Developing remote sensing indices for biodiversity studies across the conterminous US

A dissertation proposal submitted by

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Contents

	Introduction	4
	Study area	7
35	Chapter 1. Comparison of vegetation productivity summarized by the Dynamic Habitat Indices from	
	MODIS instrument and Landsat satellites	9
	Introduction	9
40	Methods	12
	The DHIs calculation	12
	Expected results	15
	Significance	16
	Chapter 2. Explaining bird richness with the Dynamic Habitat Indices across the conterminous US	18
	Introduction	18
	Methods	21
45	Calculation DHIs	21
	BBS data	21
	Environmental Variables	21
	Statistical analysis	22
	Expected results	23
50	The DHIs versus bird richness	23
	The DHIs at different scales	23
	The relative importance of the DHIs in global model	24
	Significance	24
55	Chapter 3. Explaining bird abundance with the Dynamic Habitat Indices	25
	Introduction	25
	Methods	27
	The DHIs and bioclimatic variables	27

	Bird data	
	Statistical analysis	
60	Expected Results	
	Significance	
	Overall significance	
	Reference	

Introduction

Avian diversity is declining globally, due to many threats including habitat loss from human activities, which modify ecosystems through land cover and land use change. Conservation of biodiversity is critically important for the resilience and resistance of

ecosystems to environmental change (Chapin et al. 2000). Moreover, biodiversity loss raises 70 serious concerns about services that humans receive from ecosystems (Sekercioglu 2006). Thus, there is an urgent need for better assessments of the current status of biodiversity, in order to better understand and predict future changes, and to allow timely implementation of conservation actions to prevent biodiversity loss. However, to obtain a spatially detailed map of species

richness directly is hardly possible. In this regard, remote sensing is a suitable tool for assessing 75 biodiversity (Nagendra 2001, Turner et al. 2003).

Satellite data can be used to characterize suitable habitat for each species, predict species distribution, and identify high-value habitat (Nagendra 2001). Effective management applications often require maps with higher spatial resolution. However, there is a trade-off

between spatial and temporal resolution of satellite data. On the one hand, satellites with coarse 80 spatial resolution have more observations over time, providing better estimations of annual vegetation productivity, but larger pixels can be too coarse for ecological studies and management applications. On the other hand, imagery with higher spatial resolution can provide more detailed information about spatial patterns of productivity, especially in heterogeneous 85 landscapes, but temporal resolution is lower.

Available energy has a particularly strong influence on biodiversity (Gaston 2000). Based on the species-energy hypothesis, areas with more available energy can support larger numbers of species (Wright 1983). However, measuring energy can be problematic. Vegetation productivity derived from satellite data can be used as indirect measurement of available energy

(Myneni et al. 2002). Moreover, vegetation productivity is highly associated with biodiversity

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(Skidmore et al. 2003, Cohen and Goward 2004, Pettorelli et al. 2011).

The Dynamic Habitat Indices are remote sensing metrics that summarize three aspects of vegetation productivity: overall vegetation productivity of an ecosystem, the lowest vegetation productivity over the year, and variation of productivity over a year (Coops et al. 2008, Hobi et

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al. 2017, Radeloff et al. 2019). The DHIs are important metrics for biodiversity, and effectively predict species richness for many taxa at national to global scales (Coops et al. 2009, Zhang et al.

2016, Hobi et al. 2017, Radeloff et al. 2019). The DHIs are designed specifically for assessing biodiversity, however, they might also be useful for studies of individual species (Michaud et al. 2014, Razenkova et al. 2020).

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My overarching goal is to develop remote sensing indices with different spatial and temporal resolution for monitoring avian diversity and abundance across different scales. My hope is to improve our understanding of the usefulness of higher spatial resolution satellite data for explaining patterns of avian diversity and abundance.

- In my first chapter, I will calculate the DHIs using data from two satellites which are different in both temporal and spatial resolution. One dataset comes from MODIS instrument which has high temporal resolution (1-2 days) and coarse spatial resolution (1-km). The second dataset is from Landsat satellite with low temporal resolution (16 days) and medium spatial resolution (30-m). The calculation of composite DHIs using MODIS and Landsat images will require several years of data. Including several years of imagery will increase the robustness of
- the DHIs and minimize noise from raw images and effects of cloud, but precludes analyses of changes over time. Furthermore, some changes in vegetation productivity can occur very rapidly due to land cover change or natural disturbance, such as clear-cuts and fire. In this chapter I will find the optimal time period for calculation of the DHIs, balancing the trade-off between obtaining robust metrics and avoiding or minimizing land cover change. I will assess the
- 115 uncertainties for each DHI product.

I assume that the DHIs with medium spatial resolution will provide more advantages over coarse DHIs for studies at smaller extents, because by averaging the Landsat DHIs over large areas we will lose detailed information about landscapes, and Landsat DHIs will provide similar information as MODIS DHIs. To test this hypothesis, I will run correlation analysis at two

- 120 scales: ecoregions based on level III classification of the US Environmental Protection Agency (EPA) (<u>https://www.epa.gov/eco-research/ecoregions</u>) cover large areas (Figure 1), and ecoregions based on level IV cover smaller areas. To evaluate the ability of Landsat DHIs to capture heterogeneity at a much finer scale then MODIS DHIs, especially in complex terrain and fragmented landscapes, I will develop models including commonly used metrics, such as terrain
- 125 ruggedness index and landscape metrics, to explain the variation in the standard deviation of Landsat DHIs.



Figure 1: Ecoregions based on level III classification of the US Environmental Protection Agency across the conterminous states of the USA

In my second chapter, I will evaluate the relationship between the two sets of DHIs and bird richness at three scales. I will also quantify the benefit of higher spatial resolution DHIs 130 when predicting species richness. For that, I will use the DHIs based on MODIS and Landsat calculated in first chapter and test them as predictors for bird species richness for several bird guilds across the US. Birds can serve as good indicators of biodiversity and ecosystem health, because they utilize a wide range of habitat and are sensitive to environmental changes (Cody 1981, Sekercioglu 2006). The vertical complexity of vegetation affects bird species diversity by providing more niches in places with complex vegetation structure (MacAthur and MacAthur 135 1961). Optical satellites are not suitable for measurement of vertical structure such as foliage height diversity, however they capture horizontal heterogeneity very well and indirectly capture some information related to vertical structure (Wood et al. 2012). The DHIs implicitly take into account land cover classes, many of which differ in their vertical structure. I hypothesize that the 140 DHIs with medium resolution will better capture horizontal heterogeneity of landscapes and

vertical vegetation structure, than coarse DHIs. As a result, Landsat DHIs will outperform MODIS DHIs in models of bird species richness of some bird guilds, such as forest species. In

addition, I will assess the relative importance of the DHIs versus the commonly used metrics, including topography and land cover, in multiple regression models for species richness.

- 145 **The main goal in my third chapter** is to evaluate the utility of the Landsat DHIs in explaining bird abundance across the western US. The More Individuals Hypothesis (MIH) explains heterogeneous pattern of species richness (Evans et al. 2005, 2006, Storch et al. 2018), but this hypothesis can also be directly applied to explain species abundance. More productive areas that have high biodiversity can support a higher number of individuals, because of
- 150 abundant food resources (Srivastava and Lawton 1998, Storch et al. 2018). At same time, the relationship between available energy and abundance may be stronger for rare species than for common species (Evans et al. 2005, 2006), because where there is more available energy the extinction probability may be reduced, especially for rare species (Evans et al. 2005, 2006). My first objective is to test if bird abundance varies between areas with higher vegetation
- 155 productivity and lower productivity. Then I will examine if the relationship between the DHIs and bird abundance is stronger for rare species or common species. And finally, I will explore if bird groups based on migratory behavior exhibit different relationships to the DHIs.

In total, my dissertation will a) provide a better understanding of the time period required for the calculation of DHIs from MODIS and Landsat, and their ability to capture heterogeneity;

b) quantify the benefits of higher spatial resolution DHIs for explaining bird species richness, and c) test the utility of Landsat DHIs for explaining spatial patterns of bird abundance.
 Moreover, I will produce two datasets which will be available for users, including updated MODIS DHIs and Landsat DHIs.

Study area

165 My study area encompasses the conterminous US (7.6 million km²). This large area is suitable for my research questions because it covers a wide range of ecoregions (**Figure 1**), and has diverse climatic zones and topography (**Figure 2**), resulting in a large number of habitats and large ranges of the DHIs. Moreover, rich datasets for bird richness and abundance are available for the US, particularly the western US.

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Figure 2: Elevation across the conterminous states of the USA

Chapter 1. Comparison of vegetation productivity summarized by the Dynamic Habitat Indices from MODIS instrument and Landsat satellites

175 Introduction

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A main question in ecology is which key environmental factors shape the patterns of biodiversity? The species-energy hypothesis predicts that the areas with higher amounts of biomass can support more species due to availability of abundant food resources (Wright 1983, Currie et al. 1993, Hawkins et al. 2003a, 2003b). By exploiting the spectral reflectance signal from vegetation, remote sensing vegetation indices can characterize the available environmental energy available due to photosynthesis, making them a good proxy for vegetation productivity (Myneni et al. 1995, Cohen and Goward 2004, Pettorelli et al. 2011). However, it is often unclear what satellite data to select for different purposes. On the one hand, satellite sensors with coarse resolution provide more frequent observations, but images are often too coarse for ecological

185 studies (Kennedy et al. 2014). On the other hand, imagery with medium or high resolution provide more spatially detailed information about ecosystems (Wulder et al. 2008, 2019), but the frequency of observations is lower.

The Dynamic Habitat Indices summarize three measures of vegetation productivity over the course of a year, and capture seasonal variations in energy and correlates of available food resources, which is how the DHIs are linked to patterns of biodiversity (Hobi et al. 2017). Studies have shown that the DHIs can effectively predict species richness and abundance at regional and global scales. For example, the DHIs can predict bird richness in Canada (Coops et al. 2009), US (Hobi et al. 2017), and Thailand (Suttidate et al. 2019), species richness for birds, mammals, amphibians in China (Zhang et al. 2016) and over the globe (Radeloff et al. 2019),

195 and moose abundance in Canada (Michaud et al. 2014) and Russia (Razenkova et al. 2020). So far, the DHIs have only been derived from coarse-resolution satellite data, such as AVHRR and MODIS. However, in principle these indices can be calculated from different satellites including Landsat. Having the DHIs with higher spatial resolution may make them more useful than MODIS DHIs. The DHIs with higher spatial resolution could characterize habitat heterogeneity

200 at much finer scale, especially in complex mountainous terrain and areas with fragmented land cover. Moreover, the pixel size of the Landsat DHI is closer to home territory of some bird species, and therefore may reflect bird habitat better than coarser-resolution imagery. Another

advantage of Landsat is the long data record, which creates a great opportunity to understand changes over time (Kennedy et al. 2014, Wulder et al. 2019). However, the temporal resolution

- of Landsat is low, at a 16-day return cycle, while satellites with coarse resolution obtain imagery every day. Prior studies use the MODIS DHIs as composite products calculated from different numbers of years (Coops et al. 2008, Radeloff et al. 2019). Composite products minimize effects of atmosphere and eliminate noise from raw imagery. At same time, some changes in vegetation productivity caused by anthropogenic and natural disturbance can occur very rapidly, and that
- 210 modification in landscape is critical for habitat selection. To avoid land cover change and climate change trends during the period for which monthly measures are combined, it is better to calculate composite DHIs over shorter time periods. However, there is a lack of evaluation to determine what is the optimal period for the DHIs calculation in order to provide high quality product and avoid land cover changes, and how much this period changes for different input data that are different both in spatial and temporal resolution.

In order to identify the period required for the DHIs calculation, which depends on input data differing in temporal and spatial resolution, I will use images from two satellites. One dataset will come from MODIS with 1-km spatial resolution, and another dataset is from Landsat with 30-m spatial resolution. For both products I will test the robustness of the DHIs metrics to

number of years included for calculation. I assume that the DHIs derived from MODIS will be very robust due to large number of observations, and thus will require a relatively short period of time. For Landsat DHIs it will require a much longer period of time, and it will increase the uncertainties associated with land cover change and low number of cloud-free images. I expect that the performance of the DHIs will depend on the scale of study. By averaging the Landsat
DHIs over a large area, all detailed information will be lost, and Landsat DHIs will be similar to MODIS DHIs. The comparison between MODIS DHIs and Landsat DHIs will help me to

identify at what scale the main discrepancy between them occurs.

At same time I will quantify how well the Landsat DHIs capture heterogeneity in complex terrain and fragmented landscapes. Mountains are often hot spots for biodiversity because of long evolutionary processes (Badgley et al. 2017, Rahbek et al. 2019). Furthermore, large gradients of temperature and environmental conditions can support more species than where environmental conditions are homogeneous (Letten et al. 2013). In such places, species do not need to travel long distances to find suitable environmental and climatic conditions for

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survival and reproductive success. Moreover, climate change is causing elevational shifts for many species (Freeman and Class Freeman 2014), therefore it is important to estimate the amount of habitat area is available for species following range shifts (Elsen et al. 2020b).

With limited resources for protecting important habitat, it is crucial to understand how species respond to anthropogenic modification of landscapes, which disturb the integrity of landscape pattern, and therefore affect biodiversity. Although the effect of habitat fragmentation is debated (Fahrig 2017, Fletcher et al. 2018), there is general agreement that species show

complex responses to fragmented landscapes, with some species such as habitat specialists suffering from fragmentation (Henle et al. 2004), while others benefit from it (Rybicki et al. 2020). There are numerous landscape metrics that describe compositional and spatial aspects of landscapes, but the ecological relevance of those metrics is questionable due to many limitations

245 (Kupfer 2012). Moreover, landscape metrics are usually calculated based on static land cover maps, and at inappropriate scales for organisms (Kupfer 2012). That is why it will be beneficial for biodiversity studies to have metrics which capture heterogeneity that incorporates dynamic patterns of vegetation productivity at fine spatial scales, and be free of the limitations of landscape metrics.

I assume that the temporal resolution of satellite data will be one of the main determinants for period required for calculation. However, I expect that some areas will tend to more problematic than others, due to frequent cloud formation and consequently low number of images over that area, especially for Landsat. Moreover, adjacent Landsat images have overlapping zones, therefore the non-overlap zones may require more years. In order to account
 for these uncertainties, I will generate an additional band in the DHIs that will provide information about quality of given pixel for both MODIS and Landsat DHIs.

My primary goal of this chapter is to develop the Dynamic Habitat Indices based on 30-m resolution Landsat data and 1-km resolution MODIS data across the conterminous US, and to quantify the sensitivity of the DHIs to these input data that are different both in temporal and spatial resolution. More specifically, I will focus on the following goals:

- Identify the time period required for obtaining robust DHIs metrics based on MODIS and Landsat data.
- Assess the uncertainties of the DHIs for both satellites.
- Compare the DHIs derived from MODIS and Landsat at different scales.

• Assess the ability of Landsat DHIs to capture heterogeneity in complex terrain and fragmented landscapes.

I expect that the DHIs based on MODIS will require a relatively short period of time because of the greater temporal density of images. While for Landsat DHIs it will be a much longer time period, and it will contain the uncertainties associated with land cover change.

270 However, I expect that Landsat DHIs will provide more advantages over MODIS DHIs by capturing heterogeneity in mountains and fragmented landscapes, and over small geographical extents.

Methods

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The DHIs calculation

- I will process all data in Google Earth Engine (GEE). This free cloud-based platform provides a great opportunity to develop the DHIs across the conterminous US. The entire archive of Landsat and MODIS data is available on Google Earth Engine (GEE). Moreover, GEE has powerful servers, which allow to parallelize the data processing, resulting in shorter processing times.
- 280 I will analyze atmospherically corrected Surface Reflectance (SR) Tier 1 obtained from Landsat-5 TM, Landsat-7 ETM+, and Landsat-8 OLI from 2001 to 2020. Areas covered by clouds, i.e. 'cloud shadow,' will be removed based on the pixel quality (QA). To remove water bodies, first, I will remove pixels based on QA, and, second, I will apply a water mask of permanent water bodies (Hansen et al. 2013). I will calculate the Normalized Difference 285 Vegetation Index (NDVI) using bands 4,3 for TM, ETM+ and bands 5,4 for OLI. OLI has narrow spectral bands compared to TM and ETM+, therefore I will apply a calibration correction to combine NDVI from these satellites (Roy et al. 2016). If NDVI has negative values, then those values will be replaced with zeroes. For each pixel, I will have a different number of NDVI values due to data availability, sensor problems for ETM+, and overlapping zones. In order to create comparable (MODIS versus Landsat) DHIs, I will select 16-day median NDVI values 290 over different numbers of years, starting from three years (covering 2018-2020) up to twenty, from 2001-2020. I select this time period because MODIS started collecting data in 2001. From NDVI composites, I will calculate the three components of the DHIs: 1) summing up all 16-day median NDVI values (cumulative DHI), 2) selecting the minimum NDVI (minimum DHI), and 295 3) calculating coefficient of variation (seasonal DHI).

For the DHIs calculation from MODIS Collection 6, I will use NDVI 16-day composite product with 1-km resolution (MOD13A2) and I will follow the established protocol (Hobi et al. 2017). However, for calculation of the MODIS DHIs I will use the median NDVI values for each time step over different number of years starting from three years, as described above for Landsat.

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In order to understand the effect of the number of years of input images on the DHIs, I will calculate composite DHIs using different time periods, starting from three years. For that I will generate points using a 5*5 km grid over the conterminous US, and calculate summary metrics such as mean, median, standard deviation from DHIs layers for those points, for each time period. From these summary metrics I will create boxplots and identify which time period boxplots for the DHIs have similar shape. I will do these steps both for MODIS and Landsat. To incorporate the uncertainties associated with different numbers of years included for calculation on the quality of the DHIs product, I will create an additional band showing the number of available NDVI values. I assess how many pixels will have 3 or less observations, for each time period.

To compare the DHIs based on MODIS and Landsat, I will run correlation analysis at two scales. Because I expect that by averaging the Landsat DHIs over large areas such as ecoregions level III, all detailed information about landscape will be washed out and it will be similar to MODIS DHIs. First, I will calculate the MODIS DHIs over the same time period as

- 315 Landsat DHIs. Then I will calculate the mean values of both DHIs for Environmental Protection Agency (EPA) ecoregions level III (about 85 ecoregions in US, Figure 1) and level IV (about 967 in US. Figure 3) and calculate the Pearson correlation coefficients. Ecoregions based on level III and level IV are appropriate units for the DHIs comparison, because ecoregions are defined as areas that exhibit similar characteristics of ecosystems and incorporate regional
- 320 differences (Omernik and Griffith 2014). Ecoregions based on level III cover a relatively large area, while ecoregions based on level IV are much smaller and incorporate regional differences at a finer scale.



Figure 3: Ecoregions based on level IV classification of the US Environmental Protection Agency across the conterminous states of the USA

325 To assess the ability of Landsat DHIs to capture heterogeneity in complex terrain and fragmented landscapes, I will calculate two metrics related to topography and six landscape metrics related to fragmentation. I will use elevation data from the National Elevation Dataset (NED) with 1/3 arc-second spatial resolution. From that layer I will calculate the terrain ruggedness index as following (Riley 1999):

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$$TRI = [\sum (x_{ij} - x_{00})^2]^{1/2},$$

where x_{ij} -elevation of each neighbor cell to cell (0,0), x_{00} - central pixel of eight surrounding pixels. TRI characterizes topographic heterogeneity.

335 To characterize how fragmented landscapes are, I will use the National Land Cover Database (NLCD) with 30-m resolution for 2011 and select land cover classes related to three main habitats: forest, shrubland, and grassland. I will combine three classes for forest (base on NLCD classification 41-decidious forest, 42-evegreen forest, 43-mixed forest), two classes for shrubland (51-dwarf scrub, 52-shrub/scrub) and one class for grassland (71-grassland/

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herbaceous). I will apply image morphology (Vogt et al. 2007, 2009) and calculate the percent of core areas and edge areas for combined classes of forest, shrubland, and grassland.

I will model relationships between the Landsat DHIs and topography and landscape metrics using linear regression analysis for randomly selected 10,000 MODIS pixels separated by at least 10 km to minimize spatial autocorrelation. In order to assess the ability of Landsat

- 345 DHIs to capture heterogeneity I will calculate the standard deviation of Landsat DHIs calculated within MODIS pixels as the dependent variable, and explanatory variables will include two variables related to topography (elevation, TRI) and six variables related to fragmentation (percent of core and edge areas for forest, shrubland, and grassland). Prior to modeling, I will check the collinearity between all explanatory variables and look on scatter plots between
- 350 dependent variables and explanatory variables, to identify whether assumptions of linear regression are met. Then I will use best subset regression to find several good models using the Bayesian Information Criterion (BIC). For the top five models I will calculate the adjusted coefficient of determination (adj R²) to compare the predictive performance of these models.

355 Expected results

One of my main tasks in this chapter is to develop a methodology for the calculation of Landsat DHIs with medium 30-m resolution and MODIS DHIs with coarse 1-km resolution. I expect that the DHIs with medium resolution will have more applications especially for local studies than MODIS DHIs, because of their ability to characterize habitats of some species with more details (**Figure 4**). At the same time, Landsat DHIs will be able to capture heterogeneity of complex mountain terrains and fragmented areas much better, and for some species this type of information is critical for habitat selection.

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The first question of this chapter is to find the number of years needed for the DHIs calculation in order to provide high quality DHIs products. In general, I expect that for the calculation DHIs based on MODIS will require fewer years, while the Landsat DHIs will require more, therefore for Landsat DHIs it will be hard to avoid landcover changes. I expect to have difficulty with providing high quality Landsat DHIs uniformly across the conterminous US due

to differing numbers of available images. Landsat DHIs will have more uncertainties than MODIS DHIs because of low temporal resolution.

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I expect that the pattern of the DHIs based on MODIS and Landsat will be comparable for areas with homogeneous landscapes, such as continuous forest and grassland, but will have large differences in complex terrains, fragmented areas, and heterogeneous landscapes. MODIS DHIs and Landsat DHIs will be highly correlated at ecoregions based on level III, and from moderate to low correlation for ecoregions based on level IV. I expect that metrics related to

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topography and fragmentation will be highly correlated with the standard deviation of Landsat DHIs within MODIS pixels.



Figure 4: The DHIs calculated from 1-km MODIS and 30-m Landsat (preliminary analysis) in central Colorado, US. The DHIs are shown in RGB where red = variation DHI, green = cumulative DHI, blue = minimum DHI.

Significance

The DHIs from MODIS and Landsat will be useful for many ecological studies, especially for monitoring biodiversity, and in species distribution modeling. However, I expect that the DHIs will vary substantially depending on input data. The results of this work will help to find the sweet spot for providing robust and meaningful DHIs. The new Landsat DHIs will be more useful for studies at fine scales and over heterogeneous landscapes, while MODIS DHIs will be more suitable for regional and continental studies. Having remote sensing indices which are relevant to biodiversity and cover four decades, create a great opportunity to understand the

effect of climate change on biodiversity through changes in vegetation productivity. Awareness

of limitations and advantages of the DHIs depending on input data will help users select appropriate DHIs for a given area of interest and scientific question.

Chapter 2. Explaining bird richness with the Dynamic Habitat Indices across the 390 conterminous US

Introduction

Biodiversity is declining at an unprecedented rate and a major cause of this decline is anthropogenic factors (Rockström et al. 2009, Pimm et al. 2014). Humans dramatically change
ecosystems through land use and land cover change, with profound consequences for biodiversity (Sala et al. 2000, Hansen et al. 2013, Haddad et al. 2015). Effective conservation efforts rely on understanding the drivers of biodiversity pattern at broad scales (Pereira et al. 2013). In this capacity, satellite data provide meaningful information about biophysical characteristics of ecosystems (Turner et al. 2003) and are suitable for monitoring of biodiversity patterns across the globe (Wright 1983, Gaston 2000, Mittelbach et al. 2001, Hawkins et al. 2003a, 2003b, Bonn et al. 2004).

Species richness is a key component of biodiversity and positively correlated with Net
Primary Productivity (NPP, Paruelo et al. 1997). Remote sensing based vegetation indices such as the normalized difference vegetation index (NDVI) relate to NPP at broad scales, and
consequently relate to species richness (Myneni et al. 1995, Skidmore et al. 2003, Cohen and Goward 2004, Pettorelli et al. 2011). The integrated measure of vegetation productivity summarized as a) overall productivity over a course of the year, b) available minimum productivity during winter, and c) variation in productivity named the Dynamic Habitat Indices (DHIs) are effective predictors of species richness at regional and global scales (Coops et al.
2009, Hobi et al. 2017, Radeloff et al. 2019). The MODIS DHIs are available globally at 1-km

- spatial resolution (Radeloff et al. 2019). However, these DHIs can be too coarse for some species in cases where territory size is smaller than 1-km MODIS pixel. Moreover, satellite data with higher resolution can capture spatial heterogeneity at finer scales which is an important driver of species distribution and richness. However, satellites with higher spatial resolution have less
- 415 images for a point of interest than satellites with coarse spatial resolution. That raises the several questions regarding whether it is beneficial to calculate the DHIs using satellite data with higher spatial resolution, and how much explanatory power it will add in models of species richness.

To answer the question whether higher spatial resolution provides more advantages over coarse data, I will test the predictive performance of the DHIs based on MODIS and Landsat in

- 420 bird species richness models. Birds are a good indicator of biodiversity and ecosystem health, because they quickly respond to changes in ecosystem, have diverse ecological functions, and are very mobile (Cody 1981, Sekercioglu 2006). With steep declines of birds (Pimm et al. 2014), it raises a serious concern about ecosystem health and in particular human wellbeing because humans obtain benefits from birds by receiving ecological services such as pest control,
- 425 pollination, fertilizer, and seed dispersal (Sekercioglu 2006). The North American Breeding Bird Survey (BBS, Sauer et al. 2017) is a long-term dataset of bird abundance and occurrence, and provides an opportunity to explore the relationship between the DHIs and bird richness.

The general expectation based on species-energy hypothesis is that bird richness will be higher in areas with high productivity because of more food resources (Gaston 2000, Hawkins et

al. 2003a, 2003b). However, this relationship varies across different scales, and can be 'hump-shaped' at local scales and linear at regional scales (Waide et al. 1999, Chase and Leibold 2002). It is interesting to explore if the relationship between vegetation productivity (the DHIs) and species richness will change depending on the spatial resolution of the DHIs. My expectation is that the relationship between the DHIs and species richness will be linear for both DHIs, but the
predictive performance of the Landsat DHIs will increase with zooming to smaller areas. By averaging remote sensing data over large areas, such as ecoregions, we wash out detailed information about regions, and Landsat DHIs will be similar to MODIS DHIs.

Another important determinant of species richness is habitat heterogeneity (MacArthur 1964). Vegetation heterogeneity may support higher biodiversity by providing more niche space
(Tews et al. 2004). I hypothesize that sites with high vegetation productivity have more vegetation complexity and therefore support more species. However, birds show complex response to heterogeneity, thus Landsat DHIs may provide more explanatory power in modeling birds that depend on heterogeneous landscapes, including forest and shrubland species. At the same time, small-bodied birds that are not good with regulating body temperature may require heterogeneous landscapes to escape extreme ambient temperatures (Scholander et al. 1950, Elsen et al. 2020a).

The DHIs may provide complementary information to other variables such as climate and topography (Suttidate et al. 2019) in models of species richness. To evaluate the relative importance of both DHIs compared with other commonly used variables that potentially

450 influence bird richness, I will run the global models combining the DHIs, topography and land

cover separately for 30-m and 1-km resolution. Even though topography and land cover are static variables, both variables are important drivers of biodiversity (Rosenzweig 1995). I select these variables because elevation characterizes habitat heterogeneity well, while land cover is a good estimation of potential habitats for birds including forest, shrubland and grassland guilds (Turner et al. 2003). At the same time, elevation and land cover are available at 30-m and 1-km which allow comparisons of global models.

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My primary goal is to evaluate the predictive performance of the DHIs at 1-km and 30-m resolution for modeling bird species richness and identify where the DHIs with medium resolution provide more advantages over coarse DHIs. Specifically, I will examine the following questions:

- Do the Landsat DHIs provide higher predictive power in models of bird richness than MODIS DHIs?
- For which bird guilds are the DHIs with higher resolution important?
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- What is the relative importance of the DHIs for bird richness, compared with common variables characterizing environmental heterogeneity, such as topography and land cover?

I predict that Landsat DHIs will provide more advantages over MODIS DHIs in models of some bird guilds including forest and shrubland birds, permanent residents, and birds with small body size because landscapes with greater heterogeneity will provide more niches and therefore support more species. At the same time, permanent residents and birds with small body size must regulate body temperature for survival during harsh seasons, and heterogeneous landscapes provide more places to escape unfavorable weather conditions, and lead to higher bird richness. However, I expect no difference in explaining power between MODIS DHIs and Landsat DHIs for grassland birds, because this group of birds depends on homogeneous

475 landscapes, which are probably equally well captured by both satellites. For global models I expect that the both DHIs based on MODIS and Landsat will complement the other environmental variables and increase the predictive power of the models. However, Landsat DHIs will provide more independent contribution then MODIS DHIs.

480 Methods

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Calculation DHIs

I will use the results of the first chapter, where I will calculate the DHIs. For my second chapter I will use two sets of the composite DHIs based on MODIS and Landsat for 2011-2020. The composite DHIs are calculated only over one decade to minimize the uncertainties associated with land cover change. The DHIs contain the three components: overall productivity

(Cum DHI), the lowest amount of vegetation (Min DHI), and seasonality (Var DHI).

BBS data

The North American Breeding Bird Survey (BBS) data are collected once a year during
the breeding season across North America (Sauer et al. 2017). At 50 stops along a 39.4 km long route, skilled volunteers observe and record individual birds, by species. I will exclude some observations from BBS data using the following criteria: if the weather conditions during the survey were not good, or false positive errors (first time observers). I will calculate bird richness by summing up the list of unique bird species for Environmental Protection Agency (EPA)
ecoregions level III (about 85 ecoregions in US, Figure 1), routes (more than 3,000 routes, Figure 5), and the first stop of each route within the conterminous US for 2011-2020. I will separate birds based on habitat association (forest, shrub land, grassland), and migratory behavior (residents, short-distance migrants, long-distance migrants) using BBS classifications and detailed information about bird species from Birds of the World (Billerman et al. 2020).
Also, I will separate birds by body size (small, large). For that I will calculate the average body

mass of all breeding birds from BBS data, using information about body mass (Dunning 2008). I will assign birds as small-bodied or large-bodied if their average body mass is smaller or larger than the average body mass of all birds.

505 Environmental Variables

For elevation I will use the National Elevation Dataset for the USA with 30-m spatial resolution. To characterize land cover composition, I will use land cover maps from 2016 National Land Cover Database (NLCD) with 30-m resolution. To make sure that I will compare the global models containing DHIs with different resolution and not differences in land cover or

510 topography, I will upscale elevation and NLCD to 1-km matching the resolution of MODIS

DHIs. I will focus on three main habitat types: forest, shrubland, and grassland. I will calculate the mean and standard deviation of elevation layers and proportion of forest, shrubland and grassland cover within 20-km buffers surrounding the center of BBS routes.

515 Statistical analysis

For modeling, I will calculate the mean value of two sets of the DHIs for 85 ecoregions, mean value of the DHIs within 20-km buffers surrounding the center of BBS routes, and extract the raw value of one DHIs pixel that covers the coordinates of the first stop of each route. To explore the relationship between species richness and the DHIs, I will calculate Pearson

520 correlation coefficients, and create scatter plots for visualization. For statistical analysis, I will use a linear regression where the dependent variable will be bird richness for several bird guilds and explanatory variables will be MODIS DHIs or Landsat DHIs. To compare the predictive performance of the DHIs based on Landsat and MODIS in modeling species richness, I will run a series of univariate linear models with only one component of the DHIs (8 bird guilds by 3 the
525 DHIs components by 2 resolutions by 3 scales, total 144 models) and calculate the adjusted coefficient of determination (adj R²). Also, I will check spatial autocorrelation by plotting the

semivariograms for each model.

To evaluate the relative importance of the DHIs in global models combining the DHIs and other environmental variables, I will run analysis only for BBS routes (medium scale). First, I will check multicollinearity among explanatory variable by calculating Pearson correlation coefficients and excluding variables with |r|> 0.7. I will fit a global model that include the DHIs, two elevation metrics, and three landcover metrics. I will use best subset regression that allows all possible combinations of explanatory variables, and identifies a set of good models. To rank these models, I will use Bayesian Information Criterion (BIC), which penalizes models with

large numbers of explanatory variables. For the top five models, I will calculate adjusted R² to estimate how much of the variation in bird richness is explained by the model. For the final best model, I will calculate variance inflation factors (VIF) to check for multicollinearity among final predictors. For the top model based on BIC according to results of best subset regression, I will apply hierarchical partitioning analysis to evaluate the relative importance of predictors in multivariate models (Chevan and Sutherland 1991).



Figure 5: BBS routes in conterminous United States

Expected results

The DHIs versus bird richness

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I expect that DHIs at both spatial resolutions will provide high explanatory power in species richness models. However, I expect that DHIs with medium spatial resolution will capture the difference in vertical structure of vegetation and heterogeneous landscapes much better than coarse DHIs. As a result, Landsat DHIs will have higher explanatory power for some bird guilds which depend on heterogeneous landscapes. It is expected that Landsat DHIs will be more important for forest and shrubland birds, birds with small body size, permanent residents, while there is no difference between MODIS and Landsat DHIs for grassland species. But I expect that for some bird guilds such as short-distance migrants there will be no difference in explanatory power between MODIS and Landsat DHIs due to unimportance of the DHIs for habitat selection of these birds.

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The DHIs at different scales

In terms of the scale, I think that performance of Landsat DHIs and MODIS DHIs will be similar across ecoregions. However, the Landsat DHIs will perform much better at medium scales (i.e., within the buffer of BBC routes), and at fine scales (start point of BBC routes).

The relative importance of the DHIs in global model

I expect that the DHIs will complement the elevation and landcover metrics and increase the predictive power of the model. However, I expect the Landsat DHIs will provide more independent contribution then the MODIS DHIs.

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Significance

To maintain biodiversity, it is important to monitor biodiversity pattern at different scales and identify areas that are important for biodiversity. My study will add more understanding to the importance of higher spatial resolution for characterizing the DHIs metrics and consequently

- 570 for modeling biodiversity pattern. The comparison of DHIs based on MODIS and Landsat will reveal whether higher spatial resolution of satellite data provides more detailed information about vertical structure of vegetation and heterogeneous landscapes. Moreover, having the DHIs with higher spatial resolution, my work will add more knowledge about drivers of avian diversity across broad spatial extents, that can be used to predict how biodiversity patterns will change in
- the future depending on changes in vegetation productivity.

Chapter 3. Explaining bird abundance with the Dynamic Habitat Indices

Introduction

- 580 According to the North American Bird Conservation Initiative (NABCI), 37% of all birds in North America are at risk of extinction, with many species in coastal, grassland, and aridland habitats declining steeply (NABCI 2016, Rosenberg et al. 2019). With limited resources, conservationists want to maximize conservation return (Wilson et al. 2011), and consequently often focus on identifying and protecting areas with higher biodiversity. For these purposes there 585 are different metrics such as species richness, alpha, beta, gamma diversity and many other biodiversity indices that incorporate different information about functionality of existing species in given area. However, all these metrics do not provide information about how many individuals of a given species lives in an area. By only monitoring these metrics, we may miss important signals when species start to decline, which as a result could potentially trigger changes in abundance of other species (Rosenberg et al. 2019). Moreover, there are many uncertainties 590 about species response to advancing climate change (Langham et al. 2015). That is why it is important to monitor species abundance.
- At the same time, obtaining accurate estimates of abundance data is difficult and time consuming (Buckland et al. 2008), especially in remote and hard-to-reach areas. Moreover,
 abundance can fluctuate from one year to another because there are so many factors influencing species abundance, such as unfavorable climatic conditions, low primary productivity, predation, disturbance (fire, wind fall, clear cuts, etc.), competition, disease and many others (Currie et al. 1993). Even if it is possible to obtain all these data for one species or over a small extent, it is not possible to obtain it for all species. It is important to understand the underlying mechanisms
 influencing spatial patterns of species abundance over broad scales. In this regard, remote sensing provides a great opportunity for monitoring species abundance because it provides
 - information about environmental characteristics of habitat, and captures dynamic changes on the ground. Moreover, data are collected systematically and provide wall-to-wall global coverage (Nagendra 2013).
- In this chapter, I will explore the effectiveness of the Dynamic Habitat Indices (DHIs) to explain abundance patterns of birds. Birds can easily move over long distances to find suitable habitat, hence the decline in bird abundance in some areas are not always caused by mortality, it

can be caused by outmigration (Pavlacky et al. 2017). The DHIs integrate three measures of vegetation productivity providing information about species habitat and forage conditions

- 610 (Coops et al. 2008). Birds are a good taxon for understanding the utility of the DHIs because they exhibit a range of behaviors and strategies to find food and suitable habitat. The More Individuals Hypothesis (MIH) postulates that areas with greater food resources support higher total numbers of individuals in a community (Srivastava and Lawton 1998, Storch et al. 2018). While the MIH was developed to explain spatial patterns of species richness, it can be applied to
- 615 explain patterns of species abundance as well. The underlying mechanism of MIH is closely connected to extinction rates, with the assumption that only species with viable population size can support high species richness, whereas low population sizes have a higher probability of extinction, and could not support high species richness (Storch et al. 2018).
- The mechanism of the MIH reflects abundance-dependent extinction rate, however the relationship between species richness, abundance and available energy might be different for common versus rare species (Storch et al. 2018). Because an increase of available energy should decrease the extinction risk, especially in rare species due to low number of individuals, therefore rare species will show stronger species-energy relationships (Evans et al. 2005, 2006). In this regard the DHIs are very promising for testing the MIH for individual species, because
- these indices provide information about available energy over the year and during winter time, and moreover show the stability of available energy in the system through photosynthesis activity (Radeloff et al. 2019). Having three different measure of available energy, we can explain abundance of different bird species. For example, resident birds stay close to their breeding areas all year around, but one limiting factor for this guild is available food resources during winter time. Therefore, I hypothesize that resident birds will have stronger relationship with available energy during harsh winter season. While long-distance migrants travel great
 - distances to take advantages of seasonal abundance of insect food, for this guild I expect that seasonality is more important.

While the DHIs provide information about available energy, it may not be a primary
factor influencing bird abundance patterns. Prior studies show the effectiveness of the DHIs for
explaining the abundance of large mammals (Michaud et al. 2014, Razenkova et al. 2020),
however the combination of DHIs with other environmental variables provides higher predictive
power in models (Suttidate et al. 2019). Climate and environmental heterogeneity are important

determinants shaping species distribution and abundance patterns (MacAthur and MacAthur 1961, Gaston 2000). To test the performance of DHIs in multivariate models, I will add

bioclimatic and topographic variables.

My primary goal is to evaluate the utility of the DHIs to explain bird abundance in the western US. Specifically, I will examine the following questions:

- Does bird abundance vary between productive and less productive areas?
- Is the MIH more relevant for rare species than for common bird species?
- Does abundance of resident birds have a stronger relationship with productive areas based on winter? Does abundance of long-distance migrants have a stronger relationship with productive areas based on overall productivity or seasonality?
- Do the DHIs provide information complementary to other environmental variables?

I expect to find evidence of MIH and to see higher number of individuals in more productive areas. I expect that common species will show stronger relationships with the DHIs, and different components of the DHIs will appear more important for different birds. For example, I expect the residents will show a stronger correlation with minimum DHI, while longdistance migrants will correlate with variation DHI. Whereas Evans et al. (2005) assumed a stronger species-energy relationship in rare birds, I expect to find weak or no relationship between the DHIs and abundance of rare species, because vegetation productivity is not the limiting factor for these species. I expect that the DHIs will complement environmental variables in multivariate models, but for some species I expect that bioclimatic variables or topography will more important than the DHIs.

Methods

The DHIs and bioclimatic variables

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I will use the results of the first chapter, where I will calculate the DHIs. To minimize the influence of clouds and atmosphere, I will use composite DHIs based on Landsat for 2011-2020. The DHIs contain three components: overall productivity (Cum DHI), the lowest amount of vegetation (Min DHI), and seasonality (Var DHI).

I will subset BIOCLIM variables that influence survival and reproductive success of birds such as the minimum temperature in the coldest month (BIO6), annual precipitation (BIO12),

670 and precipitation of the warmest quarter (BIO18). This dataset is available globally at 1-km resolution. For topography, I will use the elevation data based on the National Elevation Dataset (NED) with 1/3 arc-second spatial resolution.

Bird data

The ready-to-use data from the Integrated Monitoring in Bird Conservation Regions (IMBCR) Program (Woiderski et al. 2018) provides an opportunity to explore the effectiveness of the DHIs to explain bird abundance. The main advantages of IMBCR data is that they are collected using a standard protocol and data are corrected for imperfect detection. Data are publicly available for the western US since 2005 (**Figure 6**). The IMBCR design defines sampling units as 1 km² cells, each containing 16 evenly-spaced sample points, 250 m apart

(Figure 7) (Woiderski et al. 2018). They provide estimates of bird density at 1-km resolution.



Figure 6: Shaded area indicates spatial extent of IMBCR surveys, with sampled Bird Conservation Regions in different colors (Woiderski et al. 2018).



Figure 7: Example 1-km² sampling unit using the IMBCR design (Woiderski et al. 2018)

To test if bird abundance varies between productive and non-productive areas, I will select ten widely distributed bird species with sufficient numbers of observations, such as American Robin and Black–capped Chickadee. To test if the MIH is more relevant to rare species, I will select ten rare species. I will identify rare species based on IUCN status and from detailed species accounts (Billerman et al. 2020, IUCN 2020). To test if the abundance of resident and long-distance birds is related to different components of the DHIs, I will select several species from each group (residents, long-distance migrants).

690 *Statistical analysis*

To relate the DHIs to bird abundance, I will calculate the mean value of the three components of the DHIs for each grid of cells, based on the US National Grid (USNG), because the IMBCR data are summarized based on this grid. Then I will run a set of linear regressions, where the dependent variable will be bird abundance (widely distributed, common, rare,

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residents, long-distance migrants), and explanatory variables will be the three DHIs. For each model I will calculate the adjusted coefficient of determination (adj R²) in order to estimate how

much of the variation in the response variable is explained by each model. To avoid potential bias, I will check for spatial autocorrelation and plot semivariograms.

To determine the relative importance of the DHIs in determining bird abundance in 700 multivariate model that include the subset of BIOCLIM variables and elevation, I will use a multiple linear regression approach and select a set of good models based on BIC criteria. The response variable will be bird abundance of several common species, residents, and longdistance migrants, the explanatory variables will the DHIs, the BIOCLIM variables and elevation. I will apply log-transformation of dependent variables to meet assumption of linear 705 regression if it is necessary. Before fitting regression models, I will calculate correlation coefficients for all explanatory variables to check for multicollinearity, and exclude variables with |r| > 0.7 from further analysis. After applying the best subset regression, I will select the topranked model and calculate the adjusted coefficient of determination.

Expected Results

- 710 I expect to find that bird abundance will be higher in productive areas than in less productive areas for all bird groups. In general, this pattern will be more relevant for common species and widely distributed species. I expect to find that even rare species will also have higher number of individuals in more productive areas, but this relationship will be very weak because the energy measured through vegetation productivity is not limited factor. However, the
- 715 DHIs can capture some important characteristics for suitable habitat of rare species, which are dependent on complex vertical structure of vegetation. For resident birds, I expect to see a stronger energy-abundance relationship based on Min DHI, while for long-distance migrants based on Var DHI. In multivariate models the DHIs will complement the climate and topography variables, however, I expect that BIOCLIM variables will provide more independent 720 contribution than the DHIs.

Significance

Global biodiversity crisis started with the declining abundance of individual species, thus there is an urgent need to identify factors driving species abundance patterns. The proposed study will explore the potential usage of remote sensing technology for monitoring species

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abundance. The evaluation of relationships between the DHIs and bird abundance will provide insightful information about available tools for monitoring species abundance.

Overall significance

Identifying the factors driving species richness and abundance pattern across broad scales is crucial for understanding the mechanisms influencing these patterns, and predicting how species may respond to changing conditions. In order to safeguard biodiversity, we need better assessments of the current status of biodiversity. However, biodiversity patterns are very complex, many factors matter for different regions and for different species. My proposed research will provide a better understanding of the relationship between vegetation productivity, avian biodiversity, and individual bird species.

735 My proposed work will contribute to science from three perspectives. The main **methodological** contribution is to develop the Dynamic Habitat Indices using Landsat imagery, to quantify important characteristics of suitable habitat for many species over a broad scale. I will determine whether DHIs with medium resolution provide more advantages over DHIs with coarse resolution, at different scales. In addition, I will evaluate how the Landsat DHIs capture

- 740 vegetation heterogeneity in complex mountain terrains and fragmented landscapes. I will determine the time period required for the DHIs calculation in order to provide robust products and avoid uncertainties associated with abrupt changes of vegetation. Moreover, newly developed Landsat DHIs and updated MODIS DHIs will be available to the scientific community, as effective tools for explaining spatial patterns of many other taxonomic groups.
- My project will contribute to avian ecology by improving our understanding of the factors shaping broad-scale patterns of species richness. While biodiversity patterns have been studied extensively, in most cases researchers used data that are too coarse or over limited geographical extents. I will show the effectiveness of the DHIs with medium resolution to explain bird richness of those bird guilds that depend more on heterogeneous landscapes. By
 combining the DHIs with other important factors influencing biodiversity, such as topography and land cover variables, I will add to our understanding of the relative importance of these factors and the importance of higher spatial resolution of the remote sensing data.

I will add more understanding of the application of remote sensing data to **land management and conservation** efforts to reduce the biodiversity loss and the degradation of natural resources. The Landsat DHIs will be tested for assessing bird abundances for different bird guilds. I hope that the remote sensing measures of vegetation productivity will be able to

capture important characteristics of suitable habitat of common species and birds that are experiencing significant declines. Identifying critical habitats for species of high concern will have direct implementation for management of those species.

Reference

- Badgley, C., T. M. Smiley, R. Terry, E. B. Davis, L. R. G. DeSantis, D. L. Fox, S. S. B. Hopkins, T. Jezkova, M. D. Matocq, N. Matzke, J. L. McGuire, A. Mulch, B. R. Riddle, V. L. Roth, J. X. Samuels, C. A. E. Strömberg, and B. J. Yanites. 2017. Biodiversity and Topographic
- Complexity: Modern and Geohistorical Perspectives. Trends in Ecology and Evolution 765 32:211-226.
 - Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg. 2020. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA.
 - Bonn, A., D. Storch, and K. J. Gaston. 2004. Structure of the species-energy relationship. Proceedings of the Royal Society B: Biological Sciences 271:1685–1691.
 - Buckland, S. T., S. J. Marsden, and R. E. Green. 2008. Estimating bird abundance: Making methods work. Bird Conservation International 18:S91–S108.
 - Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Díaz. 2000.
- 775 Consequences of changing biodiversity. Nature 405:234–242.
 - Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity relationship. Nature 416:427-430.
 - Chevan, A., and M. Sutherland. 1991. Hierarchical Partitioning. American Statistician 45:90–96.
 - Cody, M. L. 1981. Habitat Selection in Birds: The Roles of Vegetation Structure, Competitors,

780 and Productivity. BioScience 31:107-113.

- Cohen, W. B., and S. N. Goward. 2004. Landsat's Role in Ecological Applications of Remote Sensing. BioScience 54:535–545.
- Coops, N. C., R. H. Waring, M. A. Wulder, A. M. Pidgeon, and V. C. Radeloff. 2009. Bird diversity: a predictable function of satellite-derived estimates of seasonal variation in
- 785 canopy light absorbance across the United States. Journal of Biogeography 36:905–918.
 - Coops, N. C., M. A. Wulder, D. C. Duro, T. Han, and S. Berry. 2008. The development of a Canadian dynamic habitat index using multi-temporal satellite estimates of canopy light absorbance. Ecological Indicators 8:754–766.
- Currie, D. J., J. T. Fritz, D. J. Currie, J. T. Fritz, and J. T. Global. 1993. Global Patterns of Animal Abundance and Species Energy Use. Nordic Society Oikos 67:56–68. 790 Dunning, J. 2008. CRC Handbook of Avian Body Masses. second ed. CRC Press, Boca Raton.

- Elsen, P. R., L. S. Farwell, A. M. Pidgeon, and V. C. Radeloff. 2020a. Landsat 8 TIRS-derived relative temperature and thermal heterogeneity predict winter bird species richness patterns across the conterminous United States. Remote Sensing of Environment 236.
- 795 Elsen, P. R., W. B. Monahan, and A. M. Merenlender. 2020b. Topography and human pressure in mountain ranges alter expected species responses to climate change. Nature Communications 11:1–10.

800

805

- Evans, K. L., J. J. D. Greenwood, and K. J. Gaston. 2005. The roles of extinction and colonization in generating species-energy relationships. Journal of Animal Ecology 74:498– 507.
- Evans, K. L., N. A. James, and K. J. Gaston. 2006. Abundance, species richness and energy availability in the North American avifauna. Global Ecology and Biogeography 15:372– 385.
- Fahrig, L. 2017. Ecological Responses to Habitat Fragmentation Per Se. Annual Review of Ecology, Evolution, and Systematics 48:1–23.
- Fletcher, R. J., R. K. Didham, C. Banks-Leite, J. Barlow, R. M. Ewers, J. Rosindell, R. D. Holt,
 A. Gonzalez, R. Pardini, E. I. Damschen, F. P. L. Melo, L. Ries, J. A. Prevedello, T.
 Tscharntke, W. F. Laurance, T. Lovejoy, and N. M. Haddad. 2018. Is habitat fragmentation good for biodiversity? Biological Conservation 226:9–15.
- Freeman, B. G., and A. M. Class Freeman. 2014. Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming.
 Proceedings of the National Academy of Sciences of the United States of America 111:4490–4494.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.

- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy,
 J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L.
 Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A.
 Melbourne, A. O. Nicholls, J. L. Orrock, D. X. Song, and J. R. Townshend. 2015. Habitat
 fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:1–10.
- Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D.
 Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C.
 O. Justice, and J. R. G. Townshend. 2013. High-Resolution Global Maps of 21st-Century

Forest Cover Change. Science 342:850–853.

- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J. F. Guegan, D. M. Kaufman, J. T. Kerr,
 G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, and J. R. G. Turner. 2003a.
 Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.
 - Hawkins, B. A., E. E. Porter, and J. A. F. Diniz-Filho. 2003b. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84:1608–1623.
- 830 Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. Biodiversity and Conservation 13:207–251.
 - Hobi, M. L., M. Dubinin, C. H. Graham, N. C. Coops, M. K. Clayton, A. M. Pidgeon, and V. C. Radeloff. 2017. A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness. Remote Sensing of Environment 195:142– 152.
 - IUCN. 2020. The IUCN Red List of Threatened Species. Version 2020-1. https://www.iucnredlist.org>.
 - Kennedy, R. E., S. Andréfouët, W. B. Cohen, C. Gómez, P. Griffiths, M. Hais, S. P. Healey, E.H. Helmer, P. Hostert, M. B. Lyons, G. W. Meigs, D. Pflugmacher, S. R. Phinn, S. L.
- Powell, P. Scarth, S. Sen, T. A. Schroeder, A. Schneider, R. Sonnenschein, J. E.
 Vogelmann, M. A. Wulder, and Z. Zhu. 2014. Bringing an ecological view of change to landsat-based remote sensing. Frontiers in Ecology and the Environment 12:339–346.
 - Kupfer, J. A. 2012. Landscape ecology and biogeography: Rethinking landscape metrics in a post-FRAGSTATS landscape. Progress in Physical Geography 36:400–420.
- 845 Langham, G. M., J. G. Schuetz, T. Distler, C. U. Soykan, and C. Wilsey. 2015. Conservation status of North American birds in the face of future climate change. PLoS ONE 10:1–16.
 - Letten, A. D., M. B. Ashcroft, D. A. Keith, J. R. Gollan, and D. Ramp. 2013. The importance of temporal climate variability for spatial patterns in plant diversity. Ecography 36:1341–1349.
 - MacArthur, R. H. 1964. Environmental Factors Affecting Bird Species Diversity. The American

850

- Naturalist 98:387–397. MacAthur, R. H., and J. W. MacAthur. 1961. On Bird Species Diversity. Ecology 42:594–598.
- Michaud, J. S., N. C. Coops, M. E. Andrew, M. A. Wulder, G. S. Brown, and G. J. M. Rickbeil. 2014. Estimating moose (Alces alces) occurrence and abundance from remotely derived

environmental indicators. Remote Sensing of Environment 152:190-201.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. 855 R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology 82:2381–2396.

Myneni, R. B., F. G. Hall, P. J. Sellers, and A. L. Marshak. 1995. Interpretation of spectral vegetation indexes. IEEE Transactions on Geoscience and Remote Sensing 33:481–486.

- Myneni, R. B., S. Hoffman, Y. Knyazikhin, J. L. Privette, J. Glassy, Y. Tian, P. Votava, R. R. 860 Nemani, and S. W. Running. 2002. Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. Remote Sensing of Environment 83:214-231.
 - NABCI. 2016. North American Bird Conservation Initiative. 2016. The State of North America's Birds 2016. Environment and Climate Change Canada: Ottawa, Ontario.
- 865 Nagendra, H. 2001. Using remote sensing to assess biodiversity. International Journal of Remote Sensing 22:2377–2400.
 - Omernik, J. M., and G. E. Griffith. 2014. Ecoregions of the Conterminous United States: Evolution of a Hierarchical Spatial Framework. Environmental Management 54:1249–1266.
- Paruelo, J. M., H. E. Epstein, W. K. Lauenroth, and I. C. Burke. 1997. ANPP estimates from NDVI for the central grassland region of the United States. Ecology 78:953–958. 870

Pavlacky, D. C., P. M. Lukacs, J. A. Blakesley, R. C. Skorkowsky, D. S. Klute, B. A. Hahn, V. J. Dreitz, T. L. George, and D. J. Hanni. 2017. A statistically rigorous sampling design to integrate avian monitoring and management within Bird Conservation Regions. PLoS ONE 12:1-22.

- 875 Pereira, H. M., S. Ferrier, M. Walters, G. N. Geller, R. H. G. Jongman, R. J. Scholes, M. W. Bruford, N. Brummitt, S. H. M. Butchart, A. C. Cardoso, N. C. Coops, E. Dulloo, D. P. Faith, J. Freyhof, R. D. Gregory, C. Heip, R. Höft, G. Hurtt, W. Jetz, D. S. Karp, M. A. McGeoch, D. Obura, Y. Onoda, N. Pettorelli, B. Reyers, R. Sayre, J. P. W. Scharlemann, S. N. Stuart, E. Turak, M. Walpole, and M. Wegmann. 2013. Essential Biodiversity Variables. Science 339:277-278.
- 880
- Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. Climate Research 46:15–27.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C.

- 885 M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344.
 - Radeloff, V. C., M. Dubinin, N. C. Coops, A. M. Allen, T. M. Brooks, M. K. Clayton, G. C.Costa, C. H. Graham, D. P. Helmers, A. R. Ives, D. Kolesov, A. M. Pidgeon, G.Rapacciuolo, E. Razenkova, N. Suttidate, B. E. Young, L. Zhu, and M. L. Hobi. 2019. The
- Bynamic Habitat Indices (DHIs) from MODIS and global biodiversity. Remote Sensing of
 Environment 222:204–214.
 - Rahbek, C., M. K. Borregaard, R. K. Colwell, B. Dalsgaard, B. G. Holt, N. Morueta-Holme, D. Nogues-Bravo, R. J. Whittaker, and J. Fjeldså. 2019. Humboldt's enigma: What causes global patterns of mountain biodiversity? Science 365:1108–1113.
- 895 Razenkova, E., V. C. Radeloff, M. Dubinin, E. V Bragina, M. Allen, M. K. Clayton, A. M. Pidgeon, L. M. Baskin, C. Nicholas, and M. L. Hobi. 2020. Vegetation productivity summarized by the Dynamic Habitat Indices explains patterns of moose abundance across Russia. Scientific Reports 10:1–12.

Riley, S. 1999. Index that quantifies topographic heterogeneity.

- Rockström, J., W. Steffen, K. Noone, Å. Persson, F. S. Chapin, E. Lambin, T. M. Lenton, M. Scheffer, C. Folke, H. J. Schellnhuber, B. Nykvist, C. A. de Wit, T. Hughes, S. van der Leeuw, H. Rodhe, S. Sörlin, P. K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L. Karlberg, R. W. Corell, V. J. Fabry, J. Hansen, B. Walker, D. Liverman, K. Richardson, P. Crutzen, and J. Foley. 2009. A safe operating space for humanity. Nature 461:472–475.
- 905 Rodewald, P. 2015. The Birds of North America. Cornell Laboratory of Ornithology, Ithaca, NY. Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. Science 366:120–124.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press.

- Roy, D. P., V. Kovalskyy, H. K. Zhang, E. F. Vermote, L. Yan, S. S. Kumar, and A. Egorov.
 2016. Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. Remote Sensing of Environment 185:57–70.
 - Rybicki, J., N. Abrego, and O. Ovaskainen. 2020. Habitat fragmentation and species diversity in competitive communities. Ecology Letters 23:506–517.
- 915 Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald,

L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. R. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

- Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, K. L. Pardieck, J. E. Fallon, and W. A.
- Link. 2017. The North American Breeding Bird Survey, Results and Analysis 1966–2013.
 USGS Patuxent Wildlife Research Center, Laurel, MD.
 - Scholander, P. F., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950. HEAT REGULATION IN SOME ARCTIC AND TROPICAL MAMMALS AND BIRDS. The Biological Bulletin 99.
- 925 Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. Trends in Ecology and Evolution 21:464–471.
 - Skidmore, A. K., B. O. Oindo, and M. Y. Said. 2003. Biodiversity Assessment by Remote Sensing. Proceedings of the 30th International symposium on remote sensing of the environment: information for risk management and sustainable development:1–4.
- 930 Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: An experimental test of theory using tree-hole communities. American Naturalist 152:510–529.
 - Storch, D., E. Bohdalková, and J. Okie. 2018. The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. Ecology Letters 21:920–937.
- 935 Suttidate, N., M. L. Hobi, A. M. Pidgeon, P. D. Round, N. C. Coops, D. P. Helmers, N. S. Keuler, M. Dubinin, B. L. Bateman, and V. C. Radeloff. 2019. Tropical bird species richness is strongly associated with patterns of primary productivity captured by the Dynamic Habitat Indices. Remote Sensing of Environment 232:1–10.
 - Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch.
- 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. Journal of Biogeography 31:79–92.
 - Turner, W., S. Spector, N. Gardiner, M. Fladeland, E. Sterling, and M. Steininger. 2003. Remote sensing for biodiversity science and conservation. Trends in Ecology and Evolution 18:306– 314.
- Vogt, P., J. R. Ferrari, T. R. Lookingbill, R. H. Gardner, K. H. Riitters, and K. Ostapowicz.
 2009. Mapping functional connectivity. Ecological Indicators 9:64–71.

- Vogt, P., K. H. Riitters, C. Estreguil, J. Kozak, T. G. Wade, and J. D. Wickham. 2007. Mapping spatial patterns with morphological image processing. Landscape Ecology 22:171–177.
- Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday,
- and R. Parmenter. 1999. The relationship between productivity and species richness. 950 Annual Review of Ecology and Systematics 30:257–300.
 - Wilson, H. B., L. N. Joseph, A. L. Moore, and H. P. Possingham. 2011. When should we save the most endangered species? Ecology Letters 14:886-890.
 - Woiderski, B. J., N. E. Drilling, J. M. Timmer, M. F. McLaren, C. M. White, N. J. Van Lanen,
- D. C. P. Jr., and R. A. Sparks. 2018. Integrated Monitoring in Bird Conservation Regions 955 (IMBCR): 2017 Field Season Report. Bird Conservancy of the Rockies. Brighton, Colorado, USA.
 - Wood, E. M., A. M. Pidgeon, V. C. Radeloff, and N. S. Keuler. 2012. Image texture as a remotely sensed measure of vegetation structure. Remote Sensing of Environment 121:516-

960

526.

- Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. Oikos 41:496-506.
- Wulder, M. A., T. R. Loveland, D. P. Roy, C. J. Crawford, J. G. Masek, C. E. Woodcock, R. G. Allen, M. C. Anderson, A. S. Belward, W. B. Cohen, J. Dwyer, A. Erb, F. Gao, P. Griffiths,
- D. Helder, T. Hermosilla, J. D. Hipple, P. Hostert, M. J. Hughes, J. Huntington, D. M. 965 Johnson, R. Kennedy, A. Kilic, Z. Li, L. Lymburner, J. McCorkel, N. Pahlevan, T. A. Scambos, C. Schaaf, J. R. Schott, Y. Sheng, J. Storey, E. Vermote, J. Vogelmann, J. C. White, R. H. Wynne, and Z. Zhu. 2019. Current status of Landsat program, science, and applications. Remote Sensing of Environment 225:127–147.
- 970 Wulder, M. A., J. C. White, S. N. Goward, J. G. Masek, J. R. Irons, M. Herold, W. B. Cohen, T. R. Loveland, and C. E. Woodcock. 2008. Landsat continuity: Issues and opportunities for land cover monitoring. Remote Sensing of Environment 112:955–969.
- Zhang, C., D. Cai, S. Guo, Y. Guan, K. Fraedrich, Y. Nie, X. Liu, and X. Bian. 2016. Spatial-Temporal Dynamics of China 's Terrestrial Biodiversity: A Dynamic Habitat Index 975 Diagnostic. Remote Sensing 8:1–18.