

Science/Technical/Management Section

Introduction

Understanding biodiversity patterns in relation to habitat and climate is an important to determine the need for conservation planning and action. One way to understand patterns of biodiversity at regional to global scales is by pairing remotely sensed imagery and associated indices with *in situ* biodiversity data, in order to identify factors that influence biodiversity, and areas of high conservation value and their threats¹. However, remote sensing observations used to model biodiversity distributions often have coarse resolution, which may mask relevant fine scale habitat heterogeneity. For example, many bird species respond to different configurations of fine-scale habitat features such as vegetation structure, but also to broad-scale factors such as landscape composition^{2,3}. So, one question is what resolution of satellite imagery is best for which species. While organisms may respond to fine-scale habitat features and heterogeneity, the use of very high spatial resolution (<5 m) data can introduce ‘false’ heterogeneity from in-shadow pixels,⁴⁻⁶. That suggest that medium-resolution (~10-50 m) satellite data is a good compromise as a basis for biodiversity modeling, but there is wide variation in resolution among medium-resolution sensors. For example, the spatial resolution of different “Landsat-like” sensors ranges from 10 m to 160 m⁷. In a collaborative project we found that 10-m meter resolution satellite image texture measures have higher explanatory power than 30 m texture measures when predicting bird species richness in the U.S.⁸, illustrating the need to identify the spatial resolution(s) at remotely sensed products that characterize habitat, are most effective for modelling biodiversity⁹.

Further, in models, remote sensing data are often used for one point in time, and discrete in classification, thereby missing important within-class variability and temporal changes that influence species distributions. Indeed, generalized landcover classifications often do not capture key fine-scale habitat heterogeneity as well as continuous measures derived from satellite imagery¹⁰. Seasonality (temporal variability) may alter the availability or quality of key resources and can lead to shifts in habitat use or ranges^{11,12}, and at broad scales, patterns of biodiversity are determined by phenology and climate^{13,14}. Areas with higher spatial variability in phenology and climate are more likely to host high levels of species richness¹⁵⁻¹⁷. Furthermore, high spatial variability in phenology and climate may buffer against temporal variability in phenology and temperature because some populations may be able to persist during extreme events, but it is unclear how important this is. Fortunately, satellite data can offer both spatial and temporal measures of spectral variability, which can improve biodiversity modeling because organisms respond to both the spatial patterns and temporal changes within their environments.

Understanding how spatial resolution and variation in environmental characteristics affect biodiversity patterns is important for conservation planning, but without including information on human modification of the environment, conservation planning is likely ineffective. Humans historically have settled in areas of high primary productivity^{18,19}, but those areas with high primary productivity are often the areas with the highest levels of biodiversity²⁰. This coincidence between primary productivity, human population density, and species richness can result in conflicts between human development and conservation of biodiversity^{21,22}. The percentage of protected land often declines with increasing human population density and primary productivity, and protected areas that protect high levels of biodiversity and high primary productivity are typically smaller and surrounded by human populations compared to

protected areas in sparsely populated regions that protect less biodiversity and have lower primary productivity^{20,21}. As such, it is important to identify the relationships between primary productivity, human development, and biodiversity, in order to identify areas where biodiversity conservation would be most effective, and where threats to biodiversity are most severe.

The overarching goal of my proposed research is to model avian biodiversity patterns in Argentina with remotely sensed indices to aid conservation planning. More specifically I will:

Objective 1: Assess how spatial resolution of Dynamic Habitat Indices (DHIs) derived from different sensors (1km MODIS, 30m Landsat-8, and 10-20 m Sentinel-2) differ in their ability to predict bird distributions.

Objective 2: Assess how spatial (Landsat-8 LST and EVI) and temporal variability (MODIS LST and EVI) in temperature and forest phenology influence bird species distributions.

Objective 3: Identify the relationships between primary productivity, human population size, and forest bird species richness patterns in Argentina.

My research addresses the fundamental research question of NASA Earth Sciences regarding how the global Earth system is changing by describing how differences in terrestrial productivity, forest phenology, and climate variability influence patterns of bird species richness and human settlement. To do so, my research will rely heavily on NASA assets, in particular on MODIS and Landsat-8, as well as ESA's Sentinel 2 satellites, and I will advance the understanding of the patterns and drivers of bird biodiversity and inform conservation efforts in an ecologically diverse country.

Background and relationship of my proposal to ongoing projects:

Argentina is the fourth largest country in the Americas and ecologically and climatically very diverse. It spans approximately 21 to 55 degrees south, and 53 to 73 degrees west, encompassing much of the Southern Cone in South America, and is bordered by the Andes Mountains in the west and the Atlantic Ocean in the east. Ecosystems include subtropical dry and humid broadleaf forests, grasslands, and shrublands, flooded grasslands and savannas, montane grasslands and shrublands, temperate grasslands and forests, and subpolar forests. From a conservation perspective, Argentina hosts several biodiversity hotspots^{23,24}, ecoregions at risk of being lost ('crisis ecoregions')²⁵, endemic bird areas²⁶, centers of plant diversity²⁷, priority regions for global conservation ('Global 200')^{28,29}, frontier forests³⁰, and 'last of the wild' areas^{31 32}.

Argentina is a developing nation that has still vast undeveloped areas, and many areas are quite remote. However, while this is great for biodiversity, it also means that there is a lack of information which areas are most important for maintaining the country's rich biodiversity. Indeed, Argentina a national forest land use planning strategy in 2007, but little biodiversity data has been incorporated into national or provincial plans to date, with only a few provinces including biodiversity data into plans³³. That means that under the current forest land use plans, many wilderness areas are zoned so that logging and grazing are allowed, and much of the high conservation value forest is under some level of human influence³³. Recent shifts in agricultural land use in Argentina have put highly productive and fertile areas under more intense pressure for conversion to-, or intensification of- agriculture³⁴. Existing forest land use plans can be improved when biodiversity information becomes available, and provincial governments are open to utilize such data, as our team piloted successfully in one ecoregion (Yungas)³³. So, given that biodiversity is under threat, that biodiversity data is useful for enhancing land use plans, and

that biodiversity and human settlement patterns often respond to similar gradients of primary productivity, I proposed to map and study bird biodiversity using a variety of satellite data.

Approach

Objective 1: Assess how spatial resolution of Dynamic Habitat Indices (DHIs) derived from different sensors (1 km MODIS, 30 m Landsat-8, and 10-20m Sentinel-2) affects their ability to predict bird distributions.

Vegetation productivity summarized over the course of year, in the form of Dynamic Habitat Indices (DHIs)^{35,36}, provide remotely sensed indices that capture the energy available to organisms, which makes them useful for predicting biodiversity patterns both regionally³⁵⁻⁴⁷ and globally^{48,49}. There are three components of the DHIs that capture different aspects of the relationships between species richness and available energy. Cumulative annual productivity (cumulative DHI) captures the available energy in an area and areas with high cumulative DHI values have typically higher species richness. Annual minimum productivity (minimum DHI) reflects the minimum available energy in an area, and areas with high minimum DHI values typically have higher species richness. Variation DHI captures the seasonal variability in productivity, and areas with lower variation DHI values typically have higher species richness because the environment is more stable.

Until recently, DHIs have been derived from MODIS data and those DHIs have proven useful in predicting biodiversity patterns, despite their relatively coarse resolution (250 m to 1 km). However, Landsat and Sentinel-2 derived DHIs, at 30 m and 10 m resolution, respectively, may increase predictive power of biodiversity models, because these resolutions are more likely to match the resolution at which many species select habitat. Coarse resolution environmental data may mask fine scale variability that supports higher levels of biodiversity^{2,3}, however spatial resolution that is too fine can increase within-class spectral variation and introduce noise from in-shadow pixels⁴⁻⁶. As such, I propose to compare the predictive power of DHIs derived from MODIS, Landsat, and Sentinel-2 in modelling avian species richness patterns in Argentina.

I will develop DHI measures across Argentina from Sentinel-2 and Landsat-8 data. MODIS DHIs have already been calculated globally⁴⁸, and Landsat-8 DHIs are in development in my lab for the US. After calculating the three different DHI measures (cumulative, minimum, and variation) for each sensor, I will assess how well each predicts individual bird species distributions. I will create species distribution models (SDMs) for bird species in Argentina using the BIOMOD2 package in R⁵⁰, and species occurrence data obtained from GBIF from 1998-2019. I will spatially thin the occurrence data⁵¹, and identify species which there are >30 more occurrences, which I consider the minimum number required to generate species distribution models⁵²⁻⁵⁵. During preliminary data exploration I identified 89 bird species with sufficient data, and I will retrieve additional data from GBIF, or from the National Biological Data System <http://www.datosbiologicos.mincyt.gob.ar/>.

To assess the role that the resolution of the DHIs plays in species distributions, I will use the DHIs as environmental inputs in the species distribution models, along with Landsat-8 TIRS-derived relative temperature (Elsen et al. 2020) and topography. This will result in three models for each species (Sentinel-2 DHIs, Landsat-8 DHIs, MODIS DHIs). For each species I will generate 10,000 pseudo-absence points within a buffer (2 km – 1000 km) around occurrences (to prevent absence points being close to presence points), run 10-fold cross validation on eight species distribution modelling algorithms (GLM, GBM, GAM, CTA, MARS, RF, SRE, Maxent), evaluate the models based on AUC, and select the four highest ranked algorithm types

to generate one ensemble model for each species/sensor model set. After calculating the final ensemble model for each species/sensor combination, I will rank these three models by AUC and identify which model (and sensor) predicts the species distribution the best. I will calculate variable importance to see how each DHI (cumulative, variation, minimum) affects individual bird species distributions. I will identify trends in which types of birds (foraging guild, migratory strategy, body size etc.) are best predicted at which resolution. For example, I predict that distributions of altitudinal migrants should be well predicted by Sentinel-2 DHIs because they respond to fine scale heterogeneity due to topography that may not be captured in coarser resolution data ⁵⁶. Similarly, I predict that species with large home ranges, long-distance migrations, or those that are nomadic might be better predicted by Landsat-8 or MODIS DHIs because they may respond to broader landscape features.

My research for objective 1 will help assess the generalizability of Landsat-8 and Sentinel-2 derived DHIs and their usefulness for predicting species distributions. It will also identify if spatial resolution consistently influences species distribution models in the same way. Furthermore, 10-m DHIs from Sentinel-2 data will be novel. Maps of DHIs derived from both Landsat-8 and Sentinel-2 will be useful to land managers by themselves. Maps of species distributions will be useful in conservation planning, as their resolution is management- relevant. The results of objective 1 will be a quantitative evaluation of the sensitivity of a suite of DHIs derived from different sensors in explaining bird species distributions in Argentina, as well as maps of the resulting DHIs from each sensor across Argentina. I plan to submit this work to *Journal of Applied Ecology*.

Objective 2: Assess how spatial (Landsat-8 LST and EVI) and temporal variability (MODIS LST and EVI) in temperature and forest phenology influence bird species distributions.

Patterns of biodiversity at broad scales are determined by climate and phenology ^{13,14}, and understanding these patterns is important for conservation planning, especially in the face of global climate change. Areas with warmer temperatures and greater spatial variability in temperature (i.e., due to topography) generally have higher species richness ^{15,57,58}. Seasonal variation in temperature influences the phenology of vegetation ⁵⁹⁻⁶¹, and thus patterns of biodiversity that depends on vegetation ⁶¹⁻⁶³. Spatial variability in greenness means that at fine spatial scales there is asynchrony in plant phenology and plant-dependent resources ^{17,61,64}, which can increase species richness or facilitate persistence of individuals ⁶⁴. Additionally, areas of high spatial variability in temperature or phenology may be more resilient to temporal variability, and buffer populations ⁶⁴⁻⁶⁶. Conversely, areas with stable phenology or short phenological periods are at a higher risk of phenological mismatch in a climatically extreme year ^{64,65,67}.

Given the importance of variability in temperature and phenology for biodiversity, I want to understand how spatial and temporal variability in temperature and phenology affect species distributions. First, I want to assess how risk and resilience influence distributions, and second, I want to understand which measures (temporal vs. spatial heterogeneity; temperature vs. phenology) have the strongest influence on distributions. I will use measures of spatial heterogeneity in temperature and phenology derived from Landsat-8 TIRS and EVI (2013-2018), and temporal heterogeneity in temperature and phenology derived from MODIS 8-day LST and 16-day EVI (2001-2018) ⁶⁸. These measures have already been derived for the U.S. ¹¹ and Argentina ⁶⁸, but the measures derived for Argentina have not been related to biodiversity. Temporal variability is measured as the coefficient of variation of the first day of the year in

spring when EVI or LST were >25% of the annual maximum, and spatial variability was captured by the standard deviation texture measure for EVI or LST respectively ⁶⁸.

To assess how species richness patterns respond to spatial and temporal variability in temperature and phenology, I will generate species distribution models in the same way as in Objective 1, but I will include the four measures of variability as environmental inputs instead of the DHIs, resulting in one ensemble model for each species. I will calculate variable importance to see how each measure might influence species distributions. I will identify trends in which types of birds (organized by foraging guild, migratory strategy, body size etc.) are best predicted by the measures of variability. For example, I predict that non-migratory species distributions are concentrated in areas with stable phenology, and migratory species distributions in areas with variable phenology and temperature. Similarly, I predict that aerial insectivores will be concentrated in areas with stable phenology and temperature.

The results from Objective 2 will be a quantitative measure of how well a set of heterogeneity measures explains bird species distribution patterns in Argentina and will identify areas where biodiversity may be resilient to or at risk from changes in temperature or phenology. I plan to submit this work to *Remote Sensing of Environment*.

Objective 3: Identify the relationships between primary productivity, human population size, and forest bird species richness patterns in Argentina.

Humans have modified the environment for millennia and continue to do so. Globally, 1.9 million km² of undisturbed land became highly modified between 2000 and 2013 alone ⁶⁹. The effect of this modification on biodiversity is largely negative, especially at high levels of modification, but can also be beneficial at low or intermediate levels ^{70,71}. Disentangling how human disturbance is affecting biodiversity is difficult though, because human disturbance is far from a 'random treatment.' Historically, humans settled first in highly productive areas ^{18,19}, and near sources of fresh water ⁷². Water availability also limits vegetation growth ⁷³ and spatially structured gradients of environmental variation, such as annual precipitation, are strongly correlated with primary productivity, which in turn is a strong predictor of species richness ²⁰. This means that human population density, agriculture, and species richness tend to be higher where primary productivity is high ^{21,74,75}. Unfortunately, that coincidence can give a false impression that humans are beneficial for biodiversity, and it can result in conflict between development and conservation ^{21,22,70}. On top of that, protected areas are more common where primary productivity is low, simply because there is less demand for land, and areas are less disturbed ⁷⁶. Protected areas with high productivity and high species richness are smaller in size and surrounded by the highest human population densities ^{20,21}.

I will identify the relationships between primary productivity, human settlements, and bird species richness in Argentina. I will use the individual species distribution models from Objective 1 to quantify the relationship between a given species and cumulative DHI as a measure of productivity. Based on these models, I will calculate counterfactuals. I will run species distribution models for each species twice, once based on the actual cumulative DHI, once based on a counterfactual cumulative DHI value of zero. For each of the two models, I will predict species distributions, and then stack them to estimate species richness. If productivity is important for the distributions of many species, and hence for bird richness, then the difference in richness based on actual versus counterfactual cumulative DHI will be large. This will be a first indication of the relationship of productivity and richness, but there is the caveat that actual cumulative DHI values are affected by human settlements. To address this, I will model potential

natural cumulative DHI, based on climate, topography, soils and cumulative DHI values for natural areas make predictions for human-modified areas. Based on the potential natural cumulative DHIs, I will then run my species distribution models a third time, thereby quantifying how much human modification of areas with naturally high productivity has affected richness and identifying areas where human settlements and bird species richness respond strongly to primary productivity. These areas are likely under a greater threat of biodiversity loss compared to areas with lower human pressure because human development permanently alters the landscape and negatively affects biodiversity ⁷⁸, highly productive areas are well suited for agriculture ^{21,75}, and they are under even more pressure as populations shift away from rural, low human density areas to urban, high human density areas ⁷⁹.

The results of Objective 3 will be quantification of the relationship between primary productivity, human settlement patterns, and bird species richness in Argentina, and I will identify areas of high ‘risk’ (i.e., large human population and high biodiversity) and produce maps indicating these areas. This will help inform land use plans and biodiversity conservation efforts in Argentina. I plan to submit this work to *Conservation Biology*.

Overall Significance

Biodiversity conservation and land use plans are most effective when based on accurate assessments of biodiversity patterns. Using remotely sensed variables can greatly enhance biodiversity assessments and make them more accurate. By creating biodiversity assessments with higher spatial resolution data, I will create better datasets for regional planners because 1) coarse resolution data may mask important fine scale habitat features, and 2) resulting maps will be at a finer spatial resolution (10-30 m) than those generated from 1 km MODIS data. Another way I will improve biodiversity assessments is by using data on variation in temperature and phenology. This can help identify species or areas that are at risk or resilient to climate change. Finally, conservation actions may be ineffective if they don’t account for human development. Unfortunately, human development and high levels of biodiversity are often in the same places, i.e., where primary productivity is high. I will use remotely sensed measures of primary productivity, in combination with information about species richness, and human population density or human development to identify areas where there may be conflict between conservation and human development.

Timeline of research

Task	2021				2022				2023				2024		
	Q 1	Q 2	Q 3	Q 4	Q 1	Q 2	Q 3	Q 4	Q 1	Q 2	Q 3	Q 4	Q 1	Q 2	Q 3
Derive DHIs Obj. 1															
Analysis Obj. 1															
Analysis Obj. 2															
Data/SDMs Obj. 2															
Analysis Obj. 3															
Submission of paper															

References

1. Turner, W. Sensing biodiversity. *Science* (80-.). **346**, 301–302 (2014).
2. Wood, E. M., Pidgeon, A. M., Radeloff, V. C. & Keuler, N. S. Image Texture Predicts Avian Density and Species Richness. *PLoS One* **8**, (2013).
3. Sheeren, D., Bonthoux, S. & Balent, G. Modeling bird communities using unclassified remote sensing imagery: Effects of the spatial resolution and data period. *Ecol. Indic.* **43**, 69–82 (2014).
4. Rocchini, D. *et al.* Remotely sensed spectral heterogeneity as a proxy of species diversity: Recent advances and open challenges. *Ecol. Inform.* **5**, 318–329 (2010).
5. Nagendra, H. & Rocchini, D. High resolution satellite imagery for tropical biodiversity studies: The devil is in the detail. *Biodivers. Conserv.* **17**, 3431–3442 (2008).
6. Stickler, C. M. & Southworth, J. Application of multi-scale spatial and spectral analysis for predicting primate occurrence and habitat associations in Kibale National Park, Uganda. *Remote Sens. Environ.* **112**, 2170–2186 (2008).
7. Powell, S. L., Pflugmacher, D., Kirschbaum, A. A., Kim, Y. & Cohen, W. B. Moderate resolution remote sensing alternatives: a review of Landsat-like sensors and their applications. *J. Appl. Remote Sens.* **1**, 012506 (2007).
8. Farwell, L. S. *et al.* Satellite image texture captures vegetation heterogeneity and explains patterns of bird richness. *Remote Sens. Environ.* **253**, 112175 (2020).
9. Bar-Massada, A., Wood, E. M., Pidgeon, A. M. & Radeloff, V. C. Complex effects of scale on the relationships of landscape pattern versus avian species richness and community structure in a woodland savanna mosaic. *Ecography (Cop.)*. **35**, 393–411 (2012).
10. Oeser, J. *et al.* Habitat metrics based on multi-temporal Landsat imagery for mapping large mammal habitat. *Remote Sens. Ecol. Conserv.* 1–18 (2019) doi:10.1002/rse2.122.
11. Elsen, P. R., Farwell, L. S., Pidgeon, A. M. & Radeloff, V. C. Landsat 8 TIRS-derived relative temperature and thermal heterogeneity predict winter bird species richness patterns across the conterminous United States. *Remote Sens. Environ.* **236**, (2020).
12. Elsen, P. R., Kalyanaraman, R., Ramesh, K. & Wilcove, D. S. The importance of agricultural lands for Himalayan birds in winter. *Conserv. Biol.* **31**, 416–426 (2017).
13. Jetz, W. *et al.* Essential biodiversity variables for mapping and monitoring species populations. *Nat. Ecol. Evol.* **3**, 539–551 (2019).
14. Pereira, H. M. *et al.* Scenarios for global biodiversity in the 21st century. *Science* (80-.). **330**, 1496–1501 (2010).
15. Sears, M. W., Raskin, E. & Angilletta, M. J. The world is not flat: Defining relevant thermal landscapes in the context of climate change. *Integr. Comp. Biol.* **51**, 666–675 (2011).
16. Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E. & Evans, T. A. Microhabitats reduce animal’s exposure to climate extremes. *Glob. Chang. Biol.* **20**, 495–503 (2014).
17. Farwell, L. S., Elsen, P. R., Razenkova, E., Pidgeon, A. M. & Radeloff, V. C. Habitat heterogeneity captured by 30-m resolution satellite image texture predicts bird richness across the United States. *Ecol. Appl.* **30**, (2020).
18. Faeth, S. H., Bang, C. & Saari, S. Urban biodiversity: Patterns and mechanisms. *Ann. N. Y. Acad. Sci.* **1223**, 69–81 (2011).

19. Kühn, I., Brandl, R. & Klotz, S. The flora of German cities is naturally species rich. *Evol. Ecol. Res.* **6**, 749–764 (2004).
20. Chown, S. L., van Rensburg, B. J., Gaston, K. J., Rodrigues, A. S. L. & van Jaarsveld, A. S. Energy, Species Richness, and Human Population Size : Conservation Implications at a National Scale. *Ecol. Appl.* **13**, 1233–1241 (2003).
21. Luck, G. W. The relationships between net primary productivity, human population density and species conservation. *J. Biogeogr.* **34**, 201–212 (2007).
22. Balmford, A. *et al.* Conservation conflicts across Africa. *Science (80-.)*. **291**, 2616–2619 (2001).
23. Myers, N., Mittermeyer, R. A., Mittermeyer, C. G., Da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
24. Mittermeyer, R. A. *et al.* *Hotspots Revisited. Journal of Chemical Information and Modeling* (CEMEX, 2004).
25. Hoekstra, J. M., Boucher, T. M., Ricketts, T. H. & Roberts, C. Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecol. Lett.* **8**, 23–29 (2005).
26. Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. *Endemic Bird Areas of the World. Priorities for biodiversity conservation.* (BirdLife International, 1998).
27. Davis, S. D. & Heywood, V. *Centres of Plant Diversity: a guide and strategy for their conservation, v.3. Americas.* (IUCN and WWF, 1997).
28. Olson, D. M. & Dinerstein, E. The global 200: A representation approach to conserving the earth's most biologically valuable ecoregions. *Conserv. Biol.* **12**, 502–515 (1998).
29. Olson, D. M. & Dinerstein, E. The Global 200: Priority Ecoregions for Global Conservation. *Ann. Missouri Bot. Gard.* **89**, 199–224 (2002).
30. Bryant, D., Nielsen, D. & Tangle, L. *Last Frontier Forests: Ecosystems and Economies on the Edge. Frontiers: A Journal of Women Studies* (1997).
31. Sanderson, E. W. *et al.* The human footprint and the last of the wild. *Bioscience* **52**, 891–904 (2002).
32. Brooks, T. M. *et al.* Global biodiversity conservation priorities. *Science (80-.)*. **313**, 58–61 (2006).
33. Martinuzzi, S. *et al.* Enhancing biodiversity conservation in existing land-use plans with widely available datasets and spatial analysis techniques. *Environ. Conserv.* **45**, 252–260 (2018).
34. Izquierdo, A. E. & Grau, H. R. Agriculture adjustment, land-use transition and protected areas in Northwestern Argentina. *J. Environ. Manage.* **90**, 858–865 (2009).
35. Berry, S., Mackey, B. & Brown, T. Potential applications of remotely sensed vegetation greenness to habitat analysis and the conservation of dispersive fauna. *Pacific Conserv. Biol.* **13**, (2007).
36. Mackey, B. ., Bryan, J. & Randall, L. Australia's dynamic habitat template 2003. in *MODIS Vegetation Workshop II* (2004).
37. Michaud, J. S. *et al.* Estimating moose (*Alces alces*) occurrence and abundance from remotely derived environmental indicators. *Remote Sens. Environ.* **152**, 190–201 (2014).
38. Suttidate, N. *et al.* Tropical bird species richness is strongly associated with patterns of primary productivity captured by the Dynamic Habitat Indices. *Remote Sens. Environ.* **232**, 111306 (2019).
39. Zhang, C. *et al.* Spatial-temporal dynamics of China's terrestrial biodiversity: A dynamic habitat index diagnostic. *Remote Sens.* **8**, 7–9 (2016).

40. Andrew, M. E., Wulder, M. A., Coops, N. C. & Baillargeon, G. Beta-diversity gradients of butterflies along productivity axes. *Glob. Ecol. Biogeogr.* **21**, 352–364 (2012).
41. Bonthoux, S., Lefèvre, S., Herrault, P. A. & Sheeren, D. Spatial and temporal dependency of NDVI satellite imagery in predicting bird diversity over France. *Remote Sens.* **10**, 1–22 (2018).
42. Coops, N. C., Waring, R. H., Wulder, M. A., Pidgeon, A. M. & Radeloff, V. C. Bird diversity: A predictable function of satellite-derived estimates of seasonal variation in canopy light absorbance across the United States. *J. Biogeogr.* **36**, 905–918 (2009).
43. Coops, N. C., Wulder, M. A., Duro, D. C., Han, T. & Berry, S. The development of a Canadian dynamic habitat index using multi-temporal satellite estimates of canopy light absorbance. *Ecol. Indic.* **8**, 754–766 (2008).
44. Coops, N. C., Wulder, M. A. & Iwanicka, D. Exploring the relative importance of satellite-derived descriptors of production, topography and land cover for predicting breeding bird species richness over Ontario, Canada. *Remote Sens. Environ.* **113**, 668–679 (2009).
45. Hobi, M. L. *et al.* A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness. *Remote Sens. Environ.* **195**, 142–152 (2017).
46. Holmes, K. R., Nelson, T. A., Coops, N. C. & Wulder, M. A. Biodiversity indicators show climate change will alter vegetation in parks and protected areas. *Diversity* **5**, 352–373 (2013).
47. Michaud, J. S., Coops, N. C., Andrew, M. E. & Wulder, M. A. Characterising spatiotemporal environmental and natural variation using a dynamic habitat index throughout the province of Ontario. *Ecol. Indic.* **18**, 303–311 (2012).
48. Radeloff, V. C. *et al.* The Dynamic Habitat Indices (DHIs) from MODIS and global biodiversity. *Remote Sens. Environ.* **222**, 204–214 (2019).
49. Coops, N. C., Kearney, S. P., Bolton, D. K. & Radeloff, V. C. Remotely-sensed productivity clusters capture global biodiversity patterns. *Sci. Rep.* **8**, 1–12 (2018).
50. Thuiller, W., Georges, D., Engler, R. & Breiner, F. biomod2: Ensemble Platform for Species Distribution Modeling. (2020).
51. Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B. & Anderson, R. P. spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography (Cop.)*. **38**, 541–545 (2015).
52. Mateo, R. G., Felicísimo, Á. M. & Muñoz, J. Effects of the number of presences on reliability and stability of MARS species distribution models: The importance of regional niche variation and ecological heterogeneity. *J. Veg. Sci.* **21**, 908–922 (2010).
53. van Proosdij, A. S. J., Sosef, M. S. M., Wieringa, J. J. & Raes, N. Minimum required number of specimen records to develop accurate species distribution models. *Ecography (Cop.)*. **39**, 542–552 (2016).
54. Soultan, A. & Safi, K. The interplay of various sources of noise on reliability of species distribution models hinges on ecological specialisation. *PLoS One* **12**, 1–19 (2017).
55. Støa, B., Halvorsen, R., Stokland, J. N. & Gusarov, V. I. How much is enough? Influence of number of presence observations on the performance of species distribution models. *Sommerfeltia* **39**, 1–28 (2019).
56. Malizia, L. R. Seasonal Fluctuations of Birds, Fruits, and Flowers in a Subtropical Forest of Argentina. *Condor* **103**, 45 (2001).

57. Rangel, T. F. *et al.* Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. *Science* (80-.). **361**, (2018).
58. Howard, C., Flather, C. H. & Stephens, P. A. What drives at-risk species richness? Environmental factors are more influential than anthropogenic factors or biological traits. *Conserv. Lett.* **12**, 1–9 (2018).
59. Fu, Y. H. *et al.* Three times greater weight of daytime than of night-time temperature on leaf unfolding phenology in temperate trees. *New Phytol.* **212**, 590–597 (2016).
60. Piao, S. *et al.* Plant phenology and global climate change: Current progresses and challenges. *Glob. Chang. Biol.* **25**, 1922–1940 (2019).
61. Persche, M. E. & Pidgeon, A. M. Habitat resilience for songbirds: The role of topographic position in a mixed deciduous forest. *For. Ecol. Manage.* **472**, 118238 (2020).
62. La Sorte, F. A., Fink, D., Hochachka, W. M., DeLong, J. P. & Kelling, S. Spring phenology of ecological productivity contributes to the use of looped migration strategies by birds. *Proc. R. Soc. B Biol. Sci.* **281**, (2014).
63. Chuine, I. Why does phenology drive species distribution? *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 3149–3160 (2010).
64. Oliver, T. H. *et al.* Biodiversity and Resilience of Ecosystem Functions. *Trends Ecol. Evol.* **30**, 673–684 (2015).
65. Robinson, N. M., Leonard, S. W. J., Bennett, A. F. & Clarke, M. F. Are forest gullies refuges for birds when burnt? The value of topographical heterogeneity to avian diversity in a fire-prone landscape. *Biol. Conserv.* **200**, 1–7 (2016).
66. Keppel, G. *et al.* Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Glob. Ecol. Biogeogr.* **21**, 393–404 (2012).
67. Malika, V. S., Lindsey, G. & Katherine, J. W. How does spatial heterogeneity influence resilience to climatic changes? Ecological dynamics in southeast Madagascar. *Ecol. Monogr.* **79**, 557–574 (2009).
68. Silveira, E. M. O. *et al.* Spatio-temporal remotely sensed indices identify areas of potential risk from resilience to climate variability. *Remote Sens. Environ.*
69. Williams, B. A. *et al.* Change in Terrestrial Human Footprint Drives Continued Loss of Intact Ecosystems. *One Earth* **3**, 371–382 (2020).
70. Pidgeon, A. M. *et al.* Systematic temporal patterns in the relationship between housing development and forest bird biodiversity. *Conserv. Biol.* **28**, 1291–1301 (2014).
71. Pal, M., Pop, P., Mahapatra, A., Bhagat, R. & Hore, U. Diversity and structure of bird assemblages along urban-rural gradient in Kolkata, India. *Urban For. Urban Green.* **38**, 84–96 (2019).
72. Kummu, M., de Moel, H., Ward, P. J. & Varis, O. How close do we live to water? a global analysis of population distance to freshwater bodies. *PLoS One* **6**, (2011).
73. Nemani, R. R. *et al.* Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* (80-.). **300**, 1560–1563 (2003).
74. Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E. & Hope, D. From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* (2006) doi:10.1016/j.tree.2005.11.019.
75. Luck, G. W., Smallbone, L., McDonald, S. & Duffy, D. What drives the positive correlation between human population density and bird species richness in Australia? *Glob. Ecol. Biogeogr.* **19**, 673–683 (2010).
76. Joppa, L. N. & Pfaff, A. High and far: Biases in the location of protected areas. *PLoS One*