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The role of natural regeneration to ecosystem services provision and habitat availability: a case study in the Brazilian Atlantic Forest

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ABSTRACT

Natural regeneration provides multiple benefits to nature and human societies, and can play a major role in global and national restoration targets. However, these benefits are context specific and impacted by both biophysical and socioeconomic heterogeneity across landscapes. Here, we investigate the benefits of natural regeneration for climate change mitigation, sediment retention and biodiversity conservation in a spatially explicit way at very high resolution for a region within the global biodiversity hotspot of the Atlantic Forest. We classified current land-use cover in the region and simulated a natural regeneration scenario in abandoned pasturelands, areas where potential conflicts with agricultural production would be minimized and where some early stage regeneration is already occurring. We then modeled changes in biophysical functions for climate change mitigation and sediment retention, and performed an economic valuation of both ecosystem services. We also modeled how land-use changes affect habitat availability for species. We found that natural regeneration can provide significant ecological and social benefits. Economic values of climate change mitigation and sediment retention alone could completely compensate for the opportunity costs of agricultural production over 20 yr. Habitat availability is improved for three species with different dispersal abilities, although by different magnitudes. Improving the understanding of how costs and benefits of natural regeneration are distributed can be useful to design incentive structures that bring farmers' decision making more in line with societal benefits. This alignment is crucial for natural regeneration to fulfill its potential as a large-scale solution for pressing local and global environmental challenges.

Key words: climate change mitigation; connectivity; cost-effectiveness; ecological restoration; environment services evaluation; incentives.

Tropical forests are irreplaceable to maintain biodiversity, provide ecosystem services and mitigate climate change as they globally host around two-thirds of the species (Gardner *et al.* 2010) and half of the total carbon storage of the vegetation (Strassburg *et al.* 2010). Nonetheless, tropical forests are increasingly shrinking due to habitat loss, fragmentation and degradation as a result of the land-use change for accommodating agriculture, and urban expansion (Gibbs *et al.* 2010). For example, between 1980 and 2012 more than 100 million ha of tropical forests were converted to other land-uses (Gibbs *et al.* 2010, Hansen *et al.* 2013). As a consequence, land-use changes may increase carbon emission, reduce sediment retention, and commit species to extinction (Foley *et al.* 2007, Gardner *et al.* 2009, Cardinale *et al.* 2012).

An alternative to reverse these trends is the ecological restoration of forests (Clewell & Aronson 2007, Menz *et al.* 2013). Ecological restoration is the process of helping degraded or destroyed ecosystems (SER 2004). It can be done through passive (*e.g.*, natural regeneration) or active (with human intervention) initiatives (Holl & Aide 2011, Chazdon & Uriarte 2016). As natural regeneration does not require human intervention, it is a cheaper initiative to increase forest cover (Birch *et al.* 2010). For example, in tropical regions, large-scale restoration have occurred as extensive areas of secondary forest are being recovered passively due to rural-urban migration and agricultural abandonment (Guariguata & Ostertag 2001, Aide & Grau 2004, Bowen *et al.* 2007, Chazdon *et al.* 2009, Aide *et al.* 2012, Chazdon &

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Guariguata 2016). In such cases, natural regeneration occurred in lands with low or no loss of income from agriculture (*i.e.*, low opportunity cost). However, the role of these secondary regrowth forests in providing ecosystem services and facilitating biodiversity maintenance compared to old growth forests is an open question (Gibson *et al.* 2011, Lewis *et al.* 2015, Crouzeilles *et al.* 2016). Thus, to improve the cost-effectiveness of large-scale restoration, it is timely, to raise the awareness of the socioeconomic and ecological roles of natural regeneration in tropical forests, which remains poorly understood (Gardner *et al.* 2007, Chazdon *et al.* 2009, Chazdon & Guariguata 2016).

A current leading scientific approach to evaluate the benefits of nature to humans is the ecosystem services framework (MEA 2005; Fisher *et al.* 2008, Balmford *et al.* 2011, Pascual *et al.* 2015). Although several alternative and complementary approaches exist (Pascual *et al.* 2015), the ecosystem services framework provides useful insights to estimate how ecological and socioeconomic functions interact and thus impacts human wellbeing. Natural regeneration impacts the provision of ecosystem services from the global to the local scales (Foley *et al.* 2007). Regrowing forests may sequester high amounts of carbon, helping to mitigate climate change (Finegan *et al.* 2015, Gilroy *et al.* 2014), and at the same time help to stabilize the soil, avoid sediment loss and improve water quality (Ditt *et al.* 2010).

In addition, natural regeneration also can provide suitable habitats for species, and increase species connectivity in the landscape (Chazdon *et al.* 2009). Therefore, to avoid the loss of species at the landscape scale, it is essential to maximize the amount of naturally regenerating areas available for species. Areas available for species can be measured through the habitat availability; an increasingly applied concept that consider not only the habitat amount in the landscape, but also the landscape connectivity, as even large but disconnected habitat cannot be reached and used by individuals (Saura & Pascual-Hortal 2007, Crouzeilles *et al.* 2013, 2014).

In all the considerations regarding the provision of ecosystem services made above, the overall added benefit of restoration will depend on the geographical position, area size, and shape of the places where natural regeneration is allowed to happen (*e.g.*, Verhagen *et al.* 2016). The benefits of natural regeneration for ecosystem services and habitat availability are context specific and potentially impacted by both biophysical and socioeconomic heterogeneity across landscapes (*e.g.*, Chazdon & Guariguata 2016, Poorter *et al.* 2016).

Here, we investigate the relative contribution of the natural regeneration to the provision of ecosystem services and biodiversity conservation in a spatially explicit manner, and discuss how this understanding can contribute to improve incentives structure that influence farmers' decision making. Our case study is in the Paraitinga basin, located in the Brazilian Atlantic Forest, one of the five hottest hotspots of conservation (Laurance 2009). To achieve these goals, we first classified the current land-use in the region using a combination of high-resolution (5 m) imagery and field validation. Second, we developed spatially explicit scenarios that consider potential competition for land with agriculture (Latawiec *et al.* 2015) and natural regeneration potential into consideration by selecting only areas of abandoned pasturelands with signs of early stage natural regeneration. Third, we quantified changes in biophysical functions related to two ecosystem services (climate change mitigation and sediment retention), and performed an economic valuation of them by comparing with the opportunity costs of the selected areas. Fourth, we modeled possible effects of land-use changes on habitat availability for species. Finally, we discuss how incentive structures are important for natural regeneration and how these can be informed by estimates such as the ones we produced. To our knowledge, this is the first study using spatially explicit scenarios to inform development of financial benefits from the natural regeneration to ecosystem services, and to reveal how natural regeneration affects the relative contribution of habitat availability for species' with different dispersal ability. This study might offer useful insights to different stakeholders such as researchers, policymakers, and restoration practitioners regarding the benefits and cost-effectiveness of natural regeneration for providing ecosystem services and maintaining biodiversity.

METHODS

In this section, we discuss the data inputs and the methodology used to assess the effects of natural regeneration in the functionality of the ecosystem of the Paraitinga basin, and the added economic value of a few of the services it provides. We start by describing the data images used, and the process of classification of the landscape's land-cover, which allows us to define the spatially-explicit baseline, and natural-regeneration scenarios. We then compute the additionality of natural regeneration with respect to the baseline in terms of sequestered carbon, sediment retention, and increase in habitat availability. The transition from abandoned grassland to second growth forest captures large quantities of carbon in the form of the increasing biomass of the vegetation, leading to an overall reduction in the amount of greenhouse gases in the atmosphere, in the natural regeneration scenario as compared to the baseline. Riparian forest areas may also contribute to sediment retention in rivers and may decrease the maintenance costs of water dredging purification for consumption. Finally, second growth forests can connect otherwise isolated patches of remaining pristine forest, allowing for a greater number of species in those patches to increase their habitat areas, and generally the extinction debt in the landscape.

Study area and land-use/cover classification.—The Paraitinga basin is located in the State of São Paulo (−45,6535, −23,4019; −44,6435, −22,7057), at the south-eastern coast of the Brazilian Atlantic Forest (Fig. 1) covered by evergreen tropical forest vegetation type (see Fiaschi & Pirani 2009). This basin (with 268,000 ha, *i.e.*, 0.21% of the Brazilian Atlantic Forest) has a strategic function in terms of providing water supply for São Paulo and Rio de Janeiro, two highly populated States in the Brazil. In Paraitinga basin, habitat loss and fragmentation was driven mainly by socio-economic pressures, resulting in a highly fragmented landscape with different types of land use/cover.

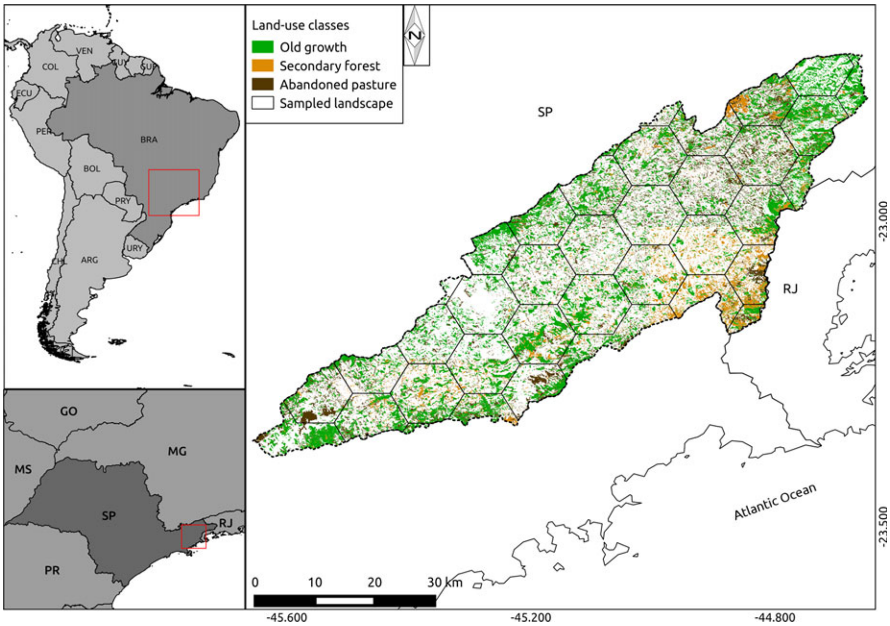

FIGURE 1. Location and land-use/cover classes used in the following analysis for the Paraitinga region, in the State of São Paulo, at the Brazilian Atlantic Forest. The hexagons represent different landscapes for the analysis of habitat availability (see this section below). [Color figure can be viewed at wileyonlinelibrary.com]

To identify the main land-use/cover classes in the Paraitinga basin, we carried out a field assessment in 155 sites from 14–17 January 2014. Then, we used 12 RapidEye images (RapidEye AG 2012) from 2012, with a pixel size of 5 m resolution, to map the current land use/cover in a scale of 1:20,000. We used a segmentation process based on region growing approach and the *Isoseg* algorithm to classify the images into 12 classes, and then performed a supervised classification and rectification to correct the mapped classes. The 12 classes used were: (1) degraded areas, (2) burned areas, (3) urban areas, (4) water bodies, (5) croplands, (6) managed pastures, (7) degraded pastures, (8) abandoned pastures (defined as pasture areas with presence of trees and shrubs.), (9) bare soils, (10) timber plantations (dense arboreal area with homogeneous texture), (11) secondary forests (arboreal area with heterogeneous texture), and (12) old growth forests (dense arboreal vegetation). The supervised process was guided by a classification key, which shows land uses ground truth and its spectral response in the image. After this classification, we carried out the second field assessment in 50 sites, randomly selected along the highway that crosses the watershed, from 22–24 October 2014, to validate our final map. The map of the current land-use/cover in the region was used as the basis for all scenarios and for the evaluation of the socioeconomic and ecological impacts of the natural regeneration on ecosystem services and biodiversity conservation. All classifications were performed using the software SPRING (Câmara *et al.* 1996).

TABLE 1. *Description of the three land use/cover scenarios.*

Spatial layer / analysis	Scenario 0 Old growth forests only	Scenario 1 Current land-cover	Scenario 2 Natural regeneration in abandoned pasturelands
Old growth forests	Included	Included	Included
Secondary forests	Not included	Included, current	Included, current + abandoned pasturelands
Abandoned pastures	Remains abandoned	Remains abandoned	Becomes secondary forests
Habitat availability	Performed	Performed	Performed
Carbon Stocks	Not Performed	Performed	Performed
Sediment retention	Not Performed	Performed	Performed

LAND USE/COVER SCENARIOS.—We considered three different land use/cover scenarios to calculate the socioeconomic and ecological benefits from natural regeneration for two ecosystem services (carbon stock and sediment retention) and habitat availability for species with different dispersal abilities (Table 1). Scenario 0 represents the land cover of old growth forests only and was used in the habitat availability analysis only. Scenario 1 is the baseline, *i.e.*, the current land use/cover. Thus, scenarios 0 and 1 differ because the former considers old growth forests only, while the latter considers old growth and secondary forests. Scenario 2 simulates natural regeneration of abandoned pasture areas. These are areas with potential for natural regeneration based on biophysical/ecological and socio-economic factors. Biophysically/ecologically these areas already present signs of natural regeneration at early successional stages, while socio-economically they would present low opportunity costs. Thus, in this scenario we assumed as a premise that abandoned pasturelands would become secondary forests in 20 yr. Thus, scenario 0 and 1 differs from scenario 2 because the latter assumes a land-use change in the next 20 yr. For the ecosystem services of climate change mitigation and sediment retention we compared the land use/cover scenarios 1 and 2, whereas we quantified the ecological benefits of habitat availability comparing land use/cover scenarios 0, 1, and 2. Land use/cover scenarios were modeled using the software ArcGis 9.3 (ESRI 2008). Table 1 summarizes the scenarios used in each separate analysis carried out in this work.

ECOSYSTEM SERVICES.—*Climate Change Mitigation*.—The natural regeneration of tropical forests sequester carbon dioxide from the atmosphere, which in the context of dangerous anthropogenic climate change is a very important global ecosystem service. Recent estimates suggest that this carbon sequestration potential of natural regeneration is very high (Chazdon *et al.* 2016). To model this climate change mitigation service, we used available data of carbon above and below the soil for each land use/cover in our map (Bernoux *et al.* 2006, Cardoso *et al.* 2012, La Scala Júnior *et al.* 2012, Table 2). We followed the approach suggested by the IPCC Good Practice Guidance for LULUCF (Penman, 2003), which is also the approach used by Brazil's National Greenhouse Gas Inventory. According to this methodology, net emissions (or sequestration) is estimated by attributing carbon stocks to different land use types, and accounting for changes in stocks based on changes in land-use. So we aggregated the carbon stock information for each pixel of the Paraitinga map in each land use/cover scenario and estimated the changes in carbon stock.

In order to estimate the economic value of the additional carbon sequestered by natural regeneration in scenario 2, we used three values for the price of carbon and three values for discount rates, generating nine distinct estimates. For the price of carbon, we used the value currently adopted by Brazil's Amazon Fund of US$ 5/tCO2, which is closer to current carbon prices in the absence of binding commitments, in addition to US$ 10/tCO_2 and US$ 15/tCO_2, values still on the conservative to intermediate range regarding estimates for carbon prices in the coming decades (Strassburg *et al.* 2012; Strassburg *et al.* 2015). The time horizon considered in this estimate is 20 years, assuming the recovery of 10 percent of the forest every two years. This follows the time horizon profile established for environmental compliance by the Brazilian Protection of Native Vegetation Law, informally known as the 'Forest Code' (Brasil 2012). Finally, we calculated the Net Present Value (NPV) of the climate change mitigation service using a conservative discount rate of 7.5 percent per year, which is the long-term interest rate in Brazil, in addition to the more widely adopted discount rate for developing countries of 5.0 percent and an optimistic discount rate of 2.5 percent (more in line with those found in developed countries). These analyses were performed in R 2.12 (R Core Development Core Team 2011).

TABLE 2. *Carbon stock in each land use/cover (ton/hectare) in the Paraitinga region, at the Brazilian Atlantic Forest.*

Land use description	Above	Below	Soil	Dead	Total (t/ha)
Degraded areas	0	0	0	0	–
Burned areas	0	0	0	0	–
Urban areas	15	3.8	41	0	60
Water	0	0	0	0	–
Croplands	7.2	1.9	62.44	1.1	73
Secondary forests	69	13.2	90.6	3.6	176
Old growth forests	134	27.6	90.6	3.6	256
Managed pastures	2.9	7.7	94.6	1.1	106
Degraded pastures	2.9	7.7	94.6	1.1	106
Abandoned pastures	2.9	7.7	94.6	1.1	106
Timber plantations	56.7	9.9	74.3	7.4	148
Bare soils	0	0	0	0	–

SEDIMENT RETENTION.—The sediment retention model is directly related to the water services. The excessive soil erosion can reduce the water quality and agricultural productivity, increase flooding, and pollutant transport (Duarte *et al.*, 2016). In relation to sediment retention, water purification is the main service provided by the forests in the study region, as the rivers are not used for navigation. In other regions, however, rivers are vital transportation networks and in that case keeping them navigable would imply additional costs that could be avoided by this same ecosystem service.

To model the sediment retention in the Paraitinga region, we used the Sediment Retention model of the software InVEST v. 3.2. The InVEST software is based on the Universal Soil Loss Equation (USLE) and estimates the potential for soil loss depending on geomorphological and climate conditions (Sharp *et al.* 2016).

The USLE uses information such as land use patterns, soil properties, rainfall data, and elevation to provide biophysical parameters to sediment retention model (equation 1). The InVEST's model considers that in areas where rainfall intensity is high, there is a high chance that soil particles will be transported (Tallis *et al.*, 2013).

$$\mathrm{USLE} = R \times K \times \mathrm{LS} \times C \times P \quad (1)$$

where R is the rainfall erosivity, K is the soil erodibility factor, LS is the slope length-gradient factor, C is the crop-management factor and P is the support practice factor. The result of the USLE is the annual estimation of soil loss due to water runoff, measured in ton/hectare/year.

The InVEST model calculates directly the LS factor, yet it does not provide all the data necessary to run the model. We estimated the other USLE parameters using Geographic Information System (SIG) tools. To estimate the rainfall erosivity we used the inverse distance-weighted method to interpolate monthly and annual rainfall data from 15 meteorological stations, during

1970–2006 yr. The Embrapa's soil map, in the scale of 1:5,000,000 was used to generate soil erodibility index. The CP factor was calculated using the land use map described above and reference data. These layers are presented in Fig. 2.

The specific values used to estimate erodibility factor were obtained from reference data considering regions with the same biophysical characteristics of our study area (Machado *et al.* 2009, Silva *et al.* 2010, Goméz 2012, Sharp *et al.* 2015, Duarte 2014, Pacher 2014, Sinisgalli *et al.* 2014, Souza-Júnior *et al.* 2014, Fig. 2). To represent the elevation we used the Digital Elevation Model (DEM), in a 30 m resolution, (TOPODATA, 2015).

To evaluate the socioeconomic benefits associated with sediment retention, we obtained local values from the literature (OIKOS 2015). These values were R$ 0.0149 (US$ 0.00383/m^3) as the regional cost of removing sediments from water in order to achieve the quality needed for domestic consumption, a usage flux of 2500 L/s based on actual water consumption in the region, and a density of the sediments suspended in the water of 3.04 ton/m^3. The sediment model was applied for all 176 subwatersheds.

We also estimated what would be the value of the sediment retention ecosystem service if the costs for dredging the river were added. In this case, we used dredging costs of US$ 4/ton.

OPPORTUNITY COSTS.—To calculate the opportunity cost of natural regeneration, we used the land prices (R$/hectare) as a proxy for the long-term expected profit of that land (*e.g.*, Crouzeilles *et al.* 2015). We used the land price values for different land uses surveyed by FNP (2015) (Table 3).

HABITAT AVAILABILITY.—To analyze the habitat availability *for species with different dispersal activities* in the landscape, we divided the

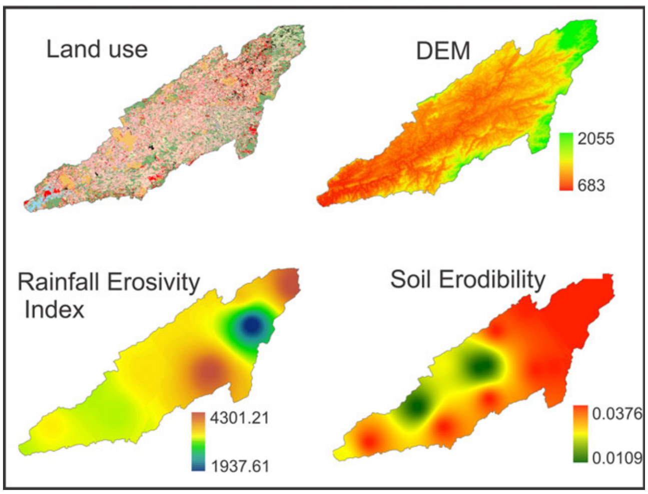

FIGURE 2. Maps of the land-use, elevation using the digital elevation model (DEM), rainfall erosivity and soil erodibility required to calculate the Universal Soil Loss Equation (USLE) for the sediment retention model in the software InVEST. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3. *Land prices (per hectare) in Paraitinga region, at the Brazilin Atlantic Forest. These prices are expressed considering the exchange rate in 18 December 2015 (US$ 1 = R$ 3.89) and where obtained from FNP (2015).*

Land use	R$	US$
Crops	26,333	6769
Pastures	11,992	3083
Degraded and abandoned pastures	10,883	2798
Timber plantations and others	14,860	3820

Paraitinga region into hexagons of 10,000 ha. Only hexagons with more than 50 percent of its area inside the study area were considered in this analysis, totaling 28 hexagons (Fig. 1). These landscape sizes, ranging from 5000 up to 10,000 ha, are consistent with previous studies that quantified the effects habitat loss and fragmentation on biodiversity in the Atlantic Forest (*e.g.*, Crouzeilles *et al.* 2014, Tambosi *et al.* 2014).

For each landscape hexagon, we analysed the habitat availability using the Probability Connectivity index (*PC*). This index considers the habitat amount through patch attribute (in this study patch size) and also the landscape connectivity through species response to habitat configuration (in this study the probability of species dispersal between habitat patches) (Saura & Pascual-Hortal 2007) as follows:

$$\mathrm{PC} = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p_{ij}^{*}}{A_L^2} \quad (1)$$

where n is the total number of patches, a_i and a_j are the patch attributes, p_{ij}^{*} is the maximum product probability of all possible paths between i and j, and A_L^2 is the square of the landscape area (Saura & Rubio 2010). The probability of a path from one patch to another is the product of dispersal probabilities for all connections between these two patches. Thus, the maximum product probability is the path with highest connection probability among all possibilities between two patches. PC index varies from 0 (no habitat available) to 1 (maximum habitat availability). We calculated PC using the software Conefor Sensinode 2.5.8 command line version (www. conefor.org; Saura & Torné 2009).

As habitat availability is species' specific, we estimated *PC* considering three mean dispersal abilities (100, 1000, and 3000 m) based on the review of Crouzeilles *et al.* (2010) for Atlantic Forest species. To represent these mean dispersal ability values, we considered a 50 percent probability of species direct dispersal between two patches, for example, a species with 100 m dispersal ability has 50 percent probability to cross patches that are 100 m apart. We used a one-way analysis of variance (ANOVA) followed by the Tukey *post-hoc* test to identify significant differences in habitat availability among the scenarios of land use/cover for each simulated species. This analysis was performed in R 2.12 (R Core Development Core Team 2011).

RESULTS

LAND-USE/COVER.—The Paraitinga basin is occupied predominantly by pastures, with 30% of the region being managed pasturelands, 21% degraded pasturelands, and 10% abandoned pasturelands showing evidence of natural regeneration – totaling 61% of the basin area (Table 4). The second predominant land use is represented by old growth forest (20.6%), while secondary forests cover 6% of the study area. In the scenario 2, the abandoned pastures were allowed to recover naturally, increasing the cover of secondary forest to 15.4% (Table 4).

ECOSYSTEM SERVICES.—*Climate Change Mitigation.*—Allowing the 24,033 hectares of abandoned pastures to become secondary forests would sequester 1.68 million tons of carbon, or 6.18 million tones of CO_2 (Table 5) in 20 yr. The economic value of this climate change mitigation service varies from US$ 21.2 million (US$ 882/restored hectare) to US$ 81.1 million (US$ 3374/restored hectare) depending on the price of carbon and discount rate used. For an intermediate scenario (US$ 10 per ton of CO_2 and a discount rate of 5%), the value is US$ 47.7 million (US$ 1,981/restored hectare) (Table 6).

Sediment Retention.—Transitioning from the current land-use to one where abandoned pasturelands are allowed regenerate (Scenario 2) would reduce sediment load into rivers by 570,000 tons annually (Table 7). On one extreme, dredging these sediments out of the river would cost US$1.17 million annually, with a net present value (using a time horizon of 20 yr and a discount rate of 5%) of US$ 14.61 million (US$ 608/hectare restored). On the other hand, rivers in the region are currently not used for transportation or electricity generation, with the main direct use being household consumption. The natural regeneration of abandoned pasturelands would reduce the costs of purifying the water that is actually consumed every year by US$ 810 per year or a NPV of US$ 10.094 (US$ 0.37 per restored hectare).

Opportunity Costs.—The opportunity costs of converting abandoned pasturelands into secondary forests were conservatively estimated at US$ 67.24 million, based on the land price per hectare for degraded pasturelands. In reality the selected areas already show signs of abandonment and it is likely that the real opportunity costs are lower than the ones estimated here.

Habitat Availability.—The habitat availability varied among the scenarios of land use/cover (scenarios 0, 1, and 2) and such result was affected by species dispersal ability (100, 1000, and

TABLE 4. *Current land use (S1) and land use if abandoned pastures recover naturally to secondary forests (S2).*

Land use description	S1 (hectares)	S1 (%)	S2 (hectares)	S2 (%)
Degraded areas	5120	2.1	5120	2.1
Burned soils	5727	2.4	5727	2.4
Urban areas	492	0.2	492	0.2
Water	3416	1.4	3416	1.4
Crops	80	0.0	80	0.0
Secondary forests	13,165	5.5	37,198	15.4
Old growth forests	46,025	19.1	46,025	19.1
Managed pastures	75,372	31.2	75,372	31.2
Degraded pastures	51,646	21.4	51,646	21.4
Abandoned pastures	24,034	10.0	–	0.0
Timber plantations	15,663	6.5	15,663	6.5
Bare soils	686	0.3	686	0.3
Total	241,425		241,425	

TABLE 5. *Carbon stocks (in ton/carbon) for scenarios 1 and 2, and the change from the scenario 1 to the scenario 2.*

Land use	Carbon Stock (S1)(tC)	Carbon Stock (S2)(tC)	Change (S2-S1)(tC)
Degraded areas	–	–	–
Burned soils	–	–	–
Urban areas	29,440	29,440	–
Water	–	–	–
Crops	5786	5786	–
Secondary forests	2,322,230	6,561,773	4,239,543
Old growth forests	11,773,198	11,773,198	–
Managed pastures	8,012,056	8,012,056	–
Degraded pastures	5,489,937	5,489,937	–
Abandoned pastures	2,554,781	–	−2,554,781
Timber plantations	2,322,872	2,322,872	–
Bare soils	–	–	–
Total	32,510,299	34,195,061	1,684,762

TABLE 6. *Economic value of the climate change mitigation service, under different assumptions.*

Discount Rate	(@5 US$/t CO_2)	(@10 US$/t CO_2)	(@15 US$/t CO_2)
7.5%	21,201,291	42,402,582	63,603,873
5.0%	23,850,352	47,700,704	71,551,057
2.5%	27,032,760	54,065,520	81,098,280

TABLE 7. *Sediment retention and export.*

	S1	S2	Difference
Total tons of sediment (Mton. / year)			
Retention	52.03	52.60	0.57
Total value for water purification service (US$)			
Retention	927,440	937,530	10,094
Area value for water purification service (US$/hectare)			
Retention	n/a	n/a	0.37
Total value for navigability services (million US$)			
Retention	1333.49	1348.10	14608.66
Area value for navigability services (US$/hectare)			
Retention	n/a	n/a	607.84

3000 m) (Fig. 3). For species with short dispersal ability (100 m), all scenarios differed significantly from each other (P = 0.04 for S0–S1 and P < 0.001 for S0–S2 and S1–S2) (Fig. 3). Secondary forests increased substantially habitat availability in relation to old growth forests (scenario 0 vs. scenario 1), while natural regeneration of abandoned pasturelands substantially increased habitat availability in relation to both old growth forests only and old growth + secondary forests (scenario 2 vs. scenario 0 and 1 respectively). For species with intermediate and large dispersal ability (1000 and 3000 m, respectively), only scenarios S0 and S2, and S1 and S2 differed significantly (P < 0.001 in all cases). Thus, for these species natural regeneration in abandoned pasturelands substantially increased habitat availability in relation to both old growth forests only and old growth + secondary forests (scenario 2 vs. scenario 0 and 1 respectively). For species with intermediate and large dispersal abilities, there was no complementary value of secondary to old growth forests (scenario 0 vs. 1) in terms of habitat availability for species.

DISCUSSION

Our results show that the natural regeneration of abandoned pasturelands can improve the provision of ecosystem services and habitat availability. Over 20 yr, the economic value of the two ecosystem services for which we performed economic valuation, climate change mitigation, and sediment retention (US$ 882 to US$ 3982), can already account for 31.5–142.0 percent of the opportunity costs in the Paraitinga region. Our central estimate for the climate change mitigation service alone would account for 71 percent of the opportunity costs. In addition, secondary forests (especially for species with short dispersal ability) and natural regeneration of abandoned pasturelands can complement the value of old growth forests in terms of habitat availability for species with different dispersal abilities.

It is broadly recognized that habitat availability increases as species' dispersal abilities increases (*e.g.*, Saura & Rubio 2010, Crouzeilles *et al.* 2013, 2014, 2015). Nonetheless, lack studies showing how species' dispersal ability affects the relative contribution of the natural regeneration to habitat availability in landscapes; the main study result we present in this article. In the Paraitinga region, even the small naturally regenerated forests that may arise as pasturelands are abandoned, would increase habitat availability for all species, although to different extents. Only for the less mobile species (100 m of dispersal ability) does the contribution of secondary forest significantly improve the amount of habitat availability when compared to scenario 0 (considering old growth forests only). It suggests that those species are more strongly affected by the spatial configuration of secondary forests. Many empirical studies have shown that species with short dispersal ability are more sensitive to habitat loss and fragmentation (Awade *et al.* 2012, Martensen *et al.* 2012, Almeida-Gomes *et al.* 2016). It is important to highlight, however, that the dispersal ability is often correlated with home range and body size (Whitmee & Orme 2012), which may affect the size of the minimum naturally regenerated forest used by species, potentially impacting habitat availability.

It is also important to mention that the effects of natural regeneration could be even more effective if allocation were spatially optimized. In that respect, our results show the importance of planning landscape restoration in a way that maximizes the increment of habitat availability (*e.g.*, Tambosi *et al.* 2014; Crouzeilles *et al.* 2015). Natural regeneration tends to occur in areas with low socioeconomic gains and high ecological resilience (Holl & Aide 2011), yet it may not result in the highest increment for habitat availability. On the other hand, active restoration, if spatially planned to occur in areas with the highest benefits for habitat availability, can greatly increase the cost-effectives of this initiative. Crouzeilles *et al.* (2015), for example, showed that planning landscape restoration considering habitat availability can result in the strategy with the highest benefits to biodiversity per unit cost in the Brazilian Atlantic Forest. Thus, our simulations demonstrate how landscape context can affect the ecological value of the natural regenerating secondary forests for biodiversity persistence (a highlighted question by Bowen *et al.* 2007). It also provides insights on how to integrate land-use change modeling and habitat availability analysis – a scarce result to be found in up-to-date literature related to landscape connectivity (Correa Ayram *et al.* 2015).

Spatial optimization is also important when considering scaling up forest restoration and to avoid potential displacement. Such displacement (or leakage) of agricultural production could

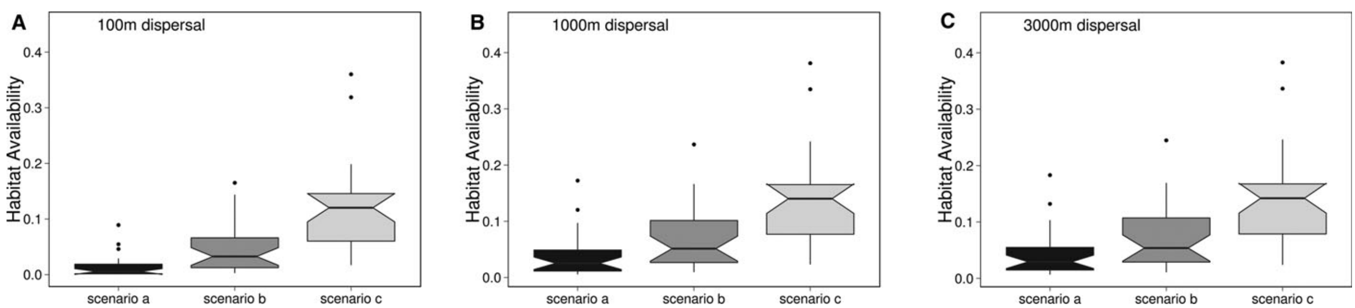

FIGURE 3. Habitat availability for species with short (100 m), intermediate (1000 m), and large (3000 m) dispersal ability in the different scenarios of land use/cover. Current old growth forests only (Scenario 0 – A), current land use (Scenario 1 – B) and land use if abandoned pastures recover naturally to secondary forests (Scenario 2 – C).

result in pressure for deforestation in other regions (Latawiec *et al.* 2015). In this regard, a properly planned large-scale restoration in the Paraitinga watershed has a high potential for avoiding this issue, since the current stocking rates of pasturelands in the region range from 0.8 to 1.4 Animal Units (AU) per hectare, while the potential stoking rate can be as high as 3.79 AU/ha (Alves-Pinto *et al.* in press). Increasing productivity in the region to half of the potential would be enough to spare 76 thousand hectares of pasture area for other uses (Alves-Pinto *et al.* in press). This means that improvement in the cattle-ranching practices alone could accommodate all the natural regeneration proposed in the scenario 2.

Our study further illustrates an important aspect about the valuation of ecosystem services: the same biophysical service can lead to very different economic values, depending exclusively on how beneficiaries relate to the service in question. In the Paraitinga basin, the utility of increased sediment retention as a consequence of natural regeneration of abandoned pasturelands is limited to avoiding the need for water purification for household consumption. This represents a very small fraction of the river flow, yielding a value of US$ 0.37 per naturally regenerated hectare. But in other basins where the rivers are used for navigation or for hydroelectric power, the economic value of this service could reach as high as US$ 608 per restored hectare.

Our results can also help in designing a payment for ecosystem services (PES) scheme. One key element is the spatial distribution patterns of sources of services and the associated beneficiaries, which should inform the allocation of incentives and costs of PES schemes. It can also suggest the potential of different ecosystem services to finance a PES scheme. In the case analyses done in this study, although the potential for such a scheme based on local ecosystem services might be relatively low, there is a very high potential for such a scheme based on the global ecosystem service of climate change mitigation (Tables 5 & 6). Therefore, our results reinforce recent outcomes that demonstrated the potential of secondary forests in the Neotropics for carbon sequestration (Poorter *et al.* 2016) and, as a consequence contribute to climate change mitigation (Chazdon *et al.* 2016). Such a scheme could provide important incentives for natural regeneration in the region.

The incentives to which a farmer is exposed, however, goes beyond direct and explicit financial incentives. The revised version of the Brazilian 'Forest Code' will make public agricultural credit conditional to environmental compliance with the Forest Code. Among other requirements, the Forest Code demands that farmers in the Atlantic Forest restore and/or preserve 20 percent of their farm's total area as Legal Reserve, also including Areas of Permanent Preservation (APP's) that considers riparian areas, hilltop, and steep slopes (Brancalion *et al.* 2016, Latawiec *et al.* 2016). Recent estimates suggest that up to six million hectares would need to be restored in the Atlantic Forest alone (Soares-Filho *et al.* 2014). Farmers must provide plans for restoring their possible forest deficits but active ecological restoration (*e.g.*, complete planting) in the country is costly, estimated around US$ 5150.00/ha, involving seedling acquisition, replanting and monitoring (Rodrigues *et al.* 2011). If an area equivalent to the abandoned pastures was actively restored, instead of naturally regenerated, it would cost US$ 124 million. Therefore, natural regeneration may offer a cheaper alternative to comply with the Forest Code, and have a positive impact on the provision of ecosystem services in the region.

A related important aspect when designing incentive schemes is that unintended consequences of 'positive' incentives should always be taken into account. For instance, natural regeneration was suppressed in the Atlantic Forest when the Atlantic Rainforest Law (Brasil 2006) was introduced. The Law prohibited the clearing of areas on which intermediate natural regeneration was observed. Although intended to help to foster natural regeneration, an unintended result was that the farmers started to regularly burn the initial stages of naturally regenerating areas in order to avoid losing the right to use that land as pasture or croplands. Similar examples can be found elsewhere (Román-Dañobeytia *et al.* 2014).

In this study, we included some elements of uncertainty in our estimation of climate change mitigation service (by using different prices of carbon and discount rates). Future studies could include improved treatment of uncertainties associated with the biophysical and socioeconomic processes involved.

CONCLUSIONS

Natural regeneration provides a range of benefits to human societies and it may play a key role if ambitious global and national restoration targets (*e.g.*, the New York Declaration on Forests and Atlantic Forest Pact, respectively) are realized (*e.g.*, Chazdon *et al.* 2016). Our analysis shows the importance of improving the understanding of costs and benefits of restoration, especially natural regeneration, and showed how this can affect the provision of ecosystem services and biodiversity conservation in a spatially explicit model. The biodiversity conservation cannot be properly valued in financial terms as its main benefit is providing the ecological base for all the other ecosystem services, *e.g.*, through species seeds dispersal. But an improved understanding of current and potential incentive structures, financially explicit, is crucial to ecosystem services, so that societal benefits can be better aligned with those of the final decision maker, the farmer. This alignment is essential for natural regeneration to realize its promise of providing cost-effective benefits to nature and human societies at large-scales.

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