

**Title:** Spatial conservation planning with ecological and economic feedback effects

## **Abstract**

Most spatial conservation prioritisations being implemented across the globe are based on static approaches to conservation planning. These use snapshots of systems to support decision-making. However, ignoring the dynamic nature of systems can result in misleading spatial prioritisations and missed opportunities to encourage participation in conservation programmes. Using a modelling approach, we show that integrating economic and ecological feedbacks into conservation planning improved social and ecological outcomes. We developed an approach that enabled accounting for feedbacks of farmland set-asides using a popular conservation planning tool. We empirically assessed the impact of ignoring feedbacks on plans to restore the Brazilian Atlantic Forest by comparing outcomes of our approach and a widely used static approach. The proposed approach attained better conservation outcomes than a static approach, at about 7% lower cost, while also allowing more farmers to benefit economically from the set-aside scheme through capitalising on the differences between their opportunity costs and the amount paid by the scheme. Accounting for feedbacks led to substantially different areas being prioritised for farmland set-asides, and to more farmers being included in the set-aside scheme. These results show important benefits from understanding, and then working with, feedbacks that inevitably accompany large-scale conservation interventions. Our approach is the first to integrate both environmental and economic feedbacks into spatial conservation planning, and model information rent capture. In doing so, it demonstrates how existing economic incentives can be used to encourage farmers to join a conservation set-aside, while still resulting in a lower overall intervention cost.

## 27 Introduction

28 Efficient allocation of conservation resources is vital, given the limited funding for  
29 conservation and rapid loss of biodiversity (Ceballos et al., 2015). Systematic  
30 conservation planning focuses on optimizing conservation outcomes cost-effectively,  
31 with thousands of systematic conservation plans developed around the globe  
32 (McIntosh et al., 2017). However, most systematic conservation plans are still based  
33 on static snapshots of the ecological and socio-economic systems to be managed  
34 (McIntosh et al., 2016). Typically, planned actions are implemented over periods of  
35 years or decades (Pressey et al., 2013), which gives opportunity for the system to  
36 react. Ignoring the dynamic nature of these systems can overlook unintended  
37 feedbacks of the conservation plan, risking undermined conservation outcomes, and  
38 even misleading recommendations (Larrosa et al., 2016).

39 Feedbacks occur when social or ecological responses to an intervention have an  
40 effect on intended outcomes, either directly or indirectly (Miller et al., 2010). The  
41 majority of research on feedbacks in conservation has been on either human or  
42 natural systems (Liu et al., 2007). Ecological mechanisms that lead to feedbacks  
43 have been widely studied within resource management (Altieri et al., 2013; Holling  
44 and Meffe, 1996), and have been integrated into conservation planning for resource  
45 management and restoration (Williams and Johnson, 2013). Dynamic optimisations  
46 explore how to use resources optimally over time, while accounting for the dynamic  
47 nature of systems. Social processes included in feedbacks from interventions have  
48 been less quantified in conservation, except for mechanisms related to land markets  
49 (Lim et al., 2016), which are mostly studied in the context of conservation planning  
50 and reserve selection (Armsworth et al., 2006; Butsic et al., 2013). Despite these  
51 studies, the impact of accounting for feedbacks on conservation planning outcomes  
52 remains unresolved, with some studies showing that planning for feedbacks  
53 improves project cost-effectiveness (Crouzeilles et al., 2015; Toth et al., 2011), whilst  
54 in others the benefits were not so clear (Butsic et al., 2013). The joint effect of social  
55 and environmental feedbacks has yet to be assessed.

56 The nature of a conservation intervention plays a crucial role in determining the  
57 feedbacks which may affect its outcomes (Armsworth et al., 2006). For example,  
58 conservation interventions that change or restrict land use can increase land prices  
59 by modifying the supply and demand for land and agricultural commodities (Lim et  
60 al., 2016). This could lead to higher future land purchase costs, increasing overall  
61 cost of the programme or affecting ecological outcomes when budget is limited.  
62 Similar feedbacks could result in market failure, which is when the market does not  
63 efficiently allocate goods and services (Mas-Colell et al., 1995). In conservation  
64 settings, market failure often leads to under-provision of public goods such as  
65 biodiversity and externalities, when those causing damage do not bear the costs  
66 (Kemkes et al., 2010; Pascual et al., 2014). Despite the relevance of market failure  
67 to conservation, few quantitative studies have explored it as a feedback mechanism  
68 (Wang and Miko, 1997).

Asymmetric information is one mechanism for market failure (Akerlof, 1970) that could underpin feedbacks of conservation interventions. For example, when signing contracts for conservation, landowners know better than programme administrators how participation in conservation actions could affect their production plans and profits (White and Hanley, 2016). The income lost by adopting conservation actions compared to current income is the opportunity cost. If the opportunity cost is lower than the compensation payment, there is an economic incentive to hide the real cost of participation to extract additional revenue. This additional revenue is called information rent. Information rent captured by landowners represents an extra income that increases their net returns per hectare, similarly to an agricultural subsidy which provides a direct payment that is not linked to production. These agricultural subsidies have been shown to increase price of farmland, and even impact rural allocation of land (Latruffe and Le Mouél, 2009; Patton et al., 2008). An incentive payment to set aside farmland could therefore result in higher future payments and increase overall project cost, because subsequent conservation payments need to approximately match the rising opportunity cost of setting aside land in order to attract farmers to the scheme (Fig.S1).

Information rent capture has been discussed in the conservation literature as something to be minimized to increase efficiency of incentive-based conservation (Ferraro, 2008; Mason and Plantinga, 2013). Methods to reduce information rent capture include estimating attributes that determine the real cost of participating in conservation and using these to calculate payments, as well as designing contracts in a way that reveals participants' real costs. These methods can be costly and the consequent gains in programme efficiency are variable (de Vries and Hanley, 2016; Ferraro, 2008). Additionally, achieving fairness can be challenging in schemes that include contracts with revelation mechanisms, such as auctions (Narloch et al., 2013). The benefits of using information rent capture reduction methods might therefore be negated at large scales due to the associated increasing costs, or when issues of fairness are considered. In this context, understanding how to manage information rent capture in spatial conservation planning at large scales is particularly important for effective conservation programmes.

Here we present the first modelling approach to spatial conservation planning that simultaneously accounts for both environmental and social feedbacks to prioritise a large-scale set-aside programme. The approach modelled both forest connectivity and incentive payment feedbacks within a conservation planning approach, designed considering real world uses of optimisation tools (Pressey et al., 2013). We tested it on a case study of ecological set-asides on private farmlands as a strategy for large-scale forest restoration in Brazil. We compared prioritisation outcomes for both the proposed approach and an established static one-off approach, and characterised information rent capture.

## 110 **Materials and Methods**

### 111 **1. Case study**

112 Our case study area was the Brazilian Atlantic forest (BAF) region, a highly  
 113 fragmented key global biodiversity hotspot (Sloan et al., 2014) that provides  
 114 ecosystem services to ~70% of Brazilian population (Joly et al., 2014). Forest  
 115 restoration and increasing forest connectivity are crucial to ensure that biodiversity-  
 116 derived ecological functions are provided across the region (Banks-Leite et al.,  
 117 2014). Ongoing restoration efforts include the Atlantic Forest Restoration Pact, a  
 118 multi-sectoral coalition with the goal of restoring 15 million ha of Brazilian Atlantic  
 119 Forest by 2050 (Pinto et al., 2014). In this case study, the aim was to set aside  
 120 enough farmland to meet both a forest restoration target and connectivity increment  
 121 target, at minimum possible cost.

### 122 **2. Overview of the modelling approach**

123 The main component of our approach was a spatial prioritisation exercise based on  
 124 a widely used static approach (Fig. 1, steps 1 to 4). The proposed approach (from  
 125 now on the “iterative” approach) integrates system’s dynamics into the planning  
 126 process by incorporating both an environmental and an economic feedback resulting  
 127 from implementing agricultural set-asides (Fig.1, grey arrows). The environmental  
 128 feedback modelled the effect that agricultural set-aside allocation has on forest  
 129 connectivity. The economic feedback modelled the effect that allocation of payments  
 130 for agricultural set-aside has on future payment price through informational rent  
 131 capture. In the following sections methods are explained in detail; see  
 132 supplementary materials (SM) text section 1 for a list of assumptions and section 2  
 133 for data and software used.

### 134 **3. Scales and units**

135 We used a nine-year time horizon, meaningful both for forest regeneration (Metzger  
 136 et al., 2009) and programme commitment. Conservation interventions at such  
 137 geographical scales are commonly implemented in phases; in our study, time moved  
 138 forward in steps, each time-step representing three years (Fig. S1). In the static  
 139 approach (the “one-off” approach), we ran one spatial conservation planning  
 140 exercise to meet forest connectivity and restoration targets. The solution was  
 141 implemented in three parts to match the defined 3-year time-steps by dividing total  
 142 restoration allocation for all priority areas into three parts. In the iterative approach,  
 143 we divided the restoration target in three and ran one spatial conservation planning  
 144 exercise at each time step to meet each third of the total restoration target. Solution  
 145 implementation followed each prioritisation exercise, enabling the iterative approach  
 146 to respond to feedbacks by adding new priority areas as payment value and  
 147 connectivity changed at each time-step. Once a priority area was included for  
 148 restoration it remained so until the end of the programme.

We used three spatial scales of relevance: municipality, biogeographical subregion, and whole Brazilian Atlantic Forest biome (BAF). The smallest unit of analysis was a municipality, because it is meaningful in policy terms, and a good compromise between ecological and social data available (Table S1). All municipalities that had at least 10 ha of forest within them were included in the analysis (SM, Section 3). Approximately 3,400 municipalities were included, covering an area of 212M ha. We grouped municipalities by 8 biogeographical subregions (from now on subregions) that span the BAF. Targets were set at subregional level to ensure their representation in priority areas and maximize beta diversity for the whole biome (after (Tambosi et al., 2014)). Targets were calculated at subregional level.

#### 4. Spatial conservation planning exercise

We had two conservation targets: a restoration target, and a forest connectivity target, to be met at minimum possible cost. Specifically, the objective function was:

$$\text{minimise } \sum_{ik=1}^{m_k} C_{ik} X_{ik} \quad (1)$$

subject to the constraint that both conservation targets ( $T_j$ ) were met as follows:

$$\sum_{ik=1}^{m_k} A_{ijk} X_{ik} \geq T_{jk} \quad \forall jk \quad (2)$$

where  $m_k$  is the total number of municipalities in a given subregion  $k$ ,  $c_{ik}$  is the cost of including set-asides (effectively the opportunity cost of the area of farmland set aside) for municipality  $i$  in subregion  $k$ ,  $x_{ik}$  is the binary decision variable indicating whether municipality  $i$  is selected ( $x_{ik} = 1$ ) or not ( $x_{ik} = 0$ ) for the solution group in subregion  $k$ , and  $A_{ijk}$  is the contribution of municipality  $i$  to target  $j$  in subregion  $k$ . Units for  $A_{ijk}$  are in hectares for both restoration and connectivity targets.

The prioritisation exercise involved four steps: (1) calculation of base metrics, (2) calculation of prioritisation inputs, (3) spatial prioritisation, and (4) solution assessment and implementation. For the iterative approach, base metrics (step 1) were updated at each time-step based on feedbacks' models (section 5, below) before running steps 2 to 4 again. Figure 1 shows how all steps and metrics involved are linked.

##### Step 1: calculation of base metrics

These calculations were the first step towards both prioritisation approaches. In the iterative approach two of these metrics (forest connectivity and farmland opportunity cost) were re-calculated at time-steps 2 and 3.

*Potential set-aside area (PSA, ha)*

For all forest patches, we delimited a one-kilometre buffer area where set-asides could potentially occur; set-asides were restricted to this potential set-aside area (PSA). This distance is a threshold for natural regeneration in the BAF (Scervino and Torezan, 2015).

#### *Forest connectivity (ECA(IIC), ha)*

We used a graph theory approach to evaluate landscape connectivity, due to its simplicity of representation, robustness, predictive power, and high potential to incorporate connectivity functional attributes (Urban and Keitt, 2001). The integral index of connectivity (IIC, (Pascual-Hortal and Saura, 2006)) is recommended as the best binary index for the type of connectivity analysis performed (Saura and Pascual-Hortal, 2007), and has been applied in many conservation planning case studies (Saura et al., 2011a).

To calculate IIC, each municipality plus a 1-km buffer was depicted as a graph in which existing forest patches are the nodes, patch area is used as the node's attribute, and biological information on organisms' dispersal capability is used to define links between nodes, which represent functional connectivity. *IIC* ranges from 0 to 1 and increases with improved connectivity. It is given by:

$$IIC = \frac{\sum_{i=1}^n \sum_{j=1}^n \frac{a_i a_j}{1 + nl_{ij}}}{A_L^2} \quad (3)$$

where  $n$  is total number of forest patches in the municipality,  $a_i$  and  $a_j$  are the sizes of patches  $i$  and  $j$ ,  $nl_{ij}$  is the number of links between patches  $i$  and  $j$ , and  $A_L$  is total landscape area (comprising both habitat and non-habitat patches). A link exists when the shortest path distance (topological distance) between patches is equal or smaller than a dispersal distance. For nodes that are not connected the numerator in the equation for *IIC* equals zero ( $nl_{ij}=\infty$ ). When  $i=j$  then  $nl_{ij}=0$ ; this relates to habitat availability (reachability) concept that applies for *IIC*, in which a patch itself is considered as space where connectivity exists. When all landscape is occupied by habitat, then *IIC*=1.

*IIC* uses species' dispersal distance to calculate functional connectivity. For this case study, we used 200 meters as the dispersal capability based on an assessment of the sensitivity of *IIC* to various dispersal capabilities under a similar scenario (Tambosi 2014). That study showed that using a dispersal capability of 200 m resulted in a restoration strategy similar to that obtained using various dispersal groups (SM, section 4).

We used the Equivalent Connected Area (ECA(IIC), henceforth "connectivity") which is preferable to *IIC* as a summary of overall connectivity because it has area units, it is easier to interpret, and has a more usable range of variation (Saura et al., 2011b). ECA(IIC) is calculated as the square root of the numerator of *IIC*, and it

219 represents the size that a single forest habitat patch should have in order to provide  
220 the same value of IIC as the actual forest habitat pattern in the landscape (Saura et  
221 al., 2011a).

222 *Farmland opportunity cost ( $R$ , US\$/yr) per year*

223 Farmland opportunity cost is the income forgone by setting aside land; in our case  
224 study, income foregone from production or rent. We used farmland price data to  
225 estimate farmland yearly rent extraction (Eq. 4), which is a proxy for opportunity  
226 costs (Ferraro, 2008).

227 
$$R_i = P_i r \quad (4)$$

228 where  $R_i$  is farmland rent extraction (from now on opportunity cost) for municipality  $i$ ,  
229  $P_i$  is price of farmland in municipality  $i$ , and  $r$  is the discount rate (annual deposit  
230 interest rate of 7.8% for Brazil in 2013, (The World Bank, 2013).

231 Step 2: calculation of prioritisation inputs

232 The prioritisation requires 5 input metrics. Two are targets, restoration and  
233 connectivity. The remaining three inputs are based on metrics calculated in step one:  
234 amount of set-aside, forest connectivity increment, and cost. In the iterative  
235 approach, the two latter are updated at each time-step with the new base metrics  
236 accordingly (Fig.1).

237 *Restoration Target*

238 The restoration target in number of hectares was calculated as restoring an area  
239 equivalent to 15% of current BAF forest extent, which amounts to a total of 2.68  
240 million hectares. The BAF is a heavily degraded biome (Banks-Leite et al., 2014;  
241 Sloan et al., 2014), and under the Convention on Biological Diversity's Aichi Targets  
242 Brazil is committed to restoring at least 15% of degraded ecosystems by 2020  
243 (National Target 15, [www.cbd.int](http://www.cbd.int)).

244 *Forest Connectivity Target*

245 For each subregion we calculated the total potential forest connectivity increment  
246 given the restoration target, and set the forest connectivity target to 90% of that total.  
247 This target was chosen based on a sensitivity analysis and enabled the algorithm to  
248 find solutions flexibly (SM section 5). Because total potential forest connectivity  
249 depends on existing connectivity, in the iterative approach connectivity target had to  
250 be updated at each time-step based on new forest connectivity values.

251 *Amount of set-aside (SA)*

252 Amount of set-aside (SA) was calculated as the set-aside required to meet the  
253 restoration target, limited to potential set-aside area (PSA) and available farmland for

each municipality. This value effectively determines municipalities' contribution to the restoration target. In the iterative approach total SA was divided into 3 equal parts so at each time-step SA was the same, i.e., if a municipality was prioritised at all time-steps it's contribution to the restoration target was total municipality's SA.

#### *Forest connectivity increment (dIIC)*

Forest connectivity increment was defined as the increment in forest connectivity promoted by set-aside allocation, and determines municipalities' contribution to the connectivity target. Given the analysis unit, and because it is unrealistic to determine exact geographical location of each 10-ha set-aside, we used forest increment simulations to measure uncertainty around the connectivity increment accrued by set-asides. Forest connectivity increment (dIIC) estimation involved two steps: (i) forest increment experiments, and (ii) calculation of changes in ECA(IIC). Forest increment experiments consisted of simulating the creation of 10-hectare patches of forest randomly 100 times within each municipality's potential set-aside area (PSA). Simulations were run for cumulative levels of set-aside amounts corresponding to one, two and three thirds of the municipalities' total amount of set-aside (SA). We calculated dIIC in each municipality  $i$  for amount of set-aside  $j$  using forest increment simulation  $k$  such that:

$$dIIC_{ijk} = ECA(IIC)_{ijk} - ECA(IIC)_i \quad (5)$$

where  $dIIC_{ijk}$  is forest connectivity increment for municipality  $i$  promoted by the amount of set-aside  $j$  for forest increment simulation  $k$ . We calculated average dIIC per municipality and SA, with its standard error. Uncertainty was aggregated using minimum, mean and maximum values of 95% adjusted bootstrap percentile confidence intervals. In the one-off approach dIIC for a municipality was dIIC accrued by total SA. In the iterative approach dIIC at any given time-step depended on whether the municipality received SA in previous time-steps or not.

#### *Cost*

The cost of including each municipality in the set-aside programme was calculated as the annual farmland opportunity cost per hectare (R, eq. 4), multiplied by the set-aside area (SA) for each municipality and number of years within the programme.

#### *Step 3: spatial prioritisation*

We used Marxan to define which municipalities needed to be included in the programme to meet defined restoration and connectivity targets at minimum cost. Marxan uses simulated annealing, a probabilistic search heuristic commonly used to find near-optimal solutions for functions that are hard to optimize with deterministic methods (Maucher et al., 2011). We set Marxan to find 1000 solutions to the objective function (Eq.1). Algorithm calibration and sensitivity analyses were run to get robust results (SM section 5) following the Good Practices Handbook (Ardrón et al., 2010).



Marxan has two spatial output files, the “best” solution and the “summed” solution. The former is the most cost-effective solution, the “summed” solution shows selection frequency for each municipality. The selection frequency counts how many times across the solutions space a municipality was chosen to be part of a solution. A “robust” solution was created by choosing municipalities sequentially by selection frequency (starting with the highest) until both conservation targets were met. This was the final solution that identified municipalities in the set-aside programme.

#### Step 4: solution assessment

For all solutions, target achievement was assessed at biogeographical subregion level.

### 5. Modelling Feedbacks

#### *Forest connectivity feedback:*

Priority areas for farmland set-asides depend on existing forest cover and connectivity (Fig.1). Set-aside allocation in the previous time-step potentially modifies these attributes, which need to be updated before finding the new priority areas. Because forest increment simulations were run for all cumulative set-aside levels in each municipality, forest connectivity (ECA(IIC)) and connectivity increment (dIIC) values were obtained for all possible restoration allocations for each municipality. These included receiving a restoration allocation once (at any time step), twice (at any two time-steps), thrice (at all time-steps), or never. The new ECA(IIC) and dIIC values after reforestation took place were obtained from the already calculated values, and depended on whether it was the first, second or third time that a municipality had received a set-aside allocation.

#### *Incentive payment feedback:*

In the case study, the programme offered a municipality-specific level of payment to set aside farmland, set at the average opportunity cost of farmland in that municipality (R). We calculated opportunity cost (R, Eq. 4) based on empirical observations of farmland prices (SM section 2) and created frequency histograms to estimate the probability distribution of opportunity costs for each municipality  $F(\theta)$  (SM section 6). *Total information rent capture (U)* for municipality  $i$  was given by:

$$U_i = \sum_{i=1}^{i=n} \sum_{j=1}^{j=b} v_{ij} (\tilde{\theta}_i - \theta_{ij}) q_i \quad (6)$$

where  $i$  denotes municipality,  $\tilde{\theta}_i$  is mean opportunity cost of farmland for municipality  $i$ ,  $\theta_{ij}$  and  $v_{ij}$  are the opportunity cost value and its probability for bin  $j$  in municipality  $i$  respectively, and  $q_i$  is the amount of farmland being set-aside in municipality  $i$ . Total information rent extracted in a municipality impacts average opportunity cost for that

328 municipality. That new opportunity cost ( $\tilde{\theta}_{i,(t+1)}$ ), which is used to estimate payment  
329 ( $p_i$ ) for municipality  $i$  in the following time-step, was defined as:

330 
$$\tilde{\theta}_{i,(t+1)} = \tilde{\theta}_{i,t} + \frac{U_{i,t}}{q_{i,t}} \quad (7)$$

331 where  $i$  denotes municipality,  $(t+1)$  denotes subsequent time-step,  $\tilde{\theta}_{i,t}$  is mean  
332 farmland opportunity cost for municipality  $i$  at time-step  $t$ ,  $U_{i,t}$  is total information rent  
333 accrued for municipality  $i$  at time-step  $t$ , and  $q_{i,t}$  is total amount of farmland set aside  
334 in municipality  $i$  at time-step  $t$ .

## 335 **6. Modelling validation**

336 Model validation and verification were an integral part of model development to  
337 ensure accurate representation of the real-world system. These included checking  
338 (1) the data for validity and consistency, (2) the validity of assumptions and  
339 conceptual model, (3) programming and implementation was correct, and (4) the  
340 range of results compared to other SCPs for the region (SM section 6).

341

## 342 **Results**

### 343 **Comparing performance of one-off and iterative approaches**

344 The iterative approach resulted in a lower overall programme cost as well as  
345 improved cost-effectiveness. Total cost of meeting both targets was US\$3,553  
346 million (\$ mill.) for the iterative solution over the 9-year period. Accounting for the  
347 increment in opportunity cost of land due to information rent capture, the real cost of  
348 the one-off approach was \$3,797 mill, but the planned estimated total cost was  
349 \$3,480 mill., i.e. there would be a deficit of \$317 mill in implementing the one-off  
350 plan. The cost of ignoring feedbacks was therefore \$244 mill. Overall, the cost of  
351 each hectare of farmland set aside for restoration was 6.4% lower in the iterative  
352 approach. Set-aside cost-effectiveness, defined as area of farmland set aside per  
353 dollar spent, also improved in the iterative approach. For each dollar spent, the  
354 iterative solution resulted in 6.9% more farmland set aside than the one-off solution.  
355 In the iterative approach, farmland opportunity costs increased over time due to the  
356 economic feedback and cost was updated at each time-step, allowing for the  
357 inclusion of the most cost-effective municipalities.

358 In terms of ecological outcomes, accounting for the forest connectivity feedback  
359 resulted in 37% more municipalities with improved forest connectivity. The highest  
360 increases in forest connectivity per hectare at municipality level were also achieved  
361 in the iterative solution (Fig. S2, Fig. S3c). At BAF level, for each hectare of land that  
362 was set aside, increment in forest connectivity in the iterative solution was 2.5-4.9%  
363 less than in the one-off solution. However, this value reflected the sum of total forest  
364 connectivity increment across municipalities and not the forest connectivity metric at  
365 the BAF level, as the scale of analysis did not allow for such a calculation.

366 At a subregional scale however, whether a one-off or an iterative approach  
367 performed better varied with subregion and metric being assessed (Fig. 2, Table S3).  
368 Cost per hectare was lower for the iterative solution in six out of eight subregions (by  
369 1-29%). A similar result was observed for set-aside cost-effectiveness, with  
370 improvements of 1-5%. For both cost per hectare and cost-effectiveness, the one-off  
371 approach sometimes performed slightly better (1-3.4%). Forest connectivity  
372 increment per hectare (i.e. the proportion of each set-aside hectare that directly  
373 contributed to forest connectivity) was higher for the one-off solution in six out of  
374 eight subregions (by 1.7-34.3%). Differences in connectivity cost-effectiveness were  
375 more evenly distributed, with the iterative solution reaching higher values in three out  
376 of eight subregions (by 4.8-23%). Despite this variability, in general terms at  
377 subregional level the iterative solution was better in terms of cost per hectare and  
378 set-aside cost-effectiveness, while solutions were similar in terms of connectivity  
379 gain per unit (ha or \$).

380 Variability in performance of approaches resulted from the distribution of  
381 municipalities with varying forest fragmentation levels and opportunity costs.  
382 Florestas de Interior, for example, is the largest (Table S4) and most degraded

subregion, with high levels of fragmentation (Tambosi et al., 2014). Additionally, it has the largest range in mean municipality farmland opportunity cost (71-1,164 \$/ha/yr), and the largest variability within municipalities (s.d. of mean municipality farmland opportunity cost as a proportion of the mean 0.1-1.14). These extreme circumstances explain why this subregion was an outlier in many ways. The iterative approach was substantially better than the one-off approach, 41% more cost-effective and 15-23% more cost-effective in terms of connectivity. Both economic and environmental feedbacks were important in this subregion. Municipalities in the one-off solution had initial low opportunity cost and intermediate forest cover but large increases in opportunity costs from the economic feedback. This resulted in lower cost-effectiveness compared to the iterative solution, which in this region had a wide choice of intermediate forest cover and low-cost municipalities to avoid the economic feedback and leverage the environmental feedback.

## **Programme priority areas**

Configuration of priority areas differed between one-off and iterative approaches (Fig.3a). Of all municipalities included in either solution, only 26% were included in the set-aside programme regardless of approach. Thirty-two percent of municipalities were included only in the iterative solution, and 7% only in the one-off solution. These proportions varied widely at subregional level (Fig.3b). For any given subregion, 6%-40% of municipalities were always priority areas, 20%-50% were only priorities in the iterative solution, and 0%-24% were only priorities in the one-off solution. Given a target set-aside amount, subregions that have many municipalities with low farmland opportunity costs are more likely to include a higher number of municipalities in the iterative solution than subregions that have lower opportunity costs but only in a few municipalities.

The one-off solution included 20-50% fewer municipalities than the iterative solution in most subregions (Table S4). This difference was not explained by number of municipalities in the subregion (Fig.S4).

## **Information rent capture**

Accounting for the economic feedback resulted in lower cost and higher cost-effectiveness, with some subregional variability. Given that the mechanism by which farmland opportunity cost increased over time was information rent capture, we expected the iterative solution to result in lower information rent capture by landowners. However, we found the opposite; information rent capture was 34% higher for the iterative solution (\$323.4 mill.) despite this solution having a lower cost. The proportion of each dollar spent captured in information rent was 43% higher in the iterative than the one-off solution. Even though variability was observed in percent difference in proportional information rent capture between subregions (11%-89%), information rent capture was always higher for the iterative approach (Fig. 2). There were more municipalities in the iterative solution for which information rent capture per hectare was higher, and for which difference between approaches reached higher values (Fig.S3b).

425

## 426 **Discussion**

427 We present the first approach to spatial conservation planning that accounts for both  
428 ecological and economic feedback effects of a conservation intervention at its initial  
429 stage. Both iterative and one-off approaches present solutions that meet the given  
430 targets within the set budget. Overall, however, applying the iterative approach  
431 resulted in increased cost-effectiveness when compared to a one-off approach,  
432 reinforcing results from other studies that form the scarce empirical evidence on  
433 economic feedbacks in conservation planning (Butsic et al., 2013). However, at  
434 subregional level the iterative approach resulted in a range of cost-effectiveness  
435 improvements, and sometimes reductions. Dynamic conservation planning studies  
436 using simulated data have also found that the extent to which accounting for market  
437 feedbacks improved cost-effectiveness depended on system and location  
438 characteristics (Armsworth et al., 2006; Dissanayake and Önal, 2011).

439 In terms of conservation outcomes, biodiversity benefits derived from forest  
440 connectivity gains were higher for the iterative approach regardless of scale,  
441 because more municipalities were included in the solution. As municipalities could  
442 not be “dropped” of the programme, in going for the most cost-effective  
443 municipalities the iterative approach engaged more municipalities. More  
444 municipalities participating in forest restoration result in regenerating areas that are  
445 more widely distributed, providing a buffer to uncertainty through a more spatially  
446 extensive network of connected forest. This is key to preserving biodiversity in the  
447 BAF, as it is mainly comprised of small isolated populations (Hatfield et al., 2018).  
448 More municipalities participating in the set-aside programme could also benefit  
449 species with smaller ranges that are currently not protected, because it is more likely  
450 that they will have regenerating forest within their range. Furthermore, more people  
451 could benefit from improved local-scale ecosystem services, such as pollination and  
452 soil retention (Farley, 2012). However, the one-off approach resulted in higher  
453 connectivity per hectare of land restored at both BAF and most subregional levels.  
454 These slightly contradictory results can be explained by the non-linear relationship  
455 between forest cover and forest connectivity, in which the same increment in forest  
456 cover results in a larger connectivity increment the larger the base forest cover is  
457 (Rappaport et al., 2015). Because in the one-off solution the same municipalities  
458 received sequential set-aside allocations, forest connectivity gains for the same set-  
459 aside amount increased over time.

460 Most literature on information rent in conservation focuses on the need to minimize  
461 its capture to improve cost-effectiveness (Ferraro, 2008; White and Hanley, 2016).  
462 By contrast, our results show that if information rent capture is allowed, increased  
463 capture (and therefore higher incentives to participate) can be obtained without  
464 increasing overall cost. In the iterative approach, Marxan provides the cheapest  
465 solution at each time-step, regardless of information rent. Municipalities with lower  
466 farmland opportunity costs are prioritised over ones with higher opportunity costs,  
467 even if the former entail higher information rent capture than the latter. In this way,  
468 the iterative solution both has a lower cost and allows more landowners to capture  
469 information rent. Our results also suggested that under the iterative approach not

only would a wider range of landowners have an incentive to participate in the programme due to information rent capture, but that incentives could also be higher.

Several studies have used contract design theory to show how auctions help reveal hidden costs and avoid adverse selection, especially in the context of agri-environmental policies (Latacz-Lohmann and Schilizzi, 2005). However, the prospect of information rent capture acts as an economic incentive for programme participation (Scheufele and Bennett, 2017). The iterative approach proposed in this study estimates total information rent capture, which enables a comparison with the cost of implementing revealed cost mechanisms for a large-scale programme. If these are similar, information rent capture is no longer a “waste” of money as it is an unavoidable cost transformed into an economic incentive. Given that asymmetric information is bound to exist in the real world, especially at large scales, our approach could be a new tool to get information rent capture working for conservation.

#### **Implications for conservation and decision-making**

Nowadays, rigorous planning methods are especially needed, given that collaborative conservation action at landscape scales is on the rise and global financial crises restrict conservation investments (Mazor et al., 2014). In our case study, ignoring the economic feedback at the planning stage resulted in a total programme cost that was \$317 mill. higher than the estimated direct cost of meeting the restoration target using a one-off approach. This difference is large enough that, if budget were fixed at the originally estimated cost, the restoration target would not have been met.

Conservation on private lands plays a crucial role in conserving biodiversity in highly fragmented areas (Paloniemi and Tikka, 2008), and this is particularly true for the Brazilian Atlantic Forest where land owners have a legal requirement to set aside 20% of their property for forest. Traditional regulation has not provided a complete solution due to large numbers of private landowners and the hidden nature of their activities, which has led to an increasing emphasis on offering financial incentives for conservation (Stern, 2006). Conservation payments can either aim to compensate costs, to change behaviour, or both (Vatn, 2010). Using the proposed iterative prioritisation, the set-aside programme could move from being only a compensation payment to providing an incentive to change behaviour, mostly by increasing information rent capture without increasing cost of the programme. Higher levels of information rent captured by more farmers, spread more evenly across more municipalities, could prove to be an invaluable benefit of the iterative approach in regions where there is low willingness to join this type of programme. Optimization studies in the PES and spatial planning literatures have begun to incorporate dimensions of equity (Halpern et al., 2013). Potential issues with large-scale set-aside payments could be the inequitable distribution of costs (land-use restrictions) and benefits (economic incentives); an iterative approach could reduce these issues. It could also enhance distributional equity and increase perceived fairness, thereby increasing probability of programme success (Pascual et al., 2014). Such a large region as the BAF, however, includes a wide range of socio-economic and land-use

514 rights profiles; the impact of local circumstances on equity would need to be further  
515 explored.

## 516 **Future work**

517 Despite feedbacks being highlighted as needing more attention (e.g. Miller et al.  
518 2010), there has been limited quantitative exploration of feedbacks in conservation  
519 planning. Here we present a method for incorporating environmental and economic  
520 feedbacks into models to inform intervention design. Further work is needed if  
521 conservation planners are to understand trade-offs in integrating varying levels of  
522 complexity of the dynamics that are at play at multiple temporal and spatial scales.  
523 Uncertainty in outputs for both approaches needs to be quantified to communicate  
524 reliability of results to decision-makers. In this study we focused on a few key  
525 optimisation parameters given the computationally intensive nature of the model.  
526 Further sensitivity analyses could include testing the performance of the model for a  
527 range of discount rates and connectivity scenarios (e.g. based on different dispersal  
528 distances). Application of the model to different geographies, targets and  
529 conservation interventions, and improvements in computational power, will enable  
530 further model validation, providing a better understanding of circumstances and  
531 scales under which the iterative approach improves cost-effectiveness compared to  
532 a one-off approach. Better availability of spatially explicit socio-economic data would  
533 also help, especially with validation of model's predictions. For example, more  
534 realistic cost estimation would be possible if the transaction costs associated with the  
535 set-aside program were known (Zheng et al., 2013); these data did not exist for the  
536 case study area. More broadly, there is a need to model other feedbacks, and test  
537 other tools to quantify these, such as agent-based modelling (Huber et al., 2013) and  
538 systems dynamics (Elsawah et al., 2017). Understanding which feedbacks are most  
539 relevant under various circumstances is key to addressing the challenge of  
540 accounting for system dynamics in conservation planning.

541

## 542 **Conclusion**

543 The proposed iterative approach to spatial conservation planning increased cost-  
544 effectiveness at biome level, improved conservation outcomes, resulted in different  
545 priority areas for farmland set-asides, and included more municipalities in the set-  
546 aside programme. These results show important benefits from modelling, quantifying  
547 and then planning for, feedbacks that inevitably accompany large-scale conservation  
548 interventions. Additionally, by modelling information rent capture, the iterative  
549 approach shows that information rent can be used as an existing economic incentive  
550 for participation while still having lower overall cost. This could potentially re-define  
551 the way in which conservation projects perceive information rent extraction, away  
552 from minimization and towards utilising the opportunities that it provides.

553

## References

- Akerlof, G.A., 1970. The Market for “Lemons”: Quality Uncertainty and the Market Mechanism. *Q. J. Econ.* 84, 488. <https://doi.org/10.2307/1879431>
- Altieri, A.H., Bertness, M.D., Coverdale, T.C., Axelman, E.E., Herrmann, N.C., Lauren Szathmary, P., 2013. Feedbacks underlie the resilience of salt marshes and rapid reversal of consumer-driven die-off. *Ecology* 94, 1647–1657. <https://doi.org/10.1890/12-1781.1>
- Ardron, J.A., Possingham, H.P., Klein, C.J., 2010. Marxan Good Practices Handbook, Version 2. *Pacific Mar. Anal. Res. Assoc.* 165.
- Armsworth, P.R., Daily, G.C., Kareiva, P., Sanchirico, J.N., 2006. Land market feedbacks can undermine biodiversity conservation. *Proc. Natl. Acad. Sci. U. S. A.* 103, 5403–8. <https://doi.org/10.1073/pnas.0505278103>
- Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, a. a., Bruscagin, R.T., Condez, T.H., Dixo, M., Igari, a. T., Martensen, a. C., Metzger, J.P., 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science* (80-. ). 345, 1041–1045. <https://doi.org/10.1126/science.1255768>
- Butsic, V., Lewis, D.J., Radeloff, V.C., 2013. Reserve selection with land market feedbacks. *J. Environ. Manage.* 114, 276–84. <https://doi.org/10.1016/j.jenvman.2012.10.018>
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., Garcia, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.* 1, e1400253–e1400253. <https://doi.org/10.1126/sciadv.1400253>
- Crouzeilles, R., Beyer, H.L., Mills, M., Grelle, C.E. V, Possingham, H.P., 2015. Incorporating habitat availability into systematic planning for restoration: a species-specific approach for Atlantic Forest mammals. *Divers. Distrib.* 21, 1027–1037.
- de Vries, F.P., Hanley, N., 2016. Incentive-Based Policy Design for Pollution Control and Biodiversity Conservation: A Review. *Environ. Resour. Econ.* 63, 687–702. <https://doi.org/10.1007/s10640-015-9996-8>
- Dissanayake, S.T.M., Önal, H., 2011. Amenity driven price effects and conservation reserve site selection: A dynamic linear integer programming approach. *Ecol. Econ.* 70, 2225–2235. <https://doi.org/10.1016/j.ecolecon.2011.06.015>
- Elsawah, S., Pierce, S.A., Hamilton, S.H., van Delden, H., Haase, D., Elmahdi, A., Jakeman, A.J., 2017. An overview of the system dynamics process for integrated modelling of socio-ecological systems: Lessons on good modelling practice from five case studies. *Environ. Model. Softw.* 93, 127–145. <https://doi.org/10.1016/J.ENVSOFT.2017.03.001>
- Farley, J., 2012. Ecosystem services: The economics debate. *Ecosyst. Serv.* 1, 40–49. <https://doi.org/10.1016/J.ECOSER.2012.07.002>
- Ferraro, P.J., 2008. Asymmetric information and contract design for payments for environmental services. *Ecol. Econ.* 65, 810–821. <https://doi.org/10.1016/j.ecolecon.2007.07.029>
- Halpern, B.S., Klein, C.J., Brown, C.J., Beger, M., Grantham, H.S., Mangubhai, S., Ruckelshaus, M., Tulloch, V.J., Watts, M., White, C., Possingham, H.P., 2013. Achieving the triple bottom line in the face of inherent trade-offs among social equity, economic return, and conservation. *Proc. Natl. Acad. Sci. U. S. A.* 110, 6229–34. <https://doi.org/10.1073/pnas.1217689110>
- Hatfield, J.H., Orme, C.D.L., Banks-Leite, C., 2018. Using functional connectivity to



predict potential meta-population sizes in the Brazilian Atlantic Forest. *Perspect. Ecol. Conserv.* 16, 215–220. <https://doi.org/10.1016/j.pecon.2018.10.004>

Holling, C.S., Meffe, G.K., 1996. Command and control and the pathology of natural resource management. *Conserv. Biol.* 10, 328–337. <https://doi.org/10.2307/2386849>

Huber, R., Briner, S., Peringer, A., Lauber, S., Seidl, R., Widmer, A., Gillet, F., Buttler, A., Le, Q.B., Hirschi, C., 2013. Modeling Social-Ecological Feedback Effects in the Implementation of Payments for Environmental Services in Pasture-Woodlands. *Ecol. Soc.* 18. <https://doi.org/10.5751/ES-05487-180241>

Joly, C.A., Metzger, J.P., Tabarelli, M., Joly, C.A., Joly, C.A., Metzger, J.P., Tabarelli, M., 2014. Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. *New Phytol.* 204, 459–473. <https://doi.org/10.1111/nph.12989>

Kemkes, R.J., Farley, J., Koliba, C.J., 2010. Determining when payments are an effective policy approach to ecosystem service provision. *Ecol. Econ.* 69, 2069–2074. <https://doi.org/10.1016/j.ecolecon.2009.11.032>

Larrosa, C., Carrasco, L.R., Milner-Gulland, E.J., 2016. Unintended Feedbacks: Challenges and Opportunities for Improving Conservation Effectiveness. *Conserv. Lett.* 9, 316–326. <https://doi.org/10.1111/conl.12240>

Latacz-Lohmann, U., Schilizzi, S., 2005. Auctions for Conservation Contracts: A Review of the Theoretical and Empirical Literature, Report to the Scottish Executive Environment and Rural Affairs Department (Project No: UKL/001/05).

Latruffe, L., Le Mouél, C., 2009. Capitalization of government support in agricultural land prices: What do we know? *J. Econ. Surv.* 23, 659–691. <https://doi.org/10.1111/j.1467-6419.2009.00575.x>

Lim, F.K.S., Carrasco, L.R., Mchardy, J., 2016. Perverse market outcomes from biodiversity conservation interventions. *Conserv. Lett.* 1–26. <https://doi.org/10.1111/conl.12332>

Liu, J., Dietz, T., Carpenter, S.R., Folke, C., Alberti, M., Redman, C.L., Schneider, S.H., Ostrom, E., Pell, A.N., Lubchenco, J., Taylor, W.W., Ouyang, Z., Deadman, P., Kratz, T., Provencher, W., 2007. Coupled human and natural systems. *Ambio* 36, 639–649. [https://doi.org/10.1579/0044-7447\(2007\)36\[639:CHANS\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36[639:CHANS]2.0.CO;2)

Mas-Colell, A., Whinston, M.D., Green, J.R., 1995. Microeconomic theory. *Can. J. Econ.* <https://doi.org/10.2307/135312>

Mason, C.F., Plantinga, A.J., 2013. The additionality problem with offsets: Optimal contracts for carbon sequestration in forests. *J. Environ. Econ. Manage.* 66, 1–14. <https://doi.org/10.1016/j.jeem.2013.02.003>

Maucher, M., Schöning, U., Kestler, H. a., 2011. Search heuristics and the influence of non-perfect randomness: Examining Genetic Algorithms and Simulated Annealing. *Comput. Stat.* 26, 303–319. <https://doi.org/10.1007/s00180-011-0237-5>

Mazor, T., Giakoumi, S., Kark, S., Possingham, H.P., 2014. Large-scale conservation planning in a multinational marine environment: Cost matters. *Ecol. Appl.* 24, 1115–1130. <https://doi.org/10.1890/13-1249.1>

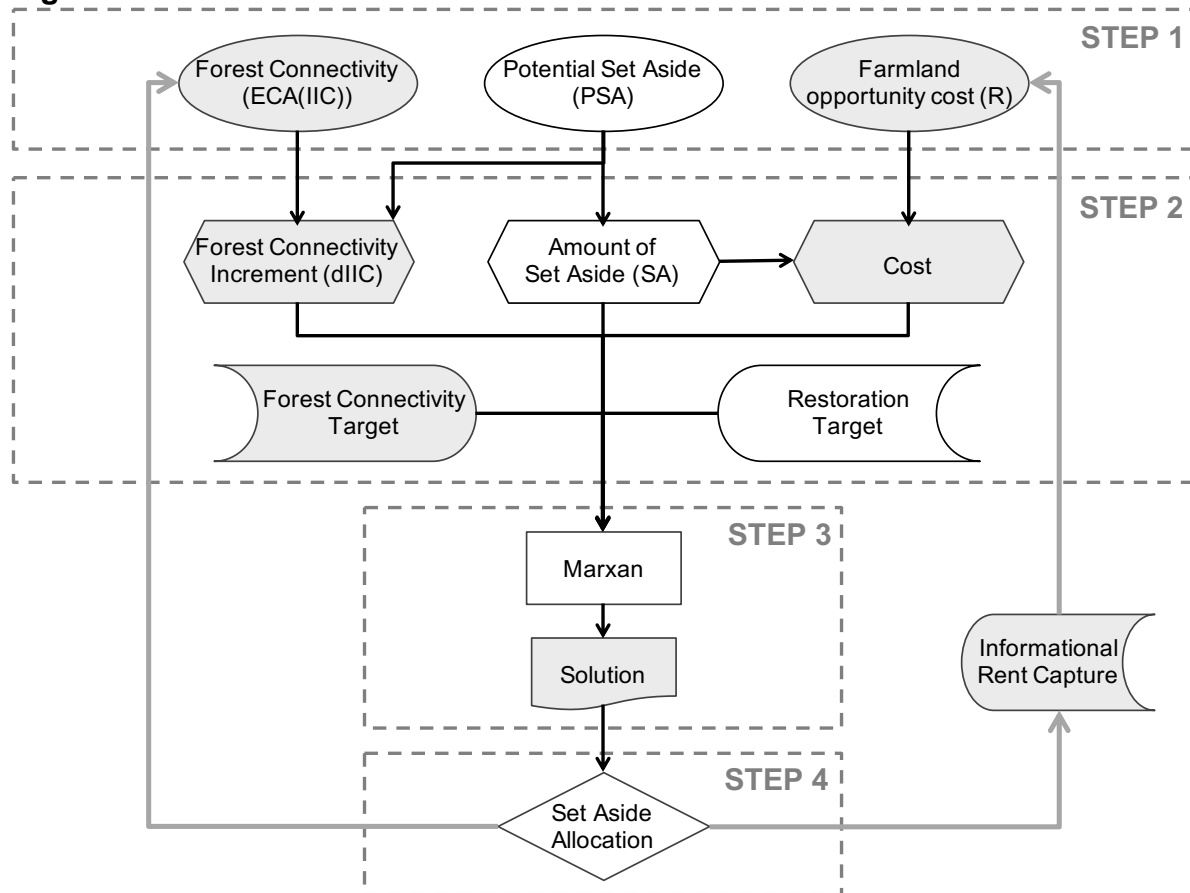
McIntosh, E.J., McKinnon, M.C., Pressey, R.L., Grenyer, R., 2016. What is the extent and distribution of evidence on effectiveness of systematic conservation planning around the globe? A systematic map protocol. *Environ. Evid.* 5, 15. <https://doi.org/10.1186/s13750-016-0069-4>

McIntosh, E.J., Pressey, R.L., Lloyd, S., Smith, R.J., Grenyer, R., 2017. The Impact

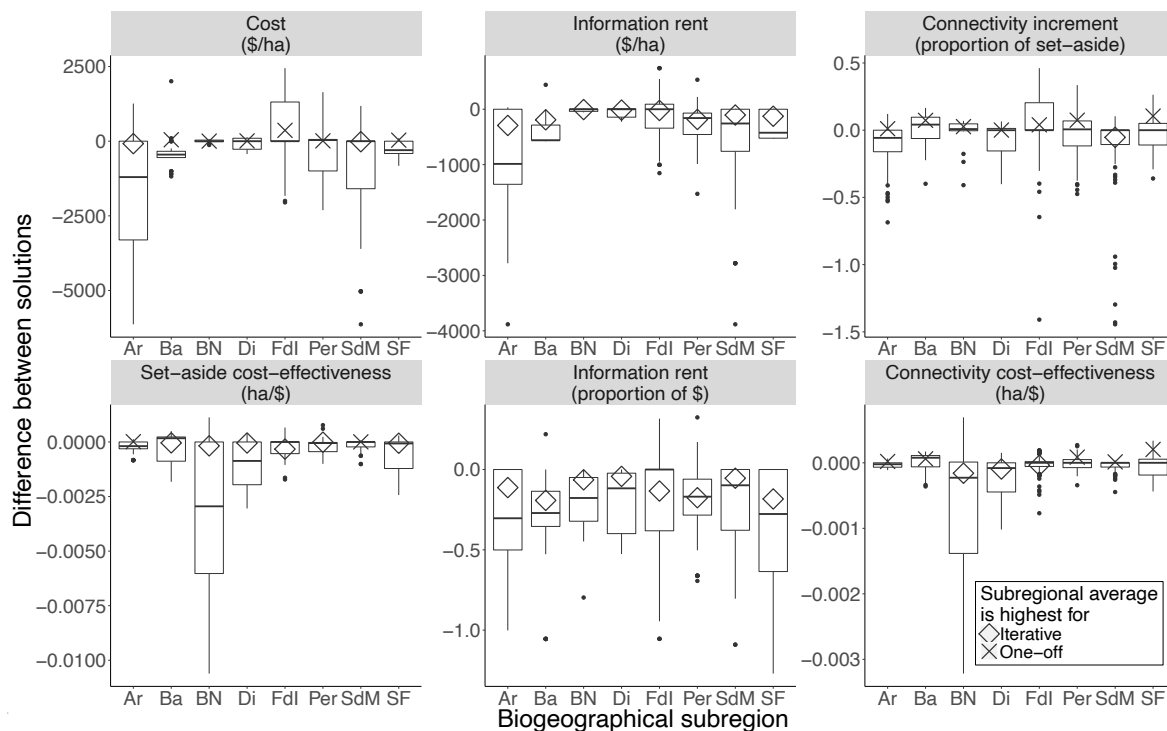
654 of Systematic Conservation Planning. *Annu. Rev. Environ. Resour.* 42, 677–  
 655 697. <https://doi.org/10.1146/annurev-environ-102016-060902>  
 656 Metzger, J.P., Martensen, A.C., Dixo, M., Bernacci, L.C., Ribeiro, M.C., Teixeira,  
 657 A.M.G., Pardini, R., 2009. Time-lag in biological responses to landscape  
 658 changes in a highly dynamic Atlantic forest region. *Biol. Conserv.* 142, 1166–  
 659 1177. <https://doi.org/10.1016/j.biocon.2009.01.033>  
 660 Miller, B.W., Caplow, S.C., Leslie, P.W., 2010. Feedbacks between conservation and  
 661 social-ecological systems. *Conserv. Biol.* 26, 218–27.  
 662 <https://doi.org/10.1111/j.1523-1739.2012.01823.x>  
 663 Narloch, U., Pascual, U., Drucker, A.G., 2013. How to achieve fairness in payments  
 664 for ecosystem services? Insights from agrobiodiversity conservation auctions.  
 665 *Land use policy* 35, 107–118. <https://doi.org/10.1016/j.landusepol.2013.05.002>  
 666 Paloniemi, R., Tikka, P.M., 2008. Ecological and social aspects of biodiversity  
 667 conservation on private lands. *Environ. Sci. Policy* 11, 336–346.  
 668 <https://doi.org/10.1016/j.envsci.2007.11.001>  
 669 Pascual-Hortal, L., Saura, S., 2006. Comparison and development of new graph-  
 670 based landscape connectivity indices: Towards the prioritization of habitat  
 671 patches and corridors for conservation. *Landsc. Ecol.* 21, 959–967.  
 672 <https://doi.org/10.1007/s10980-006-0013-z>  
 673 Pascual, U., Phelps, J., Garmendia, E., Brown, K., Corbera, E., Martin, a., Gomez-  
 674 Baggethun, E., Muradian, R., 2014. Social Equity Matters in Payments for  
 675 Ecosystem Services. *Bioscience* 64, 1027–1036.  
 676 <https://doi.org/10.1093/biosci/biu146>  
 677 Patton, M., Kostov, P., McErlean, S., Moss, J., 2008. Assessing the influence of  
 678 direct payments on the rental value of agricultural land. *Food Policy* 33, 397–  
 679 405. <https://doi.org/10.1016/j.foodpol.2008.01.001>  
 680 Pinto, S., Melo, F., Tabarelli, M., Padovesi, A., Mesquita, C., de Mattos Scaramuzza,  
 681 C., Castro, P., Carrascosa, H., Calmon, M., Rodrigues, R., César, R.,  
 682 Brancalion, P., 2014. Governing and delivering a biome-wide restoration  
 683 initiative: the case of Atlantic Forest Restoration Pact in Brazil. *Forests* 5, 2212–  
 684 2229. <https://doi.org/10.3390/f5092212>  
 685 Pressey, R.L., Mills, M., Weeks, R., Day, J.C., 2013. The plan of the day: managing  
 686 the dynamic transition from regional conservation designs to local conservation  
 687 actions. *Biol Conserv* 166. <https://doi.org/10.1016/j.biocon.2013.06.025>  
 688 Rappaport, D.I., Tambosi, L.R., Metzger, J.P., 2015. A landscape triage approach:  
 689 Combining spatial and temporal dynamics to prioritize restoration and  
 690 conservation. *J. Appl. Ecol.* 52, 590–601. <https://doi.org/10.1111/1365-2664.12405>  
 691  
 692 Saura, S., Estreguil, C., Mouton, C., Rodriguez-Freire, M., 2011a. Network analysis  
 693 to assess landscape connectivity trends: Application to European forests (1990-  
 694 2000). *Ecol. Indic.* 11, 407–416. <https://doi.org/10.1016/j.ecolind.2010.06.011>  
 695 Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate  
 696 connectivity in landscape conservation planning: Comparison with existing  
 697 indices and application to a case study. *Landsc. Urban Plan.* 83, 91–103.  
 698 <https://doi.org/10.1016/j.landurbplan.2007.03.005>  
 699 Saura, S., Vogt, P., Velazquez, J., Hernando, A., Tejera, R., 2011b. Key structural  
 700 forest connectors can be identified by combining landscape spatial pattern and  
 701 network analyses. *For. Ecol. Manage.* 262, 150–160.  
 702 <https://doi.org/10.1016/j.foreco.2011.03.017>  
 703 Scervino, R.P., Torezan, J.M.D., 2015. Factors affecting the genesis of vegetation

patches in anthropogenic pastures in the Atlantic forest domain in Brazil. *Plant Ecol. Divers.* 0874, 1–8. <https://doi.org/10.1080/17550874.2015.1044582>  
 Scheufele, G., Bennett, J., 2017. Can payments for ecosystem services schemes mimic markets? *Ecosyst. Serv.* 23, 30–37. <https://doi.org/10.1016/j.ecoser.2016.11.005>  
 Sloan, S., Jenkins, C.N., Joppa, L.N., Gaveau, D.L. a., Laurance, W.F., 2014. Remaining natural vegetation in the global biodiversity hotspots. *Biol. Conserv.* 177, 12–24. <https://doi.org/10.1016/j.biocon.2014.05.027>  
 Stern, S., 2006. Encouraging conservation on private lands: a behavioral analysis of financial incentives. *Ariz. Law Rev.* 48, 541–583.  
 Tambosi, L.R., 2014. Spatial strategies to optimize restoration efforts based on landscape ecology theory. University of Sao Paulo.  
 Tambosi, L.R., Martensen, A.C., Ribeiro, M.C., Metzger, J.P., 2014. A framework to optimize biodiversity restoration efforts based on habitat amount and landscape connectivity. *Restor. Ecol.* 22, 169–177. <https://doi.org/10.1111/rec.12049>  
 The World Bank, 2013. World Development Indicators [WWW Document]. World DataBank. URL <http://databank.worldbank.org/> (accessed 3.1.16).  
 Toth, S.F., Haight, R.G., Rogers, L.W., 2011. Dynamic Reserve Selection: Optimal Land Retention with Land-Price Feedbacks. *Oper. Res.* 59, 1059–1078. <https://doi.org/10.1287/opre.1110.0961>  
 Urban, D., Keitt, T., 2001. Landscape connectivity: A graph-theoretic perspective. *Ecology* 82, 1205–1218. [https://doi.org/10.1890/0012-9658\(2001\)082\[1205:LCAGTP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1205:LCAGTP]2.0.CO;2)  
 Vatn, A., 2010. An institutional analysis of payments for environmental services. *Ecol. Econ.* 69, 1245–1252. <https://doi.org/10.1016/j.ecolecon.2009.11.018>  
 Wang, C.-Y., Miko, P.S., 1997. Environmental impacts of tourism on US national parks. *J. Travel Res.* 35, 31–37. <https://doi.org/10.1177/004728759703500413>  
 White, B., Hanley, N., 2016. Should We Pay for Ecosystem Service Outputs, Inputs or Both? *Environ. Resour. Econ.* 63, 765–787. <https://doi.org/10.1007/s10640-016-0002-x>  
 Williams, B.K., Johnson, F.A., 2013. Confronting dynamics and uncertainty in optimal decision making for conservation. *Environ. Res. Lett.* 8, 025004. <https://doi.org/10.1088/1748-9326/8/2/025004>  
 Zheng, H., Robinson, B.E., Liang, Y.-C., Polasky, S., Ma, D.-C., Wang, F.-C., Ruckelshaus, M., Ouyang, Z.-Y., Daily, G.C., 2013. Benefits, costs, and livelihood implications of a regional payment for ecosystem service program. *Proc. Natl. Acad. Sci. U. S. A.* 110, 16681–16686. <https://doi.org/10.1073/pnas.1312324110>

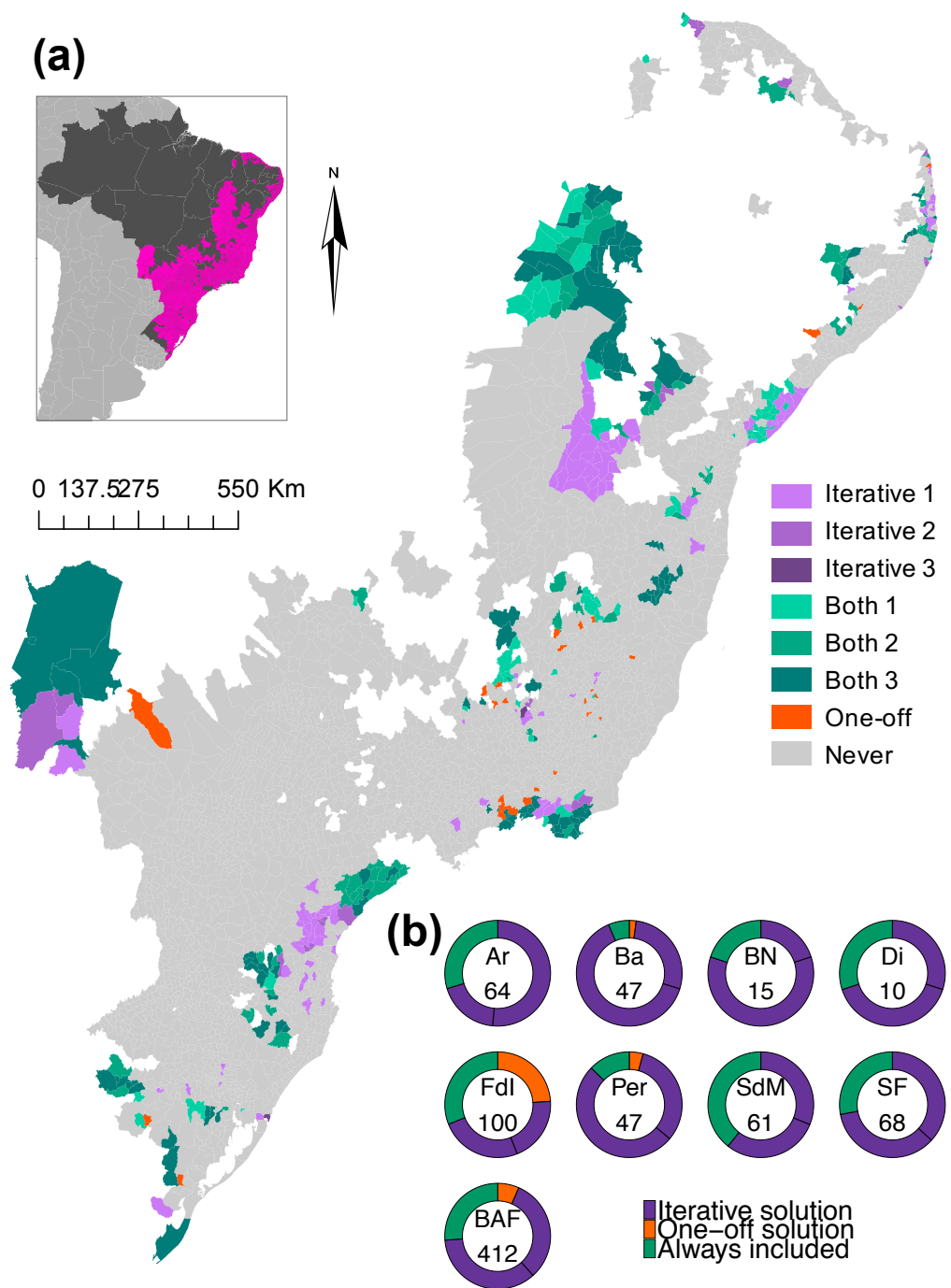
## Figures



**Fig.1. Methodological framework for prioritisation approaches.** The one-off approach involved steps 1 to 4: (1) calculation of base metrics from data, (2) calculation of prioritisation inputs, (3) spatial prioritisation, and (4) solution assessment and implementation. The iterative approach included updating metrics at step 1 before moving on to next steps. Grey arrows show feedbacks, and all stages that are updated are shaded in grey. Ovals denote starting points, hexagons denote preparation steps, “D” shaped polygons indicate that information is coming into the process, rectangle indicates a process, curved edged rectangle denotes an output, and rhombus indicates a decision.



**Fig.2. Distribution of differences in performance between one-off and iterative approaches.** Boxplots show min, max, median and interquartile range of municipality-level observations. Crosses and diamonds show the mean difference at biogeographical subregion level. Diamonds reflect negative differences, in which the iterative solution has a higher value than the one-off solution. Crosses show the opposite. Biogeographical subregions: Florestas de Araucaria (Ar), Bahia (Ba), Brejos Nordestinos (BN), Diamantina (Di), Florestas de Interior (Fdl), Pernambuco (Per), Serra do Mar (SdM), and Sao Francisco (SF). For Di, interval estimate for subregional mean connectivity increment crosses zero (-0.002,-0.004).



**Fig.3 [to be printed in colour]. Municipalities included as part of a prioritisation solution: (a)** spatial distribution. Categories: Iterative 1, 2, and 3 show municipalities included only in the iterative solution, once, twice or at all 3 time-steps respectively; Both 1, 2 and 3, show municipalities included in both the one-off and iterative solutions, once, twice or in all 3 time-steps of the iterative solution respectively; One-off shows municipalities included only in the one-off solution. In grey municipalities excluded from solutions. **(b)** The proportion of included municipalities for each category by subregion. Categories are simplified to one-off solution exclusively, iterative solution exclusively, and always included. Each ring represents a biogeographical subregion: Florestas de Araucaria (Ar), Bahia (Ba), Brejos Nordestinos (BN), Diamantina (Di), Florestas de Interior (Fdl), Pernambuco (Per),

780 Serra do Mar (SdM), and Sao Francisco (SF). The number shows municipalities  
781 included in any solution.