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Highlights

- The role of biodiversity on climate change mitigation by tropical forests remains poorly understood.
- Empirical, remote sensing and modelling studies provide complementary information.
- In more than 75% of the studies, biodiversity significantly affected carbon storage or sequestration.
- Biodiversity underpins short-term ecosystem functioning and assures long-term carbon storage and sequestration in tropical forests.
- Integrating approaches by using ‘boundary objects’ will lead to a comprehensive understanding.

Title: The integration of empirical, remote sensing and modelling approaches enhances insight in the role of biodiversity in climate change mitigation by tropical forests

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Abstract

Tropical forests store and sequester high amounts of carbon and are the most diverse terrestrial ecosystem. Studies show potentially important effects of biodiversity on carbon storage and sequestration, but a complete understanding of this relationship across spatiotemporal scales relevant for climate change mitigation needs three approaches: empirical, remote sensing and ecosystem modelling. Here, we review the contribution of these *individual approaches* to the understanding of the relationship of biodiversity with carbon storage and sequestration, and find short-term and long-term benefits of biodiversity at both broad and fine spatial scales. We argue that enhanced understanding is obtained by *combining approaches*, i.e., by using output from one approach to improve another approach and thus results in better input, validation and comparison between approaches. This can be further improved by *integrating approaches* through using 'boundary objects' (i.e., variables) that can be understood and measured by all approaches, such as the diversity of leaf traits of the upper canopy and forest structure indices. Combining and especially integrating approaches will therefore lead to a better understanding of biodiversity effects on climate change mitigation. This is crucial for making sound policy decisions.

Keywords: biodiversity-ecosystem functioning, carbon sequestration, carbon storage, forest structure, functional diversity, REDD+, species diversity

Introduction

Tropical forests play a major role in the global carbon cycle and are therefore important for climate change mitigation [1]. Tropical forests are also biodiversity hotspots and thus relevant for biodiversity conservation [2]. With ‘biodiversity’ we refer here to different vegetation properties: species and trait diversity, community-mean trait values and forest structure. Biodiversity is important for human wellbeing; it provides essential supporting, provisioning, cultural and regulating ecosystem services [3]. For example, biodiversity can potentially increase the capacity for carbon storage and sequestration, not only in temperate systems [e.g., 4,5] but also in highly diverse tropical forests [6]. In turn, this increased carbon uptake capacity may lead to a higher potential for climate mitigation. By evaluating how biodiversity affects carbon storage and sequestration, we can underscore the importance of tropical forests not only for nature conservation but also for climate mitigation.

To fully understand the effect of biodiversity on carbon storage and sequestration (hereafter referred to as “carbon”), we first need to develop a mechanistic understanding of the short-term and local-scale effects of biodiversity on carbon. For this relationship to be relevant for global climate change mitigation, it should also occur at broader spatial and longer temporal scales that will have most impact and long-term benefit on climate change mitigation. Three approaches are needed to cover these different aspects of the relationship between biodiversity and climate change mitigation: an empirical approach to understand the short-term and local-scale relationship (Figure 1, Arrow 1), a remote sensing approach to scale up to broad spatial scales (Figure 1, Arrow 2) and an ecosystem modelling approach to scale up to long temporal scales (Figure 1, Arrow 3). These approaches are complementary in their ecological realism, spatial and temporal scale and contribute differently to the understanding of the biodiversity-carbon relationship and its consequences for global climate change mitigation (Table 1, Figure 1).

In this paper, we advocate that combining and integrating empirical, remote sensing and ecosystem modelling approaches is needed to understand biodiversity effects on carbon across spatiotemporal scales. To show this, we perform a literature review to bring together evidence from the **individual approaches** to evaluate their contribution to the understanding of the biodiversity-carbon relationship. We then discuss how we can **combine approaches** to improve the assumptions, cross-validation and output of studies evaluating the biodiversity-carbon relationship. Finally, our study moves beyond the concept of combining approaches to **integration of approaches**. This is essential to link, scale and translate among the approaches, and therefore to provide the best understanding of the biodiversity-carbon relationship across spatiotemporal scales that are most relevant for climate change mitigation.

Contribution of individual approaches – a review

Empirical studies – Empirical studies and experiments in the field that control for confounding factors provide insight into mechanisms underlying the biodiversity-carbon relationship, identify important aspects of biodiversity and provide evidence whether this relationship is strong enough (i.e., detectable and significant) to have a substantial effect on the functioning of natural systems. Empirical evidence for the biodiversity-carbon relationship is increasing rapidly, starting from conceptual ideas [7] to testing this relationship for different ecosystems [e.g., 4,5]. For tropical forests, however, the evidence is still emerging and scattered among local studies [e.g., 8,9] and regional to continental studies [e.g., 6,10].

A recent review [11] evaluated 38 empirical studies on the role of different biodiversity indicators for carbon storage and dynamics (i.e., fluxes of carbon over time such as growth and mortality) in tropical forests. This review provided three main results. First, carbon dynamics increased most often with taxonomic diversity [e.g., 12], whereas carbon storage depended most on the average trait values of the tree community (i.e., community-mean traits) [13]. These results indicate that biodiversity is of major importance, but that different biodiversity indicators represent different mechanisms by which they contribute to carbon storage or dynamics: i) taxonomic (or functional) diversity can increase complementarity among species in their strategies to acquire and use resources, and as such increase overall carbon storage and sequestration [14] and ii) community-mean traits mainly represent the most dominant species in a community, which may most strongly influence carbon storage and sequestration [15]. A thorough understanding of the role of different biodiversity indicators on multiple carbon-related variables is therefore necessary to guide climate change mitigation policies. Second, the review [11] showed that this relationship is stronger in mature forests than in disturbed or plantation forests, perhaps because of stronger competition and thus higher importance of biodiversity for carbon in denser forests. Third, the biodiversity-carbon relationship was stronger at broader spatial scales across sites (e.g., across Neotropical forests [6,10]), possibly because of stronger variation in biodiversity across sites at broader spatial scale. However, since empirical studies mostly capture processes at the plot or landscape scale, the role of spatial scale in the biodiversity–carbon relationship remains unclear.

Remote sensing studies – Remote sensing allows to assess the biodiversity-carbon relationship at continuous and broader (i.e., regional to global) spatial scales relevant for policy. Remote sensing monitors changes in carbon and biodiversity over time, which is important for, among others, the measurement, verification and reporting of countries' efforts to Reduce Emissions from Deforestation and forest Degradation (REDD+). However, remote sensing is based on indirect proxies for ecosystem processes and properties and is limited in analysing site-specific conditions such as soil fertility that can co-determine carbon.

Several studies reviewed the potential and limitations of remote sensing based methods for measuring and monitoring carbon [16] and biodiversity [17,18] of tropical forests (for relevant advances in this field see Appendix S1). For forest carbon, wall-to-wall pan-tropical benchmark maps based on different techniques and resolutions have been developed [19–21]. However, remote sensing based maps of biodiversity are still rare [22], thus limiting the number of studies, especially broad scale, that evaluate biodiversity-carbon relationships. We identified and qualitatively assessed 10 studies that evaluated this relationship (Appendix S2a-c). Nine of the ten studies show a positive relationship between biodiversity and carbon storage (no studies evaluated carbon sequestration), for different biodiversity indicators: plant species diversity (7 studies), fauna species diversity (2) and plant trait diversity (1). The strength of the biodiversity-carbon relationship varied considerably among studies (r = -0.01 – 0.83) but seems to be scale-independent: both the strongest and the weakest correlations were found at the fine scale (Appendix S2a). At least three possible reasons may explain the variation in correlation strength. First, differences in environmental conditions may explain this variation. Spatial variation in rainfall seasonality and species richness was significantly positively related to the strength of the correlation between species richness and carbon storage (Figure 2,

Appendix S2), indicating that species richness effects on carbon storage increase towards more seasonal and towards more diverse forests. Second, the strength may depend on the method used to derive biodiversity and carbon variables. When biodiversity and carbon storage are derived using the same method (e.g., LiDAR), they are not independent and may show a stronger correlation compared to when the variables are obtained from independent remote sensing sources. Third, the strength of this correlation may depend on the prediction accuracy of remote sensing indicators for biodiversity and carbon. A range of retrieval methods is used to estimate carbon storage and biodiversity indicators by relating remote sensing data sources to field observations (Appendix S2b), but an optimal method is still to be agreed on [23]. Although the small number of studies does not yet allow formal testing of the biodiversity-carbon relationship, the studies indicate that hotspots for carbon storage are related to hotspots for biodiversity.

Modelling studies – Modelling studies allow assessment of the biodiversity-carbon relationship at temporal scales of up to centuries, and evaluate impacts of alternative future climate change scenarios and selected policy interventions. However, modelling is a simplification of the real world and therefore the representation of multiple interacting processes may miss relevant processes.

Testing biodiversity-carbon relationships using ecosystem models requires a modelling framework that simulates physiological and morphological processes, plant competition and mortality, and functional and structural diversity. We found only three models that studied biodiversity-carbon relationships (Appendix S4). First, a dynamic plant functional trait model was applied to Australian forests [24]. This study found that, with modest climate change, plant trait diversity increased carbon sequestration in lowland forests, but this effect decreased with strong climate change (under SRES A1FI scenario). Second, species diversity weakly increased forest productivity in northern India (simulated by the remote-sensing based Carnegie-Ames-Stanford Approach (CASA) model) under current climate conditions [25]. Third, functional trait diversity increased forest recovery of carbon stocks, and hence forest resilience, after climate change in a dynamic global vegetation model (DGVM) that accounts for competition and plant trait diversity (Lund-Potsdam-Jena managed Lands with Flexible Individual; LPJmL-FIT, [26]).

One reason for the limited amount of studies is the lack of a realistic representation of biodiversity in ecosystem models. A potentially useful modelling approach is the use of DGVMs. Initially, DGVMs had a very simplified representation of biodiversity, using several plant functional types [e.g., 27], but recent model developments focussed on implementing functional diversity or plant trait diversity in the DGVM framework. DGVMs can now include variation in some plant traits, adaptive responses, and trade-offs between traits [e.g., 28] (see Appendix S5 for more details on the models). These model developments will allow testing the biodiversity-carbon relationship at various temporal scales, including the effect of biodiversity on forest resilience.

The biodiversity–carbon relationship: state of the art

We evaluated the biodiversity-carbon relationship using three complementary approaches, and found that biodiversity significantly and positively affected carbon storage and/or sequestration in the majority of the empirical studies (75%) and remote sensing studies (90%) and a weak positive effect on long-term carbon in the most recent models. These results extend the well-known findings from experimental studies and temperate systems that ***biodiversity matters for ecosystem functioning in tropical forests***.

The different approaches provided complementary information on the role of spatial scale. Among empirical studies, the biodiversity-carbon relationship was stronger at large spatial scale (e.g., across Neotropical forests) than at fine spatial scale (e.g., within one forest type). In contrast, remote sensing studies found that the strength of the biodiversity-carbon relationship did not vary with spatial scale, perhaps because of the indirect way in which they assess both biodiversity and carbon. Modelling studies showed that biodiversity is important for carbon not only at short, but also at long temporal scales where it serves as an ‘insurance’ against environmental hazards. Hence, although scale seems to affect the strength of the biodiversity-carbon relationship, ***biodiversity underpins short-term ecosystem functioning and assures long-term carbon storage and sequestration in tropical forests, at both fine and broad spatial scales***. These results indicate that biodiversity conservation is not a mere co-benefit of management for REDD+, but should be considered as a requirement for long-term effective REDD+ activities [29].

Combining approaches

To go beyond individual contributions (Figure 3a), we advocate to ***combine approaches*** to improve the quality of input data, refine assumptions, facilitate cross-validation and evaluate the robustness of relationships across approaches (Figure 3b). We here discuss opportunities to combine the three approaches. First, empirical and remote sensing approaches can be combined (Figure 3b, Arrow 1) to validate remote sensing results, e.g. by evaluating the detection algorithm, and to facilitate accurate upscaling of local observations to broad spatial scales. Second, empirical and ecosystem modelling approaches can be combined (Figure 3b, Arrow 2) in several ways. For example, the mechanisms underlying biodiversity-carbon relationships found in empirical studies can be included in modelling approaches and used to refine model assumptions for more accurate long-term predictions. Furthermore, findings from fine-scale empirical studies can be tested in models over longer temporal scales, thus facilitating the generalisation of the mechanisms. Third, remote sensing and ecosystem modelling approaches can be combined (Figure 3b, Arrow 3) by using remote sensing data as an input for ecosystem models [30], or to validate modelled patterns and processes [31].

The combination of the three approaches would thus allow better exploration of the mechanisms behind the biodiversity-carbon relationship at broad spatiotemporal scales. Hence, combining approaches in such ways – by using output from one approach to improve another approach – leads to opportunities for better input, validation and scaling.

Integrating approaches

Integrating approaches moves beyond combining them by using similar indicators as input and/or output. Using similar indicators allows direct comparison among, and scaling between, approaches to better understand biodiversity-carbon relationships. To avoid translation problems of indicators across approaches, we propose to use '*boundary objects*', which are indicators that "are both adaptable to different viewpoints [in our case approaches] and robust enough to maintain identity across them" [32]. Boundary objects are frequently used in interdisciplinary studies to communicate across scientific disciplines (such as 'resilience' and 'ecosystem services' [33,34]). Using boundary objects that can be measured by the three research approaches could greatly facilitate scaling among them and advance our understanding of biodiversity effects on climate change mitigation.

Several potential boundary objects can be used for carbon and biodiversity (see examples in Table 2). Indicators for aboveground carbon storage are relatively easy to quantify by all approaches and are already being used. Aboveground net carbon change (i.e. net carbon uptake or net biomass growth at the ecosystem level) can serve as a boundary object for carbon sequestration as it can be measured by all approaches albeit using different methodologies. Boundary objects for biodiversity are more complicated to define as the concept of biodiversity is broadly defined, ranging from genetic to ecosystem diversity (Convention on Biological Diversity). In this review, we separated biodiversity into three important groups of vegetation properties: species and trait diversity, community-mean trait values and forest structure (Table 2 [cf. 11]). A useful boundary object for biodiversity is the diversity and the mean of leaf traits of the upper canopy, such as specific leaf area [35] and leaf nutrient concentrations [36]. Leaf trait diversity can be easily measured in the field [37] by empirical studies, can be seen from space for the upper canopy by new hyperspectral remote sensing techniques [e.g., 35] and are explicitly included in recently developed dynamic global vegetation models [e.g., 38]. Indicators for forest structure, such as crown size distribution of the upper canopy, can also serve as boundary object, as they can be captured by all three approaches (Table 1). These example boundary objects can be similarly measured by all approaches and therefore directly used to scale between approaches. Such boundary objects may thus allow for integration of empirical, remote sensing and modelling approaches. This, in turn, will help advancing our understanding of biodiversity effects on carbon across spatiotemporal scales, and thus on climate change mitigation (Figure 1).

Concluding remarks

Empirical, remote sensing and ecosystem modelling approaches each have their complementary strengths in evaluating biodiversity effects on carbon storage and sequestration. These individual approaches show that biodiversity is generally important for short-term and long-term carbon storage and sequestration, indicating that biodiversity conservation is not only a co-benefit of REDD+ activities, but is an integral and crucial component of effective REDD+ implementation [29]. However, we advocate that combining, and especially integrating these three approaches will provide an enhanced understanding of how biodiversity contributes to climate change mitigation. We propose the use of boundary objects as a means of integrating all three approaches and span across spatial and temporal scales relevant for climate change mitigations. Such integration of approaches can provide input to guide society and policies such as REDD+ to reach the goals of the UNFCCC Paris Agreement.

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Table 1: Overview of the differences among empirical, remote sensing and ecosystem modelling approaches in terms of: spatial scale, temporal scale, biodiversity variables that can be accurately estimated, how likely it is that carbon estimates are correct, the workload per unit area or time evaluated and their main strength. Please note that this overview highlights the main aspects per approach that is relevant for this manuscript, rather than that it provides an exhaustive overview of the properties of the approaches.

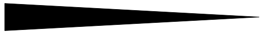
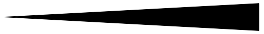
	Spatial scale	**Temporal scale**	**Biodiversity variables that can accurately be estimated**	**How likely carbon estimate is correct?**	**Workload per unit area or time evaluated**	**Main strength**
	Small Large	Short Long				
Empirical			Species, functional traits, forest structure	Very likely	High	Underpinning mechanisms
Remote sensing			Forest structure	Likely	Medium	Spatial scaling
Ecosystem modelling			Functional groups, forest structure	Likely	Medium	Temporal scaling

Table 2: Potential ‘boundary objects’ that can be used to integrate empirical, remote sensing and ecosystem modelling approaches. We identify three potential boundary objects for ‘biodiversity’ (species, functional trait and structural diversity) and two potential boundary objects for ‘carbon’ (storage and net change).

		Empirical studies	**Remote sensing studies**	**Ecosystem modelling studies**
				
Biodiversity	Species and trait diversity	Number of species Functional diversity (based on leaf traits)	Number of species, obtained from imaging spectroscopy. Variation in specific leaf area and leaf nutrient concentrations from imaging spectroscopy and hyperspectral imaging	Number of functional groups. Distribution of specific leaf area and other trait values in the modelled tree community
	Trait mean	Community-weighted mean leaf traits	Leaf trait values of tree canopy averaged by area	Average trait values of the modelled tree community.
	Forest structure	Variation in crown size (e.g. diameter)	Variation in crown shape and diameter from LiDAR	Variation in crown size
Carbon	Storage	Standing stocks per unit area	Standing stocks per unit area	Standing stocks per unit area
	Sequestration	Aboveground biomass growth or net change	Aboveground net biomass change	Aboveground gross or net primary productivity

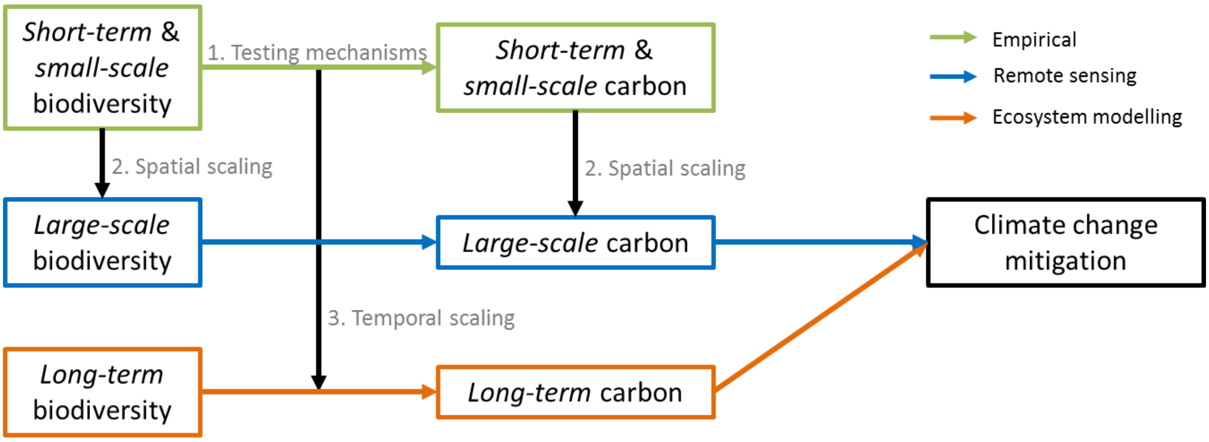


Figure 1: Conceptual framework showing how three different research approaches (empirical, remote sensing and ecosystem modelling) contribute to the understanding of biodiversity effects on carbon sequestration and storage ("carbon") and, hence, on climate change mitigation. Their main advantage and contribution to assessing the role of biodiversity for climate change mitigation is displayed in boxes, although not being exhaustive. Empirical studies (green, Arrow 1) provide a mechanistic understanding of biodiversity effects on carbon, both measured at fine spatial scales (e.g., local) and short temporal scales (e.g., a decade). Remote sensing studies (blue, Arrow 2) scale up to broader spatial scales (e.g., continental), and ecosystem modelling (orange, Arrow 3) scale up to longer temporal scales (e.g., centuries). Remote sensing scales up variables (biodiversity and carbon), whereas ecosystem models generally use the relationship to scale up.

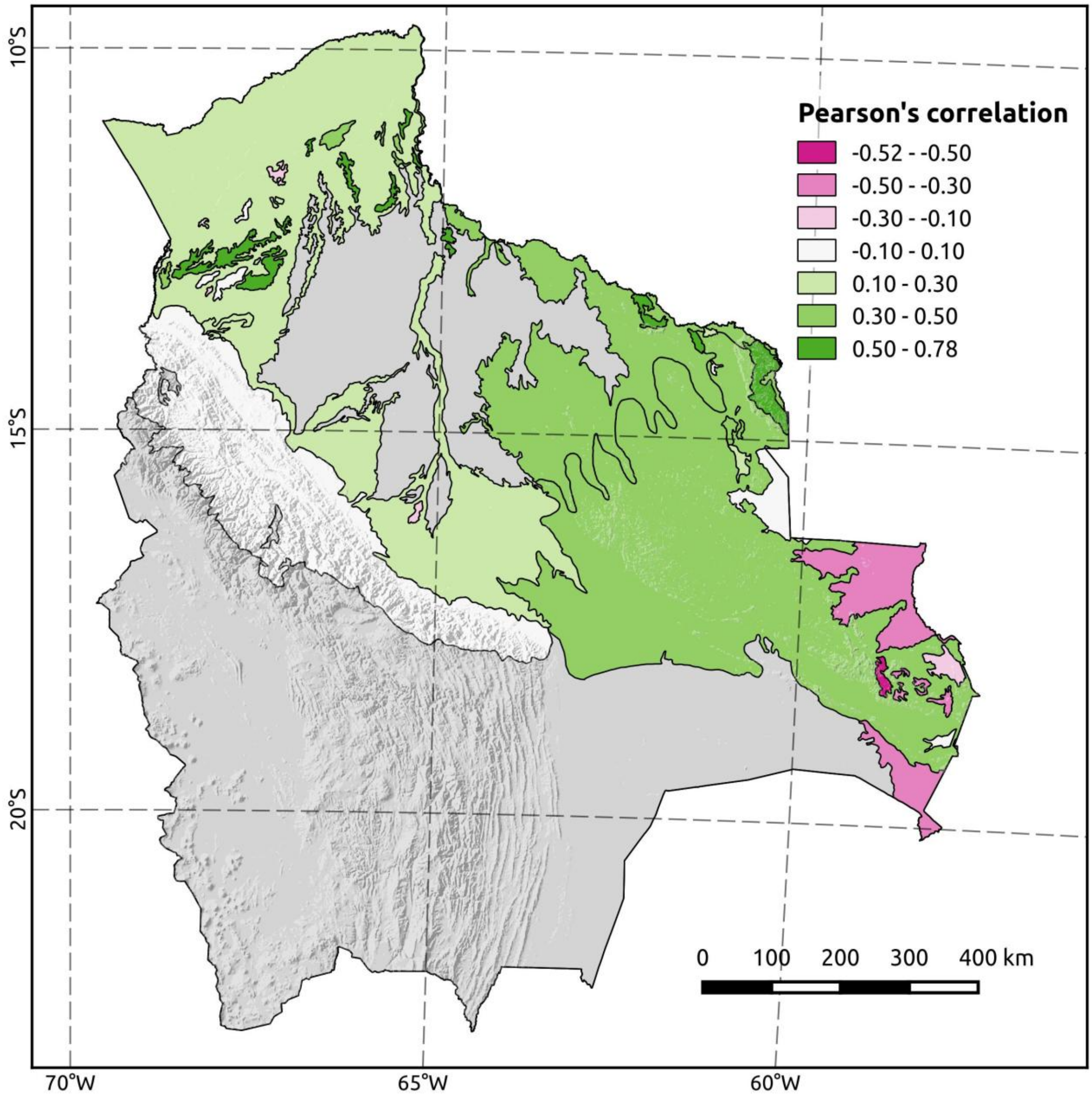


Figure 2: Spatial correlation between remote sensing-derived tree species richness and aboveground biomass for tropical forest in different biogeographic zones in lowland Bolivia (see Appendix S3 for methods). The correlation strength increased with rainfall seasonality (i.e., the coefficient of variation of monthly rainfall; $P < 0.001$, $t = 4.3$, N = 53) and with predicted species richness ($P < 0.001$, $t = 5.4$, N = 53). In both regression analyses, we included the size of the area as a variable to correct for possible effects of differences in pixel number on which the correlation coefficient was based. Rainfall seasonality and predicted species richness were not significantly correlated ($r = 0.20$, $P = 0.12$, $t = 1.55$). Data were obtained from Kooistra *et al.* [39].

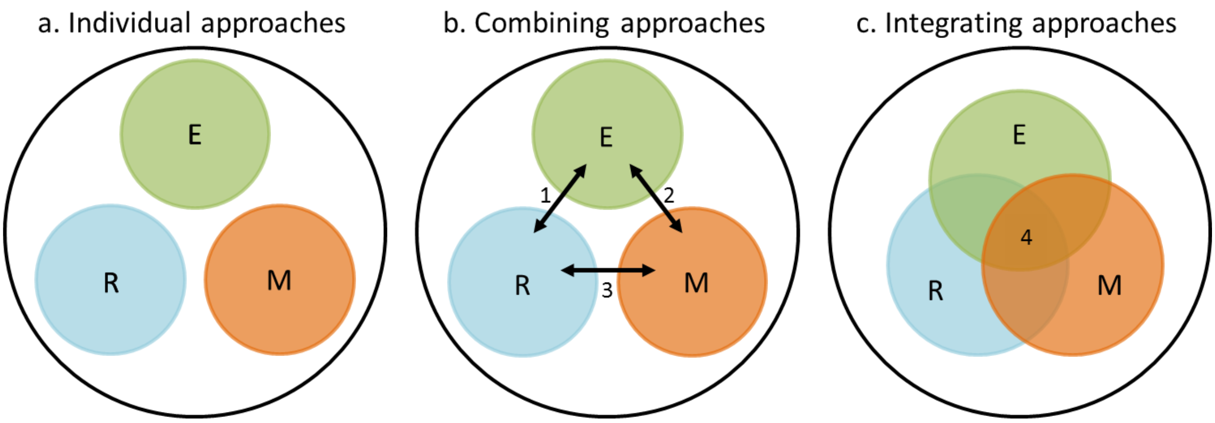


Figure 3: Representation of the differences between a) using individual approaches (E and green: empirical; R and blue: remote sensing; M and orange: ecosystem modelling) to compare results, b) combining approaches (e.g., validations and spatial and temporal upscaling) and c) integrating approaches through the use of 'boundary objects', for example by using diversity in leaf traits or indices of forest structure, which can be measured in empirical field studies, scale up over larger areas using remote sensing and included in modelling studies. Possible combinations are: empirical and remote sensing approaches to scale the biodiversity-carbon relationship to broader spatial scales (Arrow 1), empirical and modelling approaches to scale this relationship to larger temporal scales (Arrow 2) and remote sensing and modelling approaches for further validation and improvements of the approaches (Arrow 3). Integrating approaches seeks for boundary objects, i.e. indicators that can be quantified by each approach (number 4 in the figure). For examples of boundary objects, see Table 2.

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