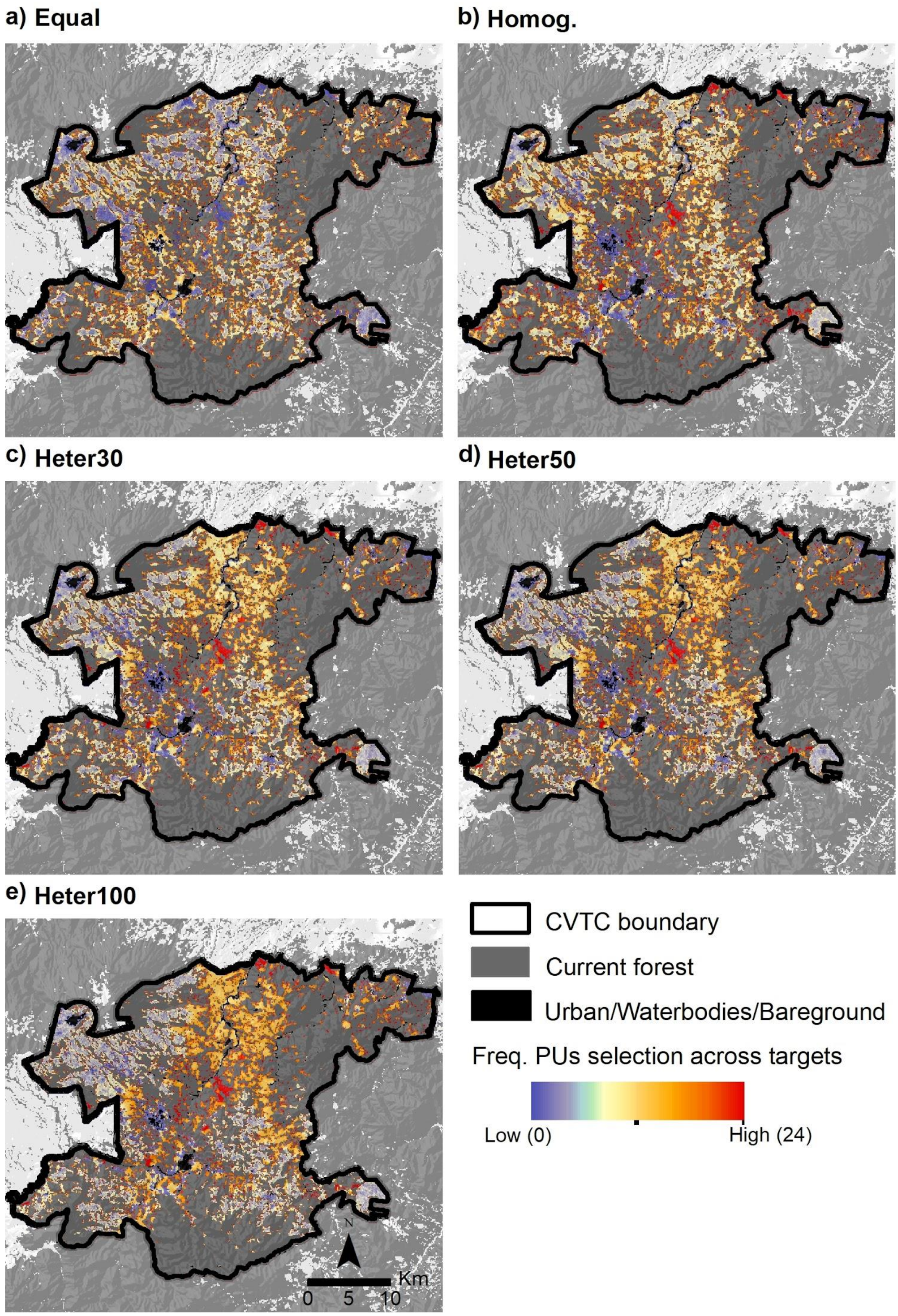
Appendix S5. Number of planning units selected for forest restoration under each combination of scenario (**Equal, Homog, Heter30, Heter50, Heter100**) and target. Colors within each bar reflect the proportion of each land use (coffee plantations, crops, pastures, and forest plantations) selected within the set of planning units in each of the Marxan's best solutions. The asterisk on top of the bar of the target 20 marks the total number of planning units available for restoration across the biological corridor.



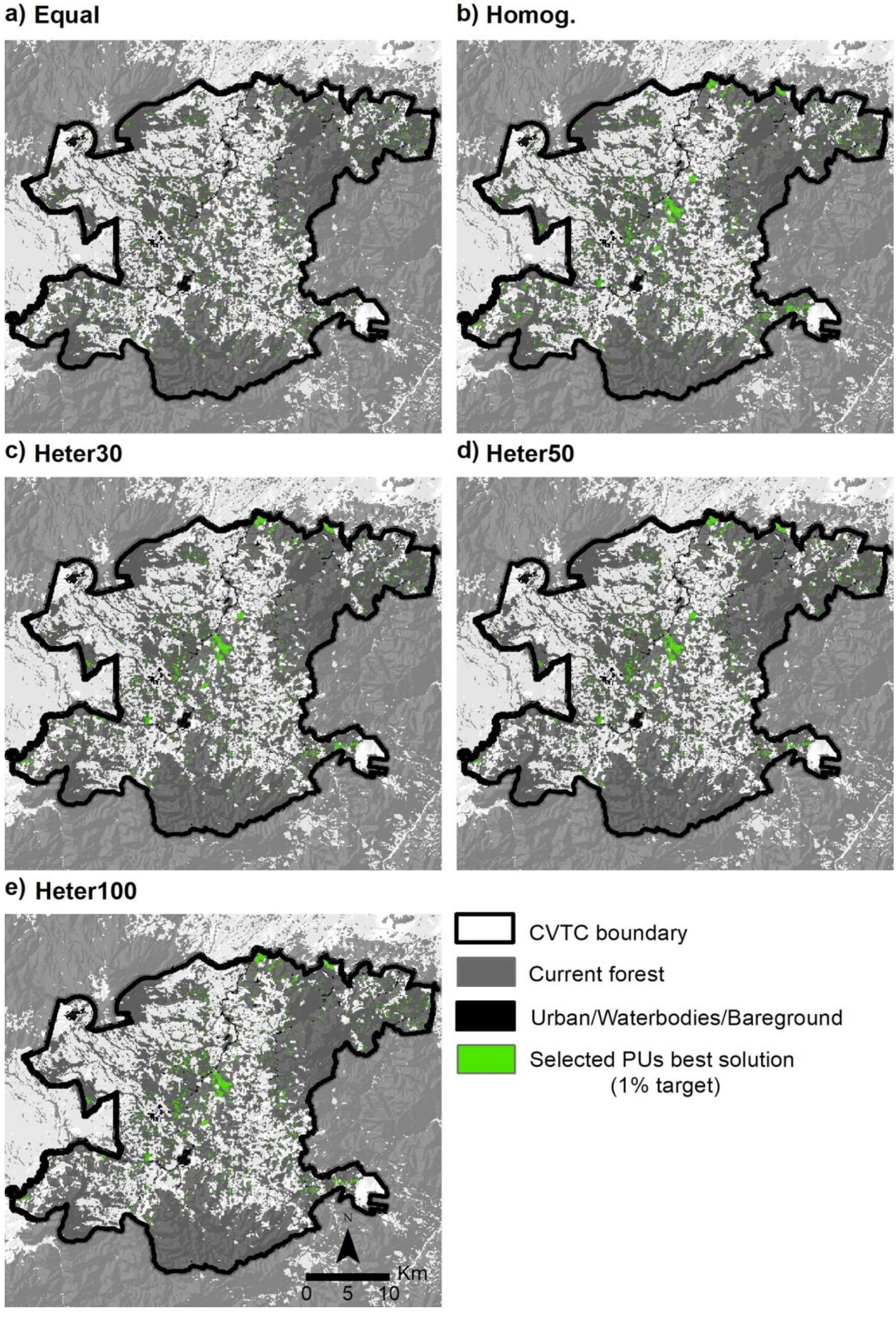
Appendix S6. Percentage of each land use (pasturelands, croplands, coffee and forest plantations), in relation to what is available across the biological corridor, selected in Marxan best solutions across different scenarios and targets. Note that forest plantations are selected in solutions for their contribution to increasing forest connectivity since they do not contribute to ecosystem service (ESS) provision.

Scenario	Target	PUs%	Pasture > 800m	Pasture < 800m	Crops > 1000m	Crops < 1000m	Coffee > 1000m	Coffee <1000m	Forest Plantation
Equal opportunity cost	0.05	3.4	3.0	4.3	2.7	2.6	1.8	2.9	4.2
	0.5	3.4	3.0	4.3	2.7	2.6	1.8	2.9	4.2
(**Equal**)	1	4.8	4.1	6.0	3.7	4.7	2.4	4.4	4.4
	5	22.8	21.1	25.3	31.1	38.4	15.9	19.2	5.7
	10	45.2	42.0	48.5	70.7	85.1	30.4	38.7	5.8
	15	69.0	68.5	74.1	91.0	94.0	49.6	60.1	7.3
	20	93.2	96.6	95.7	99.8	98.5	91.3	89.8	6.5
Homog. Oppor.	0.05	8.5	5.5	7.4	0.0	0.0	8.9	11.7	79.7
Cost	0.5	8.5	5.5	7.4	0.0	0.0	8.9	11.7	79.7
(**Homog**)	1	8.4	5.4	7.2	0.0	0.0	8.8	11.8	81.2
	5	26.9	23.7	28.0	0.0	0.0	31.4	37.8	88.9
	10	51.5	49.3	53.6	0.0	0.0	65.4	74.6	92.5
	15	75.8	77.7	80.1	0.0	0.0	94.8	89.6	94.2
	20	97.2	99.4	99.2	66.2	65.6	99.2	99.7	98.0
Heter. Opport	0.05	6.9	2.5	7.4	0.0	0.0	3.0	11.7	80.8
Cost 30%	0.5	6.9	2.5	7.4	0.0	0.0	3.0	11.7	80.8
(**Heter30**)	1	7.2	3.0	7.3	0.0	0.0	3.3	11.5	81.8
	5	26.9	15.9	36.5	0.0	0.0	21.8	49.0	86.9
	10	51.5	32.8	73.7	0.0	0.0	46.0	85.5	92.6
	15	75.8	66.7	93.2	0.0	0.1	85.8	95.9	97.0
	20	97.1	98.9	99.2	54.7	70.4	99.3	99.5	98.4
Herorg. Opport.	0.05	6.1	0.9	7.3	0.0	0.0	2.0	11.4	80.8
Cost 50%	0.5	6.1	0.9	7.3	0.0	0.0	2.0	11.4	80.8
(**Heter50**)	1	7.2	1.4	9.3	0.0	0.0	2.4	12.1	81.7
	5	26.9	11.7	41.6	0.0	0.0	15.2	52.9	88.0
	10	51.5	25.0	83.8	0.0	0.0	36.9	88.0	93.0
	15	75.8	64.1	96.2	0.0	0.4	87.3	96.3	96.4
	20	97.0	98.3	99.4	48.2	73.7	98.6	99.9	98.0
Hererog. Opport.	0.05	5.6	0.0	7.2	0.0	0.0	0.6	11.5	79.6
Cost 100%	0.5	5.7	0.2	7.3	0.0	0.0	1.0	11.5	79.6
(**Heter100**)	1	7.0	0.4	10.4	0.0	0.0	1.3	12.9	77.0
	5	27.0	4.9	49.3	0.0	0.0	8.1	59.6	88.9
	10	51.4	16.7	94.5	0.0	0.0	23.7	92.2	93.0
	15	75.8	62.2	98.6	0.0	1.3	79.3	98.5	97.5
	20	96.8	96.7	99.8	39.1	81.6	98.0	99.9	98.5

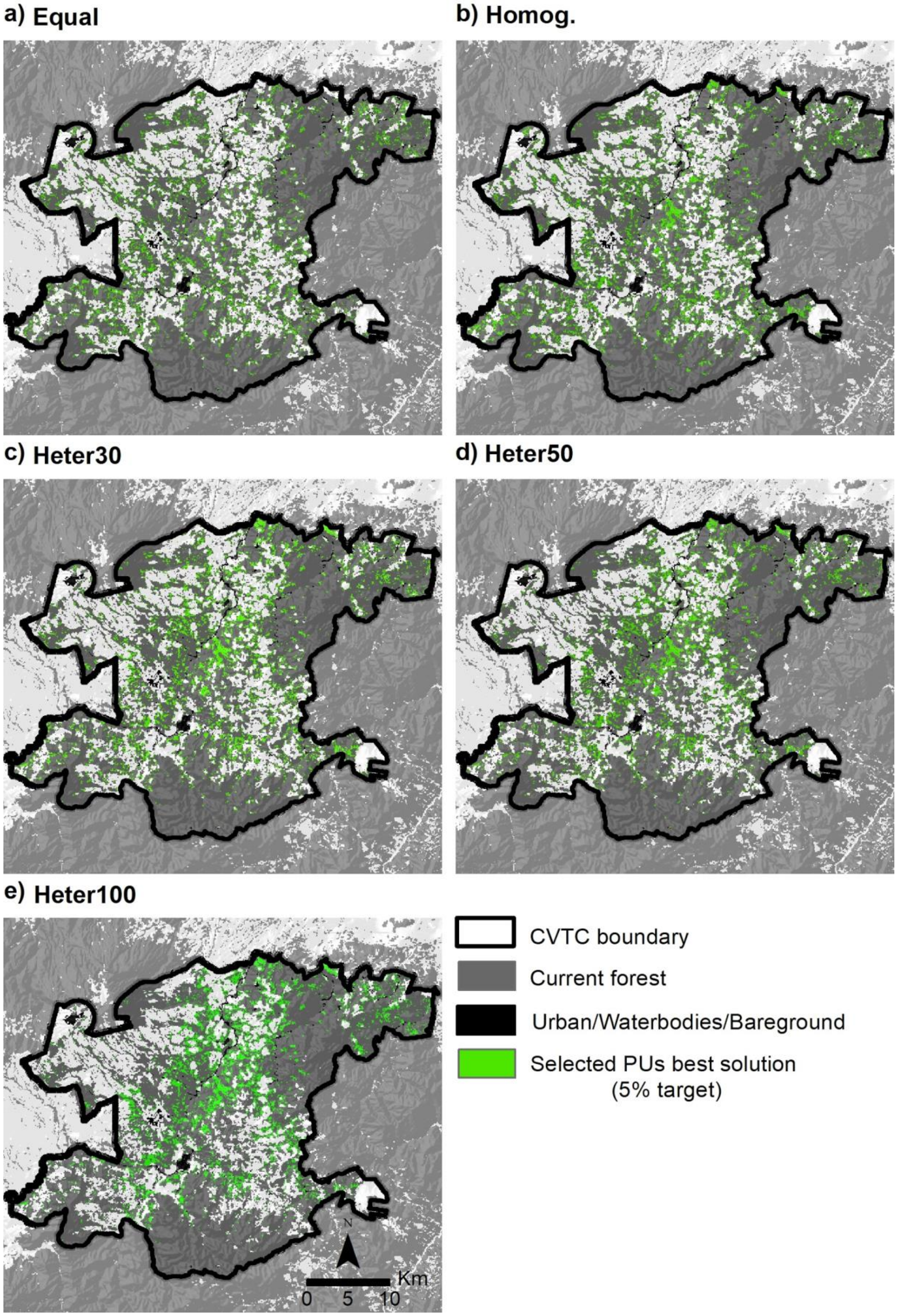
Appendix S7. Frequency of selection of planning units across all tested targets (24) in each of the tested scenarios **a)** *Equal Opportunity Cost* (**Equal**) **b)** Homogeneous Opportunity cost (**Homog**), and Heterogeneous Opportunity Costs **c) Heter30**, **d) Heter50** and **e) Heter 100**.



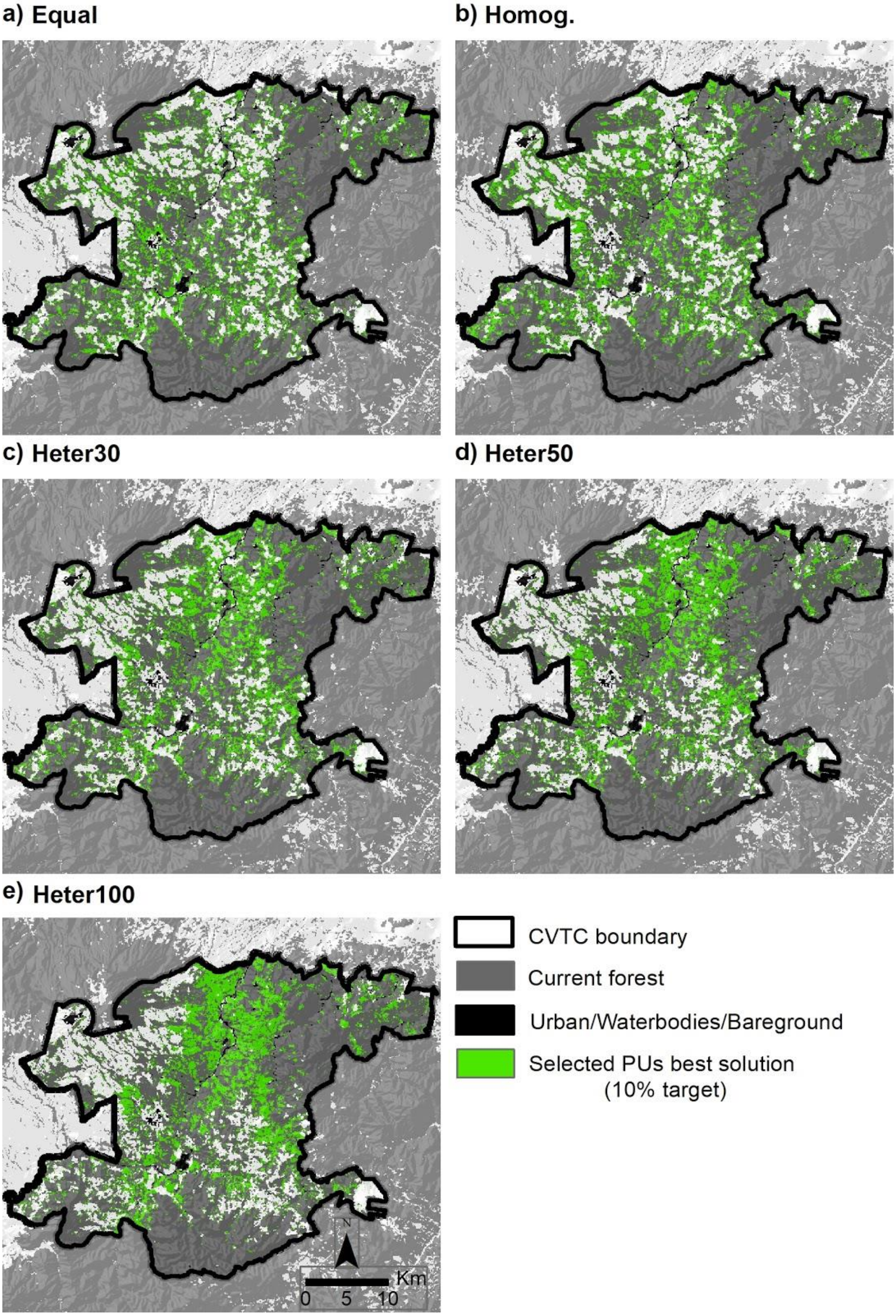
Appendix S8. Marxan best solutions across scenarios for a target of **1% increase** in ES provision.



Marxan best solutions across scenarios for a target of **5% increase** in ES provision.



Marxan best solutions across scenarios for a target of **10% increase** in ES provision.



Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: