DENVar: A global Dynamic Estimate of NDVI Variance

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1 Abstract

Since the 1980s, remote-sensing estimates of habitat productivity such as the Normalized Differnece Vegetation Index (NDVI) have helped develop and support a variety of hypotheses and inform policy and industriy-related decisions. The free availability of such data has allowed widespread access and use of well-established metrics of habitat productivity. However, historically, users tended to focus solely on (predictable) trends in productivity. In recent years, people have been recognizing the importance of envrironmental unpredictability (stochasticity), particularly as climate change and human-induced rapid environmental change transform the ecosystems species have evolved in and adapted to. We adress this gap by presenting a new global Dynamic Estimate of NDVI Variance, *DENVar*. We estimate spatiotemporal trends in mean NDVI and the variance around the mean using Hierarchical Generalized Additive Models, which provide a flexible yet transparent model structure, unlike machine learning approaches such as neural netwoks. We show that DENVar can be used as a reliable proxy of environmental stochasticity, strongly correlates with **XXX**, and can be used to test many hepotheses related to environmental stochasitcity, such as forage stochasticity, regime shifts, ... We conclude by offering some considerations around quantifying and interpreting envirnomental stochasticity, and we provide a publicly and freely available shiny app for estimating mean NDVI and the variance around it, DENVar, for given coordinates and optional dates. The app requires no knowledge of statistics or coding. Additionally, we provide a temporally static raster of mean NDVI and DENVar for the years 1981-2025 that can be used for GIS applications and does not require any knowledge of `R`.

Introduction

Developments in remote sensing since the 1970s have greatly expanded our ability to quantify and monitor landscapes using satellite imagery

- NDVI is an estimate of greenness, NPP, forage availability
- NDVI has many uses and is often convenient because it's free, well-established, and

many people focus on changes in the mean

ability to predict and respond to changes in mean conditions (forage availability, phenology, etc.) depends on the scale of changes relative to the perception scale (Levin, 1992; Frankham & Brook, 2004; Riotte-Lambert & Matthiopoulos, 2020; Steixner-Kumar & Gläscher, 2020) and memory (Abrahms *et al.*, 2019). Consequently, environmental stochasticity is also an important driver, besides changes in the mean (Mezzini *et al.*, 2025)

- variance is hard to calculate, as it depends on a correct estimate of the mean
- paper on estimating the asymptote of environmental variance globally, but variance for a closed system must converge towards a finite value (Bachmaier & Backes, 2011; Fleming *et al.*, 2014)

- we present DENVar
- HGAMs are higly flexible models that allow us to estimate trends in the data without imposing preconceived expectations
- more transparent than black-box machine learning methods like neural networks, etc.
- https://www.sciencedirect.com/science/article/abs/pii/S0034425718305625
- https://silvis.forest.wisc.edu/data/dhis/
- we provide global rasters of the mean and variance in NDVI, averaged across 1981-2025
- we provide a shiny app for people to calculate mean and variance without any knowledge of `R`

Methods

Choice of color schemes

We represent NDVI using a modified version of Fabio Crameri's divergent *bukavu* palette (Crameri, 2018; Crameri, Shephard & Heron, 2020), which has high-contrast for deuteranope and protanope vision. For NDVI values between 0 and 1 (the right half of the palette), the colors also have sufficient contrast for the colors to be distinguishable by both tritanope and achomatic vision. Appendix A contains an approximate representation of the color palette for each vision type. We obtained all color palettes from the `khroma` package (v. 1.14.0, Frerebeau, 2024) for `R` (v. 4.4.1, R Core Team, 2024).

Input data

We obtained NDVI data using the image composites from the AVHRR and VIIRS sensors (Vermote & NOAA CDR Program, 2018, 2022). The code for downloading the data directly from the NOAA server is available at https://github.com/QuantitativeEcologyLab/ndvi-stochasticity/blob/main/analysis/002-download-ndvi-rasters.R. The number of non-NA land raster cells was substantially larger than the maximum data frame size in `R` ($2.28 \times 10^{10} > 2^{31} - 1 \approx 0.21 \times 10^{10}$), so we reduced the dataset size by calculating 15-day averages of NDVI (see Fig. A2) and aggregating the averaged rasters by a factor of 2×2 with `terra::aggregate(fact = 2)`. Although this resulted in a reduction in sample size, the temporal averaging also reduced signal-related noise.

The predictor data for the models included: WWF biome (Olson & Dinerstein, 2002, see Fig. A3), ecoregion (the individual polygons from Olson & Dinerstein, 2002, see Fig. A4), integer day of year (1 to 366), integer year (1981 to 2025), and elevation above sea level (Fig. A5). We excluded all polygons that did not have any NDVI data (0.06% of land, 29% of the polygons, maximum area: $452 \text{ km}^2 \approx (21 \text{ km})^2$). We distinguished between biomes in the northern and southern hemisphere to allow for different seasonal trends between hemispheres.

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71 The 15-day averages allowed us to have non-repeating values of day of year across years, since

72 15 is not a factor of 365 or 366. We downloaded the global digital elevation model using

73 the `get_elev_raster()` function from the `elevatr` package for R (v. 0.99.0, Hollister *et al.*,

74 2023) with a resolution of 0.076 degrees.

Modeling

76   We estimated spatiotemporal trends in mean NDVI using Hierarchical Generalized Ad-

77 ditive Models (HGAMs) via the `mgcv` package for R (v. 1.9-3, Wood, 2017). To reduce

78 modeling fitting times with negligible losses to model accuracy, we used the `bam()` function

79 with fast REstricted Marginal Likelihood (`method = fREML`) and covariate discretization

80 (`discrete = TRUE`). See Wood, Goude & Shaw (2015) and Wood *et al.* (2017) for more

81 information. Ideally, NDVI should be modeled using beta location-scale models (after the

82 linear transformation $Y^* = \frac{Y+1}{2}$) to account for the fact that: (1) NDVI is bounded between

83 -1 and 1, and (2) the variance in NDVI is dependent on the mean (and vice-versa), since

84 ecosystems with very low NDVI (e.g., rock, ice, or concrete) or very high NDVI (e.g., dense

85 forest) tend to have lower variance in NDVI. However, preliminary tests showed that fitting

86 times for beta models were prohibitive, especially for beta location-scale models. In contrast,

87 Gaussian models fit substantially faster and provided very similar spatialtemporal estimates

88 of mean NDVI (see the `analysis/000-sardinia-test.R` script in the GitHub repository).

89 The global model for the mean NDVI had the structure below:

```
m_mean <- bam(
  ndvi_15_day_mean ~
    biome + # to avoid intercept shrinkage
    s(poly_id, bs = 'mrf', xt = list(nb = nbs)) +
    s(doy, biome, bs = 'fs', xt = list(bs = 'cc'), k = 10) +
    s(year, biome, bs = 'fs', xt = list(bs = 'cr'), k = 10) +
    ti(doy, year, biome, bs = c('cc', 'cr', 're'), k = c(5, 5)) +
    s(elevation_m, bs = 'cr', k = 5),
  family = gaussian(),
  data = d,
  method = 'fREML',
```

```
    knots = list(doy = c(0.5, 366.5)),
    drop.unused.levels = TRUE,
    discrete = TRUE,
    samfrac = 0.001, # find initial guesses with a subset of the data
    nthreads = future::availableCores(logical = FALSE) - 2,
    control = gam.control(trace = TRUE))
```

₉₀ Biome-specific fixed-effect intercepts allowed to account for the differences in mean NDVI

₉₁ throught biomes without coefficient shrinkage (i.e., reversion towards the global mean). A

₉₂ Markov Random Field of the ecoregions (`bs = mrf`, see page *240?* of Wood, 2017) estimated

₉₃ smoothed, ecoregion-specific deviations from the biome-level spatial means. Two factor-

₉₄ smooth interaction terms (`bs = 'fs'`) accounted for biome-specific seasonal and yearly

₉₅ trends. Seasonal terms were made cyclical by using cyclical cubic splines (`xt = list(bs`

₉₆ `= 'cc')`), which are continuous up to and including second derivative at the edge knots

₉₇ (0.5 and 366.5, which correspond to 00:00 of January 1st and 24:00 of December 31st, respec-

₉₈ tively). A tensor product interaction smooth for each biome estimated the change in seasonal

₉₉ trends over the years. Finally, a smooth of elevation above sea level accounted for the effect

₁₀₀ of altitude. See Pedersen *et al.* (2019) for more information on hierarchical modeling and

₁₀₁ the use and interpretation of factor smooth interaction terms.

₁₀₂ *will we subtract the average residual from each pixel?*

₁₀₃ A second HGAM estimated the variance in NDVI around the mean estimated by the

₁₀₄ model above. The model had an identical structure to the model for the mean, with the

₁₀₅ exception that (1) the response variable was the squared residual from the first model, such

₁₀₆ that the model estimated the mean squared residual (i.e., the variance) for a given point in

₁₀₇ time and space, and (2) a smooth term of the estimated mean NDVI. The model is available

₁₀₈ below:

```
#' *CHANGE TO SOS BASIS*
m_var <- bam(
  e_2 ~
    biome +
    s(poly_id, bs = 'mrf', xt = list(nb = nbs)) +
    s(doy, biome, bs = 'fs', xt = list(bs = 'cc'), k = 10) +
    s(year, biome, bs = 'fs', xt = list(bs = 'cr'), k = 10) +
    ti(doy, year, biome, bs = c('cc', 'cr', 're'), k = c(5, 5)) +
```

```
   s(elevation_m, bs = 'cr', k = 5) +
   s(mu_hat, bs = 'cr', k = 5),
family = gaussian(),
data = d,
method = 'fREML',
knots = list(doy = c(0.5, 366.5)),
drop.unused.levels = TRUE,
discrete = TRUE,
samfrac = 0.001,
nthreads = future::availableCores(logical = FALSE) - 2,
control = gam.control(trace = TRUE))
```

Results

General results

- two Orthographic projections of DENVar: Northern and southern hemispheres on spring solstice

Correlations with other metrics

- temperature
- seasonal temperature range
- precip
- seasonal temperature range
- spp diversity
- gross primary productivity
- max animal weight
- https://silvis.forest.wisc.edu/globalwui/
- https://silvis.forest.wisc.edu/data/dhis/: NDVI16 (Normalized Difference Vegetation Index), EVI16 (Enhanced Vegetation Index), FPAR8 (Fraction absorbed Photosynthetically Active Radiation), LAI8 (Leaf Area Index), GPP8 (Gross Primary Productivity)
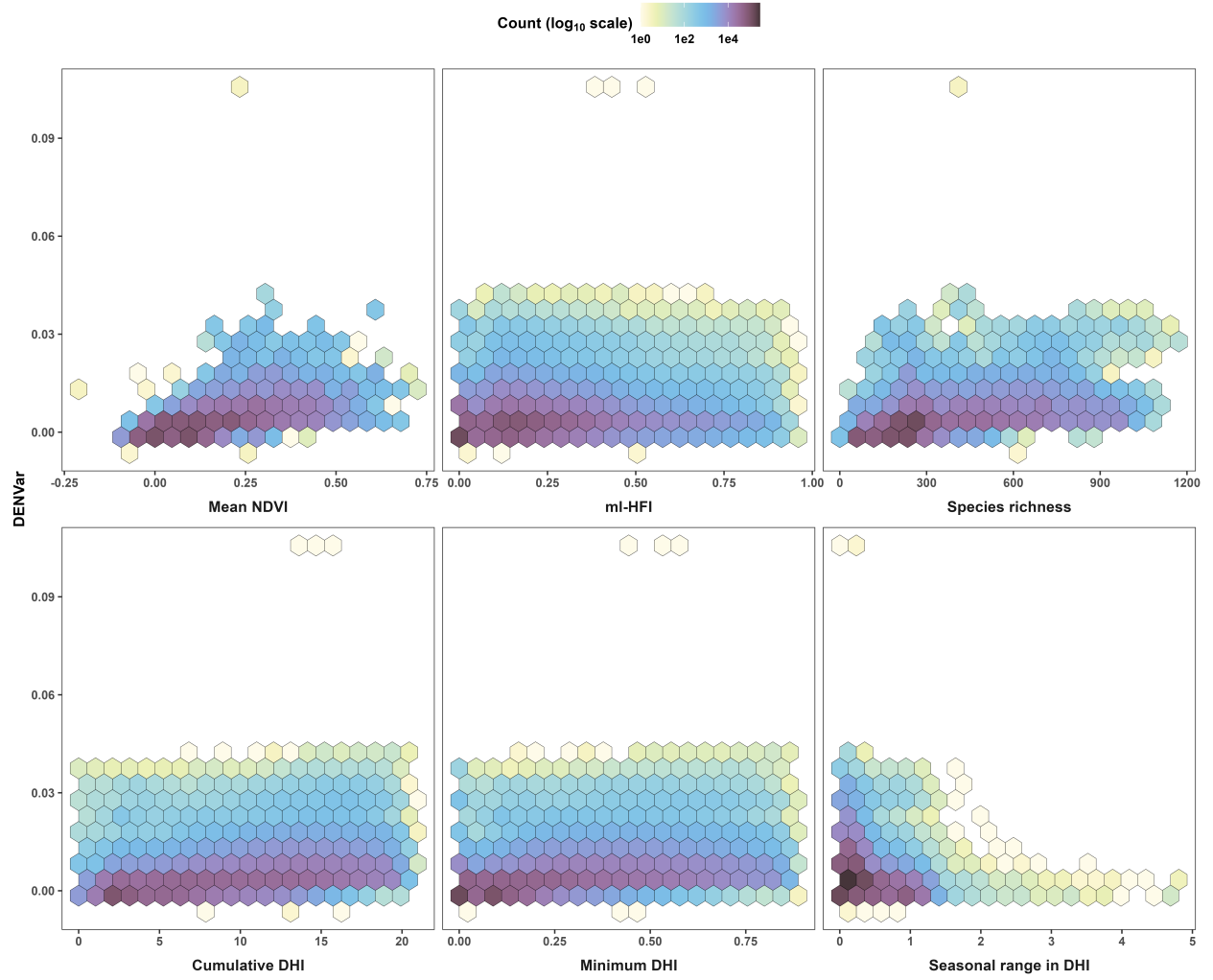
8

Figure 1: Hex plots of the relationship between the global Dynamic Estimate of NDVI Variance (DENVar) and common ecological metrics. The fill of the hexagonal cells represents the log-transformed number of points within the cell. (A) Mean NDVI (as estimated in this manuscript); (B) the machine-learning Human Footprint Index of Keys, Barnes & Carter (2021); (C-E) the 2015 cumulative, minimum, and seasonal range in the Dynamic Habitat Index of XXX, (F).

₁₂₆ **How to obtain the data**

₁₂₇ **Static rasters of mean and variance (1981-2025)**

₁₂₈ • for GIS users (tif)

₁₂₉ **Shiny app for obtaining values**

₁₃₀ • get values for specific coordinates: 1981-2025 average

₁₃₁ • get values for specific coordinates and dates (upload as a CSV, download as a CSV)

₁₃₂ • screenshot of the shiny app

₁₃₃ Discussion

₁₃₄ We have presented a new spatiotemporally dynamic metric of environmental stochasticity,
₁₃₅ which we have called the Dynamic Estimate of NDVI Variance, DENVar. In this section,
₁₃₆ we discuss the interpretation of DENVar in greater depth, and we argue the advantages and
₁₃₇ limitations of the statistical methods used. We conclude by suggsting some use cases of
₁₃₈ DENVar within animal movement ecology, landscape ecology, and phenology, but we invite
₁₃₉ readers to consider how DENVar may be of use in their field and adjacent disciplines.

₁₄₀ **Why use complicated statistics instead of machine learning?**

₁₄₁ Admittedly, the title of this section is misleading for two reasons. Firstly, some may argue
₁₄₂ that Generalized Additive Models are a form of machine-learning (here abbreviated as ML),
₁₄₃ but we intend to contrast GAMs with more "black-box" types of machine learning, such as
₁₄₄ neural networks and random forests. The second reason for which the title is misleading is
₁₄₅ that it implies that machine learning is not complicated, or at least that it is less compli-
₁₄₆ cated than the models we used. However, we argue that while traditional statistical models
₁₄₇ may seem more intimidating to some, their complexity is what allows analysts to produce
₁₄₈ interpretable results and measures of uncertainty (Wood, 2017). And while the theoretical

₁₀

basis for GAMs can discouraging for those who do not a strong background in mathematics or statistics, outputs from GAMs can be presented in an accessible manner even to those without a strong quantitative background through the use of well-designed figures, especially in a Bayesian context (when the aim is to estimate a parameter). In contrast, while ML methods will often give understandable results, it may not be possible to discern *why* such results were "chosen" by the model. Instead, GAMs produce flexible yet interpretable estimated effects that can be represented with relatively simple figures, even if the mathematical formula(e) for the model may be complicated.

Ideally, a model should estimate or explore the relationships among variables such that results can be interpreted in a transparent and unambiguous manner, such that readers can scrutinize the underlying assumptions, methods, and decisions. We recognize that the assessing GAMs requires a certain level of expertise, but we hope the readers can appreciate the option to assess the GAMs more easily than a series of consecutive, weighted regressions (as in the case of neural networks). In contrast, GAMs learn from data with no initial starting assumptions other than user-imposed limitations of wiggliness, which are clearly outlined in each basis size of the models' terms. The structure and wuggliness of GAMS can thus be grossly designed based on the system's complexity and structure while allowing the data to inform the model trends, wiggliness, and coefficient size.

Interpreting DENVar: the importance of scale

- smoothness of mean impacts smoothness and size of variance: depends on scale of interest (e.g., animals' ability to respond to, learn, and predict changes in the mean). Changes not attributed to trends in the mean are stochastic

- DENVar is a good metric as long as the spatiotemporal scale of interest is similar or larger to that of DENVar. May not work well for small-scale processes such as the movement dynamics of a small rodent, the phenology of a small orchard when spatiotemporal heterogeneity is finer than DENVar's resolution

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Environmental stochasticity and animal movement ecology

The field of animal movement ecology has long shown that animals alter their movement in response to resource abundance or availability (Burt, 1943; Charnov, 1976; Southwood, 1977; Broekman *et al.*, 2024). More recently, movement ecologists have started focusing more on resource stochasticity (e.g., Stephens & Charnov, 1982; Rizzuto *et al.*, 2021), but it is worth distinguishing between resource stochasticity and seasonality (Nilsen, Herfindal & Linnell, 2005). Seasonality is generally best interpreted as a cyclical change in the mean that many animals can learn to predict, as in the case of green-wave surfing (Middleton *et al.*, 2018; Geremia *et al.*, 2019). In contrast, environmental stochasticity refers to unpredictable changes, such as forest fires (**ref?**), sudden snow storms (Aikens *et al.*, 2025), and unusual phenology (**ref?**). Animals also respond to stochastic changes (Mezzini *et al.*, 2025), but their ability to adapt depends on behavioral plasticity (Rickbeil *et al.*, 2019; Steixner-Kumar & Gläscher, 2020), and memory (Polansky, Kilian & Wittemyer, 2015; Abrahms *et al.*, 2019; Riotte-Lambert & Matthiopoulos, 2020; Falcón-Cortés *et al.*, 2021; Ranc, Cagnacci & Moorcroft, 2022).

Botero *et al.* (2015) tipping points

Polazzo *et al.* (2024)

extreme events, black swans (Logares & Nuñez, 2012; Anderson *et al.*, 2017)

- migration routes are key habitat (Ortega et al., in prep), especially in stochastic environments
- can fail to adapt to changes in conditions Sawyer *et al.* (2019)
- https://www.sciencedirect.com/science/article/pii/S0960982220308484
- https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.15169
- industrial development affects animals' ability to respond to both predictable and unpredictable change (https://www.nature.com/articles/s41559-022-01887-9)
- effects of sudden deep snow in red desert on proghorn (https://www.sciencedirect.com/

201 science/article/abs/pii/S0960982225002957)

202 - https://www.nature.com/articles/s41467-023-37750-z

203 - https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.4238

204 - detecting regime shifts (in lakes: Bjorndahl *et al.*, 2022)

Environmental stochasticity and population dynamics

read Lande (1993)

Environmental stochasticity reduces habitats' energetic balance and carrying capacity (Chevin, Lande & Mace, 2010) as individuals struggle to rely on unpredictable resources and increase the instability of populations and communities (Lande, 1993). Additionally, stochastic environments reduce the ability of specialist species to adapt and evolve while selecting for more generalist species (Levins, 1974). Consequently, stochastic environments tend to have lower species diversity (**marcus?**).

Environmental stochasticity and fire ecology

Recent work by (**devries?**) has suggested that NDVI stochasticity is an important metric for evaluating forest recovery after large fires, while (**collinson?**) has suggested that variance in NDVI is an important predictor of the occurrence of forest fires due to ignition by lightning.

Environmental stochasticity and phenology

- Jonzén *et al.* (2006)

- effects can be compounded by cumulative effects (e.g., loss of species diversity, see Wolf, Zavaleta & Selmants (2017))

- climate change affects plant phenology, but changes in situ may not match experimental estimates (Wolkovich *et al.*, 2012)

- reproduction of painted lady butterfly (Stefanescu, Ubach & Wiklund, 2021)

- Wessling *et al.* (2018)

Useful references

- Keith *et al.* (2008)
- Chevin *et al.* (2010)
- Rickbeil *et al.* (2019)
- Mueller *et al.* (2008)
- Pettorelli *et al.* (2005)
- Keys, Barnes & Carter (2021)
- Nilsen *et al.* (2005)
- Merkle *et al.* (2016)
- Tian *et al.* (2015)
- Huang *et al.* (2021)
- Fan & Liu (2016)
- Wang *et al.* (2019)
- Pease (2024)
- Xu *et al.* (2021)
- Mezzini *et al.* (2025)

TO READ: * Site fidelity as a maladaptive behavior in the Anthropocene: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/fee.2456 * Pettorelli N., Vik J.O., Mysterud A., Gaillard J.-M., Tucker C.J. & Stenseth N.Chr. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20, 503–510. https://doi.org/10.1016/j.tree.2005.05.011

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References

Abrahms B., Hazen E.L., Aikens E.O., Savoca M.S., Goldbogen J.A., Bograd S.J., *et al.* (2019). Memory and resource tracking drive blue whale migrations. *Proceedings of the National Academy of Sciences* **116**, 5582–5587. https://doi.org/10.1073/pnas.1819031116

Aikens E.O., Merkle J.A., Xu W. & Sawyer H. (2025). Pronghorn movements and mortality during extreme weather highlight the critical importance of connectivity. *Current Biology* **35**, 1927–1934.e2. https://doi.org/10.1016/j.cub.2025.03.010

Anderson S.C., Branch T.A., Cooper A.B. & Dulvy N.K. (2017). Black-swan events in animal populations. *Proceedings of the National Academy of Sciences* **114**, 3252–3257. https://doi.org/10.1073/pnas.1611525114

Bachmaier M. & Backes M. (2011). Variogram or semivariogram? Variance or semivariance? Allan variance or introducing a new term? *Mathematical Geosciences* **43**, 735–740. https://doi.org/10.1007/s11004-011-9348-3

Bjorndahl J.A., Gushulak C.A.C., Mezzini S., Simpson G.L., Haig H.A., Leavitt P.R., *et al.* (2022). Abrupt changes in the physical and biological structure of endorheic upland lakes due to 8-m lake-level variation during the 20 $^\text{th}$ century. *Limnology and Oceanography* **67**, 1022–1039. https://doi.org/10.1002/lno.12054

Botero C.A., Weissing F.J., Wright J. & Rubenstein D.R. (2015). Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences* **112**, 184–189. https://doi.org/10.1073/pnas.1408589111

Broekman M.J.E., Hilbers J.P., Hoeks S., Huijbregts M.A.J., Schipper A.M. & Tucker M.A. (2024). Environmental drivers of global variation in home range size of terrestrial and marine mammals. *Journal of Animal Ecology* **93**, 488–500. https://doi.org/10.1111/1365-2656.14073

Burt W.H. (1943). Territoriality and home range concepts as applied to mammals. *Journal*

of Mammalogy **24**, 346. https://doi.org/10.2307/1374834

Charnov E.L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9**, 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Chevin L.-M., Lande R. & Mace G.M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology* **8**, e1000357. https://doi.org/10.1371/journal.pbio.1000357

Crameri F. (2018). Geodynamic diagnostics, scientific visualisation and StagLab 3.0. *Geoscientific Model Development* **11**, 2541–2562. https://doi.org/10.5194/gmd-11-2541-2018

Crameri F., Shephard G.E. & Heron P.J. (2020). The misuse of colour in science communication. *Nature Communications* **11**, 5444. https://doi.org/10.1038/s41467-020-19160-7

Falcón-Cortés A., Boyer D., Merrill E., Frair J.L. & Morales J.M. (2021). Hierarchical, memory-based movement models for translocated elk (cervus canadensis). *Frontiers in Ecology and Evolution* **9**, 702925. https://doi.org/10.3389/fevo.2021.702925

Fan X. & Liu Y. (2016). A global study of NDVI difference among moderate-resolution satellite sensors. *ISPRS Journal of Photogrammetry and Remote Sensing* **121**, 177–191. https://doi.org/10.1016/j.isprsjprs.2016.09.008

Fleming C.H., Calabrese J.M., Mueller T., Olson K.A., Leimgruber P. & Fagan W.F. (2014). From fine-scale foraging to home ranges: A semivariance approach to identifying movement modes across spatiotemporal scales. *The American Naturalist* **183**, E154–E167. https://doi.org/10.1086/675504

Frankham R. & Brook B.W. (2004). The importance of time scale in conservation biology and ecology. *Annales Zoologici Fennici* **41**, 459–463

Frerebeau N. (2024). *Khroma: Colour schemes for scientific data visualization*. Université Bordeaux Montaigne, Pessac, France.

Geremia C., Merkle J.A., Eacker D.R., Wallen R.L., White P.J., Hebblewhite M., *et al.* (2019). Migrating bison engineer the green wave. *Proceedings of the National Academy of Sciences* **116**, 25707–25713. https://doi.org/10.1073/pnas.1913783116

16

Hollister J., Shah T., Nowosad J., Robitaille A.L., Beck M.W. & Johnson M. (2023). *Elevatr: Access elevation data from various APIs.*

Huang S., Tang L., Hupy J.P., Wang Y. & Shao G. (2021). A commentary review on the use of normalized difference vegetation index (NDVI) in the era of popular remote sensing. *Journal of Forestry Research* **32**, 1–6. https://doi.org/10.1007/s11676-020-01155-1

Jonzén N., Lindén A., Ergon T., Knudsen E., Vik J.O., Rubolini D., *et al.* (2006). Rapid advance of spring arrival dates in long-distance migratory birds. *Science* **312**, 1959–1961. https://doi.org/10.1126/science.1126119

Keith D.A., Akçakaya H.R., Thuiller W., Midgley G.F., Pearson R.G., Phillips S.J., *et al.* (2008). Predicting extinction risks under climate change: Coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* **4**, 560–563. https://doi.org/10.1098/rsbl.2008.0049

Keys P.W., Barnes E.A. & Carter N.H. (2021). A machine-learning approach to human footprint index estimation with applications to sustainable development. *Environmental Research Letters* **16**, 044061. https://doi.org/10.1088/1748-9326/abe00a

Lande R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* **142**, 911–927

Levin S.A. (1992). The problem of pattern and scale in ecology: The robert h. MacArthur award lecture. *Ecology* **73**, 1943–1967. https://doi.org/10.2307/1941447

Levins R.A. (1974). *Evolution in changing environments: Some theoretical explorations*, 3. printing. Princeton Univ. Press, Princeton, NJ.

Logares R. & Nuñez M. (2012). Black swans in ecology and evolution: The importance of improbable but highly influential events. *Ideas in Ecology and Evolution.* https://doi.org/10.4033/iee.2012.5.5.n

Merkle J.A., Monteith K.L., Aikens E.O., Hayes M.M., Hersey K.R., Middleton A.D., *et al.* (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20160456. https://doi.org/10.1098/rspb.2016.0456

Mezzini S., Fleming C.H., Medici E.P. & Noonan M.J. (2025). How resource abundance and resource stochasticity affect organisms' range sizes. *Movement Ecology* **13**, 20. https://doi.org/10.1186/s40462-025-00546-5

Middleton A.D., Merkle J.A., McWhirter D.E., Cook J.G., Cook R.C., White P.J., *et al.* (2018). Green-wave surfing increases fat gain in a migratory ungulate. *Oikos* **127**, 1060–1068. https://doi.org/10.1111/oik.05227

Mueller T., Olson K.A., Fuller T.K., Schaller G.B., Murray M.G. & Leimgruber P. (2008). In search of forage: Predicting dynamic habitats of mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology* **45**, 649–658. https://doi.org/10.1111/j.1365-2664.2007.01371.x

Nilsen E.B., Herfindal I. & Linnell J.D.C. (2005). Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Écoscience* **12**, 68–75. https://doi.org/10.2980/i1195-6860-12-1-68.1

Olson D.M. & Dinerstein E. (2002). The global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden* **89**, 199. https://doi.org/10.2307/3298564

Pease B.S. (2024). Ecological scales of effect vary across space and time. *Ecography* **2024**, e07163. https://doi.org/10.1111/ecog.07163

Pedersen E.J., Miller D.L., Simpson G.L. & Ross N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ* **7**, e6876. https://doi.org/10.7717/peerj.6876

Pettorelli N., Vik J.O., Mysterud A., Gaillard J.-M., Tucker C.J. & Stenseth N.Chr. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution* **20**, 503–510. https://doi.org/10.1016/j.tree.2005.05.011

Polansky L., Kilian W. & Wittemyer G. (2015). Elucidating the significance of spatial memory on movement decisions by african savannah elephants using state–space models. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20143042. https://doi.org/10.1098/rspb.2014.3042

Polazzo F., Limberger R., Pennekamp F., Ross S.R.P.-J., Simpson G.L. & Petchey O.L. (2024). Measuring the response diversity of ecological communities experiencing multifarious environmental change. *Global Change Biology* **30**, e17594. https://doi.org/10.1111/gcb.17594

R Core Team (2024). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Ranc N., Cagnacci F. & Moorcroft P.R. (2022). Memory drives the formation of animal home ranges: Evidence from a reintroduction. *Ecology Letters* **25**, 716–728. https://doi.org/10.1111/ele.13869

Rickbeil G.J.M., Merkle J.A., Anderson G., Atwood M.P., Beckmann J.P., Cole E.K., *et al.* (2019). Plasticity in elk migration timing is a response to changing environmental conditions. *Global Change Biology* **25**, 2368–2381. https://doi.org/10.1111/gcb.14629

Riotte-Lambert L. & Matthiopoulos J. (2020). Environmental predictability as a cause and consequence of animal movement. *Trends in Ecology & Evolution* **35**, 163–174. https://doi.org/10.1016/j.tree.2019.09.009

Rizzuto M., Leroux S.J., Vander Wal E., Richmond I.C., Heckford T.R., Balluffi-Fry J., *et al.* (2021). Forage stoichiometry predicts the home range size of a small terrestrial herbivore. *Oecologia* **197**, 327–338. https://doi.org/10.1007/s00442-021-04965-0

Sawyer H., Merkle J.A., Middleton A.D., Dwinnell S.P.H. & Monteith K.L. (2019). Migratory plasticity is not ubiquitous among large herbivores. *Journal of Animal Ecology* **88**, 450–460. https://doi.org/10.1111/1365-2656.12926

Southwood T.R.E. (1977). Habitat, the templet for ecological strategies? *The Journal of Animal Ecology* **46**, 336. https://doi.org/10.2307/3817

Stefanescu C., Ubach A. & Wiklund C. (2021). Timing of mating, reproductive status and resource availability in relation to migration in the painted lady butterfly. *Animal Behaviour* **172**, 145–153. https://doi.org/10.1016/j.anbehav.2020.12.013

Steixner-Kumar S. & Gläscher J. (2020). Strategies for navigating a dynamic world. *Science*

369, 1056–1057. https://doi.org/10.1126/science.abd7258

Stephens D.W. & Charnov E.L. (1982). Optimal foraging: Some simple stochastic models. *Behavioral Ecology and Sociobiology* **10**, 251–263. https://doi.org/10.1007/BF00302814

Tian F., Fensholt R., Verbesselt J., Grogan K., Horion S. & Wang Y. (2015). Evaluating temporal consistency of long-term global NDVI datasets for trend analysis. *Remote Sensing of Environment* **163**, 326–340. https://doi.org/10.1016/j.rse.2015.03.031

Vermote E. & NOAA CDR Program (2018). NOAA climate data record (CDR) of AVHRR normalized difference vegetation index (NDVI), version 5

Vermote E. & NOAA CDR Program (2022). NOAA climate data record (CDR) of VIIRS normalized difference vegetation index (NDVI), version 1

Wang X., Cao L., Fox A.D., Fuller R., Griffin L., Mitchell C., *et al.* (2019). Stochastic simulations reveal few green wave surfing populations among spring migrating herbivorous waterfowl. *Nature Communications* **10**, 2187. https://doi.org/10.1038/s41467-019-09971-8

Wessling E.G., Deschner T., Mundry R., Pruetz J.D., Wittig R.M. & Kühl H.S. (2018). Seasonal variation in physiology challenges the notion of chimpanzees (pan troglodytes verus) as a forest-adapted species. *Frontiers in Ecology and Evolution* **6**, 60. https://doi.org/10.3389/fevo.2018.00060

Wolf A.A., Zavaleta E.S. & Selmants P.C. (2017). Flowering phenology shifts in response to biodiversity loss. *Proceedings of the National Academy of Sciences* **114**, 3463–3468. https://doi.org/10.1073/pnas.1608357114

Wolkovich E.M., Cook B.I., Allen J.M., Crimmins T.M., Betancourt J.L., Travers S.E., *et al.* (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature* **485**, 494–497. https://doi.org/10.1038/nature11014

Wood S.N. (2017). *Generalized additive models: An introduction with r*, Second edition. CRC Press/Taylor & Francis Group, Boca Raton.

Wood S.N., Goude Y. & Shaw S. (2015). Generalized additive models for large data sets. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* **64**, 139–155. https:

//doi.org/10.1111/rssc.12068

Wood S.N., Li Z., Shaddick G. & Augustin N.H. (2017). Generalized additive models for gigadata: Modeling the u.k. Black smoke network daily data. *Journal of the American Statistical Association* **112**, 1199–1210. https://doi.org/10.1080/01621459.2016.1195744

Xu W., Barker K., Shawler A., Van Scoyoc A., Smith J.A., Mueller T., *et al.* (2021). The plasticity of ungulate migration in a changing world. *Ecology* **102**, e03293. https://doi.org/10.1002/ecy.3293