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Towards connecting biodiversity and geodiversity across scales with satellite remote sensing

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ABSTRACT

Issue

Geodiversity—the variation in Earth's abiotic processes and features—has strong effects on biodiversity patterns. However, major gaps remain in understanding how relationships between biodiversity and geodiversity vary over space and time. Biodiversity data are globally sparse and concentrated in particular regions. In contrast, many forms of geodiversity can be measured continuously across the globe with satellite remote sensing. Satellite remote sensing directly measures environmental variables with grain sizes as small as 10s of meters, and can therefore elucidate biodiversity-geodiversity relationships across scales.

Evidence

We show how one important geodiversity variable, elevation, relates to alpha, beta, and gamma taxonomic diversity of trees across spatial scales. We use elevation from NASA's Shuttle Radar Topography Mission (SRTM) and ~16,000 Forest Inventory and Analysis plots to quantify spatial scaling relationships between and biodiversity and geodiversity with generalized linear models (for alpha and gamma diversity) and beta regression (for beta diversity), across five spatial grains, ranging from 5-100 km. We illustrate different relationships depending on the

form of diversity; beta and gamma diversity show the strongest relationship with variation in elevation.

Conclusion

With the onset of climate change, it is more important than ever to examine geodiversity for its potential to foster biodiversity. Widely-available satellite remotely sensed geodiversity data offer an important and expanding suite of measurements for understanding and predicting changes in different forms of biodiversity across scales. Interdisciplinary research teams spanning biodiversity, geoscience, and remote sensing are well-poised to advance understanding of biodiversity-geodiversity relationships across scales and guide the conservation of nature.

KEYWORDS

Alpha diversity, beta diversity, gamma diversity, biodiversity, geodiversity, satellite, remote sensing, scale-dependent, elevation, trees

INTRODUCTION

The Earth is experiencing unprecedented global change, and species face uncertain fates. Global changes including climate change can cause species to shift their geographic ranges, resulting in the (dis)assembly of communities, and novel or no-analogue communities (Williams & Jackson, 2007) and ecosystems (Hobbs *et al.*, 2009). Species' range shifts present logistical and ethical challenges for conservation prioritization (McLachlan *et al.*, 2007). In response, conservationists have proposed focusing on 'geodiversity' as a means to preserve biodiversity, as areas with high geodiversity should harbor future biodiversity even under changing species composition (Gill *et al.*, 2015; Lawler *et al.*, 2015; Shaffer, 2015). This aptly-named 'conserving nature's stage' approach has been adopted by The Nature Conservancy to prioritize conservation of climate resilient sites (Beier & Brost, 2010; Shaffer, 2015). However, major knowledge gaps lie in understanding and predicting how different forms of geodiversity influence biodiversity patterns across spatial and temporal scales (Fig. 1A), and in adopting geodiversity data sources that span these scales (Fig. 1B). Such knowledge is essential for effective conservation and policy because many ecological processes and patterns are scale-dependent (Levin, 1992; McGill, 2010).

Here we present an approach to identify relationships between biodiversity and geodiversity across scales, provide results for a case study with alpha, beta, and gamma tree diversity across a large region of the United States, and identify a suite of global and near-global satellite remotely-sensed geodiversity data sources spanning spatial and temporal scales.

Forms of Geodiversity

A range of definitions of geodiversity exist—some include climate whereas others explicitly exclude it (Parks & Mulligan, 2010; Gray, 2013; Lawler *et al.*, 2015; Tukiainen *et al.*, 2017). In addition, geodiversity has commonly been treated categorically by thematically mapping climate, geology, geomorphology, and soil features into land units (Gray, 2013; Anderson *et al.*, 2015). To enable the use of continuous metrics in addition to ordinal and categorical ones, and to evaluate scaling relationships between biodiversity and geodiversity, we adopt the following definition of geodiversity: the set of abiotic processes and features of Earth's Critical Zone (lithosphere, atmosphere, hydrosphere, and cryosphere). This comprehensive definition is inclusive of climate and reflects the fact that Earth's fluid and solid components have strong influences on each other (Jenny, 1991).

Like biodiversity, geodiversity can be described in different forms: as heterogeneity or variability within a site; as spatial turnover or the difference between sites; and as total variability across all sites. Unlike ground-based biodiversity observations, geodiversity can be spatially continuous when measured via satellite remote sensing. Some forms of geodiversity are categorical (e.g., number of distinct features) and can be summarized with measures of diversity, whereas heterogeneity in continuous variables (e.g., elevation) can be determined using various metrics such as standard deviation, kurtosis, or various texture measurements. Scaling relationships in geodiversity are common. For example, variation in soil moisture decreases with sampling extent (Choi *et al.*, 2007), and the hydraulic geometry of stream channels (Leopold & Maddock, 1953) and river networks dictate how variability in slope changes with extent (Tarboton *et al.*, 1989).

Historically, it has been difficult to obtain reliable, consistent, and continuous geodiversity data at regional or global scales. For this reason, spatial models of species distributions and biodiversity have traditionally used topographic data as a proxy variable for climatic or environmental variance, often combining it with gridded data interpolated from weather stations (Waltari *et al.*, 2014). However, recent work highlighted the wide range of methods and accuracies among products, showing that there is no ‘best’ product and that higher resolution products are not necessarily more accurate (Behnke *et al.*, 2016). Recent satellite missions such as Landsat 8, Sentinel-1 and -2, and ICESat-2 enable accurate and continuous acquisition of global geodiversity data in space and time (Fig 1B, Appendix A). The resulting data products include surface temperature, snow cover, clouds, topography, and more. In addition, reanalysis products like MERRAclim (Vega *et al.*, 2017) combine satellite Earth observations (1979-present) to develop global models of geodiversity variables with coarse spatial resolution but high temporal resolution at temporally and spatially consistent scales. Although satellite-derived estimates of temperature and rainfall have limitations (e.g., Wan *et al.*, 2004; Maggioni *et al.*, 2016), their coverage is global or near global. For other geodiversity variables, like soil moisture and groundwater (see Appendix A), no station-derived global gridded products exist; thus, satellite remote sensing provides a needed data source. Perhaps the most widely used gridded station datasets by ecologists is WorldClim (Hijmans *et al.*, 2005). The newly released WorldClim-2 dataset (Fick & Hijmans, 2017) now includes MODIS land surface temperature (LST) and cloud cover data, highlighting the importance of satellite remotely sensed data.

Satellite Remotely Sensed Geodiversity Data are Critical for Understanding Patterns of Biodiversity

Geodiversity affects patterns of biodiversity directly and indirectly. Environmental conditions map directly to individuals’ physiological limits, whereas topographic complexity, habitat patch arrangement, and geophysical feature configuration are associated with niche diversity. Physical barriers to movement and the persistence of landscape features can also indirectly affect biodiversity by enabling or restricting biotic interactions among species (Zarnetske *et al.*, 2017), and affecting dispersal ability (Urban *et al.*, 2013). Components of geodiversity provide resources for species, including energy, water, nutrients, and space (Parks & Mulligan, 2010).

Without satellite remotely sensed geodiversity data, it can be difficult to detect drivers of biodiversity patterns across large extents. With satellite remote sensing, spatially continuous, direct, and independent measures of climate and elevation provide a means to identify when and where climate and elevation covary, enabling biodiversity scientists to ask persistent questions about the drivers of patterns of biodiversity at larger extents, with finer resolutions, and at multiple scales.

Knowledge Gap: Geodiversity & Biodiversity Across Spatial Scales

Despite their inherent coupling, and individual scale-dependence (Willig *et al.*, 2003; Rahbek, 2005), biodiversity and geodiversity scaling relationships across taxa, regions, and diversity measures are not well characterized. A recent study provides important insights into scaling relationships between taxonomic alpha diversity of alien vascular plant species and geodiversity of landforms from geological surveys and airborne remote sensing across Great Britain (Bailey *et al.*, 2017). In that study, landform diversity explained the most variation in alpha diversity at smaller spatial scales, whereas climate became more important at larger spatial scales. Yet biodiversity can be calculated in several forms: as alpha (within-site), beta (turnover between sites, or the ratio of within-site to across all sites), or gamma diversity (total across all sites). Further investigations could reveal how consistent biodiversity-geodiversity relationships are across species, regions, and forms of biodiversity. Both the data and the computational tools are now becoming available to address these relationships (Appendix A). Here we ask: how do the relationships between geodiversity and different forms of biodiversity change across spatial scale? In Box 1 and associated supplemental material, we present an approach to identify these biodiversity-geodiversity scaling relationships, illustrated with a case study of trees and elevation spanning 16.5 degrees latitude in the western United States.

Globally, the highest levels of species richness are likely to be observed where high geodiversity, like topographic heterogeneity, coincides with relatively productive and stable climatic regimes such as the tropical Andes (Rahbek & Graves, 2001; Kreft & Jetz, 2007; Buckley & Jetz, 2008). One explanation for this pattern is that warmer, stable climates promote higher biodiversity (Hawkins *et al.*, 2003), and biodiversity promotes productivity and system sustainability (Tilman *et al.*, 1996), even in fluctuating environments (Yachi & Loreau, 1999) and across heterogeneous landscapes (Oehri *et al.*, 2017). In addition, geodiverse regions such as those that are tectonically active, exhibit high species richness and spatial turnover of species (Badgley *et al.*, 2017). Such heterogeneous environments provide refuge habitat to support species persistence after environmental change and can isolate populations resulting in speciation events (Stein *et al.*, 2014). Increased richness in geodiverse areas may also occur because resource and habitat partitioning allow more species to coexist. Greater environmental heterogeneity at a given site often correlates with higher species richness, but this relationship depends on the scale at which a species perceives the heterogeneity (Tews *et al.*, 2004).

Although different species may exhibit different scaling relationships with geodiversity, these relationships are likely driven by common mechanisms at certain scales, regardless of taxonomic group. At continental to global scales, broad gradients of biological diversity result from interactions among climate, the degree of connectedness among populations, and the amount of time over which evolutionary processes act (Forest *et al.*, 2007). At these broad scales, beta diversity among sampling units should have a strong positive relationship with geodiversity because of differences in biogeographic and evolutionary histories (Barton *et al.*, 2013). Regionally within a continent, variation in habitat complexity should further influence biodiversity. At regional scales, alpha and beta diversity should decline regardless of heterogeneity in geodiversity because fewer new species are added from the regional species pool (Barton *et al.*, 2013). At more local scales within an ecoregion, stochastic processes yield large variability in species occurrence among sites (Barton *et al.*, 2013), resulting in increased variation in alpha and beta diversity. At these local scales, geodiversity likely interacts with species' life history characteristics, biotic interactions, and dispersal to mediate species-specific occurrences (Shmida & Wilson, 1985; McGill, 2010).

We expect the relationship between biodiversity and geodiversity to be stronger at broader extents where gamma diversity or macro-scale richness is highest in both measures (MacArthur & Wilson, 1967; Turner, 1989; Rosenzweig, 1995). We expect that of all the forms of biodiversity, beta diversity will be linked most strongly with heterogeneity in geodiversity because variation in geodiversity can lead to concomitant shifts in abiotic resource availability that alter habitat types and drive species turnover (Ricklefs, 1977). Biodiversity-geodiversity relationships are likely to be scale-dependent due to varying influences of local community assembly processes such as dispersal limitation, biotic interactions, and environmental filtering (e.g., Tello *et al.*, 2015).

BOX 1

Biodiversity-Geodiversity Scaling Relationships in Western United States Trees

We analyzed spatial scaling relationships between geodiversity and different forms of tree biodiversity — alpha, beta, and gamma. For geodiversity, we focused on variation in elevation because it is the most commonly used form of geodiversity (Stein *et al.*, 2014), and many geodiversity variables are correlated with topography, especially at regional scales (Hjort & Luoto, 2012). We note that numerous geodiversity variables have been proposed (Parks & Mulligan, 2010; Gray, 2013) and investigating their scaling relationships with different facets of diversity (taxonomic, functional, phylogenetic) is a needed area of research. Our approach provides a means to quantify such relationships. Data sources included western United States (California, Oregon, and Washington) Forest Inventory and Analysis (FIA) plots, which consist of four 7.2 m fixed radius sub-plots in which all trees > 12.7 cm diameter at breast height are measured; (Bechtold *et al.*, 2005), and a 1-arc second (~30 m) DEM from SRTM (NASA JPL, 2013) (Appendix B).

To investigate biodiversity-geodiversity scaling relationships, we systematically varied the grain size of analysis. At different radii (5, 10, 20, 50, 100 km) centered on each of the ~16,000 FIA plots, we calculated tree taxonomic Shannon diversity (effective species number), and the standard deviation (SD) of all elevation pixels. We calculated the median abundance-weighted effective species number (Jost, 2006) of all plots falling within the radius, including the focal plot (alpha), the mean abundance-weighted pairwise dissimilarity of all pairs of plots in the radius, including the focal plot (beta), and the median abundance-weighted effective species number of all plots in the radius as if they were a single community (gamma). We used the total basal area of each tree species in each plot as a measure of their abundance. We discarded all plots within 100 km of the political borders of the study region to avoid edge effects. To avoid pseudoreplication, we used an iterative search to generate a subsample of plots separated by at least 100 km, yielding ~20 plots per subsample. We used generalized linear models (GLM) for alpha and gamma diversity (gamma distribution and log link), and beta regression for beta diversity (Cribari-Neto & Zeileis, 2010), to relate all the focal plots' univariate diversity to elevation SD. We assessed how standardized slope coefficients changed with spatial grain, and computed confidence intervals by repeating the subsampling procedure 100,000 times (Box Fig. 1).

The Effect of Elevation Variability on Biodiversity Varies with Scale and Form of Diversity

The relationship between topographic heterogeneity and tree gamma and beta diversity shows scale-dependence, increasing in magnitude between 5 and 20 km, then plateauing (Box Fig. 1d). Overall, tree gamma diversity is most strongly related to topographic heterogeneity (Box Fig. 1c, Appendix C). The maximal magnitude of the biodiversity-geodiversity relationship at intermediate to large grain sizes may be due, in part, to tree biodiversity leveling off at larger grain sizes (50-100 km), while elevational variability increases monotonically with scale (Box Fig 1 a-d). This pattern suggests that for a given extent, there is a maximum grain size where the biodiversity-geodiversity relationship is strongest. The form of this relationship is likely related to historical processes or biogeography involving topographic constraints that affect dispersal (e.g., at treeline, across large rivers, or at biome boundaries). For example, particular tree species may thrive on steep slopes whereas other species are found in flat regions or riparian zones, but this sorting is unrelated to how many species are present in these different habitats. At even larger spatial extents, such as continents or the globe, we expect that the biodiversity-geodiversity relationship will weaken as historical processes at the biome scale play a larger role in determining patterns of biodiversity.

WAYS FORWARD

The Future of Geodiversity with Satellite Remote Sensing

Satellite remote sensing elucidates biodiversity-geodiversity scaling relationships because data are continuously measured and can be aggregated across different extents and grains. The field of remote sensing is changing rapidly, with computational and engineering advances allowing researchers to measure geodiversity, capture climate variability, and map biodiversity patterns at multiple scales. Advances include new satellite missions that measure geodiversity, publicly available big data from online biodiversity repositories, and novel statistical approaches to simultaneously model abiotic and biotic drivers of multiple species' distributions. Satellite missions provide global or near global data coverage for generating geodiversity variables at increasingly fine spatial resolutions and to help address scaling questions (Appendix A). For example, with the combination of the SRTM and ASTER Global DEMs, it is possible to calculate a variety of topographic diversity variables at 30-m resolution at a near-global extent (Simard *et al*., 2016). The rise of RADAR and LiDAR technology on air- and spaceborne platforms make it possible to quantify fine scale topographic geodiversity (e.g., Parks & Mulligan, 2010). Climatic variables can be derived from MODIS (e.g., Wan *et al.*, 2004), SMAP (e.g., Chan *et al.*, 2018), GPM (e.g., Hou *et al.*, 2014), AMSR (e.g., Parinussa *et al.*, 2015), and other space-borne sensors and platforms, and provide the basis for compiling standard bioclimatic variables at multiple spatial and temporal scales. Other satellite sensors like GRACE and ICESat-2 can provide novel information about groundwater and the cryosphere, respectively (e.g., Landerer & Swenson, 2012; Kwok, 2018). These advances are coupled with a long history of optical satellite and airborne data. When coupled with multispectral (e.g., Landsat, MODIS, VIIRS, AVHRR) and hyperspectral (e.g., Hyperion and proposed future missions) capability, these data enable measures of geodiversity (soil cover, rock type) and biodiversity (ecosystem types, plant communities, functional types, species identities, and genetic variability).

Challenges for Data Integration

Scale mismatches and gaps in measurements may hinder the integration of disparate datasets (Anderson, 2018). Biodiversity measurements tend to be measured at single locations or in small plots, whereas remotely-sensed geodiversity variables are generally at least an order of magnitude larger (Fig. 1b). Remotely-sensed geodiversity measurements are more likely to be global and repeated through time, yet biodiversity observations remain relatively sparse geographically and phylogenetically, and are rarely repeated through time (Amano *et al.*, 2016; Urban *et al.*, 2016). Furthermore, the spatial and temporal resolutions of different geodiversity datasets often do not match (Fig 1b), making it necessary to model or resample variables. In general, the timescales over which biodiversity changes are likely to be shorter than those over which most geodiversity changes. However, both forms of diversity can change over short to long timescales. Geodiversity in fluvial systems can change markedly within minutes to decades or more, whereas orogenic events often span millennia (Fig. 1A). Biodiversity at a given location can change rapidly (minutes to decades) due to habitat destruction or species invasion, or gradually (centuries to millennia) due to evolution.

Using remotely sensed metrics of geodiversity to predict biodiversity at certain scales will require knowledge of the scales and processes by which geodiversity drives biodiversity for different taxonomic groups and life history characteristics. Multivariate or ensemble geodiversity measures (Parks & Mulligan, 2010) should be interpreted carefully, as their aggregate nature is likely to mask important biodiversity-geodiversity relationships. While exploratory research and data mining will help to identify key metrics and scales, more process knowledge is necessary to pair specific types of biological responses with geodiversity drivers at specific scales. Feedbacks among geodiversity drivers at multiple scales likely exist, so understanding cross-scale interactions (Soranno *et al.*, 2014) is a research priority.

Finally, although satellite remotely sensed data are often publicly available, the need to employ big data management (Kelling *et al.*, 2009) and remote sensing techniques can be a hurdle for investigators. Although many ecologists are familiar with MODIS and Landsat data products, they may not be aware of other products such as GRACE, SMAP, or Hyperion. Such underused geodiversity measures should be assessed for their ability to explain and predict biodiversity. The rise of cloud-based computing platforms, such as Google Earth Engine, can facilitate data accessibility and operability.

Networks and Interdisciplinary Research Opportunities

Coordinated observation networks and interdisciplinary research teams are well-positioned to advance knowledge of biodiversity-geodiversity linkages across scales, and ultimately improve forecasts of future biodiversity change. Observation networks such as the National Ecological Observatory Network (NEON; Keller *et al.*, 2008) provide a means to scale up ecology and can be used to investigate biodiversity-geodiversity relationships using co-located ground-based biodiversity observations and remotely sensed geodiversity from tower-based, airborne, and satellite platforms. Teams of researchers and practitioners that span disciplines can more effectively address fundamental and applied questions that are essential to forecast changes to biodiversity across scales (Reinhardt *et al.*, 2010; Heffernan *et al.*, 2014;

Pettorelli *et al.*, 2014). In this age of big data, the combination of coordinated research networks and interdisciplinary teams of investigators may be the best way forward to advance the conservation of nature.

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DATA ACCESSIBILITY STATEMENT

Tree and location data used to generate these analyses cannot be published per Forest Service Agreement No. 17-MU-11261919-021. Digital elevation model data from the NASA Shuttle Radar Topography Mission are freely available from the US Geological Survey (https://lta.cr.usgs.gov/SRTM).

FIGURES

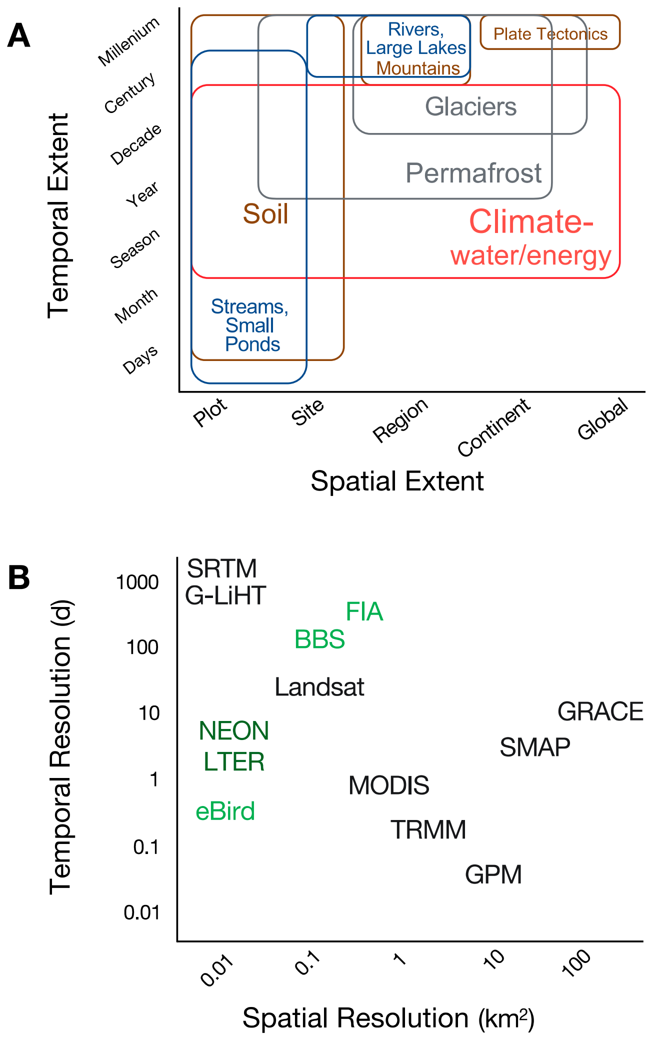
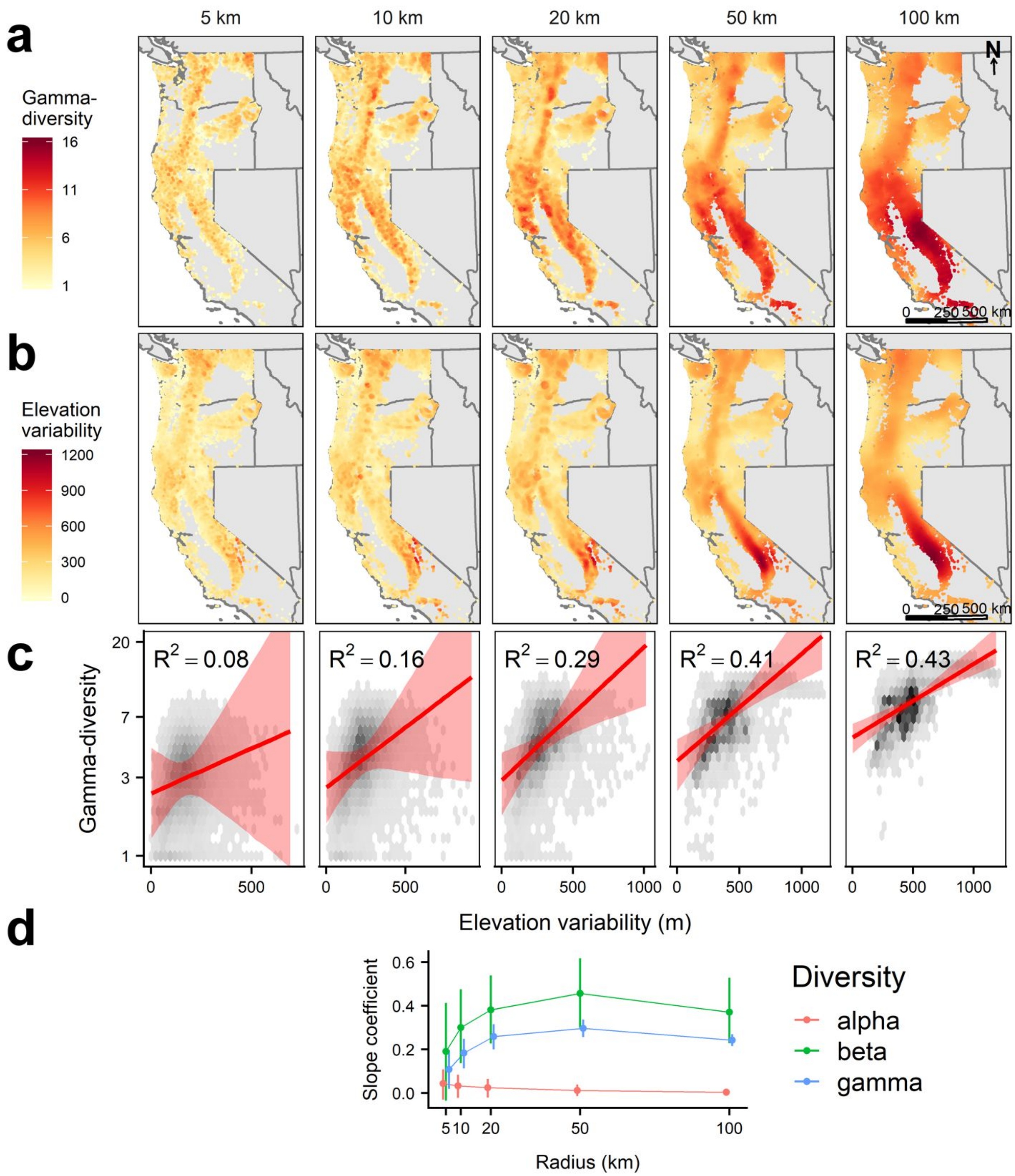


Figure 1. Geodiversity across scales. A) Examples of geodiversity variables and the spatial and temporal extents at which they vary. Geodiversity encompasses abiotic components of the Earth's Critical Zone, specifically the lithosphere (brown), atmosphere (red), hydrosphere (blue), and cryosphere (gray) (Natural Resources Council, 2001; Parks & Mulligan, 2010). In general,

511 surficial geodiversity at regional to global scales remains constant over short timeframes (e.g.,
512 days to years), whereas local scale surficial geodiversity (e.g., micro-topography and the physical
513 and chemical properties of soil) vary over short to intermediate timeframes (e.g., years to
514 centuries). B) Examples of satellite remotely sensed geodiversity (black). As point data,
515 biodiversity data (green) are often high resolution, but are lacking in spatial and temporal extent.
516 Networked sites like the National Ecological Observatory Network (NEON) and Long-Term
517 Ecological Research Sites (LTER) provide a combination of biodiversity and geodiversity (dark
518 green). See Appendix A for further details on a more complete list of NASA missions and
519 geodiversity products. Additional abbreviations are as follows: SRTM (Shuttle Radar
520 Topography Mission); G-LiHT (Goddard's LiDAR Hyperspectral Thermal imager); MODIS
521 (MODerate resolution Imaging Spectroradiometer); TRMM (Tropical Rainfall Measuring
522 Mission); GPM (Global Precipitation Measurement mission); SMAP (Soil Moisture Active
523 Passive): GRACE (Gravity Recovery and Climate Experiment); FIA (Forest Inventory and
524 Analysis); BBS (Breeding Bird Survey).
525
526



Box Figure 1. Patterns of variation in tree biodiversity and topographic geodiversity depend on the scale at which they are measured or summarized. For the analysis, total extent remained constant (California, Oregon, and Washington, USA), and grain size (radius encompassing data) varied. Locations depicted in maps are fuzzed FIA coordinates (Woudenberg *et al.*, 2010). (A) Forest Inventory and Analysis (FIA) tree taxonomic gamma diversity at 5-100 km; (B) standard deviation of elevation at 5-100 km; (C) the relationship between gamma diversity and elevation variability (SD of elevation), the median R^2 value of the models, and the shaded red band bound by the 2.5% and 97.5% percentiles of the predicted values from the models; (D) scaling relationships between variation in biodiversity and geodiversity, represented as the standardized slope coefficients from GLMs for alpha and gamma diversity, and beta regression models for beta diversity for each scatter plot in C above vs. distance (km; grain size); error bars represent 25th to 75th percentiles and points are offset slightly to avoid overlap. Standardized slopes are the increase in number of standard deviations in diversity with 1 m increase in elevation SD. See Appendix B for alpha and beta diversity maps and relationships. Gamma diversity values for each combination of point and radius are the total aggregated diversity value of all plots within the radius centered at the point.

Supplemental Materials List

Appendix A. Table of geophysical remote sensing products from NASA and their associated geodiversity variables.

Appendix B. Calculation of taxonomic diversity of FIA tree communities.

Appendix B-1. Preparation of Forest Inventory and Analysis dataset.

Appendix B-2. Diversity calculations.

Appendix B-2.1. Alpha and gamma diversity.

Appendix B-2.2. Beta diversity.

Appendix B-3. Additional figures related to Box 1.

Supplemental Figure B-1. Alpha diversity of trees in FIA plots in the Pacific Northwest region.

Supplemental Figure B-2. Beta diversity of trees in FIA plots in the Pacific Northwest region.

Supplemental Figure B-3. Generalized linear models with gamma distribution and log-link of alpha diversity versus the standard deviation of elevation.

Supplemental Figure B-4. Beta regressions of beta diversity versus the standard deviation of elevation.

Supplemental Figure B-5. R^2 values from biodiversity-geodiversity relationships shown in Supplemental Figures B-3 and B-4, and Box Fig. 1c.

APPENDICES

APPENDIX A

Table 1. Available geophysical remote sensing products from NASA which provide geodiversity variables, with their spatial and temporal scales noted.

Online interactive table available at: https://bioxgeo.github.io/bioXgeo_ProductsTable/

APPENDIX B: Calculation of taxonomic diversity of FIA tree communities

B-1. Preparation of Forest Inventory and Analysis dataset

We obtained USFS Forest Inventory and Analysis (FIA) data, including measurements and locations, for the Pacific Northwest region (California, Oregon, Washington, USA) (Forest Service Agreement No. 17-MU-11261919-021). Forest plots surveyed according to the FIA protocol consist of four subplots, each circled with 7.3 m radius, located 36.6 m from one another in a three-pointed star pattern. See Bechtold *et al.* (2005) and https://www.fia.fs.fed.us/library/field-guides-methods-proc/docs/2016/core_ver7-1_10_2016-opt.pdf for more detailed description of the survey protocols. We retained only plots identified as natural forest by excluding plots with no trees and plots identified as plantation forests, resulting in approximately 16,000 plots across the three states. Each tree in each subplot is identified to species, and its diameter at breast height is recorded. Using the diameters to calculate basal area of each individual tree, we summed the basal areas within each species to estimate the relative abundance of each species in each subplot. Any discrepancies in species names were resolved to the most recent taxonomy.

B-2. Diversity calculations

We calculated abundance (basal area)-weighted diversity metrics for species present at each plot. We used the most recent survey as a single time point for each plot. Our decision to use basal area as a surrogate for tree abundance is consistent with many previous studies that computed diversity metrics for tree communities (e.g., Risser & Rice, 1971; Liang *et al.*, 2007; Grossiord *et al.*, 2014)

We calculated alpha, beta, and gamma diversity at a number of different radii around each FIA plot by taking the median diversity of all plots in the radius, including the focal plot (alpha), the mean pairwise Sørensen dissimilarity of all pairs of plots in the radius, including the focal plot (beta), and the aggregated diversity of all plots in the radius as if they were a single community (gamma). We calculated the mean arcsine-square root transformed value in the case of beta diversity, then back-transformed to the original scale (0 to 1). The radii for which we calculated diversities included 5,10, 20, 50, and 100 km; a subset of these results are presented in the manuscript.

B-2.1 Alpha and gamma diversity

We calculated taxonomic alpha diversity (Shannon diversity of a local community) for FIA tree communities. We calculated diversity indices for communities aggregated at the plot level (aggregating the four subplots making up one plot). For each plot and radius, we calculated alpha

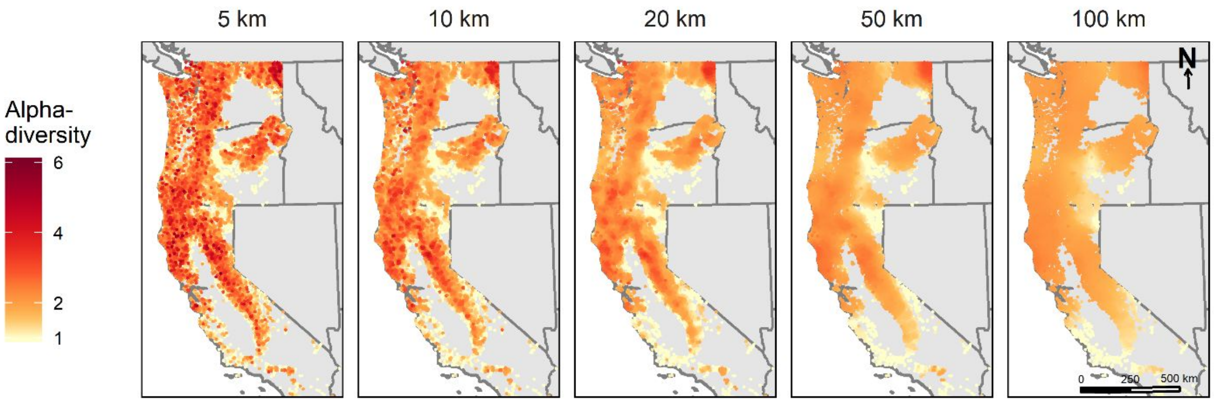
605 diversity within that radius by taking the median diversity value for all plots or routes (including
606 the focal plot) located inside the circle defined by the radius around the focal plot. For gamma
607 diversity, the diversity of a region that consists of multiple local communities, we aggregated all
608 the plots within the focal circle to a single community, and calculated taxonomic, functional, and
609 phylogenetic diversity of that community. We calculated basal-area-weighted Shannon alpha and
610 gamma diversity as follows: $H' = \sum_{i=1}^{R} - p_i \ln p_i$, where R is species richness and p_i is the
611 basal area of species i. We expressed this as true diversity, or effective species number, with q =
612 1 by exponentiating Shannon diversity (Jost, 2007).

613 B-2.2 Beta diversity

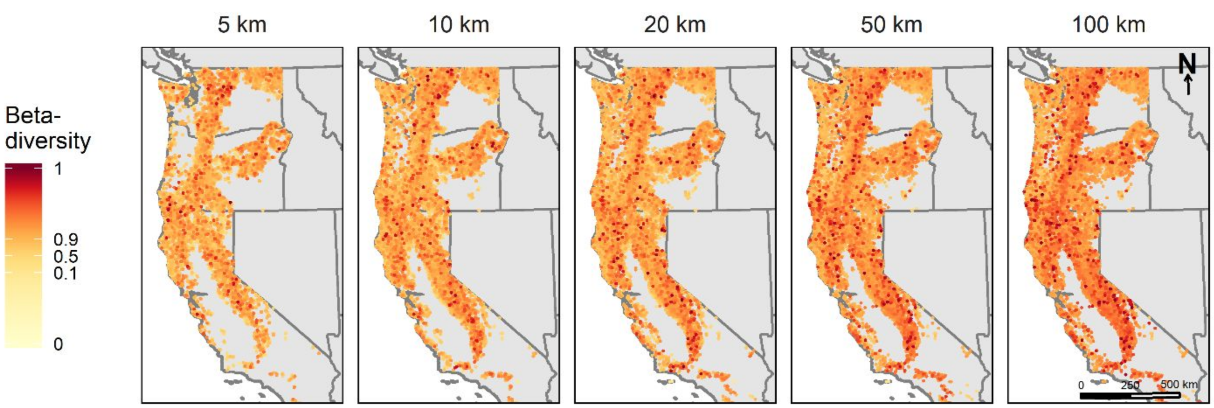
614 We calculated taxonomic beta diversity (turnover of diversity among local communities) for FIA
615 tree communities. Beta diversity is defined as the variation in community composition across
616 multiple local communities. To determine beta diversity at a point, it is necessary to define the
617 kernel or radius within which variation in community composition is taken into account. For the
618 FIA dataset, we aggregated species abundances of each plot and calculated beta diversity for
619 each plot at a number of different radii around the focal plot; as the radius increases, the number
620 of pairwise comparisons among plots also increases as more plots fall within the kernel.

621 We calculated beta diversity with the pairwise dissimilarity method using the vegdist() function
622 from the R package vegan (Oksanen *et al.*, 2018) and taking the mean of the pairwise Sørensen
623 dissimilarity (transformed with the arcsine-square root transform, then back-transformed to the
624 original scale, 0-1) of all local communities within a particular radius of the focal plot.

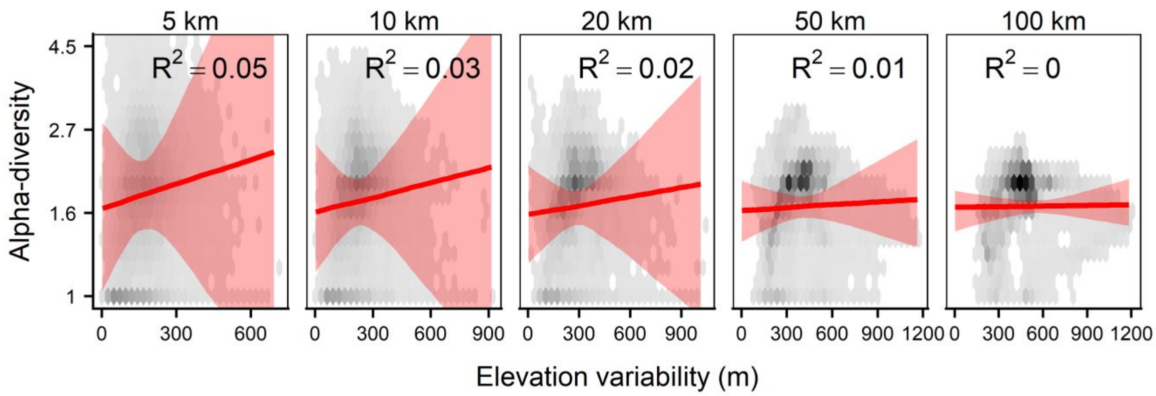
B-3. Additional figures related to Box 1.



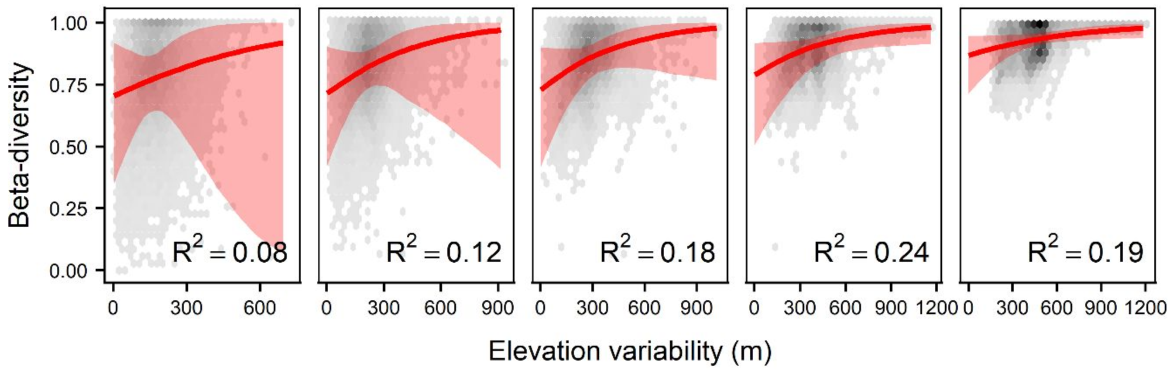
Supplemental Figure B-1. Alpha diversity of trees in FIA plots in the Pacific Northwest region, expressed as effective species number with q=1, or the exponential of Shannon diversity. Alpha diversity values for each combination of point and radius are the median diversity value of all plots within the radius centered at the point.



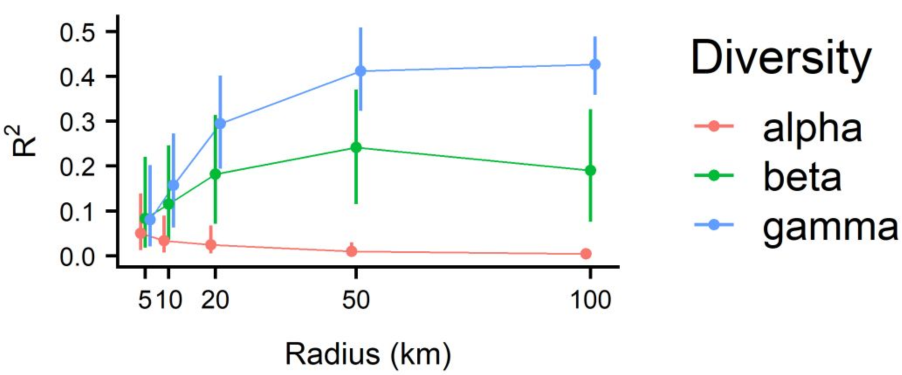
Supplemental Figure B-2. Beta diversity of trees in FIA plots in the Pacific Northwest region, expressed as effective species number with q=1, or the exponential of Shannon diversity. Beta diversity of the regions around the plots are depicted in logit scale to improve the distinction between values at the higher end of the scale near 1.



Supplemental Figure B-3. Generalized linear models with gamma distribution and log-link of alpha diversity (Shannon diversity) versus the standard deviation of elevation. Density of points in the scatterplot is represented by shading of hexagonal areas to avoid overplotting. The dark red line is the median predicted value of models fit with 100,000 spatially stratified random subsamples of the full dataset, each with approximately n=20. The shaded red area is bounded by the 2.5% and 97.5% percentiles of the predicted values from the regressions. The median R^2 value of the models is shown in each panel.



Supplemental Figure B-4. Beta regressions of beta diversity versus the standard deviation of elevation. Density of points in the scatterplot is represented by shading of hexagonal areas to avoid overplotting. The dark red line is the median predicted value of regressions fit with 100,000 spatially stratified random subsamples of the full dataset, each with approximately n=20. The shaded red area is bounded by the 2.5% and 97.5% percentiles of the predicted values from the regressions. The median R^2 value of the regressions is shown in each panel.



Supplemental Figure B-5. R^2 values from biodiversity-geodiversity relationships shown in Supplemental Fig. B-3 (alpha diversity), Supplemental Fig. B-4 (beta diversity), and Box Fig. 1c (gamma diversity) at increasing grain sizes (radii around focal plot). The x-axis is increasing radii distance (km; akin to grain size). Error bars represent 25th to 75th percentiles.

04 December 2018

Comments to Reviews on GEB-2018-0112.1:

Thank you to the editors and reviewer for these helpful suggestions. We have addressed the comments as well as the GEB style guidelines. Below we respond to each reviewer or editor comment with “RESPONSE:”.

EDITOR-IN-CHIEF'S COMMENTS TO AUTHORS

Much of the feedback from the first reviewer pertains to the title. In part I think this is just a mismatch between an ecological sounding and a research article. We do not expect (there is not space for!) more than a proof of concept.

As a sounding I do want to keep the topic in the title general, but I invite you to at least consider alternatives that might make the reviewer happier while keeping the general nature appropriate to a Sounding. One simple solution might just be to add the word "Towards" at the front (I.e. "Towards connecting biodiversity and ...") which keeps the generality while also acknowledging the limitations of the format.

RESPONSE: Thank you for the great suggestion to modify the title. We have adjusted the title to achieve the generality of a Sounding article, while also describing the intent of the article more appropriately to address the reviewer's concern. Our new title is “Towards connecting biodiversity and geodiversity across scales with satellite remote sensing.”

EDITOR'S COMMENTS TO AUTHORS

Editor: Gillespie, Thomas

Comments to the Author:

This manuscript has been massively revised. It is now very well written, clear, and a very nice example of what an “Ecological Soundings” article should look like. Most importantly, geodiversity and remote sensing metrics used to quantify aspects of geodiversity is an important and timely topic. I think this manuscript will be of interest to GEB readers and could be widely cited. Discussing the topic and summarizing geodiversity appears very similar to trying to summarize Biodiversity which is a large and complex topic. Thus I like the focus on spaceborne remote sensing datasets and applications which helps the authors focus on one aspect of geodiversity. I also like the case study now.

My only real concern is that I think the readers would like to see some excellent articles cited in the “The Future of Geodiversity with Satellite Remote Sensing" section. In Particular, I think you need citations for 1) SRTM and ASTER, 2) Radar and Lidar, 3) SMAP, GPM, AMSR, and 4) GRACE and ICESat-2. I am sure you can find excellent and up to date citations for these themes that the reader can further explore. This will make this a stronger review.

RESPONSE: Thank you for these comments about the better fit of the article and interest to GEB readers! Thanks also for the suggestion to add references to the Future section. We have added references to papers that use or help assess the satellite remote sensing data sources that we discuss.

My minor comments and suggestions are below.

Abstract
The Issue, Evidence, and Conclusions are very clear now.

The Introduction is also very clear.

Line 63. I like your clear definition of geodiversity.

Line 107. Good point.

Line 164. Excellent points and summary.

Line 183. The methods are now very clear to this reader. Thank you for that. The remote sensing metrics can also be easily repeated in other regions.

The Future of Geodiversity with Satellite Remote Sensing.
This is a nice summary of the remote sensing data that can be used to quantify aspects of geodiversity, but I think the readers would appreciate citations in this section. For examples, I might provide citations for GRACE and ICE-Sat here for the reader. In particular, articles that provide global datasets, standard metrics on geodiversity would be useful.

RESPONSE: Thank you also for the positive feedback about specific lines and sections. We are glad to hear that the manuscript has improved in terms of clarity, describing our definition of geodiversity, and in terms of the methods. We added references for GRACE and ICE-Sat and the other geodiversity measuring satellites. References range from descriptions to quality assessments to applications, depending on the maturity of the satellite being described.

Line 237. I would remove AVIRIS and G-LiHT because they are airborne and not spaceborne or satellite remote sensing. There are enough spaceborne sensors that are under-utilized for geodiversity that I do not think you need to bring in airborne sensors which only cover a relatively small geographic area. These also do not match the subheading title.

RESPONSE: Thank you for noticing that the inclusion of AVIRIS and G-LiHT in the main text do not align as well with our focus on satellite remote sensing. We agree that these should be omitted and have replaced ‘AVIRIS and G-LiHT’ with ‘and proposed future missions’.

Dr. Thomas Gillespie, Editor

REVIEWER COMMENTS TO AUTHORS

Referee: 1

Comments to the Author
1. The data in the paper relate to elevation and tree coverage in the western US states. The title and text therefore give a very misleading impression about the scope of the paper. Only one geodiversity variable (elevation) is included and therefore the paper is definitely NOT about geodiversity. The title should therefore be altered to "Connecting aspects of biodiversity (trees) and geodiversity (elevation)...". The text should be revised to reflect this point.
RESPONSE: The suggestion to modify the title is a good suggestion. We have tried to balance this concern with the editor's request to keep Soundings articles general. Therefore, we have adjusted the title to better describe the intent of the article by adding "Towards" at the beginning. The new title is "Towards connecting biodiversity and geodiversity across scales with satellite remote sensing."

2. In relation to scales, only scales of many kms are included in this paper and this is another reason for challenging the title. Many elements of geodiversity occur at smaller scales, e.g. fossils, minerals, sediments and their diversity. The paper is limited to mid-scale diversity in elevation, NOT geodiversity at all scales. So the title should read "medium-scales" (or similar) and text need to be modified to reflect this point.

RESPONSE: Thank you for the suggestions concerning scales. As the main message of this Soundings article is to emphasize the need to assess these relationships across scales, we have kept emphasis on this more general framing. The new title de-emphasizes the summative or absolute nature of our case study analysis. The methods we provide to achieve the multi-scale analysis can be applied at any set of grain sizes, or spatial extent, given the data and scope of study.

3. Finally the tile should end with "in western US states" (or similar).

RESPONSE: Thank you for the comment about the region of the study. Please see our response to Comment #2 above. With the Box we illustrate the application of this approach with 1 large region across the Western US Coast.

4. There is discussion on whether climate is part of geodiversity. The authors include a reasonable discussion of this point, which not everyone will agree with, but that is not a reason to remove this view from the paper.

RESPONSE: Thank you for this feedback. It's helpful to know that our definition of geodiversity is more clear.