Contents lists available at [ScienceDirect](www.sciencedirect.com/science/journal/03014797)





journal homepage: [www.elsevier.com/locate/jenvman](https://www.elsevier.com/locate/jenvman) 

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

Alejandra Morán-Ordóñez<sup>a,b,\*</sup>, Virgilio Hermoso <sup>b,d</sup>, Alejandra Martínez-Salinas <sup>c</sup>

<sup>a</sup> *Ecological and Forestry Applications Research Centre (CREAF), Edifici C Campus de Bellaterra, 08193, Cerdanyola del Valles, Spain* 

<sup>b</sup> Consorci Centre de Ciència i Tecnologia Forestal de Catalunya (CTFC), Ctra. St. Llorenç de Morunys, km. 2, 25280, Solsona, Spain

<sup>c</sup> CATIE – Centro Agronómico Tropical de Investigación y Enseñanza, 30501, Turrialba, Cartago, Costa Rica

<sup>d</sup> *Departamento de Biología Vegetal y Ecología, Facultad de Biología, 41012, Universidad de Sevilla, Sevilla, Spain* 

#### ARTICLE INFO

*Keywords:*  Nature-based solutions Neotropical birds Spatial conservation planning tools Species distribution models Secondary forest Tropical forests

## 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 the UN 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 restoration areas, 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. 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.

#### **1. Introduction**

Forest conservation and restoration at the global scale is key to recovering ecosystems health, and achieving Aichi Biodiversity Targets and the UN Sustainable Development Goals ([Chazdon, 2019](#page-6-0); [Griscom](#page-7-0)  [et al., 2017](#page-7-0)). 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;](#page-6-0) [Davidson et al., 2012; Lovejoy and Nobre, 2019](#page-7-0)).

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;](#page-6-0) [Fisher et al., 2019;](#page-7-0) [Zhang et al., 2019](#page-7-0)). 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

<https://doi.org/10.1016/j.jenvman.2022.114717>

Available online 23 February 2022 0301-4797/© 2022 Elsevier Ltd. All rights reserved. Received 14 September 2021; Received in revised form 9 February 2022; Accepted 9 February 2022

<sup>\*</sup> Corresponding author. Ecological and Forestry Applications Research Centre (CREAF), Edifici C Campus de Bellaterra, 08193, Cerdanyola del Vall´es, Spain. E-mail address: [a.moran@creaf.uab.cat](mailto:a.moran@creaf.uab.cat) (A. Morán-Ordóñez).

<span id="page-1-0"></span>reduction (e.g., landslides, floods) [\(Brandon, 2014\)](#page-6-0).

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\)](#page-7-0). 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;](#page-6-0) [Chazdon et al., 2020](#page-7-0)), 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 other approaches based on actively increasing forest extent using, for example, monoculture plantations ([Seddon et al., 2019;](#page-7-0) [Zhang et al., 2021](#page-7-0)). 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](#page-6-0); [Holl, 2017](#page-7-0)).

Integrating spatially-explicit planning tools and forest conservation policies and incentives can prove key to planning landscape-scale forest restoration across areas where conflicts between ecosystem recovery and socioeconomic development might arise [\(Chazdon et al., 2020](#page-7-0); [Strassburg et al., 2019\)](#page-7-0). 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). 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. Biological corridors are conservation tools designed to promote biodiversity conservation and increase forest connectivity, while pursuing sustainable development and human well-being ([Powlen and Jones, 2019](#page-7-0)). 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 maximizing spatial connectivity with already existing forested areas and minimizing the impact on existing socio-economic activities. 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.

## **2. Methods**

## *2.1. 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 established in 2003 with the main goal of restoring and/or increasing the functional connectivity between the Volcanica Central and the Talamanca Mountain ranges, (Fig. 1). The corridor focuses at the local scale on increasing connectivity between nearby protected areas, and at a broader scale, on increasing connectivity of the forested areas



**Fig. 1.** Study area. The map shows the dominant land cover types in the Volcanica Central Talamanca Biological Corridor (VCTBC; source: [Canet-Desanti, 2016](#page-6-0)). The inset map on the bottom left shows the location of the biological corridor in the context of the network of protected areas (dark gray) in Costa Rica and across Central America.

<span id="page-2-0"></span>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, followed by pastures as the second dominant land use (30%) and other agricultural uses (10%), such as coffee plantations (4%) and annual crops (2%). Beyond 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](#page-6-0)).

#### *2.2. 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](#page-7-0); [Morrison and Lindell, 2011\)](#page-7-0), providing with effective means of forest restoration in human-disturbed landscapes ([Crouzeilles et al., 2017\)](#page-7-0); 2) Ecotourism linked to birdwatching (cultural service): Costa Rica is one of the top destinations for birdwatchers in Latin America [\(Echeverri et al., 2019\)](#page-7-0), contributing to the development of ecotourism businesses and the sustainable development of local communities [\(Sekercioglu, 2002](#page-7-0)); and 3) Carbon sequestration (regulation service): low-cost natural regeneration or assisted forest regeneration of tropical forest has a large potential for contributing to climate change mitigation via carbon sequestration and storage ([Chazdon et al.,](#page-6-0)  [2016\)](#page-6-0), making forest restoration one of the main axes of the recently launched Costa Rican National Decarbonization program to 2050 [\(Costa](#page-7-0)  [Rica Government, 2019](#page-7-0)).

To map the seed dispersal and the potential ecotourism services across the corridor, we developed species distribution models using Maxent [\(Phillips et al., 2006](#page-7-0); [Phillips and Dudík, 2008](#page-7-0)) for 62 frugivorous bird species with known presence in the area, also culturally valued by birdwatchers and locals because of multiple reasons ([Echeverri et al.,](#page-7-0)  [2019\)](#page-7-0) such as the Resplendent Quetzal *(Pharomachrus mocinno*) or the Collared Aracari (*Pteroglossus torquatus*). Current predictions of habitat suitability for selected bird species were used as a surrogate 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 corridor assuming all current non-forest areas were restored to forest was used as a surrogate 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](#page-7-0)) (Appendix S1). We used the distribution of each species as an individual surrogate for the ESS. 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](#page-6-0); [Mouillot et al., 2013](#page-7-0)). 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](#page-7-0)). Using the VCTBC official land cover map as a reference [\(Canet-Desanti, 2016](#page-6-0)), the model estimated the potential change in carbon sequestration per hectare (ha) if all current non-forested areas in the 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. \(2016\)](#page-7-0). We only considered coffee plantations, annual crops and pastures as land covers with potential to be restored to forest, totaling 51852 ha across the corridor; each ha represented an individual restoration unit and corresponded to the scale at which the three ESS were mapped. These land covers represent the only ones that could potentially benefit from economic incentives associated to climate mitigation targets – i.e. Payments for

#### Environmental Services (Sánchez-Azofeifa et al., 2007).

The spatial predictions of current and future habitat suitability of the 47 frugivorous birds (surrogates 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.

#### *2.3. Spatial prioritization of forest restoration*

We used the spatial prioritization tool Marxan [\(Ball et al., 2009](#page-6-0)) to identify priority areas for forest restoration across the corridor to maximize the provision of the three ESS (i.e., seed dispersal, ecotourism and carbon storage) (objectives 1,2,3) while increasing spatial forest connectivity (objective 4). Marxan uses an optimization algorithm that seeks to minimize an Objective Function (Eq. (1)) across *I* restoration units and *J* ESS features:

$$
OF = \sum_{i}^{I} Cost_i + \sum_{j}^{J} SPF^*Feature\ Penalty_j
$$
  
+  $CSM \sum_{i}^{I} Connectivity\ Penalty_i$  (1)

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 the current land uses into forest) (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 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. \(2016\)](#page-7-0) (Appendix S2); 3) a *Heterogeneous opportunity cost* scenario (**Heter**), where the opportunity cost of each restoration unit for each land use varied across the corridor to account for differences in productivity across environmental gradients. In this case, the opportunity cost varied 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. Thus, in this study, we assumed the main constraint on the achievement of multi-objective forest restoration to be the land opportunity costs (i.e., the higher the revenues of a given current land use the lower the willingness of the owners to lose that land in favor of forest restoration). The use of these scenarios sought to evaluate how this constraint could influence the optimal spatial design of landscape-scale forest restoration plans across the corridor.

We ran a sensitivity analysis 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 and 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

*Journal of Environmental Management 310 (2022) 114717*

<span id="page-3-0"></span>set for each ESS feature (second element in Eq. [\(1\)](#page-2-0)). 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. [\(1\)](#page-2-0).

Finally, the Connectivity Penalty in Eq. [\(1\)](#page-2-0) 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 number of restoration units being selected (and therefore cost). For this reason, it is necessary to calibrate the CSM value. We calibrated the CSM (Eq.  $(1)$ ) for each scenario and target following [Andron et al. \(2010\).](#page-6-0) However, and given the large amount of forest already existing in the 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 used 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



**Fig. 2.** Number of units 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 units available for restoration across the biological corridor. See Appendix S5 for results of the Heter30 and Heter50 (not shown because of their similarity with the Heter100 solution). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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\)](#page-7-0). We also measured the selection frequency of restoration units in best solutions across all targets for each scenario.

#### **3. Results**

Restoration targets were achieved for all 95 ESS across all scenarios and tested targets (Appendix S4). For a given target, the number of ha 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](#page-3-0), Appendix S5). The selection frequency of different land uses across Marxan's best solutions also markedly differed between scenarios ([Fig. 2\)](#page-3-0). 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 to 20). On the contrary, scenarios considering opportunity costs prioritized the selection of restoration units in lowlands, where the total opportunity cost was lower (e.g., selection of restoration units over pastures at *<* 800 m were prioritized over selection of pastures *>*800m; [Fig. 2](#page-3-0); 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 land opportunity 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).

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.

Marxan best solutions across all scenarios markedly increase forest structural connectivity compared to current connectivity across all targets (Appendix S7) but especially compared to reforestation scenarios that sought to achieve ESS targets without accounting for connectivity  $(CSM = 0;$  Appendix S7). 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. 4](#page-5-0); Appendix S8, S9). 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 corridor, connecting already existing forest



**Fig. 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).

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](#page-1-0)).

#### **4. Discussion**

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.,](#page-7-0)  [2016;](#page-7-0) [Strassburg et al., 2019\)](#page-7-0); 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. 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\)](#page-7-0). 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 reality, having the largest consequences in terms of loss of cultural heritage among all tested scenarios (i.e. loss of cultural services and relational values; [Chapman et al., 2020](#page-6-0); [Daniel et al., 2012\)](#page-7-0). On the other hand, our study demonstrated that accounting for opportunity costs (scenarios **Homog**, **Heter30**, **Heter50** and **Heter100)** does not translate into loss of connectivity or ESS 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 main objectives pursued by this conservation tool.

## <span id="page-5-0"></span>a) Equal



b) Heter100



Frequency of PUs selection across targets (panels a, b)

 $24$ **CVTC** boundary **Current forest** Urban/Waterbodies/Bareground

c) Difference selection frequency b) - a)



**Both** 

*(caption on next column)* 

**Fig. 4.** 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 S8 for comparative results for the Homog., Heter30 and Heter50 scenarios. See Appendix S9 for best solutions for targets 1, 5 and 10. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Accounting for opportunity costs when designing landscape-scale forest restoration plans is critical to design realistic interventions. The estimates of opportunity costs that we used were based only on the current revenues farmers get from the goods they produce, without considering any potential changes in market demands and product prices or accounting for other intangible benefits. Given the impacts that opportunity costs had on the selection of priority areas for restoration, the selection of adequate estimates of these values deserves special attention. For example, Marxan best solutions of the **Homog**, **Heter30**, **Heter50** and **Heter100** scenarios selected more frequently coffee plantations over croplands for restoration [\(Fig. 2\)](#page-3-0), because currently, the revenue generated by coffee plantations per ha at the corridor is 25 times lower than from croplands (Appendix S2; [Vallet et al., 2016](#page-7-0)). 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 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 support greater levels of biodiversity compared to other crops and other coffee management systems (e.g., coffee monocultures). Likewise, coffee agroforestry also promote 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](#page-6-0); [De Leijster et al., 2021](#page-7-0)). 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.

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](#page-6-0); [Holl, 2017](#page-7-0)) as well as finding adequate financial incentives to landowners ([Brancalion et al., 2012](#page-6-0)). 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](#page-7-0)). This scheme, pays private landowners who own forests or who promote forest recovery in their land, in recognition of the ESS provided ([Liagre](#page-7-0)  [et al., 2021;](#page-7-0) 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\)](#page-7-0) 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 downstream

<span id="page-6-0"></span>hydroelectrical plants (under the "water resource protection" PES scheme; [Estrada-Carmona and DeClerck, 2012](#page-7-0)).

Passive restoration following natural regeneration of secondary forest could represent an interesting cost-effective landscape-scale forest restoration measure to apply across the corridor [\(Holl and Aide, 2011](#page-7-0)). In this regard, all Marxan solutions presented here suggest areas where this restoration option could be facilitated to a great extent by the presence of seed dispersers (i.e., frugivorous birds). However, in Costa Rica, forest expansion due to the regrowth of secondary forests has been hampered by several factors including the existence of a strong forest law that bans land use change over forested land, the lack of knowledge by landowners of financial mechanisms to support the management of secondary forests (option only contemplated and fully developed in Costa Rica legislation in 2016 Decreto 399952 - MINAE) as well as the lengthy and complex bureaucracy and administration processes to access them (e.g., an officially approved forest management plan is mandatory to access incentives for forest management; [Reyes et al.,](#page-7-0)  [2018\)](#page-7-0). 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](http://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 ([Figs. 2 and 4](#page-3-0); Appendix S5, S8). 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\)](#page-7-0). 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](#page-7-0); [Zhang et al., 2021](#page-7-0)). 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 [\(Estrada-Carmona and DeClerck, 2012](#page-7-0); [FONAFIFO et al., 2012](#page-7-0); [GGGI, 2016\)](#page-7-0) and thus, a multi-objective spatial prioritization protocol as the one presented here can prove key to identify areas where to maximize such investments.

## **5. Conclusions**

We have demonstrated how to identify priority areas for forest restoration for multiple objectives (promote ESS provision, increase forest connectivity and minimize impacts on local livelihoods), by using a freely available spatial planning tool. When planning blindly to opportunity costs, our results suggest that landscape-scale forest restoration plans could lead to potential socio-economic impacts and management conflicts. 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, where multiple-objectives are pursued and where potential conflicts between these could arise, being a useful tool to foster optimal restoration interventions.

#### **Credit author statement**

Alejandra Morán-Ordóñez: Conceptualization, Methodology, Formal analysis, Writing – original draft preparation; **Virgilio Hermoso**, Methodology, Writing – original draft preparation; **Alejandra Martínez Salinas:** Conceptualization, Writing – original draft preparation.

#### **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.

#### **Acknowledgments**

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. V.H. was also funded by the Junta de Andalucía through an Emergia contact (EMERGIA20\_00135) 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).

## **Appendix A. Supplementary data**

Supplementary data to this article can be found online at [https://doi.](https://doi.org/10.1016/j.jenvman.2022.114717)  [org/10.1016/j.jenvman.2022.114717](https://doi.org/10.1016/j.jenvman.2022.114717).

#### **References**

- Alexander, S., Aronson, J., Whaley, O., Lamb, D., 2016. The relationship between ecological restoration and the ecosystem services concept. Ecol. Soc. 21 [https://doi.](https://doi.org/10.5751/ES-08288-210134)  [org/10.5751/ES-08288-210134](https://doi.org/10.5751/ES-08288-210134).
- Alroy, J., 2017. Effects of habitat disturbance on tropical forest biodiversity. Proc. Natl. Acad. Sci. U. S. A 114, 6056–6061. [https://doi.org/10.1073/pnas.1611855114.](https://doi.org/10.1073/pnas.1611855114) [Andron, J.A., Possingham, H.P., Klein, C.J., 2010. Marxan Good Practices Handbook,](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref3)
- [Version 2. Pacific Marine Analysis and Research Association. Canada, Victoria, BC](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref3).
- Ball, I.R., Possingham, H.P., Watts, M.E., 2009. Marxan and relatives: software for spatial conservation prioritization. In: Moilanen, A., Wilson, K.A., Possingham, H.P. (Eds.), Spatial Conservation Prioritisation: Quantitative Methods and Computational Tools. Oxford University Press, Oxford, pp. 185–195. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.cjca.2015.05.027) [cjca.2015.05.027](https://doi.org/10.1016/j.cjca.2015.05.027). Oxford University Press.
- Brancalion, P.H.S., Meli, P., Tymus, J.R.C., Lenti, F.E.B., M Benini, R., Silva, A.P.M., Isernhagen, I., Holl, K.D., 2019. What makes ecosystem restoration expensive? A systematic cost assessment of projects in Brazil. Biol. Conserv. 240, 108274. [https://](https://doi.org/10.1016/j.biocon.2019.108274)  [doi.org/10.1016/j.biocon.2019.108274](https://doi.org/10.1016/j.biocon.2019.108274).
- [Brancalion, P.H.S., Viani, R.A.G., Strassburg, B.B.N., Rodrigues, R.R., 2012. Finding the](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref6)  [money for tropical forest restoration. Unasylva 63, 41](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref6)–50.
- Brandon, K., 2014. "Ecosystem Services from Tropical Forests: Review of Current Science.". CGD Working Paper 380. Center for Global Development, Washington, DC. http://www.cgdev.org/publication/ecosystem-services-tropical-forests-review [urrentscience-working-paper-380](http://www.cgdev.org/publication/ecosystem-services-tropical-forests-review-currentscience-working-paper-380).
- Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F., Rey-Benayas, J.M., 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends Ecol. Evol. 26, 541–549. [https://doi.org/10.1016/j.tree.2011.06.011.](https://doi.org/10.1016/j.tree.2011.06.011)
- [Canet-Desanti, L., 2016. Plan Estrat](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref9)égico del Corredor Biológico Volcánica Central -[Talamanca \(2016-2021\) \(Turrialba, Costa Rica\).](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref9)
- Chain-Guadarrama, A., Martínez-Salinas, A., Aristizábal, N., Ricketts, T.H., 2019. Ecosystem services by birds and bees to coffee in a changing climate: a review of coffee berry borer control and pollination. Agric. Ecosyst. Environ. 280, 53–67. <https://doi.org/10.1016/j.agee.2019.04.011>.
- Chapman, M., Satterfield, T., Wittman, H., Chan, K.M.A., 2020. A payment by any other name: is Costa Rica's PES a payment for services or a support for stewards? World Dev. 129, 104900. [https://doi.org/10.1016/j.worlddev.2020.104900.](https://doi.org/10.1016/j.worlddev.2020.104900)
- Chazdon, R.L., 2019. Towards more effective integration of tropical forest restoration and conservation. Biotropica 51, 463–472. [https://doi.org/10.1111/btp.12678.](https://doi.org/10.1111/btp.12678)
- Chazdon, R.L., Brancalion, P.H.S., Lamb, D., Laestadius, L., Calmon, M., Kumar, C., 2017. A policy-driven knowledge agenda for global forest and landscape restoration. Conserv. Lett. 10, 125–132. <https://doi.org/10.1111/conl.12220>.
- Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., Zambrano, A.M.A., Aide, T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Craven, D., Almeida-Cortez, J.S., Cabral, G.A.L., De Jong, B., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernández-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Lohbeck, M., Martínez-Ramos, M., Massoca, P., Meave, J. A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-

#### <span id="page-7-0"></span>*A. Morán-Ordóñez et al.*

Gaona, S., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velazquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Uriarte, M., Van Breugel, M., Van Der Wal, H., Veloso, M.D.M., Vester, H., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Poorter, L., 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Sci. Adv. 2 https:// [doi.org/10.1126/sciadv.1501639.](https://doi.org/10.1126/sciadv.1501639)

Chazdon, R.L., Lindenmayer, D., Guariguata, M.R., Crouzeilles, R., Rey Benayas, J.M., Lazos Chavero, E., 2020. Fostering natural forest regeneration on former agricultural land through economic and policy interventions. Environ. Res. Lett. 15 [https://doi.](https://doi.org/10.1088/1748-9326/ab79e6)  [org/10.1088/1748-9326/ab79e6.](https://doi.org/10.1088/1748-9326/ab79e6)

Costa Rica Government, 2019. Costa Rica National Decarbonization Plan 2018-2050. Costa Rican Government (online; last access 14/02/2022). [https://unfccc.int/sites](https://unfccc.int/sites/default/files/resource/NationalDecarbonizationPlan.pdf) [/default/files/resource/NationalDecarbonizationPlan.pdf](https://unfccc.int/sites/default/files/resource/NationalDecarbonizationPlan.pdf).

- Crouzeilles, R., Ferreira, M.S., Chazdon, R.L., Lindenmayer, D.B., Sansevero, J.B.B., Monteiro, L., Iribarrem, A., Latawiec, A.E., Strassburg, B.B.N., 2017. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. Sci. Adv. 3, 1–8. <https://doi.org/10.1126/sciadv.1701345>.
- Daniel, T.C., Muhar, A., Arnberger, A., Aznar, O., Boyd, J.W., Chan, K.M.A., Costanza, R., Elmqvist, T., Flint, C.G., Gobster, P.H., Grêt-Regamey, A., Lave, R., Muhar, S., Penker, M., Ribe, R.G., Schauppenlehner, T., Sikor, T., Soloviy, I., Spierenburg, M., Taczanowska, K., Tam, J., Von Der Dunk, A., 2012. Contributions of cultural services to the ecosystem services agenda. Proc. Natl. Acad. Sci. U. S. A 109, 8812–8819. [https://doi.org/10.1073/pnas.1114773109.](https://doi.org/10.1073/pnas.1114773109)
- Davidson, E.A., De Araüjo, A.C., Artaxo, P., Balch, J.K., Brown, I.F., Mercedes, M.M., Coe, M.T., Defries, R.S., Keller, M., Longo, M., Munger, J.W., Schroeder, W., Soares-Filho, B.S., Souza, C.M., Wofsy, S.C., 2012. The Amazon basin in transition. Nature 481, 321–328. [https://doi.org/10.1038/nature10717.](https://doi.org/10.1038/nature10717)
- De Leijster, V., Santos, M.J., Wassen, M.W., Camargo García, J.C., Llorca Fernandez, I., Verkuil, L., Scheper, A., Steenhuis, M., Verweij, P.A., 2021. Ecosystem services trajectories in coffee agroforestry in Colombia over 40 years. Ecosyst. Serv. 48, 101246. [https://doi.org/10.1016/j.ecoser.2021.101246.](https://doi.org/10.1016/j.ecoser.2021.101246)
- Echeverri, A., Naidoo, R., Karp, D.S., Chan, K.M.A., Zhao, J., 2019. Iconic Manakins and Despicable Grackles: Comparing Bird-Related Cultural Ecosystem Services across Birdwatchers, Farmers, and Urbanites in 2 Northwestern Costa Rica. [https://doi.org/](https://doi.org/10.1101/548982)  [10.1101/548982.](https://doi.org/10.1101/548982)
- Estrada-Carmona, N., DeClerck, F., 2012. Payment for ecosystem services for energy, biodiversity conservation and poverty reduction in Costa Rica. In: Ingram, J.C., DeClerck, F., Rumbaitis del Rio, C. (Eds.), Integrating Ecology and Poverty Reduction: the Application of Ecology in Development Solutions. Springer, pp. 191–210. [https://doi.org/10.1007/978-1-4614-0186-5.](https://doi.org/10.1007/978-1-4614-0186-5)
- Fisher, B., Herrera, D., Adams, D., Fox, H.E., Gallagher, L., Gerkey, D., Gill, D., Golden, C. D., Hole, D., Johnson, K., Mulligan, M., Myers, S.S., Naidoo, R., Pfaff, A., Rasolofoson, R., Selig, E.R., Tickner, D., Treuer, T., Ricketts, T., 2019. Can nature deliver on the sustainable development goals? Lancet Planet. Health 3, e112–e113. [https://doi.org/10.1016/S2542-5196\(18\)30281-X](https://doi.org/10.1016/S2542-5196(18)30281-X).
- Fonafifo, Conafor, Ministry of Environment, 2012. Lessons Learned for REDD+ from PES and Conservation Incentive Programs: Examples from Costa Rica, Mexico and Ecuador. World Bank, Washinton, D.C. (online; last access 14/02/2022). [https](https://openknowledge.worldbank.org/handle/10986/27164) [://openknowledge.worldbank.org/handle/10986/27164](https://openknowledge.worldbank.org/handle/10986/27164)
- GGGI, 2016. Bridging the Policy and Investment Gap for Payment for Ecosystem Services: Learning from the Costa Rican Experience and Roads Ahead. The Global Green Growth Institute (online; last access 14/02/2022). [https://gggi.org/report/br](https://gggi.org/report/bridging-the-policy-and-investment-gap-for-payment-for-ecosystem-services-learning-from-the-costa-rican-experience-and-roads-ahead/)  [idging-the-policy-and-investment-gap-for-payment-for-ecosystem-services-learn](https://gggi.org/report/bridging-the-policy-and-investment-gap-for-payment-for-ecosystem-services-learning-from-the-costa-rican-experience-and-roads-ahead/) [ing-from-the-costa-rican-experience-and-roads-ahead/.](https://gggi.org/report/bridging-the-policy-and-investment-gap-for-payment-for-ecosystem-services-learning-from-the-costa-rican-experience-and-roads-ahead/)
- Gourevitch, J.D., Hawthorne, P.L., Keeler, B.L., Beatty, C.R., Greve, M., Verdone, M.A., 2016. Optimizing investments in national-scale forest landscape restoration in Uganda to maximize multiple benefits. Environ. Res. Lett. 11, 114027. [https://doi.](https://doi.org/10.1088/1748-9326/11/11/114027) [org/10.1088/1748-9326/11/11/114027](https://doi.org/10.1088/1748-9326/11/11/114027).
- Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., Schlesinger, W.H., Shoch, D., Siikamäki, J.V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R.T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M.R., Herrero, M., Kiesecker, J., Landis, E., Laestadius, L., Leavitt, S.M., Minnemeyer, S., Polasky, S., Potapov, P., Putz, F.E., Sanderman, J., Silvius, M., Wollenberg, E., Fargione, J., 2017. Natural climate solutions. Proc. Natl. Acad. Sci. U. S. A 114, 11645–11650. [https://doi.org/10.1073/pnas.1710465114.](https://doi.org/10.1073/pnas.1710465114)
- Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143, 29–36. [https://doi.org/](https://doi.org/10.1148/radiology.143.1.7063747)  [10.1148/radiology.143.1.7063747.](https://doi.org/10.1148/radiology.143.1.7063747)
- Harms, K.E., Wright, S.J., Calderón, O., Hernández, A., Herre, E.A., 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404, 493–495. [https://doi.org/10.1038/35006630.](https://doi.org/10.1038/35006630)
- Hermoso, V., Morán-Ordóñez, A., Lanzas, M., Brotons, L., 2020. Designing a network of green infrastructure for the EU. Landsc. Urban Plann. 196 [https://doi.org/10.1016/](https://doi.org/10.1016/j.landurbplan.2019.103732)  [j.landurbplan.2019.103732.](https://doi.org/10.1016/j.landurbplan.2019.103732)
- Holl, K.D., 2017. Restoring tropical forests from the bottom up. Science 355, 455–456. [https://doi.org/10.1126/science.aam5432,](https://doi.org/10.1126/science.aam5432) 80.
- Holl, K.D., Aide, T.M., 2011. When and where to actively restore ecosystems? For. Ecol. Manag. 261, 1558–1563. [https://doi.org/10.1016/j.foreco.2010.07.004.](https://doi.org/10.1016/j.foreco.2010.07.004)
- Liagre, L., Pettenella, D., Pra, A., Carazo Ortiz, F., Garcia Arguedas, A., Nguyen Chien, C., 2021. How can National Forest Funds catalyse the provision of ecosystem services? Lessons learned from Costa Rica, Vietnam, and Morocco. Ecosyst. Serv. 47, 101228. <https://doi.org/10.1016/j.ecoser.2020.101228>.

Lovejoy, T.E., Nobre, C., 2019. Amazon tipping point: last chance for action. Sci. Adv. 5, 4–6. https://doi.org/10.1126/sciadv.aba29

- Molina Murillo, S.A., Pérez Castillo, J.P., Herrera Ugalde, M.E., 2014. Assessment of environmental payments on indigenous territories: the case of Cabecar-Talamanca, Costa Rica. Ecosyst. Serv. 8, 35–43. [https://doi.org/10.1016/j.ecoser.2014.02.003.](https://doi.org/10.1016/j.ecoser.2014.02.003)
- Morrison, E.B., Lindell, C.A., 2011. Active or passive forest restoration? Assessing restoration alternatives with avian foraging behavior. Restor. Ecol. 19, 170–177. <https://doi.org/10.1111/j.1526-100X.2010.00725.x>.
- Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J., Thuiller, W., 2013. Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biol. 11 <https://doi.org/10.1371/journal.pbio.1001569>
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259. [https://doi.org/](https://doi.org/10.1016/j.ecolmodel.2005.03.026) [10.1016/j.ecolmodel.2005.03.026](https://doi.org/10.1016/j.ecolmodel.2005.03.026).
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175. [https://doi.](https://doi.org/10.1111/j.0906-7590.2008.5203.x)  [org/10.1111/j.0906-7590.2008.5203.x](https://doi.org/10.1111/j.0906-7590.2008.5203.x).
- Powlen, K.A., Jones, K.W., 2019. Identifying the determinants of and barriers to landowner participation in reforestation in Costa Rica. Land Use Pol. 84, 216–225. <https://doi.org/10.1016/j.landusepol.2019.02.021>.
- Pringle, R.M., 2017. Upgrading protected areas to conserve wild biodiversity. Nature 546, 91–99. [https://doi.org/10.1038/nature22902.](https://doi.org/10.1038/nature22902)
- [Reyes, V., Cascante, S., Murillo, C., 2018. Condiciones habilitadoras y barreras para el](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref42) [desarrollo de modelos sostenibles en el manejo productivo de bosques secundarios](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref42) [en Costa Rica \(Turrialba, Costa Rica\)](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref42).
- Sánchez-Azofeifa, G.A., Pfaff, A., Robalino, J.A., Boomhower, J.P., 2007. Costa Rica's payment for environmental services program: intention, implementation, and impact. Conserv. Biol. 21, 1165–1173. [https://doi.org/10.1111/j.1523-](https://doi.org/10.1111/j.1523-1739.2007.00751.x) [1739.2007.00751.x.](https://doi.org/10.1111/j.1523-1739.2007.00751.x)
- Sánchez, O., Navarrete, G., 2017. The experience of Costa Rica with the payments for [environmental services: 20 Years of lessons learned. Trop. J. Environ. Sci. 51,](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref44)  195–[214](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref44).
- Seddon, N., Turner, B., Berry, P., Chausson, A., Girardin, C.A.J., 2019. Grounding naturebased climate solutions in sound biodiversity science. Nat. Clim. Change 9, 84–87. [https://doi.org/10.1038/s41558-019-0405-0.](https://doi.org/10.1038/s41558-019-0405-0)
- Sekercioglu, C.H., 2002. Impacts of birdwatching on human and avian communities. Environ. Conserv. 29, 282–289. <https://doi.org/10.1017/S0376892902000206>.
- [Sharp, R., Tallis, H.T., Ricketts, T., Guerry, A.D., Wood, S.A., Chaplin-Kramer, R.,](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref47) [Nelson, E., Ennaanay, D., Wolny, S., Olwero, N., Vigerstol, K., Pennington, D.,](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref47)  [Mendoza, G., Aukema, J., Foster, J., Forrest, J., Cameron, D., Arkema, K.,](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref47) [Lonsdorf, E., Kennedy, C., Verutes, G., Kim, C.K., Guannel, G., Papenfus, M., Toft, J.,](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref47)  [Marsik, M., Bernhardt, J., Griffin, R., Glowinski, K., Chaumont, N., Perelman, A.,](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref47)  [Lacayo, M.M.L., Hamel, P., Vogl, A.L., Rogers, L., Bierbower, W., Denu, D.,](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref47) Douglass, J., 2018. InVEST 3.7.0 User'[s Guide. Nat. Cap. Proj. Stanford Univ. Univ.](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref47)  [Minnesota \(Nat. Conserv. World Wildl. Fund.\).](http://refhub.elsevier.com/S0301-4797(22)00290-0/sref47)
- Strassburg, B.B.N., Beyer, H.L., Crouzeilles, R., Iribarrem, A., Barros, F., de Siqueira, M. F., Sánchez-Tapia, A., Balmford, A., Sansevero, J.B.B., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Filho, A.O., Gardner, T.A., Gordon, A., Latawiec, A., Loyola, R., Metzger, J.P., Mills, M., Possingham, H.P., Rodrigues, R.R., Scaramuzza, C.A. de M., Scarano, F.R., Tambosi, L., Uriarte, M., 2019. Strategic approaches to restoring ecosystems can triple conservation gains and halve costs. Nat. Ecol. Evol. 3, 62–70. [https://doi.org/10.1038/s41559-018-0743-8.](https://doi.org/10.1038/s41559-018-0743-8)
- 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.](https://doi.org/10.1371/journal.pone.0158615) [pone.0158615](https://doi.org/10.1371/journal.pone.0158615).
- Zhang, J., Fu, B., Stafford-Smith, M., Wang, S., Zhao, W., 2021. Improve forest restoration initiatives to meet Sustainable Development Goal 15. Nat. Ecol. Evol. 5, 10–13. [https://doi.org/10.1038/s41559-020-01332-9.](https://doi.org/10.1038/s41559-020-01332-9)
- Zhang, W., Dulloo, E., Kennedy, G., Bailey, A., Sandhu, H., Nkonya, E., 2019. Biodiversity and Ecosystem Services, Sustainable Food and Agriculture. [https://doi.](https://doi.org/10.1016/b978-0-12-812134-4.00008-x)  [org/10.1016/b978-0-12-812134-4.00008-x.](https://doi.org/10.1016/b978-0-12-812134-4.00008-x)