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IDEA AND PERSPECTIVE

The biodiversity-dependent ecosystem service debt

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Abstract

Habitat destruction is driving biodiversity loss in remaining ecosystems, and ecosystem functioning and services often directly depend on biodiversity. Thus, biodiversity loss is likely creating an ecosystem service debt: a gradual loss of biodiversity-dependent benefits that people obtain from remaining fragments of natural ecosystems. Here, we develop an approach for quantifying ecosystem service debts, and illustrate its use to estimate how one anthropogenic driver, habitat destruction, could indirectly diminish one ecosystem service, carbon storage, by creating an extinction debt. We estimate that *c*. 2–21 Pg C could be gradually emitted globally in remaining ecosystem fragments because of plant species loss caused by nearby habitat destruction. The wide range for this estimate reflects substantial uncertainties in how many plant species will be lost, how much species loss will impact ecosystem functioning and whether plant species loss will decrease soil carbon. Our exploratory analysis suggests that biodiversity-dependent ecosystem service debts can be globally substantial, even when locally small, if they occur diffusely across vast areas of remaining ecosystems. There is substantial value in conserving not only the quantity (area), but also the quality (biodiversity) of natural ecosystems for the sustainable provision of ecosystem services.

Keywords

Biodiversity conservation, biodiversity–ecosystem functioning relationships, carbon storage and sequestration, ecological production function, economic valuation, extinction debt, global ecoregions, habitat destruction, natural capital, social cost of carbon.

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INTRODUCTION

Many human activities can drive declines in biodiversity in remaining intact ecosystem fragments, including habitat destruction, nutrient enrichment, exotic species invasions, intense livestock grazing and climate change (Benayas *et al.* 2009; Murphy & Romanuk 2014). Furthermore, ecosystem functioning and services often directly depend on biodiversity (Loreau 2010; Isbell *et al.* 2011; Cardinale *et al.* 2012; Gamfeldt *et al.* 2013; Balvanera *et al.* 2014). While current ecosystem service models often account for direct effects of habitat destruction on ecosystem services through changes in land use and habitat area (Costanza *et al.* 1997; Nelson *et al.* 2009; Bateman *et al.* 2013), such models typically do not account for potentially important indirect effects of this habitat destruction on ecosystem services resulting from changes in biodiversity that occur within nearby remaining ecosystem fragments (Fig. 1). In other words, current ecosystem service models often implicitly assume that intact fragments of forests and grasslands will continue to provide the same flow of benefits per unit area in the future, even though many species could be lost from such fragments.

Here, we begin to explore the extent to which gradual plant species loss that occurs after nearby habitat destruction could diminish the future provision of ecosystem services in remaining ecosystem fragments. That is, we quantify the extent to which an extinction debt (Tilman *et al.* 1994) could create an ecosystem service debt. To do so, we integrate several relationships that have thus far been separately investigated: extinction debt relationships, which specify how nearby habitat destruction gradually drives species loss in remaining ecosystem fragments (Tilman *et al.* 1994, 1997b; Rybicki & Hanski 2013); biodiversity–ecosystem functioning relationships, which specify how species loss alters ecosystem functioning (Schmid *et al.* 2009; Cardinale *et al.* 2011; Reich *et al.* 2012); and ecological production functions, which specify how ecosystem services depend on ecosystem functioning (Daily *et al.* 2009; Nelson *et al.* 2009; Polasky & Segerson 2009; Keeler *et al.* 2012) (Fig. 1).

To what extent does habitat destruction drive species loss in remaining ecosystem fragments? Habitat destruction drives species loss not only in areas where ecosystems are converted to other land uses (He & Hubbell 2011), but also in fragments where ecosystems remain intact (Tilman *et al.* 1994, 1997b; Ewers & Didham 2006; Hanski *et al.* 2013; Rybicki & Hanski 2013). Species that were endemic to the destroyed area are quickly lost, and some additional species present in the remaining ecosystem area are gradually lost due to reduced

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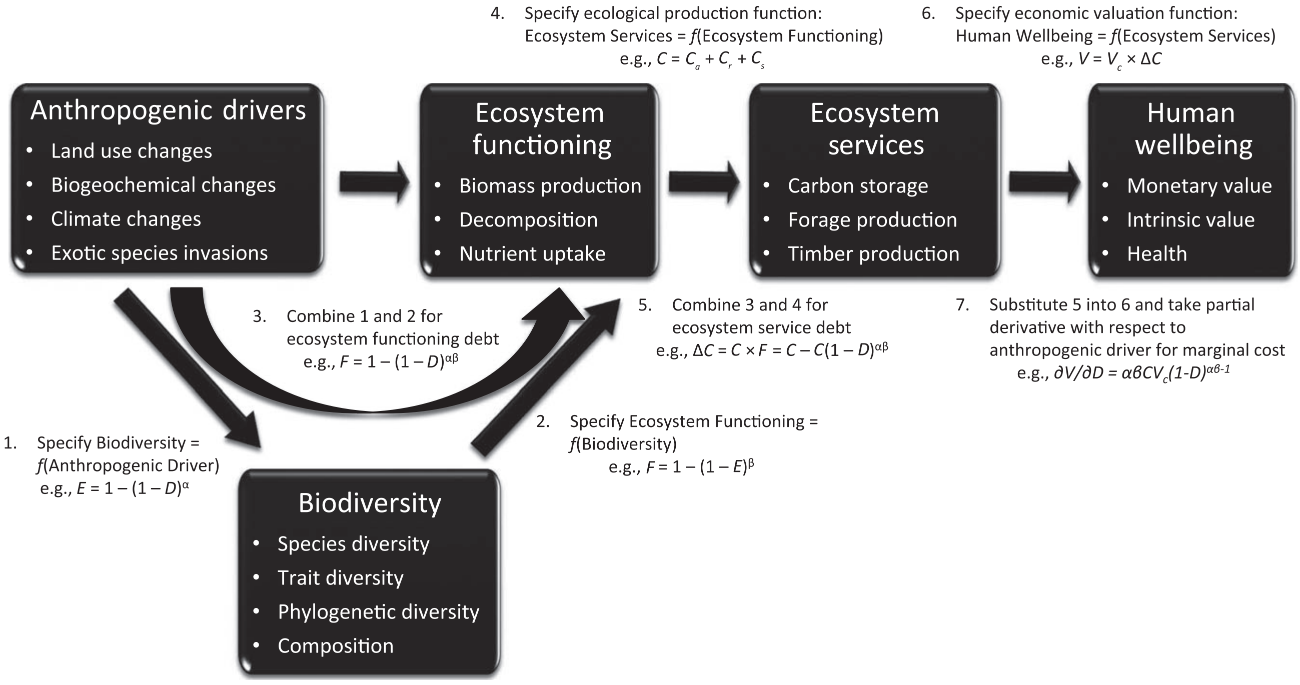

Figure 1 These seven steps outline a general approach for quantifying the extent to which anthropogenic drivers indirectly alter ecosystem services and human wellbeing by altering biodiversity within remaining fragments of ecosystems. Items in boxes are examples, rather than comprehensive lists. Example equations are provided to indicate how destruction of some proportion of habitat (D) causes loss of some proportion of species (E), which then causes loss of some proportion of ecosystem functioning (F), which then causes a given amount of carbon emissions (C_{debt}), with a corresponding social cost (V). See main text for further details on this worked example. There remains considerable uncertainty in each of these relationships, which makes it difficult to predict whether people will obtain a steady flow or a diminishing trickle of future benefits from each hectare of remaining ecosystems.

population sizes or disrupted species movements and interactions (Tilman *et al.* 1994, 1997b; Gonzalez & Chaneton 2002; Hanski *et al.* 2013; Rybicki & Hanski 2013). Here, we focus on the extinction debt: gradual species loss that occurs within remaining ecosystem fragments after nearby habitat destruction.

To what extent does species loss impact ecosystem functioning in remaining ecosystem fragments? Ecosystem processes, such as biomass production, depend on abiotic factors, such as precipitation and soil nutrients, but also strongly depend on the identities and numbers of plant species (Loreau 2010; Cardinale *et al.* 2011; Hooper *et al.* 2012; Reich *et al.* 2012; Tilman *et al.* 2012; Scherer-Lorenzen 2014). Changes in numbers of plant species over time at a particular place can impact ecosystem functioning as much as changes in species composition (Hector *et al.* 2011), global change stressors (Hooper *et al.* 2012), resources, disturbance, or herbivory (Tilman *et al.* 2012).

By combining relationships describing how habitat destruction drives species loss (Fig. 2a), and how species loss impacts ecosystem functioning (Fig. 2b), we can predict the ecosystem functioning debt (Gonzalez *et al.* 2009): the gradual loss of biodiversity-dependent ecosystem functioning caused by species loss due to nearby habitat destruction (Fig. 2c). Current ecosystem service models (e.g. Nelson *et al.* 2009; Kovacs *et al.* 2013) typically assume that remaining ecosystem fragments incur no ecosystem functioning debt, which would only occur if habitat destruction causes no species loss in habitat fragments, or if this species loss has no impact on ecosystem functioning.

APPROXIMATING BIODIVERSITY-DEPENDENT ECOSYSTEM SERVICE DEBTS

In this section we develop an analytical approach for approximating biodiversity-dependent ecosystem service debts. The numbers of the headings and equations below correspond to the numbers and relationships shown in Fig. 1.

(1) Extinction debt relationships

To determine a range of possible extinction debt relationships (Fig. 2a), we used results from multiple theoretical models (Tilman *et al.* 1994, 1997b; Rybicki & Hanski 2013) and empirical studies (Rosenzweig 1995; Leach & Givnish 1996; Gonzalez & Chaneton 2002; Benitez-Malvido & Martinez-Ramos 2003; Wilsey *et al.* 2005; Ewers & Didham 2006; Helm *et al.* 2006). We first explored the range of extinction debt magnitudes predicted by contrasting cases of a theoretical model in which species coexist by a competition-colonisation trade-off (Tilman *et al.* 1994, 1997b). This model predicts a wide range of potential magnitudes for the extinction debt, with the smallest extinction debts occurring when the most competitive species are extremely dominant, when there are few unoccupied sites, and when the ecosystem has many species (Box 1, Figs S1–S3).

Box 1 Using a competition-colonisation model to predict extinction debt magnitudes

Consider a theoretical model of species competing and coexisting by a competition-colonisation trade-off, with the following dynamics for species *i* in a community with S species (Tilman *et al.* 1997b):

$$\frac{dp_i}{dt} = c_i p_i \left(1 - D - \sum_{j=1}^{i} p_j\right) - m_i p_i - \sum_{j=1}^{i-1} c_j p_i p_j \qquad (S1)$$

where c_i, p_i and m_i are respectively the colonisation rate, proportion of sites occupied and mortality rate for species *i*, and D is the proportion of habitat destroyed. Species are ranked from best (1) to worst (S) competitors, and superior competitors ($j < i$) can displace inferior competitors from any site that they colonise. Previous studies have found that the best competitors, which are also the poorest dispersers, were among the first driven extinct by habitat destruction regardless of their abundance, dispersal distance, or reproductive strategy; and regardless of the rate that they competitively displaced other species, the spatial arrangement and rate of habitat destruction, and the size of habitat (Tilman *et al.* 1994, 1997b). The magnitude of the extinction debt, however, varies considerably, depending on the abundance of the best competitors (Tilman *et al.* 1997b). Here, we consider two contrasting cases for the abundance of the best competitors.

First, consider the case where the best competitors are most abundant, there is equal mortality, and the abundance of each species *i* is given by $p_i = z(1-z)^{i-1}$, where *z* is the abundance of the best competitor, which is the most abundant species. In this case, the extinction debt is relatively small, with the proportion of species going extinct (E) increasing with the proportion of habitat destroyed (D) according to:

$$E = \frac{\ln(1-D) + \ln(1-z)}{2\ln(v(1/z-1))} \qquad (S2)$$

where *v* is the abundance of the worst competitor, which is the rarest species ($v = z(1-z)^{S-1}$). This relationship is obtained by analytically determining the colonisation rates that allow species to stably coexist in an intact habitat, the amount of habitat destruction that deterministically drives each species extinct, and then the number of species that are driven extinct by destruction of some proportion of habitat (Tilman *et al.* 1994, 1997b). The bottom line in Fig. S1 shows this relationship for $z = 0.0046$ and S = 1000, which gives the case where 99% of the sites are initially occupied ($\sum_{i=1}^{S} p_i = 0.99$). Note that this is equivalent to assuming that $z = 0.045$ and S = 100 or that $z = 0.37$ and S = 10 for $\sum_{i=1}^{S} p_i = 0.99$. In other words, the relative abundance of the most abundant species increases as S decreases, as previously observed across many plant communities (Rosenzweig 1995). If we assume that < 99% of the sites are initially occupied (Fig. S1), or that there were fewer species (Fig. S2), then the extinction debt would be greater. We considered the relationships shown for $S = 1000$, because the mean and median number of plant species per ecoregion is on this order of magnitude (Kier *et al.* 2005). Thus, we chose parameter values that would more likely under- than over-estimate the magnitude of the extinction debt.

Second, consider the case where the best competitors are the rarest species, there is equal mortality, and the abundance of each species *i* is given by $p_i = iz$, where *z* is again the best competitor, which is in this case the rarest species. In this case, the extinction debt is relatively large, with the proportion of species going extinct (E) increasing with the proportion of habitat destroyed (D) according to:

$$E = \frac{z}{v}\sqrt{\frac{4 + z - \sqrt{(4+z)^2 - 16D}}{2z}} \qquad (S3)$$

where *v* is the abundance of the worst competitor, which is the most abundant species ($v = zS$). This relationship is obtained by analytically determining the colonisation rates that allow species to stably coexist in an intact habitat, the amount of habitat destruction that deterministically drives each species extinct, and then the number of species that are driven extinct by destruction of some proportion of habitat (Tilman *et al.* 1994, 1997b). The bottom red line in Fig. S1 shows this relationship for $z = 0.00000198$ and $S = 1000$, which also gives the case where 99% of the sites are initially occupied ($\sum_{i=1}^{S} p_i = 0.99$). Again, if we assume that < 99% of the sites are initially occupied (Fig. S1), or that there were fewer species (Fig. S2), then the extinction debt would be greater. Thus, our chosen parameter values could underestimate the extinction debt.

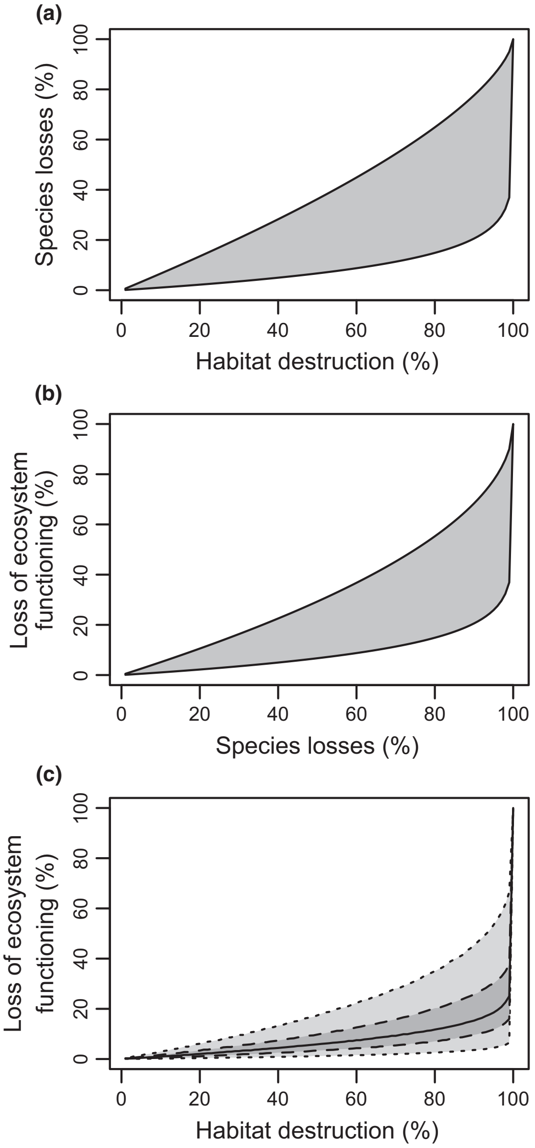

Figure 2 Potential magnitudes of extinction debt (a), biodiversity-ecosystem functioning (b), and ecosystem functioning debt (c) relationships. Habitat destruction creates an ecosystem functioning debt (i.e. gradual loss of biodiversity-dependent ecosystem functioning) when it drives species loss in remaining ecosystems (a), and when species loss causes loss of ecosystem functioning (b). We used theoretical and empirical studies to determine likely magnitudes of these relationships (see *Extinction debt relationships* and *Biodiversity–ecosystem functioning relationships* sections in main text). Combining all possible combinations of curves drawn from uniform distributions within the shaded regions shown in (a) and (b) produces the ecosystem functioning debt relationships shown in (c), where the solid black line indicates the median (0.5 quantile), the dark grey region indicates the interquartile range (0.25 and 0.75 quantiles) and the light grey region indicates the extreme range (0.025 and 0.975 quantiles) of the potential ecosystem functioning debt relationships.

We next explored empirical estimates for the magnitude of the extinction debt. The magnitude of the extinction debt can be empirically estimated by comparing species–area relationships between habitat islands and intact habitats (Gonzalez *et al.* 2009). There are often fewer species per unit area in habitat islands than in intact habitats (Rosenzweig 1995; Leach & Givnish 1996; Benitez-Malvido & Martinez-Ramos 2003; Wilsey *et al.* 2005; Helm *et al.* 2006), resulting in a steeper scaling relationship between species and area for habitat islands (e.g. $S \approx cA^{0.25}$, where S is richness, A is area and c is a constant) than for intact habitats (e.g. $S \approx cA^{0.15}$) (Gonzalez *et al.* 2009). The difference between these relationships reflects the extinction debt that has occurred in habitat islands (Gonzalez *et al.* 2009). That is, if a proportion of habitat of size A has $cA^{0.15}$ species before habitat destruction and only $cA^{0.25}$ species after habitat destruction (where $A = 1 - D$, and D is the proportion of habitat destroyed), then the proportion of species driven extinct (E) is given by: $E = 1 - (cA^{0.25}/cA^{0.15}) = 1 - A^{0.1} = 1 - (1 - D)^{0.1}$ (Fig. S3). For example, this relationship would predict that previous conversion of all but 0.1% of tallgrass prairie in Iowa, USA would leave only 450 of the previously known 897 plant species in the short term ($897 \times 0.001^{0.1} = 450$), which is close to the 491 species found in recent surveys (Wilsey *et al.* 2005). Note, however, that this should be considered a lower bound for the extinction debt. If habitat destruction leads to very slow loss of species (Tilman *et al.* 1994, 1997b; Benitez-Malvido & Martinez-Ramos 2003; Ewers & Didham 2006; Helm *et al.* 2006) such that some species are currently persisting with unviable populations, then contemporary observations of the numbers of species in habitat islands, which are the empirical basis for the species-area exponent of 0.25 for habitat islands (Rosenzweig 1995; Gonzalez *et al.* 2009), will underestimate the extinction debt. Even so, this empirically based lower bound for the magnitude of the extinction debt is close to the lower bound case from the competition-colonisation model (Fig. S3).

Other models that include different assumptions about population and community dynamics can also theoretically estimate the magnitude of the extinction debt. For example, the extinction debt was recently estimated from spatially explicit simulations of habitat destruction for a community consisting of many non-interacting species in a heterogeneous environment (Rybicki & Hanski 2013). For this model (Rybicki & Hanski 2013), the total proportion of species eventually driven extinct (i.e. based on one-fragment species–area relationships; OF-SARs) by a given proportion of habitat destruction (D) was given by: $1–(1–D)^{0.24}$, and the proportion of the species immediately driven extinct because they were endemic to the destroyed area (i.e. based on remaining species–area relationships; RARs) was given by: $1–(1–D)^{0.04}$. The extinction debt, which is the proportion of species driven extinct within remaining habitat (i.e. excluding extinctions of species endemic to the destroyed area), can be given by the difference between these two proportions: $(1–D)^{0.04}–(1–D)^{0.24}$. On average, across a range of parameter space, this model predicts extinction debt magnitudes that are intermediate to those produced by the contrasting cases of the competition-colonisation model (Fig. S3). Breaking the remaining habitat up into multiple fragments, and moving these fragments farther from one another, would tend to increase the extinction debt (Hanski *et al.* 2013; Rybicki & Hanski 2013).

We found that many functional forms can describe extinction debt relationships (Fig. S3). A fairly flexible and generic form for the extinction debt is given by:

$$E = 1 - (1 - D)^{\alpha} \tag{1}$$

where the proportion of species driven extinct (E) increases with the proportion of habitat destroyed (D), and α is a constant that indicates the magnitude of the extinction debt (Figs 2a, S3, S4).

(2) Biodiversity–ecosystem functioning relationships

To determine a range of possible biodiversity–ecosystem functioning relationships (Fig. 2b), we considered results from multiple theoretical models (e.g. Tilman *et al.* 1997a; Loreau 2010) and empirical studies (e.g. Schmid *et al.* 2009; Cardinale *et al.* 2011; Reich *et al.* 2012; Hulvey *et al.* 2013; Scherer-Lorenzen 2014), dozens of which have been conducted in temperate grasslands, where substantial previous habitat destruction has occurred (Hoekstra *et al.* 2005), and some of which have been conducted in forests (Gamfeldt *et al.* 2013; Hulvey *et al.* 2013; Scherer-Lorenzen 2014), drylands (Maestre *et al.* 2012), and other ecosystems.

Biodiversity–ecosystem functioning relationships can be approximated by a power function (Cardinale *et al.* 2011; Reich *et al.* 2012): $Y \sim \kappa S^{\beta}$, where Y is the ecosystem functioning of a community with S species, and κ and β are constants. Results from many previous theoretical (e.g. Tilman *et al.* 1997a; Loreau 2010) and experimental (e.g. Schmid *et al.* 2009; Cardinale *et al.* 2011; Reich *et al.* 2012) studies suggest that the strength of biodiversity effects on ecosystem functioning range from weak and saturating relationships, to strong and approximately linear relationships. The strength of biodiversity effects partly depends on which species are lost (Bunker *et al.* 2005; Hector *et al.* 2011) and on whether results from short- or long-term biodiversity experiments are considered (Reich *et al.* 2012). In particular, the loss of initially abundant species can reduce ecosystem functioning more than the loss of initially rare species (Smith & Knapp 2003; Isbell *et al.* 2013), and results from long-term experiments suggest that short-term studies underestimate the strength of biodiversity effects (Reich *et al.* 2012). We considered a range of β-values that correspond to approximately saturating ($\beta = 0.1$, increasingly saturating as β approaches 0) and approximately linear ($\beta = 0.5$, increasingly linear as β approaches 1.0) relationships between biodiversity and ecosystem functioning, based on previous results (e.g. Tilman *et al.* 1997a; Schmid *et al.* 2009; Loreau 2010; Cardinale *et al.* 2011; Reich *et al.* 2012; Hulvey *et al.* 2013; Scherer-Lorenzen 2014). Other results suggest that β-values can be much greater than the strongest effects that we consider here, including β-values > 1 (Mora *et al.* 2014). Specifically, β-values > 0.5 can occur for some types of non-random biodiversity loss (Isbell *et al.* 2013; Mora *et al.* 2014), and when considering the greater proportion of biodiversity that is required to maintain multiple ecosystem functions (Hector & Bagchi 2007) at multiple times and places under global changes (Isbell *et al.* 2011).

The biodiversity–ecosystem functioning relationship can be reformulated to predict the proportion of ecosystem functioning lost (F) as an increasing function of the proportion of species driven extinct (E):

$$F = 1 - (1 - E)^{\beta} \tag{2}$$

This reformulation is directly analogous to reformulating the species–area relationship to predict the proportion of species driven extinct due to habitat destruction (Tilman *et al.* 1994; Rybicki & Hanski 2013).

(3) Ecosystem functioning debt relationships

Habitat destruction creates an extinction debt (see *Extinction debt relationships* above), and species loss drives declines in ecosystem functioning (see *Biodiversity–ecosystem functioning relationships* above). The combination of these two effects produces an indirect effect of habitat destruction on ecosystem functioning via its effects on biodiversity (Gonzalez & Chaneton 2002) (Fig. 1), which has been termed an ecosystem functioning debt (Gonzalez *et al.* 2009). We combined the relationships shown in Fig. 2a and Fig. 2b to approximate the range of possible ecosystem functioning debt relationships shown in Fig. 2c. Specifically, we sampled 100 lines from uniform distributions within each of the inclusive ranges shown in Figs. 2a, b; combined all pairs of these lines to produce ecosystem functioning debt lines; and then determined the median (0.5 quantile), interquartile range (0.25 and 0.75 quantiles) and extreme range (0.025 and 0.975 quantiles) for these ecosystem functioning debt relationships (Fig. 2c). Sampling from normal, rather than uniform, distributions would lead to narrower ranges in Fig. 2c.

Next, we derived an analytical approximation for these ecosystem functioning debt relationships. Combining the extinction debt relationship and the biodiversity–ecosystem functioning relationship, which are respectively given in eqns 1 and 2, gives the following form for the ecosystem functioning debt relationship:

$$F = 1 - (1 - D)^{\alpha\beta} \tag{3}$$

which can be used to predict a gradual loss of ecosystem functioning due to species loss in remaining ecosystems. For example, this relationship, with $0.015 \leq \alpha\beta \leq 0.25$ (Fig. S4), can approximate the range of ecosystem functioning debt relationships shown in Fig. 2c.

(4) Ecological production functions

Each ecosystem service has an ecological production function that describes its dependence on one or more ecosystem functions (Daily *et al.* 2009; Nelson *et al.* 2009; Polasky & Segerson 2009). For example, the ecological production function for ecosystem carbon storage is particularly simple as it equals the sum of various carbon pools (Conte *et al.* 2011):

$$C = C_a + C_r + C_s \tag{4}$$

where C_a, C_r and C_s respectively correspond to carbon stored in aboveground plant tissues, roots and soils, quantified as mass per unit area. Other ecological production functions that translate ecosystem functions to ecosystem service flows, such as water-related ecosystem services, are more complex (Keeler *et al.* 2012).

(5) Biodiversity-dependent ecosystem service debts

Biodiversity-dependent ecosystem service debts can be quantified by accounting for ecosystem functioning debts in ecological production functions. In general, ecosystem service debts are the product of each biodiversity-dependent ecosystem function in the ecological production function, and the corresponding ecosystem functioning debt. For example, if we assume that eqn 3 can approximate the ecosystem functioning debt for ecosystem carbon storage, then we obtain the following biodiversity-dependent ecosystem service debt relationship:

$$\Delta C = C \times F = C - C(1 - D)^{\alpha\beta} \tag{5}$$

where ΔC is Mg C ha^{-1} emitted because of species loss resulting from habitat destruction elsewhere in the habitat, D is the proportion of habitat destroyed and α and β are respectively the strengths of the extinction debt and of the biodiversity–ecosystem functioning relationships. Note that eqn 5 could also be applied to particular carbon pools, such as root carbon, if one does not wish to assume that all carbon pools depend on plant diversity.

(6) Economic valuation functions

Economic valuation functions monetise, or otherwise assign weights to, various ecosystem services according to relative preferences. For example, the economic valuation function for carbon is simply the product of the social cost of carbon (V_c) and the change in the mass of carbon stored (ΔC):

$$V = V_c \times \Delta C \tag{6}$$

The social cost of carbon is the net present value of damages due to an additional unit of carbon emissions, with units of monetary value per unit of carbon emitted, such as U.S. \$ Mg^{-1} C.

Economic valuation is not necessary for all applications of ecosystems service investigations, but it can be useful in several ways. First, economic valuation functions can help transparently communicate relative preferences in explicit mathematical expressions that convert each biophysical ecosystem service unit to a common currency, monetary or otherwise (Daily *et al.* 2009). This helps rigorously explore trade-offs between the responses of various ecosystem services to changes in land use, biodiversity or other anthropogenic drivers. Second, economic valuation functions can help explicitly account for the presence or absence of beneficiaries, distinguishing between the supply of, and the demand for, ecosystem services (Keeler *et al.* 2012). Third, economic valuation functions can help quantify returns on conservation investments (Kovacs *et al.* 2013).

(7) Marginal value of further anthropogenic perturbations

How costly is a further incremental anthropogenic perturbation? Substituting eqn 5 into eqn 6, and then taking the partial derivative with respect to D, gives the marginal cost of an additional proportional unit of habitat destruction elsewhere in the habitat:

$$\frac{\partial V}{\partial D} = \alpha\beta C V_c (1 - D)^{\alpha\beta - 1} \tag{7}$$

with units of U.S. \$ ha^{-1}. Alternatively, the marginal cost of an additional absolute unit of habitat destruction would be given by eqn 7 divided by the area of the habitat. Thus, unsurprisingly, an additional absolute amount of habitat destruction incurs a greater cost in small than in large habitat. In other words, as the area of a habitat becomes increasingly large, there is an increasingly small cost of destroying an additional hectare of habitat nearby. We avoid this inevitability by considering marginal habitat destruction on a proportional scale.

EXPLORATORY ANALYSIS OF A GLOBAL BIODIVERSITY-DEPENDENT CARBON DEBT

In this section, we demonstrate how the analytical approach developed in the previous section can be empirically explored.

Estimating carbon storage

Although results from several long-term experiments suggest that soil carbon depends on plant diversity (Fornara & Tilman 2008; Steinbeiss *et al.* 2008; Cong *et al.* 2014), there have been relatively few tests of this relationship. Thus, we empirically estimate the potential global biodiversity-dependent carbon debt (eqn 5) assuming either that only vegetation carbon depends on plant diversity ($C = C_a + C_r$ in eqn 5) or that both vegetation and soil carbon depend on plant diversity ($C = C_a + C_r + C_s$ in eqn 5). Our Figures show the first case, which considers only vegetation carbon. See Appendix 1 for details regarding quantification of soil carbon storage.

To empirically estimate the potential global biodiversity-dependent vegetation carbon debt we used a previously developed global map of biomass carbon stored in aboveground and belowground (root) living plant tissues (Ruesch & Gibbs 2008). This map was developed by using the Intergovernmental Panel on Climate Change (IPCC) Tier-1 methodology (IPCC 2006) to estimate aboveground biomass for ecofloristic zones by continent; root biomass was then estimated according to the IPCC root to shoot ratios for each vegetation type; and biomass was then converted to carbon according to the per cent carbon by vegetation type (Ruesch & Gibbs 2008). This produced 124 zones with unique vegetation carbon estimates, which were then mapped at approximately 1 km^2 spatial resolution according to global land cover during the year 2000, continental regions, ecofloristic zones and forest age (Ruesch & Gibbs 2008). The map is available online from the Carbon Dioxide Information Analysis Center at Oak Ridge National Laboratory (http://cdiac.ornl.gov). Carbon in destroyed habitat was masked out (see Estimating habitat destruction in global ecoregions below) because our study considers the previously unquantified carbon emissions that could occur at places where fragments of ecosystems remain, due to plant species loss, rather than the previously quantified carbon emissions that occur at places where ecosystems are no longer present, due to swapping carbon-rich ecosystems for carbon-poor land uses.

Estimating habitat destruction in global ecoregions

We estimated habitat destruction by ecoregion (*D* in our Equations) as the proportion of grid cells on a global land cover map that were designated as *Cultivated and Managed Areas* or *Artificial Surfaces* within each of the World Wildlife Fund's terrestrial ecoregions (Hoekstra *et al.* 2005) (Fig. 4). Areas that were designated as *Snow and Ice*, *Water Bodies* or *Bare* were ignored because these areas have little or no vegetation by definition. The land cover and ecoregion maps are both available online (Hoekstra *et al.* 2005). As in previous studies (Hoekstra *et al.* 2005), we consider habitat destruction within ecoregions, which are defined as 'relatively large units of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use change' (Olson *et al.* 2001).

The land cover and ecoregion maps (Hoekstra *et al.* 2005), and the vegetation carbon map (Ruesch & Gibbs 2008), were projected to the World Cylindrical Equal Area spatial reference, with cell size of 1000 by 1000 m. The land cover map was then reclassified with the original land cover categories 1–15, and 17–18 reclassified as habitat (value = 1), original categories 16 (*Cultivated and Managed Areas*) and 22 (*Artificial Surfaces*) reclassified as destroyed (value = 0), and original categories 19–21 (*Bare Areas, Water Bodies, Snow and Ice*) reclassified as ignored (value = NoData). Next, to ignore carbon where habitat was destroyed, we multiplied the reclassified binary habitat raster by the vegetation carbon map to produce the map shown in Fig. 3. We then summed the carbon values by ecoregion to produce the values in Table S1. We also quantified proportions of ecoregions that were designated as destroyed, and rasterised this shapefile to produce Fig. 4. These operations were performed with the Project Raster, Project Feature, Reclassify, Raster Calculator, Zonal Statistics as Table, Tabulate Area and Feature to Raster functions in ESRI ® ArcMap 10.0.

Quantifying biodiversity-dependent carbon debts and marginal values

After creating the vegetation carbon in habitat (Fig. 3) and proportion of habitat destroyed (Fig. 4) maps, we applied our eqns 5 and 7 within each grid cell, assuming a moderate ecosystem functioning debt relationship ($\alpha\beta = 0.067$; median line Fig. 2c, Fig. S4) and a moderate social cost of carbon emissions (V_c = 2012 U.S. \$39.91 Mg^{-1} CO_2 = \$146.49 Mg^{-1} C, discount rate = 3.0%). This produced our biodiversity-dependent vegetation carbon debt (Fig. 5) and marginal value (Fig. 6) maps. These operations were performed with the Raster Calculator function in ESRI ® ArcMap 10.0. We then aggregated values by ecoregion to consider correlations among ranks in plant species richness (Kier *et al.* 2005), habitat destruction (Fig. 4), vegetation carbon (Fig. 3), vegetation carbon debt (Fig. 5) and marginal value of an additional proportional unit of habitat destruction (Fig. 6).

Global biodiversity-dependent carbon debt estimates

We estimate that habitat destruction has created a global biodiversity-dependent vegetation carbon debt of approximately 4 Pg C (Fig. 5), assuming a moderate ecosystem functioning debt ($\alpha\beta = 0.067$ in eqn 5; median line in Fig. 2c, Fig. S4). Accounting for uncertainties in how many species will be lost (Fig. 2a), and how much species loss will impact ecosystem functioning (Fig. 2b), gives the interquartile ranges, 2–6 Pg C, and extreme ranges, 1–13 Pg C, for these values (Fig. 2c). Further accounting for the possible dependence of soil carbon on biodiversity, which has been observed in several long-term experiments (Fornara & Tilman 2008; Steinbeiss *et al.* 2008; Cong *et al.* 2014), could approximately triple these estimates, giving a median of 12 Pg C, interquartile range of 8–21 Pg C, and extreme range of 3–44 Pg C (see Appendix S1).

The extreme ranges are the unlikely cases where few species are lost *and* each species loss has a small impact on ecosystem functioning worldwide (lower extreme), or where many species are lost *and* each species loss has a large impact on ecosystem functioning worldwide (upper extreme). If we instead focus on the interquartile ranges, then overall we estimate that the biodiversity-dependent carbon debt is likely somewhere between 2 and 21 Pg C, depending on the magnitude of extinction debts, the strength of biodiversity–ecosystem functioning relationships, and whether soil carbon depends on plant diversity. We offer this as a first-order approximation for the global biodiversity-dependent carbon debt, and we encourage future studies to refine this estimate.

Where might the social costs of carbon emissions be most sensitive to further habitat destruction elsewhere in the ecoregion? The marginal cost of further habitat destruction is predicted to be greatest in carbon-rich ecoregions (Figs 3, 6, 7, 8). For example, the Cerrado ecoregion is predicted by our analyses to have the largest biodiversity-dependent carbon debt and one of the largest marginal costs of additional habitat destruction (Fig. 7, Table S1). That is, previous habitat destruction in the Cerrado will likely gradually decrease both biodiversity and carbon storage over time within the remaining fragments of this savanna ecosystem, and further habitat destruction in the Cerrado will likely create substantial costly carbon emissions not only at the places where land is converted, but also nearby where Cerrado savanna fragments remain intact but lose species and carbon over time. The marginal cost of further nearby habitat destruction strongly depends on the amount of carbon stored in an ecoregion, while the current carbon debt strongly depends on the extensiveness of previous habitat destruction (Fig. 8). In other words, additional habitat destruction will likely lead to costly carbon emissions in remaining fragments of carbon-rich ecoregions, regardless of whether these ecoregions are currently largely destroyed or intact; and previous extensive habitat destruction will likely lead to substantial carbon emissions in remaining ecosystem

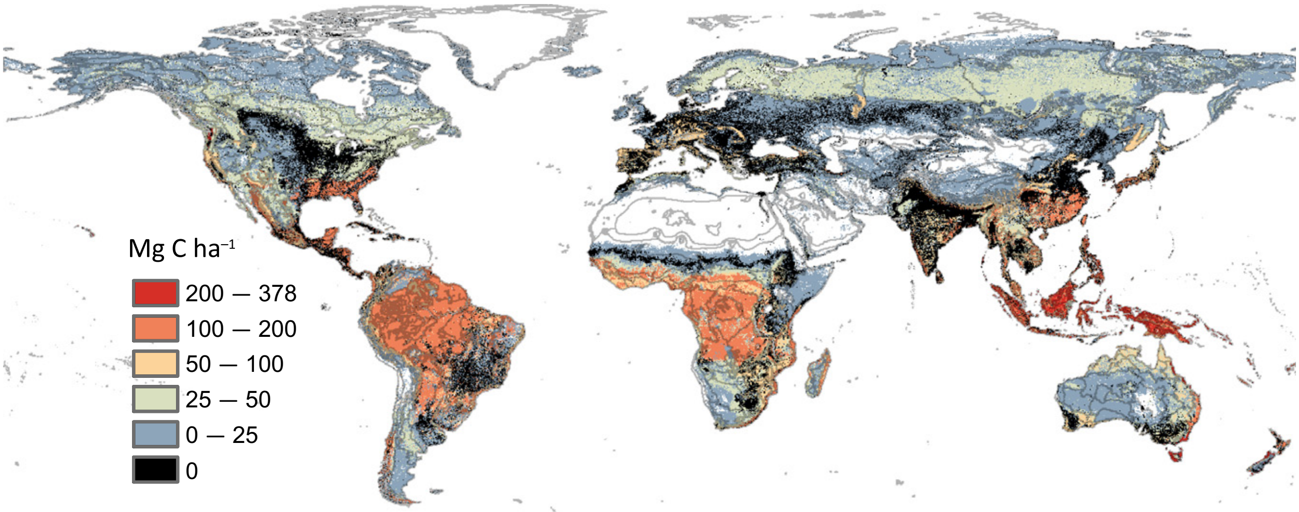

Figure 3 Vegetation carbon (C in our equations) stored in aboveground plant tissues and roots of remaining ecosystems. Destroyed habitats are shown in black. Our analyses ignore carbon stored in destroyed habitats because many previous studies have considered carbon emissions from land conversion at these places. Uniquely, here we focus on carbon stored in remaining ecosystem fragments, which are shown in the blue to red colour gradient.

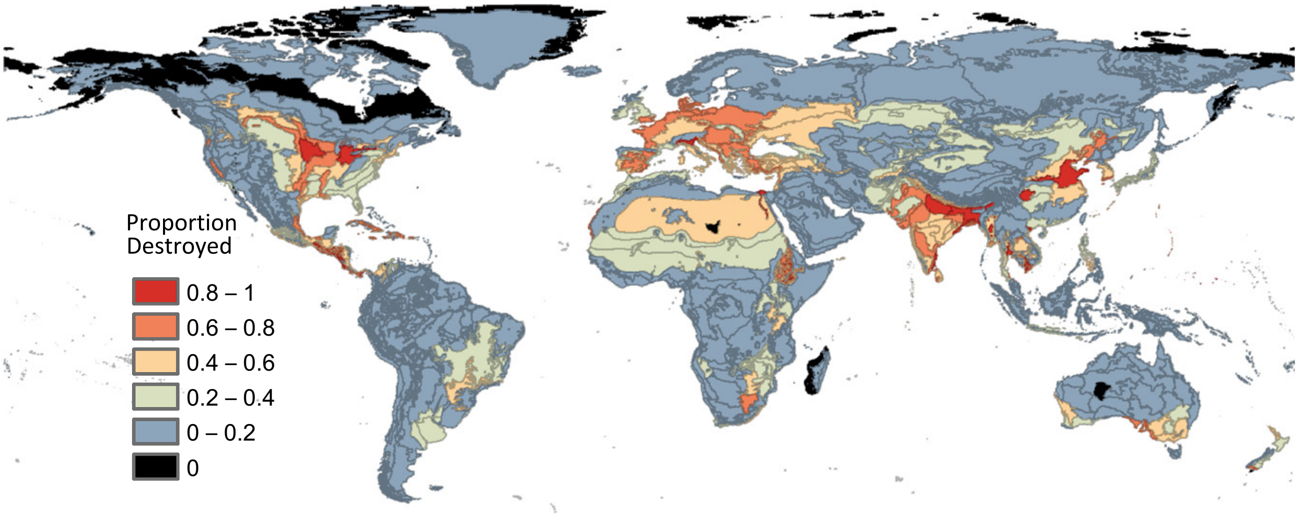

Figure 4 Proportion of each ecoregion destroyed (D in our equations). Areas designated as *Cultivated and Managed Areas* or *Artificial Surfaces* on a global land cover map were considered destroyed (see black areas in Fig. 3). Areas that were designated as *Snow and Ice* or *Bare* were ignored because these areas have little or no vegetation by definition.

fragments, regardless of whether these ecoregions are carbon-rich or carbon-poor.

DISCUSSION

Placing the biodiversity-dependent carbon debt in context

There are many benefits and costs of land conversion. The biodiversity-dependent carbon debt considered here is one previously unquantified cost of land conversion that is in addition to previously considered direct carbon emissions from land-use changes. It accrues where ecosystem fragments remain intact, due to loss of plant species in remaining ecosystems. This contrasts with previously considered carbon emissions from land-use changes (Friedlingstein *et al.* 2010), such as the biofuel carbon debt (Fargione *et al.* 2008), which accrue where habitat has been destroyed, due to swapping carbon-rich ecosystems for carbon-poor land uses. Although these carbon emissions from plant species loss are locally relatively small, they are globally substantial if they occur diffusely across extensive areas of remaining natural ecosystems. Carbon emissions per unit land area tend to be greater for land conversion (Fargione *et al.* 2008) than for plant species loss caused by nearby habitat destruction (Fig. 3). Our first-order approximation of 2–21 Pg C for global carbon emissions from plant species loss amounts to approximately 2–20 years of global carbon emissions from direct land conversion, or approximately 2 months–2 years of global

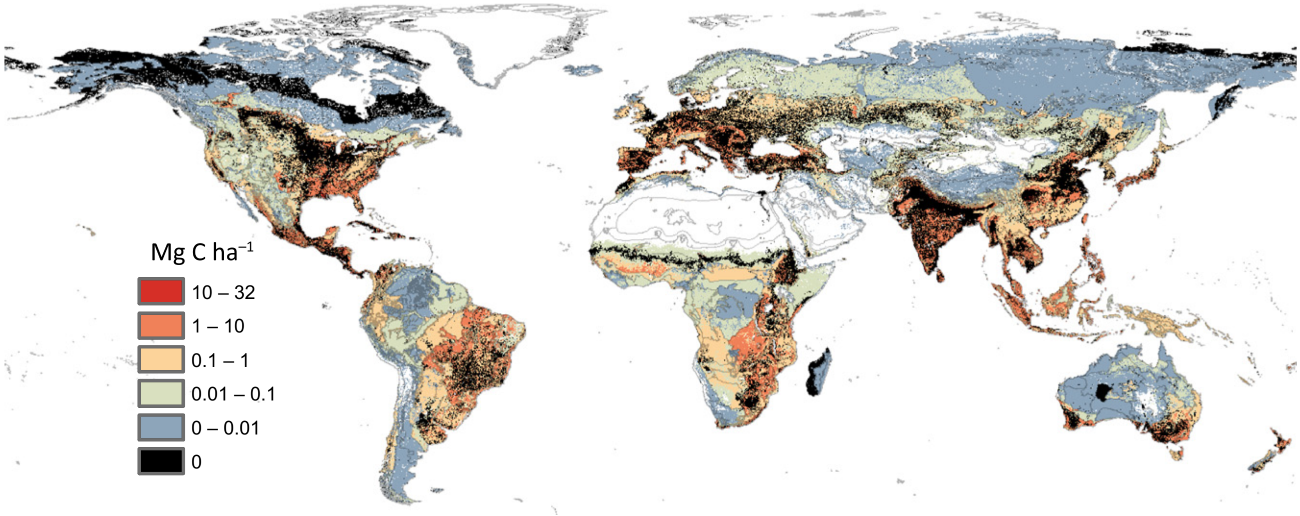

Figure 5 Estimated loss of a biodiversity-dependent ecosystem service. Carbon emissions caused by gradual plant species loss in remaining ecosystem fragments due to previous nearby habitat destruction. Ecosystem fragments that are predicted to lose the most species and carbon over time are shown in red and orange. No biodiversity-dependent carbon debt is predicted in black areas, which include areas where land cover is designated as *Cultivated and Managed Areas* or *Artificial Surfaces* (black areas in Fig. 3) and ecoregions where there has been no significant habitat destruction (black areas in Fig. 4). These estimates assume moderate species loss and impacts on ecosystem functioning ($\alpha\beta = 0.067$ in eqn 5; median line in Fig. 2c). Our exploratory analysis suggests that biodiversity-dependent ecosystem service debts can be globally substantial, even when locally small, if they occur diffusely across extensive areas of remaining ecosystems.

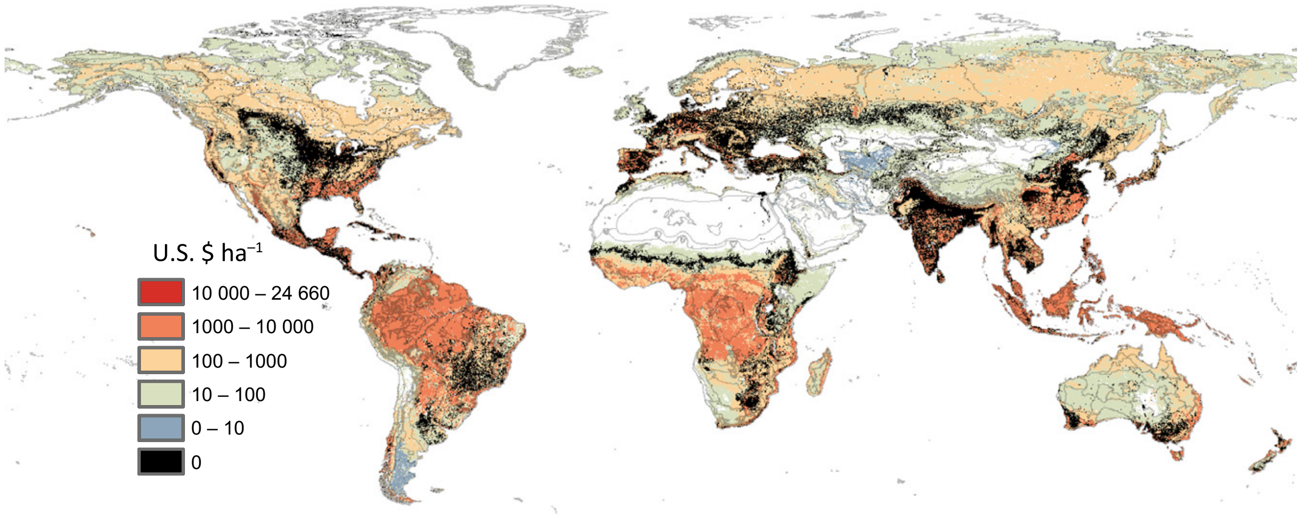

Figure 6 Marginal costs of further land conversion. Social costs of carbon emissions caused by plant species loss in remaining ecosystem fragments that could result from an additional proportional unit of habitat destruction elsewhere in the ecoregion. Previous habitat destruction occurred in black areas, where land cover is designated as *Cultivated and Managed Areas* or *Artificial Surfaces*. These estimates assume moderate species loss, impacts on ecosystem functioning and social costs of carbon emissions ($\alpha\beta = 0.067$ and $V_c = \$146.49\ \mathrm{Mg}^{-1}$ C in eqn 7; median line in Fig. 2c).

carbon emissions from all human activities (Friedlingstein *et al.* 2010).

The biodiversity-dependent carbon debt is a gradual transfer of carbon from remaining ecosystem fragments to the atmosphere that could slowly occur over decades or centuries. There remains considerable uncertainty in rate of species loss following habitat destruction. Given that more species loss will likely occur sooner than later after habitat destruction (Tilman *et al.* 1997b; Rybicki & Hanski 2013), and that species might become extremely rare and thus 'functionally extinct' before they are globally extinct, we expect more biodiversity-dependent carbon emissions in the short- than in the long-term. Some of this species loss and consequent emissions have likely already occurred.

Testing the predictions of our framework will require new observational, experimental and theoretical modelling studies. Many previous studies have considered whether biodiversity and carbon storage positively covary across space (e.g. Nelson *et al.* 2009; Jonsson & Wardle 2010; Strassburg *et al.* 2010; Gamfeldt *et al.* 2013). Note, however, that biodiversity and

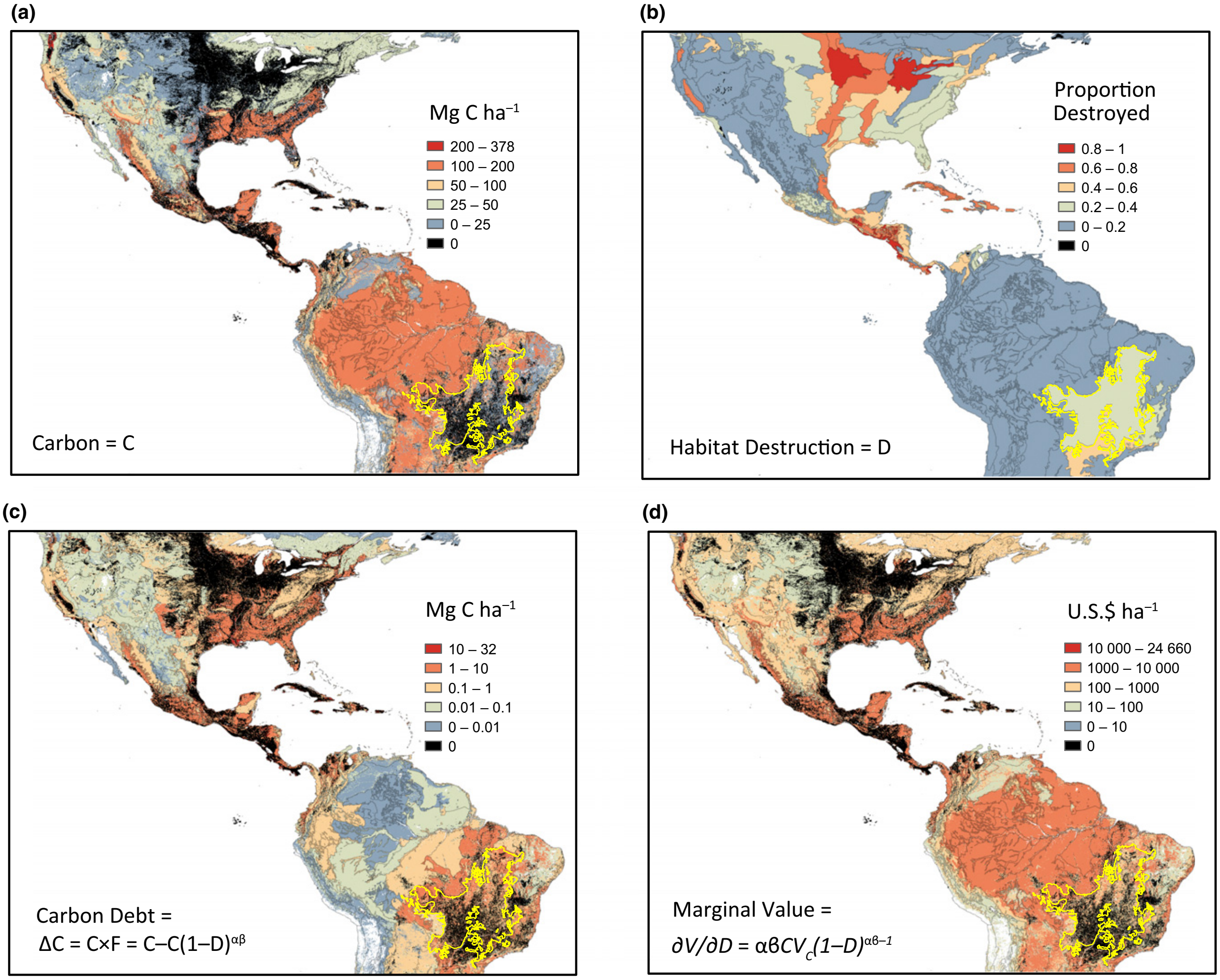

Figure 7 Zooming in on the Cerrado ecoregion, which is predicted to have the greatest biodiversity-dependent carbon debt, and which is highlighted in yellow in the lower right area of each panel. Panels (a–d) are respectively close-up views of portions of Figures 3-6. See Figs 3–6 for further details regarding each map.

ecosystem services will not necessarily be positively correlated across space even when they are causally related (Loreau 1998). Thus, the framework presented here does not predict that biodiversity and ecosystem services will necessarily be positively correlated across space, but rather that changes in biodiversity within any particular place will often cause changes in ecosystem services at that place. Testing the predictions of our framework will require new observational studies that consider the temporal covariance of biodiversity and ecosystem services, new experiments that consider the responses of both biodiversity and ecosystem services to manipulations of anthropogenic drivers, and new theoretical studies that integrate extinction debt relationships with biodiversity–ecosystem functioning relationships and ecological production functions.

There is already some experimental evidence that habitat destruction, and other drivers of biodiversity loss, such as nitrogen enrichment, can produce ecosystem functioning debts. For example, in a moss-based microecosystem experiment, habitat destruction caused loss of microarthropod diversity and biomass over time within the remaining moss fragments (Gonzalez & Chaneton 2002). Additionally, although chronic nitrogen enrichment initially increased grassland productivity, it also led to substantial loss of plant species over time, which then caused substantial diminishing returns of productivity from fertilisation (Isbell *et al.* 2013). These results support the predictions of our ecosystem services debt framework by showing that the long-term impacts of human activities on ecosystem services can strongly depend on how such human activities gradually alter biodiversity.

Landscape-scale habitat destruction experiments also provide rigorous tests of our predictions for tree species loss and associated carbon emissions. During the first few decades of a tropical deforestation experiment, the Biological Dynamics of Forest Fragments Project, habitat destruction caused net loss of understory plant species diversity, which includes tree seedlings, lianas, herbs and palms (Benitez-Malvido & Martinez-Ramos 2003). Our framework predicts that such tree species

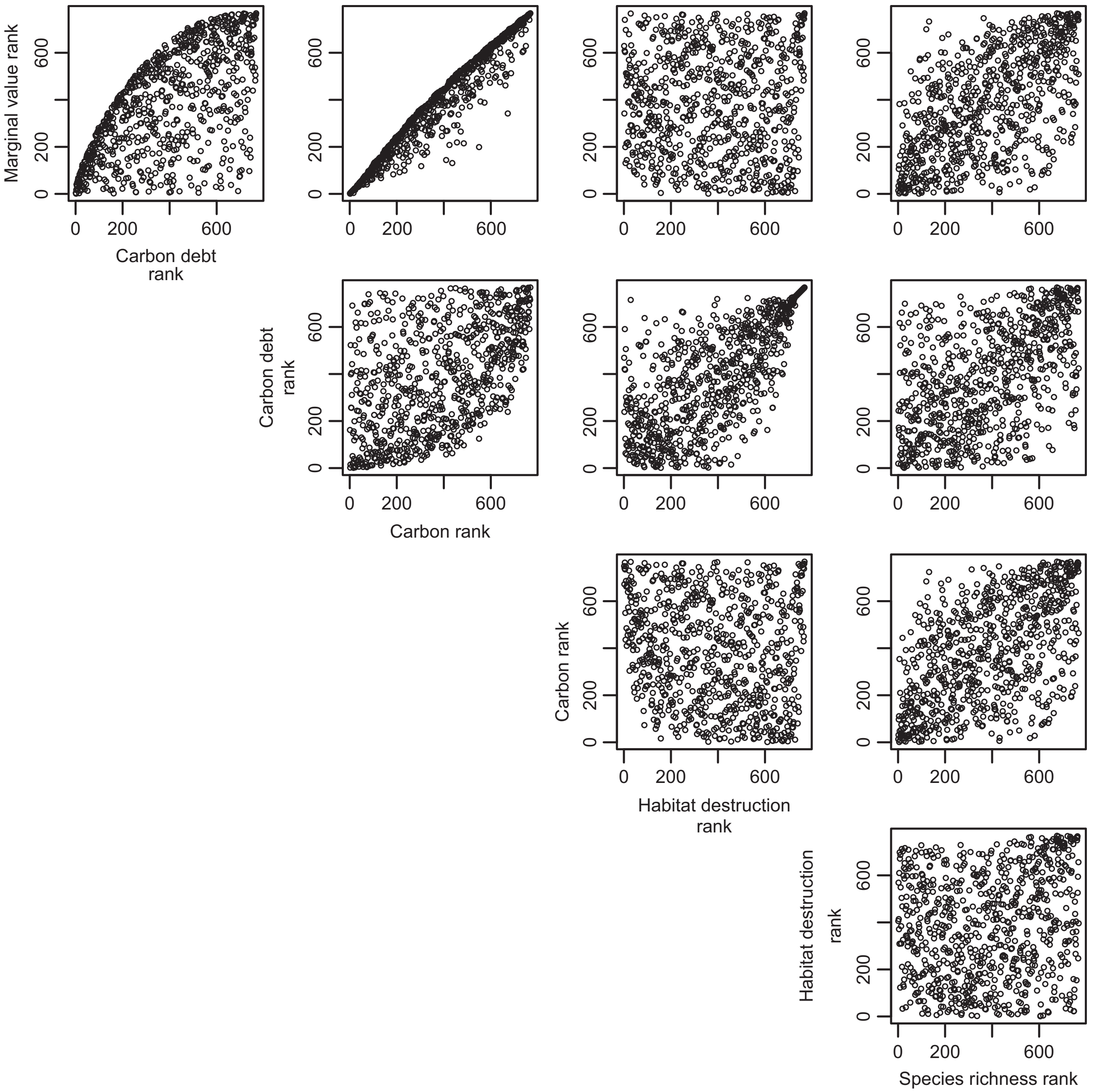

Figure 8 Correlations among ecoregion ranks in plant species richness (Kier *et al*. 2005), habitat destruction (Fig. 4), carbon (Fig. 3), carbon debt (Fig. 5) and marginal value of an additional proportional unit of habitat destruction (Fig. 6). Each open circle is an ecoregion. Note that the marginal value strongly depends on the amount of carbon stored in an ecoregion, while the carbon debt strongly depends on the extensiveness of previous habitat destruction. The lack of strong correlations between species richness rank and other variables indicates that conservation priorities for minimising the biodiversity-dependent carbon debt are not necessarily the ecoregions with the most plant species. See Table S1 for ecoregion details.

loss will gradually lead to carbon emissions as these depauperate tree seedlings replace the current diverse tree community during the coming decades and centuries. Given that individuals of Amazonian tree species can live for centuries or millennia (Chambers *et al*. 1998), these could be slowly emerging and long-lasting changes in ecosystem carbon storage. Thus, in addition to previously reported loss of carbon from these forest fragments due to elevated tree mortality (Laurance *et al*. 1997) and early shifts in species composition (Laurance *et al*. 2006) that occurred during the first few decades after nearby deforestation, our framework predicts further loss of carbon during the coming decades and centuries due to tree species loss. The Stability of Altered Forest Ecosystems Project (Ewers *et al*. 2011) will also provide a rigorous test of our predicted decline in tree diversity and consequent carbon emissions.

Future habitat destruction will tend to amplify the biodiversity-dependent carbon debt for several reasons. First, we expect accelerating loss of species and carbon given the predicted nonlinear responses to habitat destruction (Fig. 2). Second, previous habitat destruction has primarily occurred in temperate grassland ecoregions (Hoekstra *et al.* 2005), which store considerably less carbon than tropical forest ecoregions, where habitat destruction continues to expand (Hansen *et al.* 2013). Third, habitat destruction could interact with climate change or other anthropogenic drivers to synergistically drive species loss (Sala *et al.* 2000).

We did not consider other potentially important biodiversity-dependent changes in ecosystem services that might occur within destroyed habitats. First, an unknown portion of carbon emissions from land conversion could be due to species loss. This makes it difficult to tease apart the relative magnitudes of the direct and indirect (via changes in biodiversity) pathways shown in Fig. 1. Second, there can be spillover of biodiversity from ecosystem fragments into destroyed habitats, which could affect the provision of ecosystem services there either favourably, such as when pollinators promote crop yields, or unfavourably, such as when wildlife spread zoonotic diseases.

Substantial sources of uncertainty for the biodiversity-dependent carbon debt

Our exploratory analysis reveals substantial uncertainties at each step shown in Fig. 1. For example, our approach likely underestimates habitat destruction (D) for two reasons. First, we were unable to quantify the additional habitat destruction that has occurred on grid cells designated as Mosaic Croplands, which include both cropland and habitat. Second, the global land cover map that we used does not distinguish between habitat that has never been destroyed and habitat that has recovered after earlier destruction. By treating recovering ecosystems as equivalent to remnant ecosystems, we assume that recovering ecosystems are as diverse as remnant ecosystems, which is likely true for some (Jones & Schmitz 2009) but not other (Benayas *et al.* 2009) ecosystems. This assumption might cause us to under-estimate the biodiversity-dependent ecosystem services debt, especially for slowly recovering ecosystems. We made several other simplifying assumptions that could also cause us to underestimate the extinction debt (Box 1).

We assume that species loss causes a net decrease in carbon storage. Species loss will likely decrease plant biomass production (Cardinale *et al.* 2011), which would decrease the amount of CO_2 that is removed from the atmosphere. However, species loss will also likely decrease rates of decomposition (Handa *et al.* 2014), which would decrease the amount of CO_2 that is returned to the atmosphere. The available evidence suggests that species loss decreases productivity more than it decreases decomposition in terrestrial ecosystems (Cardinale *et al.* 2011), which would lead to net carbon emissions. Similarly, two experiments found that when biomass production decreased with richness, net ecosystem exchange, which accounts for both gain and loss of carbon, also decreased with richness (Stocker *et al.* 1999; Wilsey & Polley 2004). In other words, as species were lost, the decrease in carbon gain was incompletely offset by decreases in carbon loss, and thus species loss resulted in a net transfer of carbon from the terrestrial biosphere (including soil) to the atmosphere. Here, for simplicity, we assume that aboveground and root carbon pools similarly depend on plant diversity. We also separately consider the case where soil carbon is equally dependent on plant diversity. Further study is required to determine ecosystem function-specific parameter values for β.

Our assumptions and results differ from those of another study which considered how tree species loss could impact carbon storage in a tropical forest (Bunker *et al.* 2005). This previous study assumed that there were no species interactions, and thus that random species loss would have no effect on ecosystem functioning (Bunker *et al.* 2005). In this case, species loss could increase or decrease carbon storage, depending on whether carbon-poor or carbon-rich species were lost (Bunker *et al.* 2005). In contrast, based on many previous results (e.g. Schmid *et al.* 2009; Loreau 2010; Cardinale *et al.* 2011; Hector *et al.* 2011; Hooper *et al.* 2012; Reich *et al.* 2012; Tilman *et al.* 2012; Scherer-Lorenzen 2014), here we assume that species loss will decrease ecosystem functioning to a lesser or greater degree, depending in part on which species are lost. We suspect that our chosen β-values might underestimate the dependence of ecosystem functioning on biodiversity because they do not account for the fact that different sets of species can promote ecosystem functioning during different years, at different places, for different functions, and under different global change scenarios (Hector & Bagchi 2007; Isbell *et al.* 2011; Gamfeldt *et al.* 2013).

We used species richness, a simple measure of biodiversity, to formally bridge these relationships (Figs 1 and 2) because species richness is often a response variable in extinction debt theory (Tilman *et al.* 1994, 1997b; Hanski *et al.* 2013) and a predictor variable in biodiversity-ecosystem functioning theory (Tilman *et al.* 1997a; Loreau 2010). An important next step will be to incorporate other aspects of biodiversity and species composition that may mediate the effects of human activities on ecosystem services, such as functional trait diversity (Laliberte & Tylianakis 2012), phylogenetic diversity (Cadotte *et al.* 2008), species evenness (Wilsey & Polley 2004), native or exotic species origin (Isbell & Wilsey 2011) and widespread shifts in functional composition, such as increases in liana abundance (Laurance *et al.* 1997) and decreases in legume abundance (Leach & Givnish 1996).

Although our analyses accounted for considerable uncertainties in the strengths of extinction debt relationships (Fig. 2a) and biodiversity–ecosystem functioning relationships (Fig. 2b), we were unable to account for uncertainty in the spatial scaling of these relationships. There could be a mismatch between the local scales at which biodiversity experiments have typically been conducted, and the regional scales at which habitat destruction and extinction debts have typically been investigated. By analytically combining these relationships (Fig. 2), we assume that habitat destruction drives loss of the same proportion of species both regionally and locally. If a smaller or larger proportion of species is lost locally than regionally, then our analytical assumptions could respectively over- or under-estimate this ecosystem functioning debt. Furthermore, if ecosystem functioning additionally depends on species diversity at larger spatial scales than those considered in most biodiversity experiments (Isbell *et al.* 2011; Pasari *et al.* 2013), then our approach could underestimate the ecosystem functioning debt. Further study will be required to quantify and reduce uncertainty in the spatial scaling of these relationships.

There is currently some debate as to whether and how local biodiversity is changing in many ecosystems. Some meta-analyses have found that many human disturbances tend to decrease local biodiversity (Benayas *et al.* 2009; Jones & Schmitz 2009; Murphy & Romanuk 2014), while other meta-analyses have found no systematic loss of local biodiversity (Vellend *et al.* 2013; Dornelas *et al.* 2014). These two groups of studies have defined species loss with respect to two different baselines. Change in biodiversity is measured against levels of local biodiversity observed either: (1) in remnant ecosystems (Benayas *et al.* 2009; Jones & Schmitz 2009; Murphy & Romanuk 2014), which by definition have minimal human disturbance, or (2) at earlier points in time (Vellend *et al.* 2013; Dornelas *et al.* 2014), when ecosystems might have been more or less disturbed by people than during recent observations. Many of the observed plant species gains occur during post-disturbance succession (Vellend *et al.* 2013; Dornelas *et al.* 2014) (Fig. S5). Therefore, these meta-analyses together provide considerable evidence that many human disturbances can substantially decrease local biodiversity, and that reducing human disturbances can lead to substantial recovery of local biodiversity (Benayas *et al.* 2009; Jones & Schmitz 2009; Vellend *et al.* 2013; Dornelas *et al.* 2014; Murphy & Romanuk 2014). The assumptions of our framework do not conflict with these recent results. By assuming that recovered ecosystems are as diverse as remnant ecosystems, our framework acknowledges the tendency for species gains above disturbed levels of plant diversity following relaxation of anthropogenic disturbances.

There are some cases where human activities have increased plant diversity above remnant levels, such as the gain of many exotic plant species at regional spatial scales on islands (Sax *et al.* 2002). Further study is required to determine the extent to which such species gains cause increases in carbon storage that counter-balance the carbon debt from extinction debt that we consider here. The gain of exotic species might have a smaller impact on carbon storage than the loss of native species. First, the nonlinear relationship between biodiversity and ecosystem functioning (Fig. 2b) means that ecosystem functioning tends to be impacted less by species gain than by species loss. Second, changing exotic plant diversity can impact ecosystem functioning less than changing native plant diversity, partly due to reduced complementarity between exotic species with no coevolutionary history of interaction (Isbell & Wilsey 2011). In general, though, species gain or loss due to other anthropogenic drivers could counter-balance or exacerbate changes in ecosystem services due to the extinction debt that we consider here.

Conservation implications of ecosystem service debts

Our results suggest that there is substantial value in conserving not only the quantity (area), but also the quality (biodiversity) of natural ecosystems. If we assume a moderate social cost of carbon (Interagency Working Group on Social Cost of Carbon United States Government 2013) (2012 U.S. \$39.91 Mg^{-1} CO_2 = \$146.49 Mg^{-1} C, discount rate = 3.0%), then our first-order approximation (i.e. using the range 2–21 Pg C) for the global value of conserving plant diversity for carbon storage alone in remaining ecosystems is between U.S. \$0.3–3.1 trillion. This amounts to approximately 15–155 years of current global conservation expenditures (Waldron *et al.* 2013), or approximately 4–40 years of greater investments that could reduce the risk of extinction for all globally threatened species (Mccarthy *et al.* 2012). Current conservation funding tends to support land acquisition and protection of charismatic species. Our results suggest that there is also considerable value in maintaining plant diversity within protected areas, which will likely require changes in human activities both inside and outside protected areas (Kareiva *et al.* 2007), possibly including assisted migrations and species reintroductions. For example, restoring carbon-rich ecosystems with native plant species can not only store considerable amounts of carbon where ecosystems are restored, but can also prevent carbon emissions where species loss is prevented in nearby remaining ecosystem fragments. Given uncertainty in the timing of species loss and declines in ecosystem functioning following habitat destruction, here we assumed that each unit of carbon emissions would have the same monetary cost, regardless of when it occurred. This assumption likely causes us to underestimate the social cost of carbon emissions because at least some species loss will not immediately occur (Tilman *et al.* 1994, 1997b; Rybicki & Hanski 2013) and the social cost of carbon is expected to increase over time (Interagency Working Group on Social Cost of Carbon United States Government 2013). Further accounting for substantial uncertainties in the social cost of carbon emissions (Interagency Working Group on Social Cost of Carbon United States Government 2013) could approximately double or halve these monetary value estimates.

Quantifying other ecosystem service debts

The approach developed here can be modified to estimate any ecosystem service debt. In general, ecosystem service debt relationships specify changes in ecosystem service provision in intact ecosystem fragments as a function of anthropogenic drivers of biodiversity declines (Fig. 1). Ecosystem service debts can be quantified by accounting for ecosystem functioning debts in ecological production functions (Fig. 1). Here, we have demonstrated how to approximate changes in carbon storage due to species loss caused by habitat destruction. Further study is required to approximate ecosystem service debts that specify relationships for other widespread drivers of contemporary biodiversity declines, including climate change (Thomas *et al.* 2004) and nutrient enrichment (Isbell *et al.* 2013), other dimensions of biodiversity, including phylogenetic (Cadotte *et al.* 2008) and functional diversity (Laliberte & Tylianakis 2012), and other ecosystem services, including those dependent on water quality (Keeler *et al.* 2012). Given the widespread influences of climate change, nitrogen deposition, intense livestock grazing and other drivers of biodiversity declines, and given that remaining natural ecosystems still cover most of the earth's land surface, we expect substantial global magnitudes for many ecosystem service debts. Improved estimates of biodiversity-dependent ecosystem service debts are required to determine whether people will obtain a steady flow or a diminishing trickle of future benefits from each hectare of remaining nature.

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AUTHORSHIP

FI conceived and designed the study, conducted analyses and wrote the first draft of the paper. All authors contributed substantially to revisions.

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