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Valuable habitat and low deforestation can reduce biodiversity gains from development rights markets

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Abstract

1. Illegal private land deforestation threatens global biodiversity, even in areas with native habitat requirements stipulated by law. Compliance can be improved by allowing landholders to meet legal reserve requirements by buying and selling the rights to have deforested land through a Tradeable Development Rights system (TDR). While this policy mechanism may prevent native habitat area loss, the spatial pattern of reserved areas will shift, creating novel landscape patterns. The resulting altered fragmentation and connectivity of habitat will impact biodiversity. TDR may also allow landholders to earn rent on land they never intended on converting, resulting in additional deforestation elsewhere and net habitat loss.
2. We construct a simulation model to explore the potential implications for biodiversity when development rights can be traded, compared with the landscape resulting from enforced individual compliance with deforestation laws.
3. We find that where future deforestation is very likely, a TDR market can provide better outcomes for both biodiversity and agriculture, resulting in more connected habitat networks with larger fragments and fewer edge effects. However, the TDR market can be harmful if future deforestation is unlikely, or if one habitat type is tightly spatially correlated with high economic returns from agriculture.
4. *Policy implications*. Allowing landholders to buy and sell the rights to keep more cleared land than legally stipulated will result in transformed multiuse landscapes. Losses of native habitat in some areas will be offset in others. We conclude that trading forest development rights has the potential to improve habitat configurations, but that careful consideration should be given to current species distributions and likely future deforestation scenarios.

KEYWORDS
biodiversity conservation, deforestation, economic incentives, land-use change, market mechanisms, offsets, tradeable development rights, transferrable quotas

1 | INTRODUCTION

Balancing economic development and ecological sustainability is a complex problem. One way to achieve both goals is by setting quotas and distributing permits for environmentally degrading activities. This method can be extended to allow permits to be traded between stakeholders. Quotas place a rigid, legal limit on the extent and magnitude on destructive economic activities with the aim of reducing the overall impact of, for example, fishing (Branch, 2009), hunting (Whitman, Starfield, Quadling, & Packer, 2004), greenhouse gas emissions (Springer, 2003) or deforestation (Corbera & Schroeder, 2011). In areas with a significant threat of land-use change, Tradeable Development Rights (TDR) can be allocated to landowners, stipulating the proportion of their land that can legally be developed (Harman, Pruetz, & Houston, 2015; Menghini, Gemperle, Seidl, & Axhausen, 2015; Pruetz & Standridge, 2008). Landholders must decide whether to meet their development allowance and conservation requirements on their property, or sell their development rights to other landholders (Wissel & Waetzold, 2010).

Allowing permits to be traded ensures that the magnitude of any degradation is maintained but redistributes the impacts throughout communities, time and space. Resulting landscape patterns are affected by the decisions of individual landholders, acting to maximize individual utility, and therefore are unlikely to produce configurations that are optimal for conservation (Armsworth et al., 2012). Some ecological services, such as carbon storage, are mostly unaffected by spatial distribution—the location of the stored carbon is largely irrelevant, only the amount matters (Potts, Kelley, & Doll, 2013). On the other hand, biodiversity conservation and other localized ecosystem services are heavily dependent on spatial distribution and composition (De Oliveira, De Carvalho Júnior, Gomes, Guimarães, & McManus, 2017; Pickett & Cadenasso, 1995). Global food demand is causing substantial land-use change in high biodiversity areas, where the spatial distribution of agricultural expansion affects biodiversity and ecosystem function through fragmentation, isolation and increased proliferation of destructive species (Chaplin-Kramer et al., 2015; Gibbs et al., 2010; Luskin et al., 2017). Generally, fragmentation reduces species diversity and homogenizes species composition with a shift towards edge, generalist and highly dispersive species (Uehara-Prado, Brown, & Freitas, 2007). Increased access to habitat areas can increase the opportunity for harmful invasive species introduction (Coutts, Helmstedt, & Bennett, 2017; Southwell et al., 2016). Therefore, altering the spatial distribution of environmentally degrading activities through tradeable permits has the potential to significantly alter ecological outcomes.

Because of this spatial dependency, the ecological implications of TDR are not fully understood. Recent TDR research has focused on revisions to Brazil's Forest Code that allow for trading of existing legally mandated development rights (Soares-Filho et al., 2014). Most conservation land in Brazil is on private property, so compliance with private land-use regulations drives conservation outcomes in Brazil. Almost a third of landholders Mato Grosso have illegally cleared more than the legal limit on their properties, while around a sixth of landholders are yet to clear up to the limit (Stickler, Nepstad, Azevedo, & McGrath, 2013). To promote participation and compliance, new provisions will allow under-compliant landholders to buy land-clearing rights from over-compliant landholders who have more native vegetation than required (Silva et al., 2011). Increased deforestation would be a perverse and undesirable outcome from this law, so no future illegal deforestation will be allowed within this market; trades will only be allowed for deforestation that occurred prior to implementing the law (Nunes et al., 2016). A TDR market in Brazil could erase over half of current legal reserve debt as well as prevent millions of future deforested hectares on over-compliant properties (Soares-Filho et al., 2014).

Predicted ecological outcomes from a TDR in Brazil have been modelled only at a coarse scale. Area of supply and demand of development rights have been identified nationally, giving broad-scale insight into areas that will increase or decrease in native forest under the policy, and estimates of total area that will be preserved (Chomitz, 2004; May, Bernasconi, Wunder, & Lubowski, 2015; Micol, Abad, & Bernasconi, 2013). Trading is predicted to lead to increased development in agriculturally productive areas, paired with greater native habitat protection in less productive areas. Finer scale predictions of TDR trades across Brazil identify whether municipalities are net buyers or net sellers of development rights (Soares-Filho et al., 2016). These utilize precise data and provide an excellent basis for understanding the economic, carbon storage and greenhouse gas implications of the TDR market. However, changes to habitat connectivity and fragmentation occur at a much finer, sub-property scale. Environmental and economic data are not available at such a fine-scale level across most of the country (and indeed across most countries).

Existing analyses of TDR schemes in Brazil and elsewhere do not explicitly model the uncertainty around landholder actions. In emissions trading schemes, this uncertainty is manifested in the potential for "hot air" trades, where an over-compliant participant who has no intention to exercise their excess rights sells them to an under-compliant participant (Den Elzen & De Moor, 2002). The purchaser can then exceed legal limits without effectively reducing the environmental impact of the whole system. In a deforestation context, landholders with more native habitat than needed may not ever intend to develop their entire permitted area. Biodiversity conservation, rather than money, is the motivation of many landholders (87%) who participate in conservation schemes (Horton, Knight, Galvin, Goldstein, & Herrington, 2017). Landholders who gain yield-increasing ecosystem services from native habitat are also likely to maintain more native habitat than required (Costanza et al., 1998; Dee, De Lara, Costello, & Gaines, 2017), while others have a sense of social or environmental responsibility to maintain native vegetation (Chan et al., 2016). In these circumstances, TDRs may allow landholders to earn rent on land they never intended on converting (May et al., 2015). These resulting "hot air" trades offset clearing elsewhere with no realized ecological benefit (Den Elzen & De Moor, 2002).

Addressing this gap requires exploring how different land-use change scenarios resulting from a TDR market will affect biodiversity. While these markets can prevent the net conserved area loss, the reserved areas are spatially shifted creating novel landscape patterns. The new reserved site network might not retain the same connectivity or fragmentation as the previous landscape, and specific habitat types might not be equally represented. Here, we investigate how trading environmental reserve quotas changes biodiversity conservation outcomes compared with enforced individual compliance. The spatial configuration of habitat on each property affects the biodiversity implications of a TDR trading scheme. Since land-use maps and change predictions are not available at that scale, we use simulation models to determine general trends likely to emerge in different land-use scenarios. We model the predicted native habitat and agriculture patterns resulting from these two policies, assessing outcomes with multiple graph-based landscape metrics. We incorporate potential agricultural profits into the model and assess the economic impact as the total agricultural income from the landscape. We compare outcomes under four different assumptions about the initial land-use patterns, from random initial land-use patterns to those predicted by economic value. We observe predicted land-use outcomes first in a heterogeneous landscape, then around a permanent conservation reserve or area of irreplaceable habitat, and finally with different levels of deforestation pressure.

2 | MATERIALS AND METHODS

To explore and quantify the impact of a TDR market on biodiversity, we developed and assessed simulated land-use changes. First, we constructed a Monte Carlo simulation model of landscapes and land use with spatially autocorrelated agricultural productivities and habitat distributions. Second, we applied an economic model to predict the landowners who traded part of their quota of development rights. Third, we measured impact on biodiversity with a suite of landscape metrics (connectivity, fragment spatial distribution, edge-to-area ratios and habitat representation). We used graph theory to assess these landscape quality metrics quickly and transparently by considering each patch as a node, and borders between patches as edges (Urban & Keitt, 2001). We used R version 3.0.3 and igraph package version 1.0.1 for all our analyses. All code is deposited at Dryad Digital Repository (Helmstedt & Potts, 2018).

2.1 | Initial landscape

For a given landscape, we divided the area into L equally sized, individually owned, square properties (see all model parameters in Table 1). Each property, represented by the binary vector $\{h_1 \ldots h_N\}$, was divided into N land parcels each either agriculture ($h_i = 0$) or native habitat ($h_i = 1$). The amount of native habitat on a landholder's property is $H = \sum_{i \in [1,N]} h_i$. Landholders earn profits either by using their land for agriculture or by selling their environmental reserve quota. We omitted the potential profits gained from timber sales after clearing native habitat, as these values are likely to be small on average in comparison with cumulative agricultural profit over many years. Each parcel in the landscape has a potential economic return from agriculture v_i, representing the maximum possible economic returns from an agricultural crop on that parcel. Soil quality, rainfall and distance to roads, markets and towns are drivers of agricultural productivity, and are autocorrelated in space (Chomitz & Thomas, 2003; Rosa, Purves, Souza, & Ewers, 2013). We simulated these economic returns randomly according to a multivariate normal distribution, which was spatially autocorrelated and therefore tends towards a clustered pattern (Appendix S1).

Land use, ownership, agriculture technology and specific crop productivity all change and can influence the way spatial agricultural patterns have evolved through time (Chomitz, 2004). Therefore, there exist many land-use patterns in different regions even within one country. To explore various potential patterns, we considered four initial land-use scenarios describing the agricultural land and native habitat distribution in a region: "random"; "split" (approximating a forest conversion front); and two types of economic maximizers, "local" and "regional" (Table 1).

To investigate the performance of policy mechanisms in a heterogeneous landscape, we simulated landscapes with multiple (up to 4), spatially aggregated habitat types (Appendix S2). We assumed that each of these habitat types is associated with a suite of species, and so equal protection of habitat classes approximates equal protection of species. Our initial assumption was that there is no correlation between economic returns from agriculture and type of habitat. Relaxing this assumption, we then included a habitat class

TABLE 1 Initial land-use scenarios and model parameters

Name	Distribution of agricultural land
Random	Random according to a uniform distribution
Split	Native habitat on one side of a dividing line and agricultural land on the other (approximates a forest conversion frontier)
Local	Random deforested proportion (uniform distribution), cleared most profitable parcels up to that level
Regional	Random deforestation with probability of clearing scaling positively with economic returns from agriculture (Hargrave & Kis-Katos, 2013)
Parameter	**Definition, value**
L	Number of landholders, 400
N	Number of parcels per property, 4
τ	Proportion of native habitat required on each property, 0.5
τ_0	Initial proportion of landscape that is native habitat, 0.5 (results robust across range [0.25–0.75])
d	Probability of legal deforestation of native habitat, [0–1]
p	TDR price (single parcel), Determined by agricultural profitability of supply and demand parcels

that occurred only on land with high potential economic returns from agriculture.

We also investigated the results both in with and without a permanent native habitat reserve (25% of the total area) centred in the landscape. This area is not available for the TDR, and must remain as native habitat. In a policy context, this could either be a pre-existing legal reserve or an area recognized as irreplaceable habitat (e.g. where high endemism occurs).

2.2 | Baseline scenario: Individual compliance

A legally mandated target proportion T of each property l must be preserved as native habitat and cannot be converted to agriculture resulting in a requirement for τ parcels to be preserved (Table 1). This proportion is the same for both individual compliance and TDR, and therefore the same total native habitat area is preserved in each scenario. In our baseline policy scenario, we assume landholders will preferentially deforest the most productive parcels up to the threshold. Under-compliant landholders (who have more agriculture than allowed) must reforest $\tau - S_l$ parcels; we assumed they will choose to reforest their least productive parcels (Appendix S1). We assumed that landholders have intentionally and rationally chosen where on their lands to deforest, so we did not model any landholders who both reforest and deforest.

Each landholder aims to maximize the profit they earn from their agricultural land, by reforesting or deforesting enough parcels to bring them into compliance. We defined x_i as a decision variable indicating whether an under-compliant landholder chooses to reforest parcel i ($x_i = 1$), an over-compliant landholder chooses to deforest parcel i ($x_i = -1$), or no change is made to the parcel ($x_i = 0$). Each landholder is therefore choosing the set of actions for each parcel, $X = \{x_1, \ldots x_N\}$, according to

$$X^* = \underset{X=\{x_i\}}{\operatorname{argmax}} \sum_i^N v_i(1 - h_i - x_i),$$

subject to the requirements that (1)

$$\tau \leq \sum_i h_i - x_i \leq N$$

and $x_i \epsilon \{-1,0,1\} \forall i$, where v_i is the potential agricultural return on parcel i and h_i is the initial land use of parcel i (1 if habitat, 0 if agriculture).

2.3 | TDR market scenario

Trading development rights allows environmental reserve quotas to be traded for a price rather than forcing de- or reforestation on individual properties. Each landholder is initially allocated the rights to develop up to a legally mandated target $N - \tau$ parcels on their property. Landholders who are initially under-compliant or exactly compliant have expended their rights from the outset. Over-compliant landholders have excess reserve quota, and they face a choice: develop the land they have the rights for, or sell those rights to an under-compliant landholder and commit to maintaining extra native habitat in perpetuity.

In this scenario, a second decision variable is available to each landholder, and they aim to maximize their total profit not only from agriculture but also from trading development rights. Over-compliant landholders will choose to sell development rights for $y \in [0, H - \tau]$ parcels on the market. They will then deforest $H - \tau - y$ parcels, which they will choose to maximize their returns from agriculture. Under-compliant landholders will purchase development rights for $y \in [H - \tau, 0]$ parcels (represented as a negative number sold for this analysis), and then must reforest $\tau - H - y$ parcels. The number of parcels traded, and therefore the number of parcels re- or deforested will depend on the market price of the development rights, and the landholders' potential agricultural profits. Each landholder is therefore choosing both the number of parcels to trade, y, and the reforestation/deforestation actions, X, according to

$$(y^*, X^*) = \underset{(y,X)}{\operatorname{argmax}}\, py + \sum_i^N v_i(1 - h_i + x_i),$$

subject to the condition that (2)

$$\tau \leq \sum (h_i - x_i) - y \leq N,$$

and $x_i \epsilon \{-1, 0, 1\} \forall i$. Here, the terms remain the same as the individual compliance case, while p denotes the market price for a parcel unit of development rights.

The market price and quantity of the quota traded are determined by the parcel potential economic returns from agriculture, and were defined by the supply and demand curves intersection (Menghini et al., 2015). For our simulated landscapes, we mapped those curves and calculated the market price of a single parcel development rights. We used that price to determine which parcels over-compliant landholders would sell, which under-compliant landholders would choose to buy development rights, and which parcels would be either reforested or deforested instead of trading. The results of these trades determined the final land-use maps for analysis. See Appendix S3 for further details of the market model.

2.4 | Modelling hot air trades

Deforestation pressure can vary significantly across landscapes, ranging from almost certain future clearing to areas with very little clearing even of unprotected land (Nolte, Agrawal, Silvius, & Soares-Filho, 2013). To investigate the impact of this heterogeneity on the outcomes from TDR, we defined $d \in [0, 1]$ as the uniformly distributed probability that an over-compliant landholder plans to deforest their excess native habitat. Alternatively, $(1 - d)$ gives the probability that the landholder will never clear that land. When considering the counter-factual individual compliance case for those parcels, we assumed they will remain native habitat even though this pushes the landholder above the required target. In the TDR case, however, this results in hot air trades. In this scenario, we assumed the landholder receives a payment for keeping that parcel as native habitat, and cleared land is offset elsewhere. This results in a net loss of habitat area compared to the individual compliance scenario. This is the only time our model will predict that a different total area is preserved in the two policy scenarios.

2.5 | Assessing biodiversity outcomes

We used five graph theory derived landscape metrics to evaluate how land-use change alters habitat configuration. We used each metric to quantify the ecological value of the predicted landscape resulting from the individual compliance and TDR scenarios. In our results, we focus on the difference between these two scenarios, since this indicates the change in outcome achieved by choosing one policy scenario over the other. To calculate these metrics, we converted landscapes to mathematical graphs, with a node representing each native habitat parcel and an edge connecting orthogonally adjacent parcels (Figure 1). A contiguous patch of native habitat is a cluster of nodes that are connected to each other, but not connected to any other clusters. Where multiple habitat types were modelled, we separated each habitat type into a separate graph.

First, we calculated the probability of connectivity (after Saura & Pascual-Hortal, 2007, see Supporting information), which measures how connected patches of habitat that are separated by space are. A higher probability of connectivity measure indicates that there are more, and shorter, paths of continuous habitat from distant patches. Second and third, we calculated the mean and maximum sizes (i.e. number of nodes) of contiguous native habitat in the predicted landscapes. Fourth and fifth, we calculated two measures of fragmentation: number of fragments, and mean edge-to-area ratio. The number of fragments is given by the number of clusters in the graph, and the edge-to-area ratio of each contiguous patch is the number of potential edges in the cluster that are not connected (which therefore must be connected to agriculture) divided by the number of nodes in the cluster.

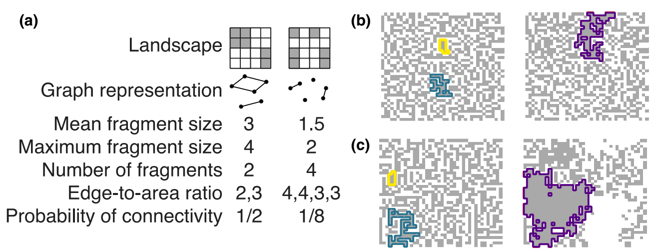

FIGURE 1 Grey indicates native habitat, white indicates agricultural land. Example of (a) metric calculations for two simple landscapes. Edge-to-area ratio is calculated for each fragment as the number of possible edges for each node (4 in this case study) minus the number of actual edges divided by the number of nodes in the fragment. Probability of connectivity is calculated according to (Saura & Pascual-Hortal, 2007); (b) simulated Random land-use landscape with projected individual compliance (left) and Tradeable Development Rights (TDR) market (right), each stemming from identical initial land use; (c) simulated Split land-use landscape. A green border indicates the largest contiguous native habitat fragment, yellow the fragment with the smallest edge-to-area ratio, and purple that both occur in the same fragment

3 | RESULTS

When future deforestation was certain to occur, our modelled TDR market predicted better outcomes for biodiversity than enforced individual compliance for all landscape metrics we considered (Figure 2). Our individual compliance model resulted in a very diffuse landscape, which TDR counteracted resulting in a more connected landscape (at least twice but up to 23.9 times higher mean probability of connectivity, Figure 2a) with fewer and larger maximum fragment sizes (2–9.2 times higher), and significant but small benefits for economic productivity and edge-to-area ratio (Figure 2a).

Not all initial land-use patterns resulted in equal potential improvements with a TDR scheme (Figure 2b–d). The largest gains were possible where the most economically productive areas in a region had been preferentially cleared (the "regional" scenario) and around a forest conversion frontier (the "split" scenario). We saw smaller but significant ecological and economic benefits of TDR in landscapes with random clearing ("random" land use), or randomly distributed local maximizers ("local" scenario). Increased habitat heterogeneity also corresponded with a decreased benefit of trading (Figure 2b). Connectivity and mean fragment size showed the largest relative reductions in landscapes with increased habitat heterogeneity (Figure 2b). When 25% of the area cannot be cleared (for example is already designated as a reserve or irreplaceable habitat), the benefits of a TDR were reduced but were still positive (Figure A1).

When one habitat type exists only on the most profitable land, the result changes. A TDR market disproportionately harms to the economically valuable habitat. This effect depends on the initial land-use pattern. The largest impact occurred when past land clearing was also correlated with high economic returns from agriculture. Our model showed that in this scenario, the TDR can result in the total loss of that valuable habitat type. Random initial land use results in a 14% reduction in that habitat type; a landscape where landholders have maximized their individual profits results in a 21% reduction; and a split landscape shows a 51% reduction.

A TDR was also detrimental to biodiversity if deforestation is halted (Figure 2c,d), and provides negligible benefit if deforestation is controlled (Figure 2c,d) according to our model. Higher benefits were achieved by a TDR market if future legal land clearing is more likely. Above a deforestation probability of 75% ($d = 0.75$), TDR was beneficial according to all habitat metrics and with the highest gains achieved through reduced fragmentation (Figure 2c,d).

Finally, when agricultural profitability was modelled as aggregated strongly in the landscape, a TDR had high benefits compared to individual compliance (Figure 3a–c). As the spatial autocorrelation of profitability decreases (i.e. the landscape becomes more random, see Appendix S1), the magnitude of that benefit decreases. Overall, uncertain deforestation pressure reduces the potential benefits of a TDR but even where deforestation is 75% likely and there is low spatial autocorrelation of profits, a TDR was still slightly beneficial (Figure 3d,e).

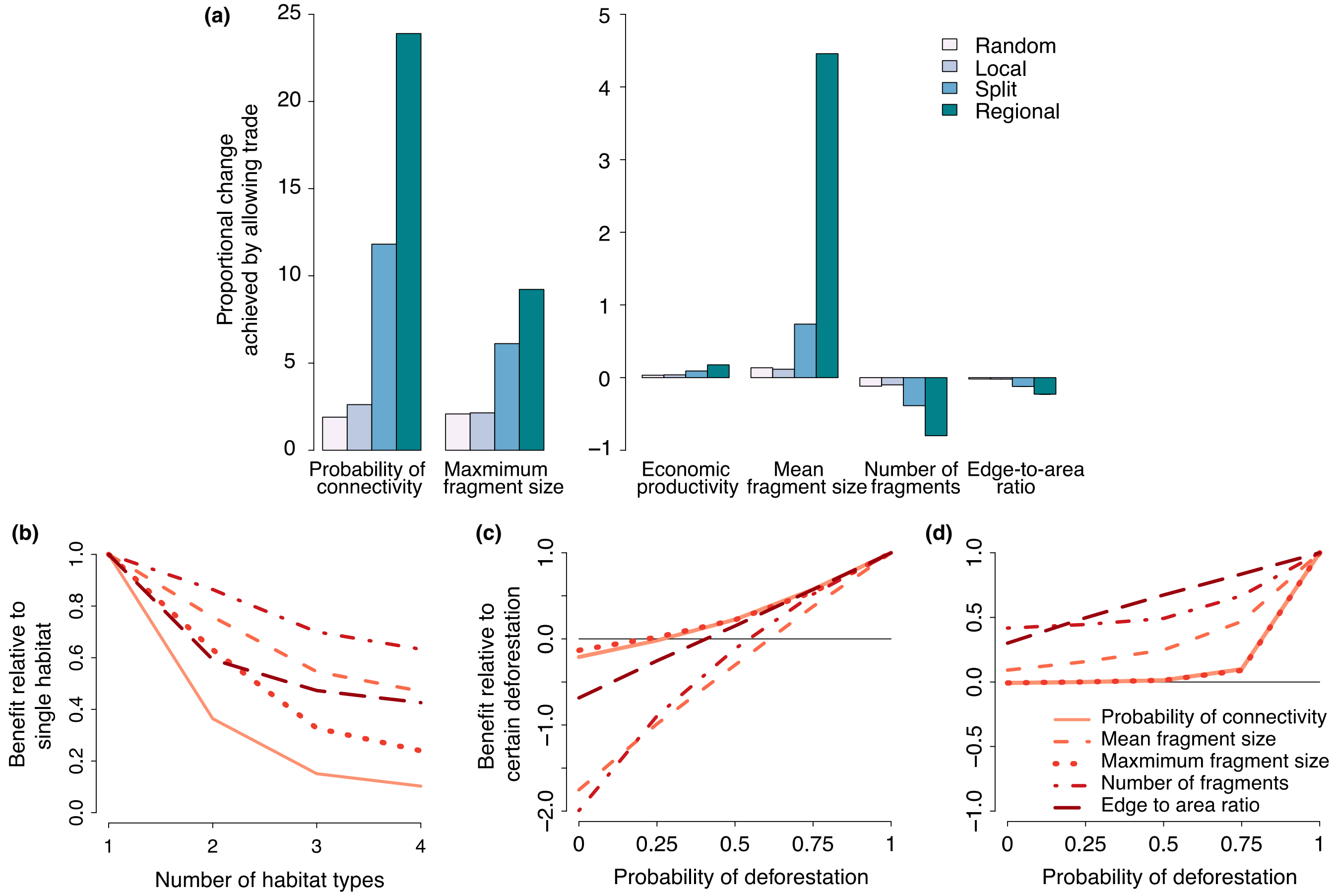

FIGURE 2 (a) Metric outcomes from a post-market landscape compared to a landscape with individual compliance in an area with no reserve, with 50% deforestation allowance, and initial compliance 50% of the entire landscape. Change is measured by (Tradeable Development Rights (TDR)-individual)/individual. Histogram shows mean change. All are proportional changes—positive change means that trade scores higher according to that metric, negative change means individual compliance scores higher. Relative benefits compared to (a) of allowing a trade with: (b) uncertain probability that over-compliant landholders will deforest and a "random" initial landscape (a locally distributed landscape shows similar relationships); (c) uncertain probability that over-compliant landholders will deforest and a "split" initial landscape (a regionally distributed landscape shows similar relationships which are also always positive; (d) "split" initial landscape composed of more than one habitat type (all other initial landscape configurations showed same trend

4 | DISCUSSION

Our model showed that, in general, allowing landholders to trade development rights can result in a more connected native habitat with larger fragments that will have fewer edge effects. However, this result does not hold where either future deforestation is very unlikely, or where one habitat type is strongly spatially linked to potential economic returns from agriculture. We conclude that efforts to implement a TDR market would be detrimental in those areas, and implementation of the market should focus on single-habitat areas with high deforestation pressure. In areas where a TDR is implemented, other interventions must be explored for any species that requires habitat that is strongly correlated with high potential economic returns from agriculture.

If continued legal deforestation is unlikely and therefore hot air trades are a threat, we found that any benefit of TDR markets is dramatically reduced and individual compliance will likely give better ecological outcomes. Specifically, if the probability of clearance on over-compliant properties is less likely than 50%, trading provides no benefit in these simulated landscapes. In these situations, a TDR market allows landholders to earn rent on land they would have protected anyway. Clearing allowed from trades thus results in a net loss for the system—deforestation is offset by land that would never have been cleared, and these hot air trades severely undermine the benefits gained by operating a TDR market. These results confirm predictions and fears of potential perverse outcomes arising from trading development rights where deforestation pressure is low (Den Elzen & De Moor, 2002; May et al., 2015).

Although based on simulation analyses, our results give general insight into where implementing TDR might be most successful from a conservation perspective. We found overwhelmingly that the predicted benefits from TDR are most notable in landscapes where deforestation is observed, where a permanent reserve is absent, habitat is roughly uniform, and the current deforestation patterns have been driven by land values in the region. Landscapes that have been

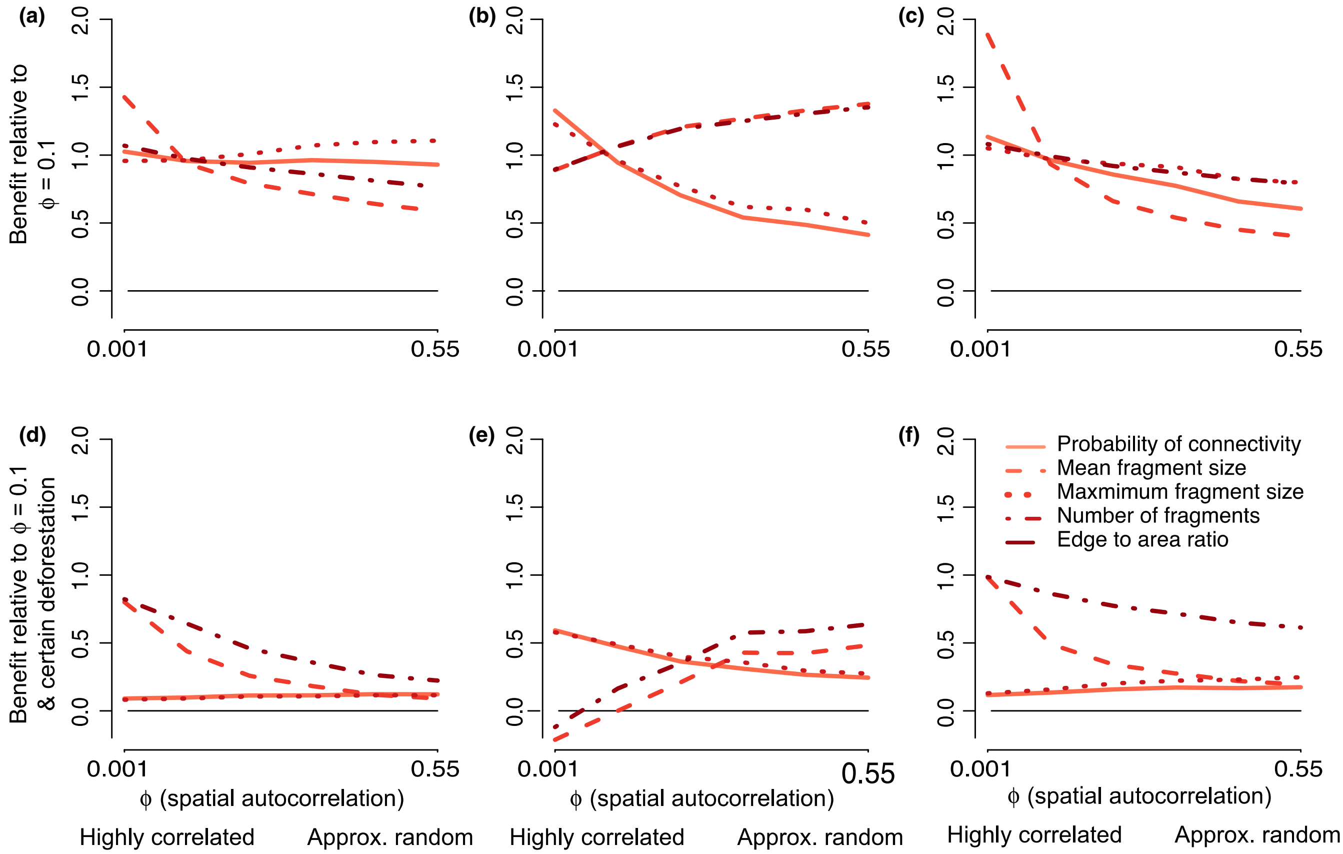

FIGURE 3 Relative benefits compared to Figure 2(a) (which uses $\phi = 0.1$) of allowing trade with varied strengths of agricultural profit autocorrelation (by varying ϕ in Equation A1), probability of deforestation equal to 1 (top row) and 0.75 (bottom row) and (a, d) "split," (b, e) "local", and (c, f) "regional" initial land use

deforested along a forest conversion frontier also benefit substantially from TDR. Future investment in achieving a successfully functioning TDR market would be best spent in these landscapes.

However, implementing TDR trading is not without its risks. It may compound drivers of non-compliance. Inconsistent laws and changing regulations can impede landholders' ability and willingness to maintain working knowledge of a complex forestry policy (Schmidt & McDermott, 2015), and enforcing compliance may be costly and uncertain. We have implicitly assumed that these costs would be equal for either policy by omitting them from our comparison. TDR trading is one of many potential market-based mechanisms for private land conservation, including direct payments for ecosystem services (McDonald et al., 2018). Implementing any of these participatory management strategies will require careful communication and collaboration with relevant stakeholders (Helmstedt, Stokes-Draut, Larsen, & Potts, 2018).

Conservation planning is complex when human behaviour drives outcomes. Here, we have considered two types of landholder utility: economic profit and some environmental utility captured by the hot air trades. In considering those utilities, we have assumed that all landholders have the same attitude to risk and future earnings. Additionally, to compare two potential policies, here we have assumed that these policies will be implemented successfully; that all landholders will comply with either law. This, of course, cannot be guaranteed for either scenario. We do not explore in this study the many, multifaceted legal and policy options available to ensure compliance with the law. Significant areas of non-compliance will impact the results presented here, and will have strong consequences for biodiversity. If this is the case, the biodiversity impacts are caused by the lack of native habitat area rather than its configuration.

Our conclusions are general, without local specificity. They are based on well-supported ecological understanding but could be refined when detailed and fine-scale (within-property) information about ecosystem services, species presence, species response to land-use change, land value drivers, and agricultural conversion drivers become available. Although we have incorporated some habitat heterogeneity and the notion of habitat irreplaceability with the inclusion of habitat classes, this does not capture the full spatial complexity of biodiversity. In reality, biodiversity is unevenly distributed in space even within one habitat type. With current spatial biodiversity data, fine-scaled modelling of these components over broad areas is infeasible. Further advances in remote sensing allowing mapping of fine-scale, sub-property level forest cover across large areas will provide opportunities to test our general findings across real landscapes in Brazil and elsewhere (Pau & Dee, 2016).

Certainly in Brazil, and likely in any area considering a TDR market to limit native habitat loss, there are other unrelated land-use laws and policies enacted. We have made initial steps to consider these here by considering the presence of a legal reserve, but largely these have been omitted. Brazil's Forest Code, for example, requires the preservation of native riparian areas and hilltops over and above any threshold proportion requirements. In some areas, these additional requirements make up most of the over-compliant native habitat Nunes et al. (2016). These additions will alter the connectivity of the landscape regardless of which of the two policy options we have considered is used.

More broadly, TDRs can offer more than biodiversity benefits. Socially, it is an opportunity for small farmers to escape illegal land use permanently and legally (Sparovek, Berndes, Barretto, & Klug, 2012). Ecologically, spatial forest patterns affect ecosystem services other than the biodiversity (Fischer & Lindenmayer, 2007). Forested areas can increase available water quantity, store carbon, and provide habitat for pollinators, whereas agricultural use decreases water quality (Costanza et al., 1998). These ecosystem services increase with contiguous forest area, which we have shown occurs under a TDR scheme. Many ecosystems services beyond biodiversity conservation are highly dependent on the spatial structure of the landscape, and future work on the impacts of TDR on various ecosystem service provisioning would further aid decision makers. We have assumed that all native habitat provides biodiversity benefit, omitting the potential need for assisted migration into remaining fragments (Helmstedt & Possingham, 2017).

Overall, our results indicate TDR have potential for improving habitat connectivity and conserving biodiversity if care is taken in spatial planning. Markets such as those proposed in the Brazilian Forest Code 2012 can result in a more connected landscape with larger fragments and fewer edge effects than enforced individual compliance. This can have substantial benefits for native biodiversity, at no average loss of agricultural profits. However, if the markets are implemented in areas that are unlikely to be deforested in the future or where one habitat type is closely linked to potential economic returns from agriculture, biodiversity will be under even higher threat.

AUTHORS' CONTRIBUTIONS

K.J.H. and M.D.P. conceived the ideas and designed methodology; K.J.H. designed and wrote the model and code; K.J.H. analysed the results; K.J.H. led the writing of the manuscript; M.D.P. edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Code available from the Dryad Digital Repository https://doi.org/10.5061/dryad.344hs (Helmstedt & Potts, 2018).

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