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Economic valuation of ecosystem services fails to capture biodiversity value of tropical forests

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ABSTRACT

The reconciliation of biodiversity conservation, ecosystem service provision and agricultural production in tropical landscapes requires recognition of the trade-offs between competing land-uses. It is especially relevant for conservation planning to assess whether the economic value of ecosystem services is spatially congruent with biodiversity. Previous analyses have largely focused on ecosystem service provision or assumed homogeneous economic values across land uses within biomes. We relax this assumption by carrying out a spatially explicit meta-analysis based on 30 studies of ecosystem service values in tropical forests from The Economics of Ecosystems and Biodiversity (TEEB) database, while controlling for economic, environmental and methodological variables. Our results demonstrate a lack of spatial congruence between the economic value of ecosystem services and biodiversity in tropical forests. Instead, we find that economic value presents a nonlinear inverted-U relationship with site accessibility and economic activity, highlighting the importance of matching supply and demand between each ecosystem service and its beneficiaries for economic values to be realized. The implications are that conservation policies focusing solely on the economic value of ecosystem services will fail to protect biodiversity in remote and less disturbed regions.

1. Introduction

The tropical forest ecosystem is one of the most biodiverse in the world and provides a wide range of goods and services that are fundamental to human populations locally and globally (Balmford, 2002; Costanza et al., 1997; Ricketts et al., 2004). Tropical forests are currently subject to strong pressure from agricultural expansion, leading to unprecedented deforestation rates (Hansen et al., 2013; Margono et al., 2014; Miettinen et al., 2011). Mapping the economic value of the ecosystem services of tropical forests is thus necessary to support land-use decisions that can capture the trade-offs between ecosystem service provision, biodiversity conservation and agricultural production (Koh and Ghazoul, 2010; Millennium Ecosystem Assessment, 2005). Given the mounting pressure to convert forests into agriculture, particularly for highly profitable crops such as oil palm in Southeast Asia (Koh et al., 2011) or soya bean in Brazil (Ewers et al., 2008), knowing the distribution of the economic values of ecosystem services could facilitate the spatial planning and management of landscapes to maximize agricultural production while maintaining ecosystem service benefits (Sayer et al., 2013).

Previous evaluations of potential payment for ecosystem services schemes have led to mixed results (Naidoo et al., 2008; Strassburg et al., 2010). In terms of the provision of ecosystem services, such as carbon storage and sequestration, grassland production and water, strategies that target biodiversity-rich areas would not perform better than randomly distributed strategies (Naidoo et al., 2008). Whereas in other cases, congruence between carbon storage and sequestration services and biodiversity was observed (Strassburg et al., 2010). More importantly, for most ecosystem services (an example of an exception are carbon related services), the magnitude of a service provided at a site might not necessarily coincide with its realized economic value, as value will be influenced by existing demand for the service at the place where it is provided (Burkhard et al., 2012; García-Nieto et al., 2013).

Previous studies have mapped the value of tropical forests by directly transferring the average economic value of ecosystem services from existing studies in the tropics to the rest of the tropical biome. For instance, one study averaged 11 estimates of the value of climate regulation in tropical forests from previous studies and assumed that this value was homogeneous across the tropical

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biome (Costanza et al., 1997). Indeed, this study has been used to demonstrate congruence between ecosystem service value and biodiversity (Turner et al., 2007), even though it failed to account for within-biome variation in economic values—a crucial assumption that is the focus of our current analysis.

Benefit transfer meta-analysis is an alternative approach to direct benefit transfer that takes into account the potential environmental, economic and study-specific factors that might influence the estimation of economic values. Given the limitations of direct benefit transfer, meta-analyses are increasingly demanded (Hoehn, 2006; Richardson et al., 2014; Wilson and Hoehn, 2006). Meta-analyses have been successfully applied to the valuation of coastal and wetland ecosystem service values (Brander et al., 2007; Ghermandi and Nunes, 2013; Woodward and Wui, 2001). Although there have been previous applications of the meta-analytical method for assessing the value of biodiversity (Nijkamp et al., 2008) and temperate forests (Zandersen and Tol, 2009), a comprehensive meta-analysis of ecosystem services in tropical forests has, to the best of our knowledge, not yet been attempted.

Here we carry out a spatially explicit meta-analysis using The Economics of Biodiversity and Ecosystems (TEEB) dataset (de Groot et al., 2012; Van der Ploeg and de Groot, 2010), which is arguably the most comprehensive ecosystem services value database. We evaluate the environmental, economic and methodological factors that drive economic value for tropical forest ecosystem services, *inter alia* climate regulation, disturbance regulation, provision of raw materials and provision of recreation in tropical forests. The main objective of our analysis is to assess whether the economic value of ecosystem services is spatially congruent with biodiversity in tropical forests. Any demonstrable spatial congruence between biodiversity and economic value of ecosystem services would suggest the possibility of win–win conservation strategies that bundle ecosystem services with biodiversity.

2. Methods

2.1. Data collection

The TEEB dataset was queried for ecosystem service values in tropical forests (Van der Ploeg and de Groot, 2010). Studies based on benefit-transfer approaches were excluded since they did not represent independent valuation studies. The list of studies obtained was compared and complemented with the list obtained in the recent estimation of ecosystem service values of the TEEB dataset (de Groot et al., 2012) leading to 78 observations from 31 studies in 24 different countries (Table S3, "TEEB dataset" in the Electronic Supplementary Material (ESM)). The TEEB dataset is the result of selecting primary ecosystem service valuation studies that were scrutinized by TEEB experts for their originality and availability of information on surface area, valuation method and location of the study (de Groot et al., 2012).

To evaluate how well the meta-analytic model could predict the value of other studies for which it had not been trained we performed a review of the literature and compiled a combination of peer-reviewed articles, reports and theses that reported primary economic values of ecosystem services in tropical forests and that were not included in the TEEB dataset (Table S4, "validation dataset" in ESM).

The location of each study was geo-referenced using Google Earth following the name of the reserve, village or district. For studies referring to larger areas, the centroid of the referred forested area was chosen. Studies with a global or national scope were excluded from the analysis. A total of 53 value observations from 20 studies were compiled (Table S3, "validation dataset").

In both the TEEB dataset and the validation dataset, the variance associated with each economic observation was not systematically reported. This reflects the nature of economic valuations that might apply to methods that do not necessarily rely on statistical sampling, e.g. cost-based methods. Hence variance or standard errors could not be used to place weights on the certainty of each value (less variance indicating less uncertainty) as it is customary in meta-analytical studies. As a consequence all observations were implicitly given the same weight in the model.

2.2. Economic value elicitation

In the case of the TEEB dataset, economic values that were reported in different years and sometimes in different currencies have been standardized to international dollars of 2012 using purchasing power parity and deflator tables. We followed the same approach for the validation dataset so that all observations were expressed in the same units. As for the TEEB dataset, all values were expressed per hectare and per year. Some cases in the validation dataset involved eliciting the area of study and dividing the total value by it. Studies for which information on the area was not available were removed. Some studies reported benefits as a net present value. The values were annualized using the discount rate and time horizon reported in the study. Studies that did not report the discount rate and the time horizon were removed.

2.3. Variables

The variables used to explain economic value were derived from theory and previous meta-analytic approaches (Table 1 describes the variables, their estimation and rationale for their inclusion in the meta-analysis). They were grouped into three categories: (i) *methodological variables* describing valuation method (15 categories Tables S2 and S3), ecosystem service (13 categories described in Table S1), whether studies were peer-reviewed or not, and year of publication; (ii) *context variables* capturing the local factors affecting value, which were average temperature and precipitation (New et al., 2002), accessibility (Nelson, 2009), elevation (New et al., 2002), geographically-based GDP (Nordhaus et al., 2006), area of the forest, protected area status (WDPA Consortium, 2004), type of soil (Zobler, 1986), species richness of birds (Jenkins et al., 2013) (species richness of vascular plants (Kreft and Jetz, 2007) was also used as an alternative), types of land use (Bartholomé and Belward, 2005) and carbon content (Ruesch and Gibbs, 2008); and (iii) *variables controlling for sources of non-independence*: country and continent (Table 1).

2.4. Regression meta-analysis

The statistical model had the following form:

$$V_i = \alpha + \sum_{1}^{J}\beta_{Cj}X_{Cji} + \sum_{1}^{K}\beta_{Sk}X_{Ski} + \varepsilon_i \text{ where } \varepsilon_i \sim N(0, \sigma^2)$$

where V_i represents the logarithmic transformation of the economic value estimate of observation i; α is the intercept; β_C and β_S are the coefficients for the J context variables (X_{Cji}) and K methodological variables (X_{Ski}) respectively; and ε is the error term that will be modified when considering heterogeneity of variance, spatial autocorrelation and non-independence using random effects.

For most ecosystem services there were not enough observations to conduct a separate analysis, so the analysis was conducted simultaneously for all the ecosystem services. This was done by adding an explanatory categorical variable indicating the type of ecosystem service (Zuur et al., 2009). Before proceeding to fit the meta-analytic models, multicollinearity was checked using a linear regression model containing the main effects and using variance inflation factors in the R statistical environment (R Development

Table 1
Variables used in the meta-analysis, their description, estimation and rationale for inclusion. The values correspond to the TEEB dataset.

Variable	Units/type of variable[a]	Mean (SD)/number of levels[b]	Rationale/expectations	Source/estimation/notes
Dependent variable				
Economic value	I$/(ha year)	266 (821)	–	Log transformed to prevent negative predictions. Source (de Groot et al., 2012)
Methodological variables				
Peer reviewed	Binary (yes/no)	yes 54%, no 46%	Potential bias to publish high economic value results (Rosenberger and Johnston, 2009)	Generated by authors
Type of ecosystem service	Categorical	13	Different values depending of the nature of the service	See Table S1. (de Groot et al., 2012)
Valuation method	Categorical	15	Contingent valuation methods might lead to lower estimates (Bateman and Jones, 2003; Brander et al., 2007)	E.g. avoided cost, hedonic pricing, replacement cost, travel cost. (See Table S2) (de Groot et al., 2012)
Year of publication	Year	1999 (5)	Techniques might be refined or preferences change over time	Generated by authors
Context variables				
Protection status (protected areas, PA)	Categorical	8 Levels. IUCN I: 13%, III 4%, IV 9%, V 1%, VI 3%. No PA: 71%	Value might increase due to high value site selection bias (Rosenberger and Johnston, 2009) or decrease as use is restricted in protected areas	IUCN categories for protected areas (WDPA Consortium, 2004). The equivalence with the categories in de Groot et al. (2012) was: I–IV: "protected"; V–VIII: "partially protected". The rest were "not protected"
Area of the forest	ha	145 (516)	Smaller areas present services of higher value due to scarcity	Generated by authors and de Groot et al. (2012).
Elevation	m	862 (1154)	Difficult access with altitude, different plant communities	(New et al., 2002)
Geographically based GDP	2005 US $ per 1°·1° grid cell	6 (18)	Economic activity might influence willingness to pay and accessibility	Spatially explicit GDP at purchasing power parity exchange rates per unit of area (Nordhaus et al., 2006)
Population density	Persons/1° 1° grid cell	954,238 (1,799,918)	Higher use and value of the service with higher population	(Nordhaus et al., 2006)
Accessibility	Minutes	601 (803)	Higher value due to higher capacity to use the service	Time of land-based travel to the nearest city >50,000 people in the year 2000 (Nelson, 2009)
Mean monthly temperature	°C	22.2 (7.7)	Might affect the ecosystem and provision of services (Dale et al., 2001)	Mean temperature from 1980 to 2008 (New et al., 2002)
Mean monthly precipitation	mm/month	1946 (869)	Might affect the ecosystem and provision of services (Dale et al., 2001)	Mean precipitation from 1980 to 2008 (New et al., 2002)
Biodiversity	Number of bird and vascular plant species	287 (109) 2008 (755)	Higher provision of services in biodiversity richer ecosystems (Balvanera et al., 2006)	Expressed as the total number of bird species recorded as breeding in each grid cell (Jenkins et al., 2013). Vascular plants (Kreft and Jetz, 2007)
Carbon content	Tons CO_2/ha	226 (140)	Proxy for type of forest. Primary forests have the highest aboveground content of carbon[c]	Expressed as potential CO_2 emissions if deforested. Estimated from maps of carbon aboveground (Ruesch and Gibbs, 2008) that combined with IPCC tables were used to estimate carbon belowground, stored in soil and in dead organic matter (IPCC, 2006)
Global land use 2000	Categorical	14 types	Type of forest might lead to different services (e.g., evergreen, deciduous)	(Bartholomé and Belward, 2005)
Soil type	Categorical	20 types	Type of soil influences plant communities and land use	E.g. cambisol and andosol are suitable for agriculture (Zobler, 1986)
Variables controlling for potential non-independence: random effects				
Country	Categorical	24	Non-captured social, political or environmental circumstances in a country that can affect values	(de Groot et al., 2012)
Continent	Categorical	4	Non-captured social, political or environmental circumstances in a continent that can affect values	(de Groot et al., 2012)

[a] Unit of measurement is reported for continuous variables, type of variable for categorical and binary variables.
[b] Mean and standard deviation are reported for continuous variables, number of levels for categorical variables.
[c] We do not consider carbon content in the soils of peat swamp forests as no comprehensive maps of peat swamp forests across the tropical biome could be found.

Core Team, 2012). Variables with variance inflation factors greater than 4.0 were eliminated or grouped.

There were not enough degrees of freedom to fit a saturated model with all the variables and their interactions. Instead, we fitted a model containing only the main effects of the variables. Because exploratory plots indicated potential nonlinear relationships of value with accessibility and GDP, their quadratic terms were also included. The model was then checked for heteroscedasticity by inspecting plots of the residuals vs. fitted values and vs. each of the explanatory variables. To correct for heteroscedasticity, generalized least squares (GLSs) models were fitted to the data with exponential and categorical variance structures combining the variables that presented heteroscedasticity from visual inspection. The models were compared using the Akaike information Criterion (AIC).

To correct for potential problems of non-independence due to observations coming from the same country or continent, we constructed linear mixed-effects models (LMEs) keeping the fixed part and variance structures similar to the GLS models. The models evaluated were random intercept models using continent and country as random intercepts. To correct for spatial autocorrelation in the LMEs due to a potential tendency for over-studying certain areas, spatial autocorrelation was modeled as a random slope where the mean distance from each observation to the rest was employed (Sodhi et al., 2008).

The random effects part of the LMEs was simplified through the comparison of the AIC of the LME with the equivalent GLS. The fixed part of the models were simplified stepwise using likelihood ratio tests while the model was fitted using the maximum likelihood method. The final models were visually further checked for heteroscedasticity to confirm that the residuals presented no patterns and re-fitted using restricted maximum likelihood (Zuur et al., 2009).

2.5. Meta-analysis validation and representativeness

We compared the results of using the meta-analytic model to scale up ecosystem service values across tropical forests to the rest of the biome with results from two simpler direct-transfer methods: (i) mean value transfer where the average of the values of the observations per ecosystem service apply to all tropical forests and (ii) mean value transfer using observations grouped by continent if data were available and using the global mean when there were not data for a specific service type and continent.

Two validation procedures were employed: (a) leave-one-out cross-validation where the model was fitted to all but one observation in the TEEB dataset. Then the fitted model is used to predict the unused observation. The process is repeated for all the observations, leaving each observation out at a time; (b) prediction of the validation dataset. In both cases the mean predictive error was calculated using the mean absolute percentage error (MAPE). Models pseudo-R^2 was calculated by regressing model fitted response values to the observed values.

The representativeness of the fitted model to the rest of tropical forests elsewhere was assessed by comparing the mean and inter-quartile range of the explanatory variables for the locations for which observations were available with the distributions of those values across the forests in the tropical biome. The more similar both distributions are, the smaller the expected generalization error will be (Rosenberger and Stanley, 2006).

The fitted model was then used to scale-up the results for tropical forests in the tropical biome. For those variables that were not available for extrapolation such as year of publication or area of the forest, the average value in the TEEB dataset was employed. In the case of random effects by country, to extrapolate to those countries for which observations were not available, a value of zero for the random effect was assumed. To estimate the total value of ecosystem services by tropical forests in each map cell we added up 20 ecosystem services according to the three categories of services (provisioning, regulating and cultural) that were used in the data to construct the models (according to the ecosystem services classification in de Groot et al., 2012). A fourth category "habitat services" that contains the services "nursery service" and "gene pool protection" was not included in the benefit transfer as no data on this service category were originally available in the dataset. The values corresponding to supporting services were removed from the datasets to avoid potential double-counting (Boyd and Banzhaf, 2007).

3. Results

3.1. TEEB and validation datasets

The observations in the TEEB dataset were distributed across all continents containing tropical forests: eight in Africa, 23 in Latin America, 33 in Asia and 14 in Oceania. Some countries presented higher number of observations (Australia with 14, India with eight, Indonesia and Malaysia with six, Table S1 in ESM). The year of publication ranged from 1988 to 2007 with the highest number of observations corresponding to the period 2003–4 with 18.

In the validation dataset, 25 of the observations were located in Latin America, five in Africa and 22 in Asia (Fig. S1 in ESM shows the location of the studies in both datasets). The countries with the most observations were Indonesia with 13, Cameroon with eight and Brazil with five. Publication years ranged from 1989 to 2011 and were evenly distributed.

The values for each ecosystem service and dataset showed high variability (Table S1). The mean values for some ecosystem service were markedly different in the TEEB and the validation datasets, in some cases by an order of magnitude (e.g. disturbance regulation and recreation (Table S1)). In contrast, the ranges of values of other ecosystem services were similar across the two datasets (e.g. climate regulation, food, water supply, Table S1).

3.2. Statistical modeling

The Global Land Use 2000 dataset, type of soil, elevation and population density presented high variance inflation factors and were removed stepwise from the analysis. The type of ecosystem service and type of valuation method were also highly collinear. These variables were re-classified into higher hierarchical orders that encompassed all the observations. Ecosystem services were classified into three types: cultural, provisioning and regulating. Valuation methods were classified into three types: cost-based (e.g. avoided cost, replacement cost, restoration cost), revealed preference (e.g. direct market pricing), and stated preference (e.g. contingent valuation) (Van der Ploeg and de Groot, 2010). The removal and re-classification of the variables solved the problems of multicollinearity.

Potential sources of heteroscedasticity were observed for the variables elevation, type of ecosystem service, precipitation, protected status and type of valuation method under visual inspection. The variance structure from the model that attained the lowest AIC was a combined structure where the variance was allowed to vary per type of valuation method and per type of ecosystem service. After implementing this variance structure, visual inspection of the plot of model residuals showed no further problems of heteroscedasticity.

3.3. Meta-analysis

The final meta-analytic model indicated that the economic value was influenced by both context and methodological variables (Table 2). The model was able to explain a large proportion of the variance presenting a pseudo-R^2 of 86%. A negative relationship between the values of ecosystem services with bird species richness was found, showing incongruence between economic value and biodiversity. This relationship was also found if bird richness were substituted by vascular plant richness. Related to this incongruence, a quadratic inverted-U relationship between accessibility and geographically-based GDP on ecosystem services economic value was observed (Table 2, Fig. 1). The contribution of time to travel to cities on economic values was slightly smaller for locations beside cities, then the contribution increased up to $\sim$1000 min of travel, where it peaked, and then decreased with time to travel. Low geographically-based GDP was associated with lower ecosystems services values, peaking at \$60 per $1°{\cdot}1°$ grid cell and then decreasing (Table 2, Fig. 1). A positive relationship between the value of ecosystem services and area of the forest providing the service was also found (Table 2, Fig. 1).

Table 2
Linear mixed-effects model resulting from the meta-analysis of studies from the TEEB dataset. homogBT and contBT: MAPE from direct homogeneous benefit transfer at the biome and continent level. MAPE was estimate for the prediction of the validation dataset and using leave-one-out cross-validation. SD: standard deviation.

	Value	Standard error	*t*-Value	*p*-Value
Intercept	435.691	79.599	5.474	$<10^{-4}$
Service type: provisioning	0.857	0.394	2.177	0.035
Service type: regulating	1.189	0.457	2.604	0.013
Service area (m^2)	1.02×10^{-7}	$<10^{-4}$	5.888	$<10^{-4}$
CO_2 storage (ton/ha)	0.002	0.003	0.659	0.514
Average precipitation	2×10^{-4}	2×10^{-4}	1.255	0.216
Average temperature	−0.013	0.034	−0.374	0.710
Accessibility (min)	0.003	0.001	1.886	0.066
Bird species richness	−0.009	0.003	−3.199	0.003
GDP ($/1°·1°)	0.137	0.057	2.397	0.021
Year of publication	−0.216	0.040	−5.442	$<10^{-4}$
GDP^2	−0.001	0.001	−2.324	0.025
$Accessibility^2$	-1.23×10^{-6}	$<10^{-4}$	−2.367	0.023
Random effects	1|country: SD intercept: 1.77; SD residual: 0.87			
Variance structure parameter estimates	1|method: revealed preference: 1; stated preference: 0.31; cost based: 1.84			
	1|service type: provision: 1; regulative: 1.25; cultural: 1.28			
MAPE cross-validation	308 (homogBT = 332, contBT = 426)			
MAPE validation dataset	264 (homogBT = 135, contBT = 278)			
Pseudo-R^2	0.86			

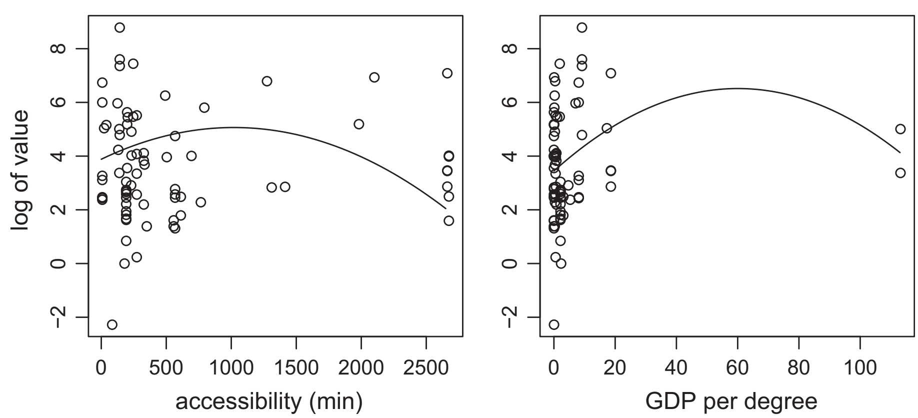

Fig. 1. The relationship between accessibility and spatial GDP with value of ecosystem services. The predictions were made using the fixed part of a LME with only the main effect and quadratic term of accessibility and spatial GDP respectively.

With regard to study variables, regulative services presented higher value than those for supporting and provision services respectively (Table 2). Year of publication was also found to decreased value. Among the variables accounting for potential sources of non-independence, the simplification of the random effects indicated that average distance between observations did not improve the model, showing no problems of spatial autocorrelation. Inspection of a semivariogram plot of model residuals confirmed this result. The final model with a random effect by country presented lower AIC than the equivalent GLS model and the random effect by country was retained. The random effect indicated that higher economic values were expected in countries such as India, Kenya, Costa Rica, Peru, Brazil or Cambodia. Lower economic values were expected for countries such as Madagascar, Nepal, or Cameroon (Table S4).

3.4. Economic value per hectare for the tropical biome

The meta-analytic model was used to generate a raster map of economic values across tropical forests globally with resolution of 0.25° (Fig. 2, shapefiles are available upon request). The estimated values have a mean of international dollars (I$) I$1312/(ha year) and an interquartile range of I$276–1611/(ha year). The spatial distribution of predicted values was complex, responding to the multiple variables contained in the model (Table 2). The random effects, representing factors at the national level such as corruption or governance that could not be captured by the spatial model, were influential. For instance they shifted the value upwards in countries like India, Costa Rica or Peru (Fig. 2). Accessibility (Nelson, 2009) also contributed to explain the complex patterns observed in the Amazon, Borneo and Papua New Guinea.

Under leave-one-out cross validation, we estimated that prediction errors were lower than a direct mean value transfer approach by 7% and 28% when using the value transfer by service type and continent respectively. The model performed worse than direct value transfer by service type when predicting the validation dataset (MAPE of 264 vs. 135 for direct transfer). However, it performed better than direct transfer by continent and service type (MAPE of 278). When bird species richness was substituted by vascular plant species richness the predictive power of the model was considerable reduced (MAPE of 1981 in leave-one-out cross validation and 3496 when predicting the validation dataset).

The mean of the values of the explanatory variables utilized in the meta-analysis showed that the model captured the variability across the tropical biome well (Table 3). All of the median values of the variables in TEEB dataset were contained within the interquartile range of the dataset for the tropical biome. Interquartile ranges were also relatively similar in both datasets (Table 3). In

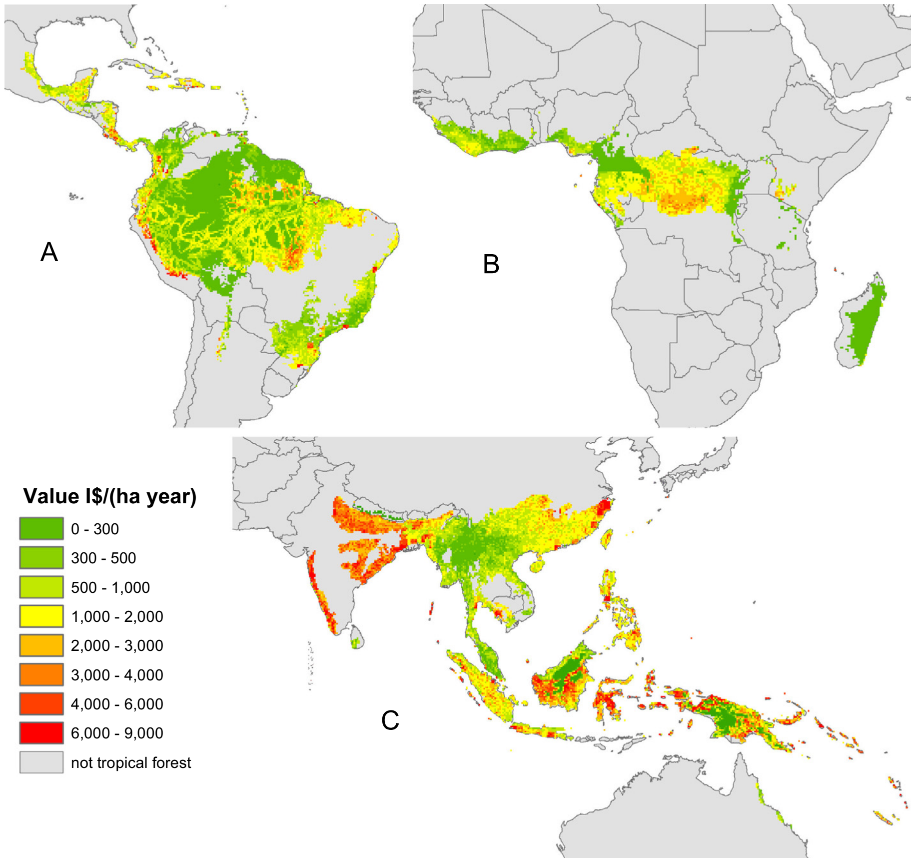

Fig. 2. Total ecosystem service values by tropical forests in America (A), Africa (B) and Asia and Oceania (C) as predicted by the meta-analytic model (Table 2).

the case of protected status, the proportion of non-protected areas was similar in both datasets, although a higher proportion of type I protected areas (12% vs. 4%) was present in the TEEB dataset (Table 3).

4. Discussion

Our results show incongruence between biodiversity and economic values of ecosystem services, indicating that policies that focus solely on ecosystem services economic values will not contribute as much to biodiversity conservation in tropical forests. The link between ecosystem service provision and economic value depends on the complex interactions between the supply and demand of ecosystem services across space. Our results highlight this concept by showing that economic value depends on accessibility to the use of the service—measured as time to travel to cities—in a nonlinear inverted-U fashion (Fig. 1). This could indicate higher degradation or pollution in locations very close to cities, making value increase further away, and then decrease due to the increasing travel cost incurred to benefit from ecosystem services and the lower demand for ecosystem services. Similarly, a nonlinear inverted-U relationship was found with spatially explicit GDP (Fig. 1). This could indicate that economic resources can be a limiting factor to realizing the services of nature, but that beyond a certain economic activity level, perhaps due to availability of alternative livelihoods, the value of ecosystem services by forests decreases. Under these results, due to lower demand, ecosystem services in remote but generally less disturbed and more biodiverse tropical forests would be expected to provide ecosystem services of lower aggregated economic value. The incongruence between biodiversity and the economic value of ecosystem services is complex and could indicate that in undisturbed habitats, that contain the highest species richness, it is more difficult to realize the full use of ecosystem services (e.g. due to low population

Table 3
Representativeness of the TEEB database of tropical forests for the variables used in the meta-analytic model. PA: protected area status IUCN categories. perc.: percentile.

Variable	TEEB dataset			Tropical biome		
	Median	25% perc.	75% perc.	Median	25% perc.	75% perc.
CO_2 storage	220.6	128.9	304.6	192.40	136.94	263.53
Average precipitation	1986.0	1258.0	2766.0	1986.40	1285.90	2640.40
Bird species richness	277.0	201.0	349.8	277.00	219.00	343.00
GDP	0.94	0.07	4.31	2.03	0.12	3.07
Elevation	480.1	361.8	782.8	536.29	361.79	689.12
Accessibility	239.5	192.0	568.0	217.00	192.00	568.00
Average temperature	23.8	22.6	26.78	23.80	23.35	26.70
PA (categories, %)	no PA: 71; I: 13; II: 0; III: 4; IV: 9; V: 1 VI: 3; VII: 0; VIII: 0			no PA: 75; I: 4; II: 0.1; III: 0.4; IV: 12; V: 0.8; VI: 1; VII: 2; VIII: 0.1		

density, remoteness or poor livability conditions to humans). This shows a disconnect between ecosystem service provision—that has been shown to increase with biodiversity (Balvanera et al., 2006)—and economic value, reinforcing the idea that demand and supply need to be matched spatially for the full value of the services provided to be realized.

Because of the spatial relationship between economic value and demand of ecosystem services, the value of ecosystem services is thus likely to vary spatially and with time. The value of ecosystem services in the context of economic activity and accessibility is not fixed geographically but dependent on the forest frontier that is itself related to the demand for ecosystem services. As the forest frontier moves, it will be expected that the location of the fraction of forest that meets the highest demand for ecosystem services also changes. This has implications for the use of ecosystem services value maps as they will need to be updated as economic activity and accessibility to the forest change.

The results that isolated and biodiverse forests have lower economic value of ecosystem services should however be taken with caution as they are limited to economic values. Even though isolated forests have fewer beneficiaries from their services, making the demand for ecosystem services and their aggregated economic value lower, the cultural and food security reliance on forests from those beneficiaries could be much higher than those beneficiaries living near urban areas. Through a global comparative analysis, the Poverty and Environment Network of the Centre for International Forestry Research has shown that up to one-fifth of household income is derived from forest products in developing tropical and sub-tropical countries (Angelsen et al., 2014). For instance, villagers actively harvest bush mango (*Irvingia gabonensis* and *I. wombolu*), *Ricinodendron*, *Aframomum*, rattans, *Gnetum* and *Cola* in Central Africa, particularly during times of agricultural downtime, i.e. post-planting (Sunderland and Ndoye, 2004). The role of forest products as an economic safety net including benefits for dietary diversity, child nutrition and health for millions of people living in the tropics is thus evident (Angelsen and Wunder, 2003; Ickowitz et al., 2014; Wunder et al., 2014), but cannot be captured by economic analyses alone. Although challenging due to data paucity, a way to identify the reliance on ecosystem services by different beneficiaries could be to disaggregate human well-being in different components (Daw et al., 2011).

We found a positive relationship between area of the forest and economic value of the services provided. This relationship contradicts the hypothesis of decreasing marginal returns of value to size of the forest (de Groot et al., 2012). Closer inspection indicated that this relationship was highly influenced by an outlier in which the service area was the largest in the dataset (29 times larger than the average). Repeating the analysis without the outlier did not affect the results of the other variables but made the effect of service area non-significant. These results could be due to different area–service value relationships for different types of ecosystem services. We also found that economic value decreased with year of publication. This could show a refinement of methods making estimates more conservative.

Although, it has been shown that meta-analytic models perform worse than simple value transfers in datasets of contingent valuation studies of non-timber benefits in Norway, Sweden and Finland (Lindhjem and Navrud, 2008), our models present mixed results. They perform better than direct benefit transfer under cross-validation, in line with recent findings of a global meta-analysis of coastal recreation services (Ghermandi and Nunes, 2013) but perform worse than direct benefit transfer when trying to predict the validation dataset. This lower performance could respond to the lack of data in some countries, preventing the use of the random effects when predicting in those countries.

Our analysis presents several limitations: (i) because of data paucity, it was not possible to produce individual models for each ecosystem service or to consider the interactions between specific services and the context variables considered. This required us to produce models for higher hierarchical orders of ecosystem services (cultural, provisioning and regulative), preventing a specific understanding of the behavior of individual services. This has obvious limitations, for instance it was not possible to tease out the fact that carbon sequestration services, that provide benefits at the global scale, are not dependent on local economic activity or accessibility. To overcome this, given the special nature of carbon related services, the maps we generated could be complemented with maps of carbon density (e.g. Ruesch and Gibbs, 2008) and carbon prices to estimate the value of carbon storage. The model should thus be treated as an analysis of common trends in aggregated combination of service types. The analysis could be refined in the future provided that further observations on ecosystem service values at the local scale in the tropics become available. More observations would facilitate a more detailed analysis, notably for ecosystem services such as biocontrol or disturbance regulation for which we found very few estimates (Table S1). (ii) Related to the previous limitation, as a result of data paucity, total ecosystem service values were estimated by addition of specific types of ecosystem services. As more data become available, the trade-offs and synergies between specific ecosystem services could be accounted for. (iii) We approximated biodiversity using bird diversity through their breeding ranges. This is commonly undertaken due to the wide availability of data for birds compared to other taxa and has been shown to be a good surrogate of overall biodiversity especially where birds are speciose (Larsen et al., 2012) as in tropical forests. As a way of uncertainty analysis, we also fitted the models using species richness of vascular plants (Kreft and Jetz, 2007) instead of bird species richness. A similar significant negative relationship between species richness and economic value was found, although the model presented very poor predictive power. This could be explained by the ten times lower resolution of vascular species maps with respect to bird richness maps. As a result, bird species richness was employed as a surrogate of biodiversity in the model. (iv) Although our maps could be used as a first step to support large scale conservation planning, given the broad scale of the analysis, our maps should not be used in isolation to support local policy. The unavoidably coarse resolution of the maps given the large scale of the analysis fails to capture the nuances of ecosystem values at the local scale and should be complemented and verified with on-the-ground studies.

We generated maps of ecosystem services values by tropical forests that should be regarded as a first step toward producing pantropical maps of economic values of ecosystem services. These maps are urgently needed given the rapid transformation of forest cover into agriculture in these regions. The take-home message from these maps is that policies that are based on the economic values of ecosystems services might fail to protect biodiversity and food security of isolated communities. Our results thus call for multi-criteria approaches where biodiversity is considered at the same level as ecosystem services values. It would thus not be advisable to use ecosystem services values as the only criterion or as bundled objectives with biodiversity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.08.007.

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