Disentangling linkages between satellite derived forest structure and productivity essential biodiversity variables.

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**Abstract:** Under a changing climate and in light of the biodiversity crises, monitoring change in biodiversity at broad scales has become ever more imperative. Key to regular biodiversity monitoring over time and space is the definition and selection of variables capable of accurately monitoring biodiversity trends. One framework is the Essential Biodiversity Variables (EBV), which are designed to be analogous to the Essential Climate variables and capable of monitoring biodiversity globally while also being complementary to one another within EBV classes. Five of six EBV classes are well suited to being monitored using satellite remote sensing, with particular focus warranted on the ecosystem structure and function classes. In this paper, we seek to address the complementarity of variables describing forest structure, as imputed across the entirety of British Columbia, Canada, with variables representing ecosystem functioning, namely the Dynamic Habitat Indices, a yearly summary of productivity indices. Both sets of variables have previously been linked with biodiversity metrics across a range of scales. Using redundancy analysis, we find that forest structural attributes and the DHIs are essentially decoupled from each other, with the forest structure variables explaining 14% of the variation in the DHIs. Further, we explore how the proportion of variance explained in the DHIs varies with either primary structure variables, such as canopy height and cover, vs more complex modelled forest structural attributes, such as aboveground biomass and volume. Results suggest there is large overlap between the two types of forest structure variables suggesting little added benefit of derived attributes beyond height and cover, in this context. Overall, we find that forest structure as an ecosystem structure EBV and the DHIs as an ecosystem function EBV represent markedly different processes as observed by remote sensing and they are highly complementary across large environmental gradients, suggesting that in an earth-observation based monitoring program both are needed.

# Introduction

With biodiversity in decline, and facing extinction rates above the background extinction rate (Thomas et al., 2004; Urban, 2015), as well as the homogenization of communities at various scales (McGill et al., 2015), it is integral to be able to monitor how biodiversity is changing across the globe. In response, the global biodiversity community is making efforts to assess and halt the degradation of biodiversity. The Group on Earth Observations Biodiversity Observation Network has developed the Essential Biodiversity Variables (EBVs, Pereira et al., 2013), designed as an analog to the Essential Climate Variables framework (Bojinski et al., 2014). EBVs are designed to be global in scope, relevant to biodiversity information, feasible to use, and complementary to one another (Skidmore et al., 2021). While it can be difficult, time consuming, and expensive to collect data on biodiversity across wide swaths of land and varying ecosystems, EBVs, which can be correlated to sampled biodiversity information, allow for the monitoring and assessment of protected area effectiveness and ecosystem health at large spatial scales (Hansen et al., 2021). There are six EBV classes, each of which correspond to a different facet of biodiversity: species populations, species traits, community composition, ecosystem structure, ecosystem function, and genetic composition (Pereira et al., 2013).

Satellite remote sensing has proven to be capable of measuring five of the six EBV classes, the exception being genetic composition, which requires in-situ observation and sampling (Skidmore et al., 2021). Species populations, and in turn community composition, can be assessed with very-high-resolution imagery to identify tree species at the tree-crown scale (Fassnacht et al., 2016; Graves et al., 2016). Additionally, species traits such as vegetation phenology have been observed at the single-tree scale using, for example, PlanetScope imagery and drone-based measurements (Wu et al., 2021). However, the spatially limited and often *ad-hoc* data collection approaches associated with monitoring individuals is not conducive to the global or regional scales required for biodiversity trend assessment (Valdez et al., 2023), in addition to the difficulties associated with extending species-level analyses to broader extents (Fassnacht et al., 2016; Graves et al., 2016).

The two landscape-level EBVs (ecosystem structure and function) are well suited to be examined at large spatial scales using coarser spatial measurements, such as those taken from satellites by the Moderate Resolution Imaging Spectroradiometer (MODIS, Zhang et al., 2003), the Landsat imaging systems (Fisher et al., 2006), or Sentinel-2 (Darvishzadeh et al., 2019; Helfenstein et al., 2022) programs. These mid-resolution satellites can monitor processes at broader extents, but their coarse spatial resolution removes the ability to relate these traits to individual organisms. As a result, satellite remote sensing data has been shown to be arguably the most effective at monitoring ecosystem based EBVs focused on structure and function. These EBVs classes can be monitored at regional to global extents through the use of optical imagery (Cohen and Goward, 2004), as well as active sensors such as lidar (light detection and ranging) and radar (Coops et al., 2016; Guo et al., 2017; Lang et al., 2021; Lefsky et al., 2002; Neuenschwander and Pitts, 2019).

## EBV - Ecosystem Structure

Forest structural diversity has been linked to biodiversity at various scales (Bergen et al., 2009; Gao et al., 2014; Guo et al., 2017). Structural attributes range in complexity from simple (canopy cover; canopy height), to more complex (vertical and horizontal structural complexity) to modelled (aboveground biomass; basal area), all of which can be assessed using lidar data (Coops et al., 2021). A suite of these lidar-derived attributes have been used as local indicators of biodiversity, including simple metrics such as canopy cover and canopy height as well as derived metrics including vertical profiles, aboveground biomass, or lidar derived indices (Coops et al., 2016; Guo et al., 2017; Lefsky et al., 1999). Other second order derived metrics such as canopy texture, height class distribution, edges, and patch metrics have also been used to examine habitat and biodiversity at landscape scales (Bergen et al., 2009). Advances in satellite remote sensing processing have now allowed 3D forest structure data to be imputed across wide spatial scales (Coops et al., 2021; Matasci et al., 2018) using data fusion approaches involving collected lidar data and optical/radar data.

Increased forest structural complexity has been hypothesized to create additional niches, leading to increased species diversity (Bergen et al., 2009), which has been frequently demonstrated using avian species diversity metrics (Macarthur and Macarthur, 1961). For example, Herniman et al. (2020) used spectral and lidar derived forest structure data to model avian habitat suitability; Clawges et al. (2008) found that lidar derived forest structural attributes are capable of identifying habitat types associated with avian species in pine/aspen forests; Goetz et al. (2007) used canopy structural diversity to predict bird species richness, finding that canopy vertical distribution was the strongest predictor of species richness. Forest structural metrics have also been used to study biodiversity in other clades as well (Davies and Asner, 2014; Nelson et al., 2005).

## EBV - Ecosystem Function

With respect to ecosystem function, energy availability in an ecosystem has shown to be a predictor of species richness and abundances at various scales (Chase and Leibold, 2002; Coops et al., 2019; Radeloff et al., 2019; Razenkova et al., 2023), and is measurable using satellite remote sensing via the use of various vegetation indices (Huete et al., 2002; Radeloff et al., 2019). Vegetation indices, which are indicative of photosynthetic activity, are commonly used as proxies of gross primary productivity (Huang et al., 2019). These vegetation indices have also been used to assess patterns in biodiversity at single time points (Bonn et al., 2004), and more recently, through yearly summaries of productivity (Berry et al., 2007; Radeloff et al., 2019). The relationship between energy availability and biodiversity occurs via various hypothesized mechanisms, such as the available energy hypothesis (Currie et al., 2004; Wright, 1983), the environmental stress hypothesis (Currie et al., 2004), and the environmental stability hypothesis (Williams and Middleton, 2008). These three hypotheses have in turn been linked to patterns of annual surface reflectance in remote sensing data (Berry et al., 2007; Radeloff et al., 2019).

Berry et al. (2007) first explored this idea by proposing the linkage of intra-annual summaries of MODIS-derived GPP to dispersive bird species. This idea was further refined into the Dynamic Habitat Indices (DHIs, Coops et al., 2008), which have now been shown to be well suited to assess the three aforementioned hypotheses at global scales (Radeloff et al., 2019). The cumulative DHI calculates the total amount of energy available in a given pixel over the course of a year. Cumulative DHI is strongly linked to the available energy hypothesis, which suggests that with greater available energy species richness will increase (Wright, 1983). The minimum DHI, which calculates the lowest productivity over the course of a year can be matched to the environmental stress hypothesis, which proposes that higher levels of minimum available energy will lead to higher species richness (Currie et al., 2004). Finally, the variation DHI, which calculates the coefficient of variance in a vegetation index through the course of a year, corresponds to the environmental stability hypothesis which states that lower energy variation throughout a year will lead to increased species richness (Williams and Middleton, 2008).

## Biodiversity Monitoring with EBVs

Biodiversity monitoring programs often require a range of information in order to accurately assess changes in ecological integrity (Lindenmayer and Likens, 2010). Choosing datasets that are most closely related to the phenomenon of interest in a given application allows for direct connections to monitoring results and management actions (Pressey et al., 2021). With the advent of large-extent monitoring methods like satellite remote sensing, and a proliferation of potential EBVs datasets, it becomes important to assess the interrelationships between these datasets, and assess their complementary of the information to reduce the duplication of efforts (Pereira et al., 2013; Skidmore et al., 2021). When strong relationships are present between EBVs, it is possible to assess the ecological relationships between potential EBVs. On the other hand, when datasets do not appear related, they may be well suited to be used in monitoring programs together, as complementary EBVs.

Linkages between forest ecosystem structure and function have been examined within a remote sensing context for over 20 years Knyazikhin et al. (1998). While there is significant theoretical and empirical evidence for their relationship at single time points (e.g. within a single image) (Myneni and Williams, 1994), various relationship directions and shapes have been found between forest structure and function metrics (Ali, 2019). Hypothesized mechanisms such as niche complementarity have shown that aboveground biomass increases with stand structure (Zhang et al., 2012), while asymmetric competition for light can reduce forest productivity with increased structural complexity (Bourdier et al., 2016). The relationship in particular between forest structural diversity metrics - which are now more accurately and comprehensively derived from lidar data - and temporal variation in functional metrics, specifically the metrics of ecosystem productivity via the DHI framework, have yet to be fully examined.

The overall goal of this paper is to assess patterns of forest ecosystem structure and function, as observed using remote sensing technologies, and their complementarity across a wide range of ecosystems encompassing significant environmental gradients. To do so, we synthesize data from moderate-scale remote-sensing derived metrics of forest structure, represented as both simple ALS-extracted metrics of canopy height, cover and vertical complexity, as well as modelled forest structure attributes including volume and aboveground biomass, with a well-established remote sensing derived index on ecosystem function. First, we examine how ecosystem structure and function complement one another across a large environmental gradient and then compare the simple and modelled representations of forest structure to different levels of ecosystem function. This question is important as it provides insights to the EBV community around complementarity of remote sensing metrics when describing the structure and function of ecosystems and proposes a method to examine potential overlap when generating remote sensing EBVs.

Our second question examines the independent and shared relationships of lidar derived forest structural attributes, with modelled forest structure, on ecosystem function. This provides insight into the selection of remote sensing attributes to use when developing EBVs within a single EBV class. Remote sensing datasets can comprise relatively unprocessed observations, in this case lidar-imputed measures of height and cover vs modelled attributes, such as biomass and volume, which involve the use the statistical relationships with field data to transform the observations into more refined data products. Assessing which of these two (or combination of the two) approaches has stronger or weaker relationships with estimates of ecosystem function provides insights into the choice of data used to build EBVs. Lastly, we examine how the primary and modelled structure variables partition the variance of the DHIs within key biomes and forest types across a large environmental range, examining to what extent ecosystem and forest types impacts these relationships and thus providing insight into the applicability of these results globally.

# Methods

## Study Area

British Columbia is the westernmost province of Canada, and is home to a variety of terrestrial ecosystems. Approximately 64% of the province is forested, with large environmental and topographic gradients (BC Ministry of Forests, 2003; Pojar et al., 1987). The Biogeoclimatic Ecosystem Classification (BEC) system identifies 16 zones based on the dominant tree species and the ecosystems general climate ([Figure 1](#fig-study-map)).

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| Figure 1: Location of biogeoclimatic ecosystem classification (BEC) zones in British Columbia. |

These zones can be further split into subzones, variants, and phases based on microclimate, precipitation, and topography (Pojar et al., 1987). To examine trends across the large environmental gradients, we group the BEC zones into five broad biomes: the southern interior, northern interior, montane, alpine, and coastal groups similar to Hamann and Wang (2006). We also report each BEC zone’s average climate data, according to Wang et al. (2020) ([Table 1](#tbl-bec-group)).

Table 1: BEC Zones, their aggregate groups, and their average climate values for precipitation, maximum temperature, and minimum temperature. Climate data from Wang et al. 2016.

| **BEC Group** | **BEC Zone** | **Full Name** | **Precipitation (mm/yr)** | **Max Temperature (°C)** | **Min Temperature (°C)** |
| --- | --- | --- | --- | --- | --- |
| Alpine | BAFA | Boreal Altai Fescue Alpine | 1357.3 | 1.9 | -5.6 |
| Alpine | CMA | Coastal Mountain-heather Alpine | 2878.1 | 4.5 | -2.4 |
| Alpine | IMA | Interior Mountain-heather Alpine | 1621.7 | 3.1 | -4.2 |
| Coastal | CDF | Coastal Douglas-fir | 986.1 | 12.9 | 5.9 |
| Coastal | CWH | Coastal Western Hemlock | 2518.8 | 10.6 | 3.5 |
| Montane | ESSF | Engelmann Spruce – Subalpine Fir | 1087.6 | 5.3 | -3.1 |
| Montane | MH | Mountain Hemlock | 2666.2 | 7.2 | -0.2 |
| Montane | MS | Montane Spruce | 622.1 | 8.3 | -2.5 |
| North | BWBS | Boreal White and Black Spruce | 516.3 | 5.9 | -5.3 |
| North | SBPS | Sub-Boreal Pine – Spruce | 480.1 | 9.0 | -3.7 |
| North | SBS | Sub-Boreal Spruce | 619.1 | 8.1 | -2.3 |
| North | SWB | Spruce – Willow – Birch | 730.7 | 3.6 | -5.7 |
| South | BG | Bunchgrass | 320.0 | 13.1 | 1.4 |
| South | ICH | Interior Cedar – Hemlock | 901.4 | 9.5 | -0.3 |
| South | IDF | Interior Douglas-fir | 476.8 | 10.6 | -0.7 |
| South | PP | Ponderosa Pine | 352.2 | 13.6 | 2.9 |

## Data

### Forest Structure

We used a suite of forest structure variables (canopy height, canopy cover, structural complexity [coefficient of variation of height returns], basal area, aboveground biomass, and gross stem volume). This dataset was created for the year 2015 at a 30 m spatial resolution according to Matasci et al. (2018). In brief, the method used a set of lidar collections and field plots across Canada, and imputed the remaining pixels using a random forest k-Nearest Neighbour approach on Landsat-derived surface reflectance and auxiliary data such as topography. Detailed information on the creation of this dataset can be found in Matasci et al. (2018).

### Dynamic Habitat Indices

We use an established set of indices of annual productivity shown to be related to global biodiversity trends: the Dynamic Habitat Indices (Radeloff et al., 2019). The DHIs are a set of satellite remote sensing derived productivity variables that summarize the cumulative amount of available energy, the minimum available energy, and the variation in available energy throughout a given year (Berry et al., 2007; Radeloff et al., 2019). The DHIs have previously been produced at a global extent using MODIS imagery, and have previously been used to assess alpha (Radeloff et al., 2019) and beta (Andrew et al., 2012) diversity, species abundances (Razenkova et al., 2023), and construct novel ecoregionalizations (Andrew et al., 2013; Coops et al., 2009). Recent studies have began to examine how these indices can be constructed at a finer spatial resolution by using multi-annual Landsat imagery to generate a single synthetic year of monthly observations (Razenkova et al., 2022).

The DHIs were calculated according to (Razenkova et al., 2022, Razenkova et al., In Press) for all of terrestrial British Columbia. In brief, Google Earth Engine (Gorelick et al., 2017) was used to obtain all valid Landsat pixels for a given study area, filtering out pixels containing shadows, clouds, and cloud shadows within each image using the fmask algorithm (Zhu and Woodcock, 2012), then calculated the NDVI for each pixel in each image. They then calculated the median NDVI value for each month across a ten year time span (2011-2020) to generate a synthetic year of monthly data. The sum, minimum, and coefficient of variation across this synthetic year of NDVI values was then calculated. More detailed information can be found in Razenkova et al. (In Press).

A summary of remote sensing derived datasets can be found in Table 2.

Table 2 Remote sensing derived datasets utilized in this study.

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| **Name** | **Sensor** | **Date Range** | **Metric** | **Metric Group** | **Citation** |
| Canopy Height | Landsat and ALS | 2015 | 95th percentile of ALS returns | Primary; Extracted directly from the point cloud | Matasci et al. (2018) |
| Canopy Cover | Landsat and ALS | 2015 | Proportion of ALS returns above 2m |
| Structural Complexity | Landsat and ALS | 2015 | Coefficient of variation of ALS returns |
| Gross Stem Volume | Landsat and ALS | 2015 | Total volume of trees / plot area | Modelled; Modelled based on the plot point clouds, lidar data, and ancillary information |
| Basal Area | Landsat and ALS | 2015 | Total cross sectional tree area / plot area |
| Aboveground Biomass | Landsat and ALS | 2015 | Total tree biomass / plot area |
| Cumulative DHI | Landsat | 2011-2020 | Sum of synthetic year of NDVI observations | Response variables | Radeloff et al. (2019); Razenkova et al. (2022);  Razenkova et al. (In Press) |
| Variation DHI | Landsat | 2011-2020 | Coefficient of variation of synthetic year of NDVI observations |
| Cumulative DHI | Landsat | 2011-2020 | Minimum of synthetic year of NDVI observations |

# Sampling

We implement two sampling schemes – one for ecosystems, and one for forest types – across the terrestrial ecosystems of British Columbia ([Figure 1](#fig-study-map)). For both sampling schemes, each individual sample was taken from a forested pixel which was surrounded by the same land cover class. The land cover class map was generated for the year 2015 following (Hermosilla et al., 2022) using a best-available-pixel composite, and an inverse-distance weighted random forest classification approach across Canada. Additionally, each pixel had to have a coefficient of variation less than 0.5 in surrounding pixels in the two simplest forest structure variables, canopy height and canopy cover. A minimum sampling distance of 1 km was implemented to reduce the effects of spatial autocorrelation, and samples that had been disturbed in the last 30 years were discarded by using a disturbance mask generated for the forested ecosystems of Canada by Hermosilla et al. (2016).

The ecosystem sampling scheme was implemented by randomly sampling pixels matching the above criteria within each BEC zone of British Columbia, up to a maximum of 3000 pixels, regardless of forest class. The forest type sampling scheme was similar in that each BEC zone was sampled, however, it implemented stratified sampling on each forest class, up to a maximum of 500 pixels per BEC zone and forest class.

Each sampling scheme was natural-log transformed and standardized to Z-scores. Variables containing zeros were natural-log plus one transformed. Sampling was conducted in R (R Core Team, 2022) version 4.2.2 using the **sgsR** package (Goodbody et al., 2023). Focal analyses for the land cover classes and coefficient of variations of canopy height and cover were calculated in Python version 3.9.

## Analysis

### Redundancy Analysis and Variation Partitioning

Redundancy analysis (RDA) and variation partitioning were used to relate the primary and modelled forest structure variables to ecosystem function across a broad environment range. Redundancy analysis functions similarly to a multiple linear regression, except it is capable of predicting multiple response variables. It accomplishes this by first running a multiple linear regression of each predictor variable on each response variable, then running a principle component analysis on the residuals from each multiple linear regression. This reduces the dimensionality of the output, and allows the relationship strength to be assessed by calculating the loadings of both predictor and response variables on the RDA axes. Partial redundancy analysis functions similarly, except also considers co-variates (Legendre and Legendre, 2012). Redundancy analysis has widely been used in community ecology where environmental variables of interest are compared to species composition (Blanchet et al., 2014; Kleyer et al., 2012) and has similarities to partial least squares regression – namely, their multivariate approach, usage of dimensionality reduction, and linearity assumptions – which is commonly used in remote sensing literature (Burnett et al., 2021; Roelofsen et al., 2014).

Following the RDA, we employ ANOVAs to determine which axes are significant, and calculate the proportion of variance attributable to each axis using the eigenvalues generated from the RDA. We calculate axis loadings for both forest structure and DHI variables by calculating the correlation between each variable and the RDA axes. Forest strcuture variable axis loadings represent the strength of relationship between a given variable and the RDA axis, while DHI loadings indicate what is being represented by the RDA axes. We only consider and display significant axes. To visualize the RDA for both predictor and response variables, we display the results as path diagrams, with loadings from each predictor to the RDA axis to the response variables. The variance explained by each axis is also displayed in the RDA box ([Figure 2](#fig-rda-var)).

Variation partitioning is an extension of partial RDA which can assess the overlap between the explanatory power of two datasets by utilizing multiple partial RDAs and exchanging which datasets are considered the predictor, and which is considered the co-variate (Legendre and Legendre, 2012). Variation partitioning is traditionally displayed using a Venn diagram, in which the percentage of variance explained by each dataset is in a circle, and the overlap between circles represents the overlap in variance explained.

RDA and variation partitioning analyses were conducted for all samples in the ecosystem sampling scheme, as well as individually across each ecosystem and forest type. The results were aggregated to BEC zone groups (see [Section 2.1](#sec-study-area)). All RDA and variation partitioning calculations were done in R (R Core Team, 2022) version 4.2.2 using the **vegan** package (Oksanen et al., 2022).

All code associated with the processing and analysis is available at https://github.com/emuise/code-structProdSem.

# Results

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| Figure 2: A) Axis loadings from redundancy analysis of primary and modelled forest structure variables on the dynamic habitat indices. B) Results from variation partitioning of primary and modelled forest structure variables on the DHIs. Both visualized analyses are across all collected samples. See supplementary information for results from each BEC zone and forest type. |

To examine the relationship between ecosystem structure and function across a large environmental gradient, we present the results of a redundancy analysis of forest structure variables on the dynamic habitat indices across the entire sampled dataset in [Figure 2](#fig-rda-var) A. While there are three RDA axes associated with the full dataset, the third axis explains 0.05% of the variance in the DHIs, and as a result is not shown. The first axis strongly represents all the DHIs (loadings > 0.85 for all DHIs), with the highest loadings from canopy cover, basal area, aboveground biomass, and gross stem volume. The other input variables (canopy height, structural complexity) have smaller loadings. The second axis primarily represents the seasonality (Minimum and Variation) of the DHIs, with no correlation to Cumulative DHI, and has the highest loadings from canopy cover and complexity, with the remainder of the forest structure variables having negligible influences([Figure 2](#fig-rda-var) A).

The results from the variation partitioning analysis ([Figure 2](#fig-rda-var) B) show that the majority of the variance explained by the input datasets is shared across both primary and modelled forest structure variables. Of the 13.4% of the variation in the DHIs being explained by the structural information, 9.4% is common across both sets of structure variables. The primary and modelled variables only explain 2.7% and 1.3% of the variation uniquely ([Figure 2](#fig-rda-var) B).

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| Figure 3: Radar plots of average loadings strength by group. A and B show input and response loadings, respectively. C) Boxplots of BEC zone, forest types, and all data loadings for predictor and response variables. |

Further, we wanted to examine the strength of the relationship between the DHIs and primary structure variables vs modelled structure variables across the forest types and ecosystems of the province. [Figure 3](#fig-radar) A and B show the axis loadings for structure variables and the DHIs, respectively. Across the BEC zone groups, the loadings are generally similar in the structure variables. Variations in the DHIs in the southern ecosystems, which are typically warmer and drier, have low or non-significant variance explained by the structure variables. Conversely, across the forest types (coniferous, broadleaf, mixed wood, and wetland-treed) structural complexity is often the highest loading. The loadings for the DHIs in the first axis are generally larger than the loadings for the structure variables, with the cumulative DHI often being the strongest loading overall. In alpine BEC zones, the minimum DHI loading is smaller than the variation and cumulative DHIs. In contrast to the first RDA axis, the secondary RDA axis is primarily driven by variation in the minimum DHI, with medium loadings in the variation DHI, and small loadings in the cumulative DHI ([Figure 3](#fig-radar) A & B). [Figure 3](#fig-radar) C shows boxplots of individual BEC zone loadings for structure variables and the DHIs. Across the province, canopy cover generally has the highest loadings, with structural complexity generally being the weakest.

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| Figure 4: Stacked bar plot proportion of DHI variation explained by extracted, modelled, and the overlap between primary and modelled structure variables. |

[Figure 4](#fig-fracts-bar) shows stacked bar plots of the proportion of variation explained in the DHIs by primary, modelled, and the overlap between primary and modelled variables. Forest types sampled across the environmental gradient generally show higher amounts of variance explained, which is especially prevalent in broadleaf and mixed wood forests. The overlap between modelled and primary structure variables is generally than the primary and modelled attributes individually, with the exception being mixed wood and broadleaf forests and colder, wetter forests. Higher elevation and colder forest stands have larger amounts of DHI variance explained by the forest structure variables than other environments in the province. Notably, the variation explained by the primary and modelled structure variables is commonly presented through a single RDA axis, which generally corresponds to overall productivity through the year ([Figure 3](#fig-radar)). Overall, the DHIs are decoupled from the structure variables, as shown by the overall variance explained being under 30%, regardless of whether the attribute is directly extracted from the point cloud or is a modelled variable.

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| Figure 5: False colour maps of axis loadings for the first RDA axis (top) and second RDA axis (bottom). All colour values are normalized to the maximum loading of each variable. A and D show axis loadings for canopy height (r), canopy cover (g) and structural complexity (b). B and E show axis loadings for basal area(r), total biomass (g) and gross stem volume (b). C and F show axis loadings for the cumulative DHI (r), variation DHI (g) and minimum DHI (b). |

[Figure 5](#fig-fcc) shows false colour composites of the primary (A & C) and modelled (B & D) loadings across the ecosystems of British Columbia. In the first RDA axis there is spatial variation in the primary structure variables, with interior zones being primarily driven by canopy cover (green), the coastal regions having strong structural complexity and canopy height loadings, and the boreal in the northwest having the strongest loading in canopy height ([Figure 5](#fig-fcc) A). The modelled structure variables generally show gray-scale colour, indicating that basal area, total biomass, and gross stem volume explain similar variation in the DHIs ([Figure 5](#fig-fcc) B). All ecosystems with a secondary axis are located away from the Pacific coast in cooler, drier environments. Canopy cover has the strongest secondary axis loading in the northern boreal stands, while the secondary axis in the remaining four zones have the highest loadings in canopy height ([Figure 5](#fig-fcc) C). Again, the modeled structure variables are in grayscale, indicating similar loadings across the three modelled structure variables ([Figure 5](#fig-fcc) E).

# Discussion

Complementarity plays a crucial role in the context of Essential Biodiversity Variables (EBVs) and holds significant importance for monitoring and understanding biodiversity (Pereira et al., 2013; Skidmore et al., 2021). At the ecosystem scale, the interconnectedness and interdependence of ecosystem structure and function is important to recognize and disentangle. In forested environments, forest structure and productivity have been shown to be linked in multiple studies spanning three decades (Ali, 2019; Myneni and Williams, 1994), however, a linkage between intra-annual production and forest structure has yet to be shown. In this study, we use statistical analyses commonly used in community ecology - namely redundancy analysis and variation partitioning - to assess the complementarity of forest structure and yearly productivity summaries. While RDA is common in the ecological literature, this analysis represents one of the first times this technique has been applied to assess the complimentary of proposed satellite-derived EBVs. We find that the example EBVs do not strongly overlap, with forest structure explaining 13.4% of the variation in the DHIs in samples taken across a broad environmental gradient ([Figure 2](#fig-rda-var) B). This indicates that they are suitable to be used in tandem with one another when used as ecosystem EBVs across wide environmental gradients.

Across most of British Columbia’s ecosystems, we identified a single RDA axis associated with the DHIs, encompassing the variation in annual productivity ([Figure 2](#fig-rda-var) A). Within this first axis, the strongest loadings were canopy cover and the modelled structure variables. In Alpine ecosystems the relationship between the first axis and the Minimum DHI was lowest, likely due to the low amount of variation in the Minimum DHI in these ecosystems. When a second axis was significant, it consistently had strong loadings on the minimum and variation DHIs, which indicates a complex internal productivity relationship in certain ecosystems. This secondary axis has smaller axis loadings associated with the primary and modelled structure variables, with the strongest loadings being canopy cover and structural complexity across the entire dataset ([Figure 2](#fig-rda-var) A).

Our second question sought to explore whether modelled structure variables (basal area, gross stem volume, aboveground biomass) add additional explanatory information when predicting the DHIs, as compared to primary forest structure variables. We generally found that canopy cover had the largest axis loadings in the first RDA axis ([Figure 3](#fig-radar)). Modelled structure variables such as basal area, aboveground biomass, and gross stem volume shared similar loading magnitudes across the range of studied ecosystems, indicating they do not add additional value when utilized with one another ([Figure 3](#fig-radar) C; [Figure 5](#fig-fcc) B). The loadings between the modelled structure variables and canopy cover are often similar, and as such, in this context we recommend utilizing the structure variables derived directly from the point cloud in the case of ALS data, or selecting a single modelled attribute, such as aboveground biomass alone (Duncanson et al., 2022).

During the analysis we found a higher amount of total variance explained in deciduous forests (mixed-wood and broadleaf) when compared to the other two forest types and most BEC zones ([Figure 4](#fig-fracts-bar)). This could potentially be due to the temporal linkages between canopy cover in deciduous forests and productivity. In evergreen coniferous forests where canopy cover is present year-round, there is likely a temporal mismatch between forest structure variables and the DHIs. Further, the strongest loadings in these two forest types was vertical structural complexity, rather than canopy cover. This indicates that the DHIs are more closely related to forest structure in deciduous forests, however even there significant decoupling remains.

Finally, we explored the amount of variation explained by primary vs modelled structure variables, as well as their overlap ([Figure 4](#fig-fracts-bar)). We generally found that the overlap between the primary and modelled structure variables explained most of the variation, with some exceptions, indicating that using either set of forest structure variables may be suitable when monitoring biodiversity. The exceptions are especially prominent in the broadleaf and mixed wood forest classes, as well as cool, highly productive forests where there is no variation explained by the overlap between the two datasets. The majority of the variance explained in the broadleaf and mixed wood forests was in the forest structure variables derived directly from the point cloud. This was expected, as the modelled structure variables are calculated based on the derived structure variables as well as site index and ancillary information (Coops et al., 2021).

Recent advances in creating synthetic yearly observations have allowed the DHIs to be generated at a finer scale (30 m; Razenkova et al., In Press), rather than the previously used 1 km DHIs derived from MODIS (Radeloff et al., 2019; Razenkova et al., 2022). This represents a significant advancement when assessing the utility of EBVs, as the 30 m scale is well suited to examine a range of ecological applications, including forest structure and productivity, and more closely approximates the scale at which species perceive habitat (Cohen and Goward, 2004; Kennedy et al., 2014). In addition to more closely matching the scale of ecological phenomenon, this allows these datasets to be matched and analyzed with other datasets generated from the Landsat archive.

In conclusion, we used redundancy analysis and variation partitioning to assess the complementarity of two potential EBV datasets - forest structure and the DHIs. We also separated the forest structure datasets into primary and modelled structure variables in order to assess the need to develop more complex structure variables, or if data derived directly from lidar datasets was suitable. We found that the structure variables are not strongly related to the DHIs, indicating that they are suitable to be used together as ecosystem scale EBVs when monitoring forest environments. We also found that variation explained by the overlap between primary and modelled structure variables was often higher than the variation explained by either individually.

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