

Observing changing ecological diversity in the Anthropocene

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Abstract

As the world enters the Anthropocene, the planet's environment is changing rapidly, putting critical ecosystem services at risk. Understanding and forecasting how ecosystems will change over the coming decades requires understanding the sensitivity of species to environmental change. The extant distribution of species and functional groups contains valuable information about the performance of different species in different environments. However, with high rates of environmental change, information inherent in ranges of many species will disappear, since that information exists only under quasi-equilibrium conditions. The information content of distributional data obtained now is greater than data obtained in the future. New remote sensing technologies can map chemical and structural traits of plant canopies and allow inference of trait and in many cases, species ranges. Current satellite remote sensing data can only produce relatively simple classifications, but new techniques have dramatically higher biological information content.

In a nutshell

Today, the Earth's environment is changing faster than species ranges can re-equilibrate to new environmental conditions, leading to growing inconsistencies between environmental conditions and ranges.

Species ranges are a key source of information about climate sensitivity but given high rates of change, information about niches inherent in species range-environment correlations is being lost.

New remote sensing technologies, deployed on aircraft and spacecraft, can provide vast quantities of distributional data for vegetation and can be deployed quickly enough to observe species range-environment correlations before they are lost.

Next-generation remote sensing allows identifying taxonomic entities from observed canopy traits, opening the possibility of global maps of plant species and traits at high resolution.

Introduction

Information derived from species ranges is a central resource for the science of ecology. Current patterns of species and physiological trait distributions contain important information about their functional relationships to climate and other environmental controls (Cody and Mooney, 1978, Rödder et al 2011, Davis 1986, Bonan and Sirois 1992, Kearney and Porter 2009). In a foundational paper, Ter Braak and Prentice (1988) wrote, "All species occur in a characteristic, limited range of habitats, and within their range, they tend to be most abundant around their particular environmental optimum". While this appraisal of the range-niche relationship is overly simplistic, ignoring the effects of species interactions (competition, mutualisms, and predation, parasitism and herbivory), distributional information is nonetheless crucial for constructing models to understand future ecological responses to climate and global change. Some modeling paradigms extract information directly from ranges to estimate model parameters, while others rely on distributions to validate models based on mechanistic approaches.

Current rates of climate change equal or exceed the highest rates observed in the recent paleorecord (Loarie et al 2009), while impacts of land use and invasive species are unprecedented. Given current rates of environmental change the information inherent in species or trait ranges is being lost, as ranges are displaced from quasi-equilibrium states and begin to reflect transient, rather than steady-state conditions (Figure 1). While vagile, fast-reproducing species plants and animals may track shifts in climate and its impacts on key resources, (Tingley et al 2009), the abundance and spatial distribution of many species will diverge more and more from their historical climate limits. High rates of environmental change imply that distributional data will contain less and less information about species niches. The further the planet moves from the pre-Anthropocene biome configuration, the more important modeling community reassembly into new configurations becomes.

Observations are urgently needed to provide a baseline global inventory of the biosphere. This information will be critical for developing robust relationships between environmental characteristics and biotic properties. It will also serve as a useful initial condition for describing the current state of the terrestrial biosphere that can be used to initialize global ecological forecasts. Given our current state of knowledge, we cannot know at what point the distributions of particular species will move out of their Holocene quasi-equilibria; however, the sooner the baseline is measured, given current rates of climate and environmental change, the better. Traditional methods of field identification and mapping, and lab-based assays of variability, are too slow and limited to obtain new information at accelerated rates.

Technological innovation is required, and the sooner those innovations are put in place, the more information on the extant distribution of diversity prior to the onset of the Anthropocene will be captured.

Species ranges as legacy information

What is the current status of climate-vegetation relationships? The modern-day configuration of biomes began late in the Holocene period, a 12,000-year long period of relatively stable climate conditions, during the latter part of which global mean temperatures varied by only a degree or so (Figure 1). Species ranges contain information because of conditions prevailing during the Holocene, and while the details remain unclear, and indeed we do not fully understand the reasons, Holocene conditions allowed range equilibria to be established for many taxa. Stable species ranges do not imply stable local populations: rather, ranges are a statistical estimate, and always include absences in some sites suitable for a species as a result of local population and metapopulation dynamics, and may include presence in refugia not suited to long term occupancy.

Later in the Holocene, evidence from atmospheric CO₂ and its isotopes support the idea that, despite emerging human activity, (Stocker et al 2011), the global land biosphere and its large-scale carbon balance were relatively quiescent, although again, fine-grained variation was continuous (Elsig et al 2009). The late Holocene left a legacy of biological information in the form of species-climate correlations. Ecologists have found links between the distribution of species and their traits, often supported mechanistically by experimental studies (Mooney 1977, Kearney and Porter 2009). Evidence for strong physical control over species distributions comes from microhabitat levels, where subtle meter-scale topography influences vegetation composition (Ackerly et al 2002) from the classic regional orographic scales of Whittaker's studies (Whittaker and Niering 1965) to the global level (Emanuel et al 1986). While the preponderance of evidence links climate and plant species traits closely, there is sufficient evidence of dynamic processes (Davis 1986, Davis and Botkin 1985, Cohen and Pastor 1991) to suggest that stable species-climate relationships are being disrupted in a changing climate, leading to complex dynamics.

Dynamics in the paleorecord can be viewed hierarchically (Whitlock and Bartlein 1998). At any given site, species composition over time is typically very dynamic, reflecting local disturbance regimes, interspecific competition and climate variability. When large ensembles of data are assembled, more-stable species range patterns emerge, even though some sites suitable for occupancy are stochastically vacant, and some unsuitable sites may be still be occupied. Because of this, geographic range data provide insights complementary to site-based time series. Range data provides information on climate dependence in the context of trophic relationships: some apparent species range correlations may in fact be correlations with prey or forage species climate sensitivity (Tingley et al 2009).

The apparent stability of the mid-late Holocene (Figure 1) allowed many species to develop spatial distributions reflective of their underlying realized niches (*sensu* Holt 2009) and those distributions are an important resource for modeling. Fine-grained patterns of variation do not prevent, given sufficient time, large-scale correlations with coarser-grained climate patterns from emerging (Whitlock and Bartlein 1998). The correlations may not be stable in climates unlike today's or the recent past. Under climate conditions with no modern analog, some important North American species had different realized niches relative to climate than these same species do today, while other species appear more stable (Veloz et al 2012). This suggests that current-day realized niches may provide limited guidance for the future. The generality of this problem is unknown. By contrast, another recent study (Perrypierre et al 2012) showed that most invasive species expand into a similar climatic niche to the one they inhabit in their home range, suggesting present-day climate relationships to be robust, a conclusion also reached for birds by Tingley et al (2009). The proportion of species for which present-day ranges are, or are not, robust predictors of future behavior remains open.

The global climate is changing, and patterns of change have complex signatures in time and space (Solomon et al 2007). Figure 2 shows interpolated average annual air temperatures (1951-2006) for the conterminous US, and their change over that same period. In the parts of the US, temperatures have changed between 1 and 2.5° over this period, more than enough to disrupt the calibration of temperature-species range analyses, and precipitation rates have also changed. Case studies show some species apparently responding directly to temperature (Erb et al 2011), while other species respond to climate via both physiological and habitat or trophic effects (Tingley et al 2009). Other observational evidence that bioclimate is changing abounds: a graphic demonstration is found in the changes to the Plant Hardiness Zones, defined by the US Department of Agriculture to indicate the regions suitable for different horticultural and crop plants (<http://www.arborday.org/media/mapchanges.cfm>).

Loarie et al (2009) calculated velocities of climate change, or the rate of movement required for a species to maintain its range within the same temperature as its current range as the climate warms, based on climate model projections. This index suggests a global mean of 0.5 km yr⁻¹ with many areas as high as 1-10 km yr⁻¹. This high rate of movement implies that, especially in fragmented or managed landscapes, many species will have difficulty in keeping pace (Figure 3). Species ranges have already begun to change (Parmesan 2006, Root and Weckstein 1994, Wake et al 2009) and data on species distributions collected in the future will be less and less likely to be reflective of adjustment to climate and more and more likely to exhibit dynamic and disequilibrium responses (Wikle 2003). These equilibrium responses may be near-linear responses to changing climate variables, as has been exhibited by some migratory species (Root and Weckstein 1994) but transient nonlinear responses to climate may not even have the same sign as steady state adjustments (Schimel et al 1990).

Techniques exist for ecological forecasting in complex systems (Scheffer et al 2001). In some situations, the actual future trajectory of a system may be predicted, while in other situations, only the likelihood of a dramatic change may be quantifiable (Scheffer et al 2009). In terrestrial ecosystems, one of the best-understood examples of complex dynamics occurs in the dynamic tension between grass and woody vegetation in savanna ecosystems. Changes to climate, fire and grazing regime can drive shifts between a grassy state with sparse trees, and a woodland state with minimal grass cover (Scholes and Archer 1997, Scheffer et al 2001). The savanna is one of the simpler multi-state systems and contains a relatively small number of interacting species, yet can produce very complex dynamics.

While abstract and idealized simulations of ecosystems can be made with very simple models (Eagleson and Segarra 1985), quantitative forecasting requires not only an appropriate model, but also detailed observations of the current state of the system (Hibbard et al 2001, 2003). The paleo-record suggest that many ecosystems that have no analog in present-day or paleo-communities will emerge from climate, invasions and land use change impacts, and so community re-assembly will be occurring at the species level, reducing the utility of simpler, biome or functional-type oriented modeling techniques. The likelihood of complex changes further highlights the need for comprehensive range observations at the species and trait level as early as possible in the Anthropocene.

The range *scale gap* and the potential of new remote sensing tools

The time that would be needed to collect comprehensive ground-based measurements of the planet's species distributions is long enough that critical information about species ranges and niches would be lost: Jetz et al (2011) wrote "Global knowledge about the spatial distribution of species is orders of magnitude coarser in resolution than other geographically-structured environmental datasets such as topography or land cover". Land cover, topography, and climate are all now observed from space using remote sensing techniques that provide global coverage. There is a significant gap between the fine scales of these abiotic data and the coarse resolution of most species distribution data. Global coverage allows analyses and models based on complete coverage, rather than on sparse statistical samples (Buermann et al 2008).

Remote-sensing observations are of unique value because of their complete spatial sampling even when, as with land cover, the measurements only reveal part of a complex reality. Recent advances in the remote sensing technology are poised to move terrestrial remote sensing beyond the monitoring of land-cover change to mapping of functional diversity and habitat. Such regional and global remote sensing data on vegetation diversity has the potential to bridge the Jetz et al (2009) "scale gap" between species distribution and other environmental data.

A global baseline dataset obtained while biogeographic distributions are in the early stages of change will allow empirical estimation of parameters governing biospheric

responses to climate from the spatial correlations between species distributions and climate and between species traits and climate. The baseline will also provide a global scale measurement of the initial state of the terrestrial biotic system, in terms of the distribution of different species, traits or functional types that can serve as a basis for initializing predictive models of vegetation change.

While current multispectral remote sensing techniques can only detect biological information variation crudely, typically classifying into tens of land cover classes rather than identifying many hundred thousands of species, new techniques have much higher spectral information content (Figure 4), and signal-to-noise ratio (SNR). Spectral resolution controls how many distinct plant constituents can be detected, although the dimensionality of the data is much less than the number of channels, because of the broad-band nature of many key chemical and structural features (Figures 4 and 5). The SNR defines how large a physical difference can be detected in any channel. Current and near-term sensors (MODIS, LANDSAT and LDCM) have SNRs over typical vegetation of 60-300, while modern spectrometers have SNRs of >600, increasing their ability to resolve biological variation beyond the additional degrees of freedom evident in Figure 4.

Unique opportunities exist for remote sensing technology to produce a dramatic increase in the amount of information, using airborne and spaceborne systems. Airborne and spaceborne approaches are complementary. Airborne data coverage from systems like NASA's AVIRIS series and Carnegie and NSF-supported systems is limited in time and space (Asner and Martin 2009, Kampe et al 2010), but is at the scale of individual trees (~1 m²) while spaceborne data (at 30-70 m²) can provide global and seasonal coverage, albeit at coarser resolution. With regard to spaceborne measurements, NASA's proposed HypsIRI (Hyperspectral and InfraRed Imager) satellite mission scheduled for the 2020s would provide a global dataset of vegetation functional diversity. Successful studies of diversity have been carried out using sensors with a wide range of spatial resolutions, but research is critically needed on the impact of resolution in retrieving species identify and diversity to guide future tradeoffs between spaceborne sensor coverage, frequency and resolution.

Quantitative remote sensing techniques produce data on the distributions of species and their traits (Table 1) by directly measuring the chemical composition of plant canopies (Figure 5, Asner and Martin 2009) and by retrieving signatures linked to water, light and nutrient use (Ustin and Gamon 2010, Ollinger 2011). Considerable success has been realized with this approach, taking advantage of airborne and the limited existing spaceborne data. Table 1 lists recent studies that have demonstrated the retrieval of diversity-related information from a wide range of current airborne and spaceborne sensors. These studies show that hyperspectral data can aid in plant species identification and diversity estimation in temperate and tropical forests, grasslands and shrublands, and a range of wetland ecosystems (Luoto et al 2010). Some of these studies were clearly able to identify individual plants to species, while others were able to classify vegetation into multiple

functional types, based on canopy signatures, in a way that could be more-or-less directly used in models of ecosystem function.

Imaging spectroscopy is reaching performance levels that allow quantification of canopy chemistry at large spatial scales. Many of the leaf traits controlling photosynthesis rates can be measured using spectroscopic remote sensing, including canopy nutrients (Kokaly et al 2009), leaf mass per unit area (Asner et al, 2011), photosynthetic pigments (Ustin et al 2009). In addition to mapping process controls, preliminary studies show photosynthesis rates, and consequently key traits like resource use efficiencies, may be directly estimated spectroscopically by measuring chlorophyll fluorescence (Frankenberg et al 2011). Spectroscopic measurements can also estimate key constraints over decomposition and subsequent soil nutrient cycling, such as nitrogen, lignin and cellulose content (Kokaly et al 2009). By affecting decomposition rates, species changes can influence productivity (Schimel 1995, Aber and Melillo 1982) and plant successional dynamics (Hobbie et al 1993). While taxonomic and evolutionary relationships may be deduced from spectral data (Asner and Martin 2011), the actual retrievals often focus on traits related to growth, longevity and defense and can be directly used in mechanistic models. As Davis et al (2005) showed, these traits and their diversity within populations are important drivers of plant community responses to climate change.

Complementary measurements of vegetation structure, and by extension, key habitat variables, may be measured using LiDAR techniques and possibly using active microwave techniques as well (NRC 2007, Hyde et al 2005,). LiDAR works by detecting the time delay of laser light pulses and, by retrieving the waveform of returns, the vertical distribution of foliage may be inferred. The architectural information obtained from LiDAR can be used in process studies and to aid in identifying plant traits, and in mapping their distributions (Dalponte et al 2008). Active LiDAR and new microwave techniques are proving to be robust and informative and provide information highly complementary to canopy chemistry. LiDAR can provide information about the structure of canopy layers, weighting of leaves between the top and bottom of canopies and presence of understory.

While this article focuses on the potential for remote sensing measurements to inform our understanding of plant distributions in relation to climate, trends in the distribution and abundance of higher trophic levels -- herbivores, carnivores, and pests and pathogens -- are also critical. While these taxa cannot be observed remotely, detailed global coverage of habitat data from remote sensors will provide information critical to modeling distribution and dynamics of higher trophic levels (Vierling et al 2010). Chemical and structural measurements provide information on food resources and quality for herbivores and heterotrophs, and 3-dimensional vegetation structure provides habitat information for many taxa. Today's relatively crude biological remote sensing data have been used successfully in modeling animal and microbial distribution and activity, but the qualitatively more advanced

sensors within technological reach will greatly enhance this type of modeling (Goetz et al 2007, Hyde et al 2005, Gilbert et al 2011).

If present-day realized niches are not stable, or if they only represent one of a family of possible niches accessible to a species, then current distributional information may produce limit our ability to make forecasts (Veloz et al 2012). Novel species interactions and effects of within-species variability in traits may result in niche-based processes having limited predictability (Beckage et al 2009). The amplitude of trait variability within species may influence their future distributional and evolutionary responses to climate change (Davis et al 2005).

Spectroscopy and allied techniques map traits from which species identity may be inferred, complementing direct taxonomic identification. Spectroscopy can, in principle, provide additional insights to those derived from maps of species distributions by quantifying spatial variability in key traits within taxa. This capability is unavailable from methods that map taxonomic identity, unless these are supplemented by labor-intensive genomic or physiological measurements. Remote sensing also intrinsically maps biological variation in the context of land use, and land use change, and so allows scientists to integrate human effects on landscape structure with other drivers of biotic change. Only the most intensive ground-based species range mapping can provide the detail to integrate land cover and the broad coverage required to assess climate effects (Jetz et al 2011).

If climate and other environmental changes lead to complex, evolving niches (Beckage et al 2012), sustained imaging of dynamic species ranges over time will be crucial. The level of effort required to track changing species ranges or trait variability within species with traditional field methods is such that only a relative few taxa could ever be tracked. Satellite observations can be sustained over decades, as has been shown by the LANDSAT, AVHRR and MODIS time series, and so are an appropriate means of observing dynamic change in geographic patterns. NASA's current plan, based on the National Research Council's Decadal Study (NRC 2005, Schimel et al 2006) calls for launching an appropriate mission (HyspIRI; hyspiri.jpl.nasa.gov/), but not for a decade or more, at a time when, given current rates of climate change, much of the data inherent in species ranges will already be lost.

Conclusions

Forecasting the future of ecosystems will increasingly require species and trait level data. Today, data with the spatial/temporal coverage and resolution to define species ranges and niches at the scale of variation in climate, land use, soils and other key controls does not exist (Jetz et al 2011). High-resolution data are required to underpin the new theory, and models are required to understand and forecast the dynamics of newly assembling communities and ecosystems. The biogeographic patterns that provide the information on niche dimensions needed to construct this theory and models is being disrupted and the information inherent in these patterns

is being lost. This information is being lost at a time when forecasting will become on the one hand an ever-more-critical tool, and on the other, increasingly challenging as complex and nonlinear behavior accelerates.

As a result of human development, the world is now committed to an era of rapid biological change. Ecologists must collect the data needed to understand, forecast and ultimately manage the biosphere. With accelerating rates of environmental change, species ranges are shifting, lagging the environmental drivers by varying amounts and reducing the amount of information about niche dimension and environmental sensitivity inherent in the relative stable pre-anthropocene spatial patterns. The information content of distributional data obtained now is greater than if obtained to the future, lending urgency to the need for investment in new remote sensing technology and platforms now. At the same time, continuous observations from space of these changes will provide critical constraints on models of movement and range dynamics. Hyperspectral and active laser and microwave technologies for remote sensing can map chemical and canopy structural traits for plants, and by extension, provide information on food resources and habitat structure for other taxa.

Typically, life form classifications are used to assign plant physiological and structural properties in models. Mapping species and life forms from canopy traits reverses this, and identifies taxonomic entities from their physiological and structural characteristics and opens the possibility of inferring species, trait and habitat distributions globally. When traits are assigned based on mapped species of functional types, only very limited information exists about variation within taxonomic entities. Mapping traits directly, and inferring identify from those traits, allows for much fuller estimation of within-taxon or type variability, which may be critical information for predictive ecological models. Space-based observations will qualitatively increase the amount and resolution of data relevant to both species and trait distributions and will transform the science, similar to the way global observations have affected climate, topographic and land cover science.

A consistently collected global dataset, obtained soon, will provide a trove of information that will be mined for niche information over the coming decades, and will provide both initial conditions and observations of change. Such a baseline can only be obtained by combining traditional field approaches with innovative new remote observation techniques, and the development of techniques for combining information across scales. Ecologists have not typically focused using technology increasing the pace of collecting species-level data; however, it is now imperative to obtain global synoptic coverage of the abundance and spatial distribution of biological diversity. The National Science Foundation has supported the construction of three airborne remote sensing systems as part of the National Ecological Observatory Network (Kampe et al 2011), the Carnegie Institution for Science operates a similar system, and NASA supports two such systems. Spectroscopic data will soon be far more available, and from a more diverse range of ecosystems, than ever before. However, the most important opportunity for range

four vegetation data arises from the planned NASA HypsIRI spectroscopic satellite mission, which would provide global coverage over a period of years. However, the timeliness of the HypsIRI mission is questionable and no firm date for its launch has been determined.

The timing of this mission is extremely important and, unlike missions in many other areas of the Earth Sciences, the information content depends on when the measurements are made. The longer before a global mission is deployed, the less information will exist about realized niches. The timing of launch of all missions affects the pace of scientific discovery, but in the case of HypsIRI, timing actually affects the science that may be done. Realizing the value of planned satellite missions such as HypsIRI requires substantial research to be conducted before the value of a global hyperspectral mission can be fully exploited. Extracting the information about biodiversity inherent in spectroscopy novel requires the development of algorithms to extract diversity-related data and appropriate ground truth for calibration and validation. Not only are species being lost to extinction, information about species is being lost to high rates of environmental change. The sooner global observations are collected, the more scientific value they will provide.

Acknowledgements

This paper emerged from a workshop convened at the Carnegie Institution for Science, Stanford, California in 2010, and supported by NASA. The authors acknowledge their colleagues for an inspiring two days of discussion. The Carnegie Airborne Observatory is made possible by the Gordon and Betty Moore Foundation, the John D. and Catherine T. MacArthur Foundation, W. M. Keck Foundation, the Margaret A. Cargill Foundation, Grantham Foundation for the Protection of the Environment, Mary Anne Nyburg Baker and G. Leonard Baker Jr., and William R. Hearst III. DS acknowledges financial support from NEON and great contributions from the NEON airborne science team. NEON is sponsored by the National Science Foundation. Part of this research was carried out at the Jet Propulsion Laboratory, California Institute of Technology, under a contract with the National Aeronautics and Space Administration.

References Cited

- Aber, J. D. and J. M. Melillo. 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. *Canadian Journal of Botany* 60:2263-2269.
- Ackerly, D.D., C.A. Knight, S.B. Weiss, K. Barton, and K.P. Starmer. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia* 130: 449-457
- Araújo, M. B., Pearson, R. G., Thuiller, W. and Erhard, M. 2005. Validation of species-climate impact models under climate change. *Global Change Biology*, 11: 1504-1513.
- Asner, G. P., M. O. Jones, R. E. Martin, D. E. Knapp, and R. F. Hughes. 2008. Remote sensing of native and invasive species in Hawaiian forests. *Remote Sensing of Environment* 112:1912-1926.
- Asner, G.P., and R. E. Martin. 2009. Airborne spectranomics: Mapping canopy chemical and taxonomic diversity in tropical forests. *Frontiers in Ecology and the Environment* 7:269-276.
- Asner, G. P. and R. E. Martin. 2011. Canopy phylogenetic, chemical and spectral assembly in a lowland Amazonian forest. *New Phytologist* 189:999-1012.
- Asner, G.P., R.E. Martin, R. Tupayachi, R. Emerson, P. Martinez, F. Sinca, G.V.N. Powell, J. Wright, and A. Lugo. 2011. Taxonomy and remote sensing of leaf mass per area (LMA) in humid tropical forests. *Ecological Applications* 21:85-98.
- Barnosky, A.D. 2001. Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. *Journal of Vertebrate Paleontology* 21:172-185
- Belluco, E., M. Camuffo, S. Ferrari, L. Modenese, S. Silvestri, A. Marani, and M. Marani. 2006. Mapping salt-marsh vegetation by multispectral and hyperspectral remote sensing. *Remote Sensing of Environment* 105:54-67.
- Biggs, R., S.R. Carpenter and W.A. Brock. 2009. Turning back from the brink: Detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences* 106(3): 826-831.
- Bonan G. and L. Sirois. 1992. Air temperature, tree growth and the northern and southern range limits to *Picea mariana*. *J Vegetation Sci* 3: 495-506

- Buermann, W., S. Saatchi, T. B. Smith, B. R. Zutta, J. A. Chaves, B. Milá, and C. H. Graham. Predicting species distributions across the Amazonian and Andean regions using remote sensing data. *Journal of Biogeography* 35: 1160-1176.
- Carlson, K. M., G. P. Asner, F. R. Hughes, R. Ostertag, and R. E. Martin. 2007. Hyperspectral Remote Sensing of Canopy Biodiversity in Hawaiian Lowland Rainforests. *Ecosystems* 10:536-549.
- Carter, G. A., A. K. Knapp, J. E. Anderson, G. A. Hoch, and M. D. Smith. 2005. Indicators of plant species richness in AVIRIS spectra of a mesic grassland. *Remote Sensing of Environment* 98:304-316.
- Clark, M. L., D. A. Roberts, and D. B. Clark. 2005. Hyperspectral discrimination of tropical rain forest tree species at leaf to crown scales. *Remote Sensing of Environment* 96:375-398.
- Cody M.L. and H.A. Mooney. 1978. Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics* 9:265-321
- Cohen Y. and J. Pastor. 1991. The responses of a forest model to serial correlations of global warming. *Ecology* 7: 1161-1165.
- Crutzen, P. J. 2002. Geology of mankind. *Nature* 415:23
- Davis, M. B., R.G. Shaw, and J. R. Etterson. 2005. Evolutionary responses to changing climate. *Ecology* 86:1704–1714.
- Davis M.B. Climatic instability, time lags and community disequilibrium. In Diamond and Case 1986. *Community Ecology*, Harper and Row, New York. pp. 269-284
- Davis M.B. and D.B. Botkin. 1985. Sensitivity of cool-temperate forests and their fossil pollen record to rapid temperature change. *Quaternary Research*. 3:327-340.
- Dalponte, M., Bruzzone, L., Gianelle, D., 2008. Fusion of hyperspectral and LiDAR remote sensing data for classification of complex forest areas. *IEEE Transactions on Geoscience and Remote Sensing* 46, 1416-1427.
- Dent, C. L. Cummings, G. S. Carpenter, S. R. 2002. Multiple states in river and lake ecosystems. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 357 (1421): 635–645
- Eagleson, P. S., and R. I. Segarra. 1985, Water-limited equilibria of savanna vegetation ecosystems. *Water Resour. Res.*, 21, 1483–1493.

Elsig, J., J. Schmitt, D. Leuenberger, R. Schneider, M. Eyer, M. Leuenberger, F. Joos, H. Fischer, T. F. Stocker, 2009. Stable isotope constraints on Holocene carbon cycle changes from an Antarctic ice core. *Nature*, 461, 507-510.

Erb, L. P., C. Ray and R. P. Guralnick. 2011. On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology* 92: 1730–1735

Emanuel, W.R., H.H. Shugart and MP Stevenson. 1985. Climate change and the broad-scale distribution of terrestrial ecosystem complexes. *Climatic Change* 7: 29-43.

Féret, J.-B. and G. P. Asner. 2011. Spectroscopic classification of tropical forest species using radiative transfer modeling. *Remote Sensing of Environment* 115:2415-2422.

Fitzpatrick, Matthew C., Evan L. Preisser, Adam Porter, Joseph Elkinton, and Aaron M. Ellison. 2012. Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. *Ecological Applications* 22:472–486

Frankenberg, C., A. Butz, and G. C. Toon. 2011, Disentangling chlorophyll fluorescence from atmospheric scattering effects in O₂ A-band spectra of reflected sun-light. *Geophysical Research Letters* 38: L03801, doi:10.1029/2010GL045896.

Goodenough, D. G., A. Duk, K. O. Niemann, P. S. Jay, C. Hao, H. Tian, M. Murdock, and C. West. 2003. Processing Hyperion and ALI for forest classification. *IEEE Transactions on Geoscience and Remote Sensing* 41:1321-1331.

Gong, P., R. Pu, and B. Yu. 1997. Conifer species recognition: exploratory analysis of hyperspectral data. *Remote Sensing of Environment* 62:189-200.

Gates, DM. 2003 *Biophysical Ecology*. Courier Dover Publications. 635 pp.

Gilbert J.A., Steele J, Caporaso J.G., Steinbruck L, Somerfield P.J., Reeder J, Temperton B, Huse S, Joint I, McHardy A.C., Knight R, Fuhrman J.A., Field D. Defining seasonal marine microbial community dynamics. *ISME J*. doi:10.1038/ismej.2011.107. OMID:

Goetz, S.J., Steinberg, D., Dubayah, R.O., Blair, B., 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. *Remote Sensing of Environment* 108, 254-263.

Held, A., C. Ticehurst, L. Lymburner, and N. Williams. 2003. High resolution mapping of tropical mangrove ecosystems using hyperspectral and radar remote sensing. *International Journal of Remote Sensing* 24:2739-2759.

- Hibbard, K.A., S.R. Archer, D.S. Schimel & D.V. Valentine. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* 82:1999-2011
- Hibbard, K.A., D.S. Schimel, S.R. Archer, D. Ojima & W. Parton. 2003. Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. *Ecological Applications* 13: 911-926.
- Hobbie, S. E., D. E. Jensen, and F. S. Chapin, III. 1993. Resource supply and disturbance as controls over present and future plant diversity. Pages 385-408 In E.-D. Schulze and H. A. Mooney (Eds.), *Biodiversity and Ecosystem Function*. Springer-Verlag, Berlin.
- Holt, R.D., 2009. Colloquium Papers: Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *PNAS* 106 (Supplement 2): 19659-19665
- Hyde, P., R. Dubayah, B. Peterson, J.B. Blair, M. Hofton, C. Hunsaker, R. Knox and W. Walker. 2005. Mapping forest structure for wildlife habitat analysis using waveform lidar: Validation of montane ecosystems, *Remote Sensing of Environment*, Volume 96, Issues 3-4, 30, Pages 427-437
- Jetz, W., J. MacPherson and R. P. Guralnick. 2011. Integrating Biodiversity Distribution Knowledge: Toward A Global Map Of Life. *Trends in Ecology and Evolution* [doi:10.1016/j.tree.2011.09.007]
- Kampe, T. U., B. R. Johnson, M. Kuester, and M. Keller. 2010. NEON: the first continental-scale ecological observatory with airborne remote sensing of vegetation canopy biochemistry and structure. *Journal of Applied Remote Sensing*, Vol. 4, 043510
- Kearney, M. and Porter, W. (2009), Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12: 334-350.
- Keller, M. Schimel, D. S. Hargrove, W. W. Hoffman, F. M. 2008. A continental strategy for the National Ecological Observatory Network. *The Ecological Society of America*: 282-284
- Kittel, T.G.F., N.A. Rosenbloom, J.A. Royle, C. Daly, W.P. Gibson, H.H. Fisher, P. Thornton, D. Yates, S. Aulenbach, C. Kaufman, R. McKeown, D. Bachelet, D.S. Schimel, and VEMAP2 Participants. 2004. The VEMAP Phase 2 bioclimatic database. I: A gridded historical (20th century) climate dataset for modeling ecosystem dynamics across the conterminous United States. *Climate Research* 27:151-170.

Kokaly, R. F., G. P. Asner, S. V. Ollinger, M. E. Martin, and C. A. Wessman. 2009. Characterizing canopy biochemistry from imaging spectroscopy and its application to ecosystem studies. *Remote Sensing of Environment*. 113: S78-S91

LaDeau, S. L., G. E. Glass, N. T. Hobbs, A. Latimer, and R. S. Ostfeld. 2011. Data-model fusion to better understand emerging pathogens and improve infectious disease forecasting. *Ecological Applications* 21:1443–1460.

Loarie, S.R. , P.H. Duffy, H. Hamilton, G.P. Asner, C.B. Field, D.D. Ackerly. 2009. The velocity of climate change. *Nature* 462:1052-1055

Lucas K.L. & Carter G.A. (2008). The use of hyperspectral remote sensing to assess vascular plant species richness on Horn Island, Mississippi. *Remote Sensing of Environment*, 112, 3908-3915.

Luoto, H. Nagendra, J. Oldeland, C. Ricotta, J. Southworth, and M. Neteler. 2010. Remotely sensed spectral heterogeneity as a proxy of species diversity: Recent advances and open challenges. *Ecological Informatics* 5:318-329.

Martin, M. E., S. D. Newman, J. D. Aber, and R. G. Congalton. 1998. Determining Forest Species Composition Using High Spectral Resolution Remote Sensing Data. *Remote Sensing of Environment* 65:249-254.

Mooney, H.A., 1977. Convergent evolution in Chile and California. Dowden, Hutchinson & Ross 224pp.

Ollinger, S. V. 2011. Sources of Variability in Canopy Reflectance and the Convergent Properties of Plants. *New Phytologist* 189:375-394.

Papeş, M., R. Tupayachi, P. Martínez, A. T. Peterson, and G. V. N. Powell. 2010. Using hyperspectral satellite imagery for regional inventories: a test with tropical emergent trees in the Amazon Basin. *Journal of Vegetation Science* 21:342-354.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637-669

Petitpierre B, C Kueffer, O Broennimann, C Randin, C Daehler, and A Guisan. 2012. Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. *Science*: 335, 1344-1348

Rödger D, S Schmidlein, S Schick and S Lotters. 2011 Climate envelope models in systematics and evolutionary research. in Hodkinson et al, (Eds) 2011 Climate change, ecology and systematics. Cambridge University Press, 524 pp.

Root, T. L. and J. D. Weckstein. 1994. Changes in the distribution patterns of select wintering North American birds from 1901 to 1989. *Studies in Avian Biology* 15: 191 - 201

Sacks W.J., Schimel D.S., Monson R.K. 2007. Coupling between carbon cycling and climate in a high-elevation, subalpine forest: a model-data fusion analysis. *Oecologia*, 151: 54-68.

Scheffer, M.; Carpenter, S.; Foley, J.A.; Folke, C.; Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature* 413. p. 591 - 596.

Scheffer, M.; Bascompte, J.; Brock, W.A.; Brovkin, V.; Carpenter, S.R.; Dakos, V.; Held, H.; Nes, E.H. van; Rietkerk, M.; Sugihara, G. 2009. Early warning signals for critical transitions. *Nature* 461 . p. 53 – 59.

Schimel, D. S. 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biology*, 1: 77–91.

Schimel, D. S., W. J. Parton, T. G. F. Kittel, D. S. Ojima and C. V. Cole. 1990. Grassland biogeochemistry: links to atmospheric processes. *Climatic Change* 17:13-25.

Schimel, D., Inez Fung, and Ruth Defries. 2006. Space-based ecological observations: the NASA decadal survey. *Frontiers in Ecology and the Environment* 4: 171–171

Scholes, R.J. and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517-544.

Sitch S., Smith B., Prentice I.C., Arneth A, Bondeau A., Cramer W., Kaplan J., Levis S., Lucht, W., Sykes M., Thonicke K., Venevsky S. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9: 161–185.

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.) 2007. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007 Cambridge University Press. Cambridge, United Kingdom and New York, NY, USA.

Stenseth , N.C. 1979. Where Have All the Species Gone? On the Nature of Extinction and the Red Queen Hypothesis. *Oikos* 33: 196-227.

Stocker, B. D., K. Strassmann, F. Joos, 2011. Sensitivity of Holocene atmospheric CO₂ and the modern carbon budget to early human land use: analyses with a process-based model. *Biogeosciences* 8: 69-88.

ter Braak, C. J. F., and I. C. Prentice. 1988. A theory of gradient analysis. *Adv. Ecol. Res.* 18:271-313.

- Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz. 2009. Colloquium Papers: Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences* 106: 19637-19643.
- Ustin, S. L. and J. A. Gamon. 2010. Remote sensing of plant functional types. *New Phytologist* 186:795-816.
- Ustin, S. L., A. A. Gitelson, S. Jacquemoud, M. Schaepman, G. P. Asner, J. A. Gamon, and P. Zarco-Tejada. 2009. Retrieval of foliar information about plant pigment systems from high resolution spectroscopy. *Remote Sensing of Environment* 113: S67-S77.
- Wake, D. B, E. A. Hadly, and D. D. Ackerly. 2009. Biogeography, changing climates, and niche evolution. *Proceedings of the National Academy of Sciences* 106: 19631-19637.
- Wessman, C.A., J. D. Aber, D. L. Peterson & J. M. Melillo. Remote sensing of canopy chemistry and nitrogen cycling in temperate forest ecosystems. 1988. *Nature* 335: 1541-56.
- Whittaker R.H., 1967. Gradient analysis of vegetation. *Biological Reviews*. 42: 161–326.
- Whittaker, R.H. & W.A. Niering 1965. Vegetation of the Santa Catalina mountains: a gradient analysis of the South slope. *Ecology* 46: 429-452.
- Wikle, Christopher K. 2003. Hierarchical Bayesian Models For Predicting The Spread Of Ecological Processes. *Ecology* 84: 1382–1394.
- Williams, J. W., B. N. Shuman, T. Webb, P. J. Bartlein, and Phillip L. Leduc. 2004. Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecological Monographs* 74: 309–334.
- Veloz, S., Williams, J.W., Blois, J.L., He, F., Otto-Bliesner, B., and Z. Liu.(2012). No-analog climates and shifting realized niches during the late Quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology* 18: 1698-1713.
- Vierling, K.T., Bäessler, C., Brandl, R., Vierling, L.A., Weiß, I., Müller, J., 2010. Spinning a laser web: predicting spider distributions using LiDAR. *Ecological Applications* 21: 577-588.
- Yates, C. J., Elith, J., Latimer, A. M., Le Maitre, D., Midgley, G. F., Schurr, F. M. and West, A. G. 2010, Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: Opportunities and challenges. *Austral Ecology* 35: 374–391.

Yu, Q., P. Gong, N. Clinton, G. Biging, M. Kelly, and D. Schirokauer. 2006. Object-based detailed vegetation classification with airborne high spatial resolution remote sensing imagery. *Photogrammetric Engineering and Remote Sensing* 72:799-811.

Table 1. Examples of identifying species or functional diversity using imaging spectroscopy. S indicates studies that classified to taxonomic species, F indicates studies that primarily identified functional types, and I indicates identification of invasive species.

Ecosystem Type	Sensor	Spatial Resolution (m)	Source
Sub-tropical broadleaf forest (S)	CAO	0.5	Féret and Asner (2011)
Sub-tropical broadleaf forest (F)	AVIRIS	3.0	Carlson et al. (2007)
Temperate broadleaf forest (F)	EO-1 Hyperion	30.0	Goodenough et al. (2003)
Temperate grasslands (S)	AVIRIS	19.0	Carter et al. (2005)
Temperate mixed forest (S)	AVIRIS	20.0	Martin et al. (1998)
Temperate needleleaf forest (S)	DAIS	1.0	Gong et al. (1997)
Temperate shrubland-grassland (F)	DAIS	1.0	Yu et al. (2006)
Temperate wetlands (F)	CASI, other	1.0-3.0	Belluco et al. (2006)
Temperate wetlands (S)	HyMap	3.0	Lucas and Carter (2008)
Tropical broadleaf forest (S)	HYDICE	1.6	Clark et al. (2005)
Tropical broadleaf forest (F)	EO-1 Hyperion	30.0	Papeş et al. (2010)
Tropical lowland-to-montane rainforest (S,I)	AVIRIS	3.0	Asner et al. (2008)
Tropical mangroves (S)	CASI	2.5	Held et al. (2003)

CAO = Carnegie Airborne Observatory; AVIRIS = Airborne Visible and Infrared Imaging

Spectrometer; EO-1 Hyperion = Earth Observing-1 (spaceborne); DAIS = Digital Airborne Imaging

System; CASI = Compact Airborne Spectrographic Imager; HyMap = Hyperspectral Mapper

(airborne); HYDICE = Hyperspectral Digital Imagery Collection Experiment (airborne)

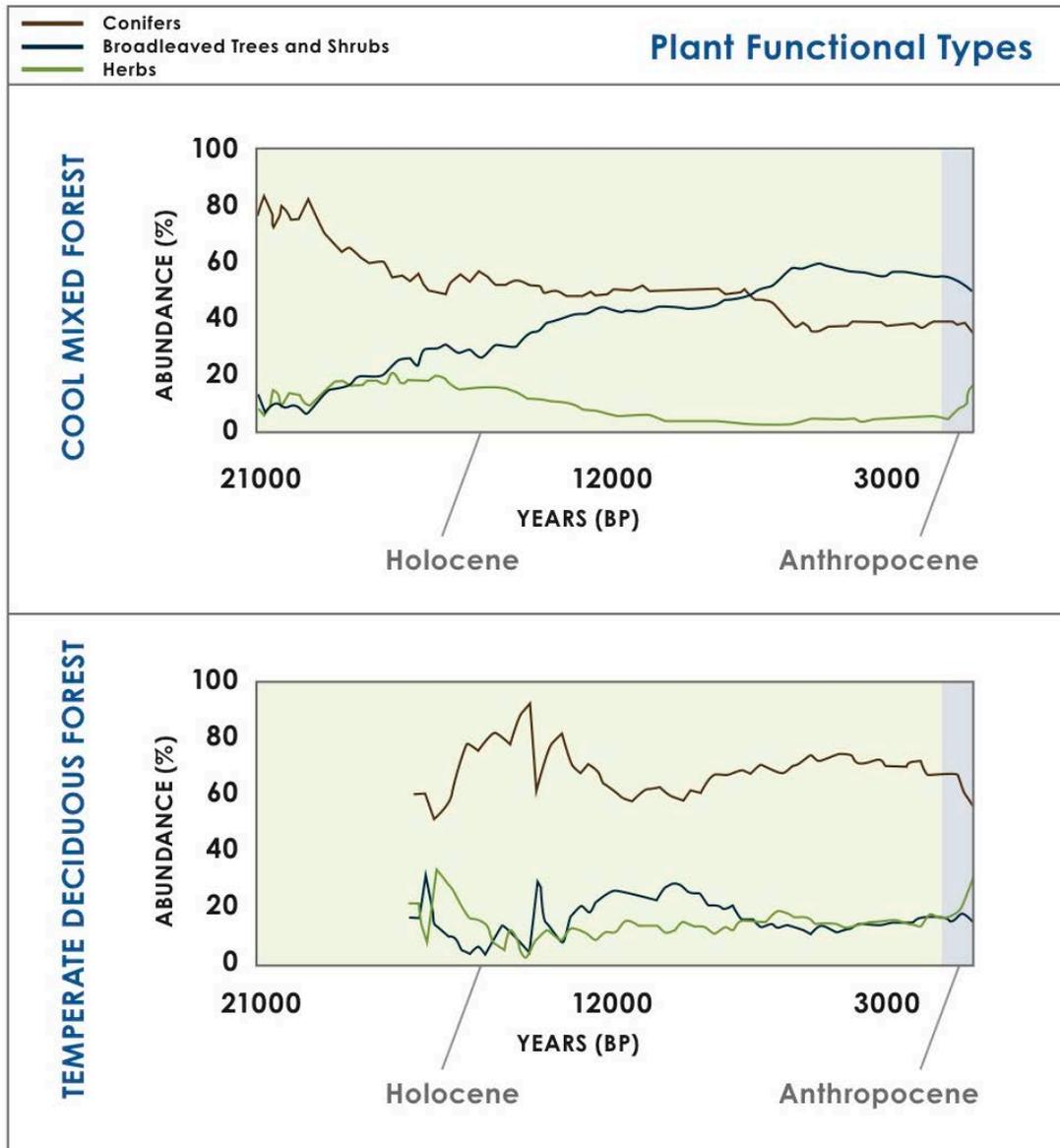


Figure 1. Rates of biotic change in the Holocene and Anthropocene (adapted from Williams et al 2004). Rates of ecosystem compositional change over 21,000 years in two North American ecosystems, cool mixed and temperate deciduous forests. Following the deglaciation of North America, relatively rapid changes are seen during the early Holocene. This was followed by a period of relative stability during the mid- (12000-6000) and later Holocene (6000 – 3000 BP). Rates of change then accelerate in the Anthropocene. The Anthropocene changes seen here primarily reflect the impacts of land use following the European settlement of North America, but may include some early effects of climate change.

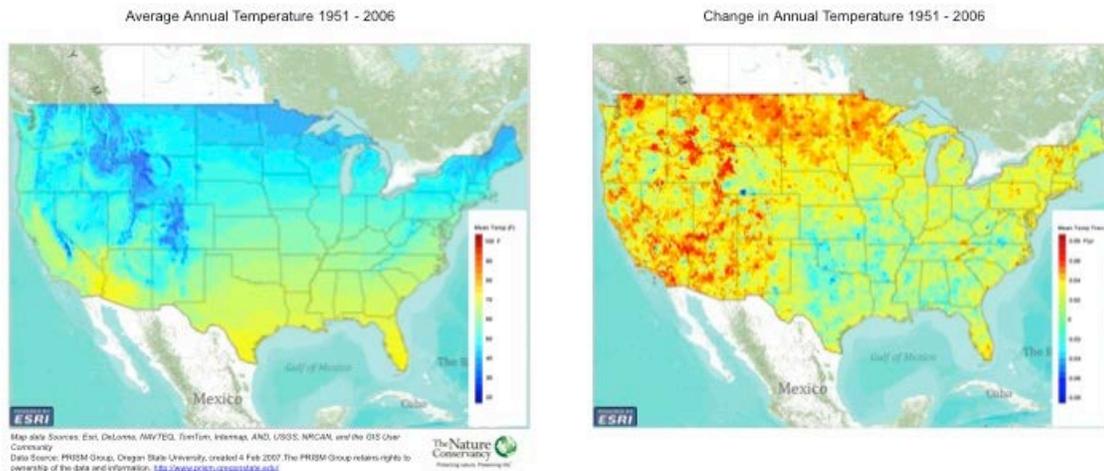


Figure 2. Rates and spatial variability of temperature change across the US. While patterns of mean climate are complex, spatial variation in rates of change adds even more complexity. Left panel, average temperatures for the US, and, right panel, rates of temperature change, both for the period 1951-2006. The data are based on assembled station data, interpolated using a terrain-sensitive algorithm. (Data from Climate Wizard (www.climatewizard.org), developed by the University of Washington, the University of Southern Mississippi and The Nature Conservancy).

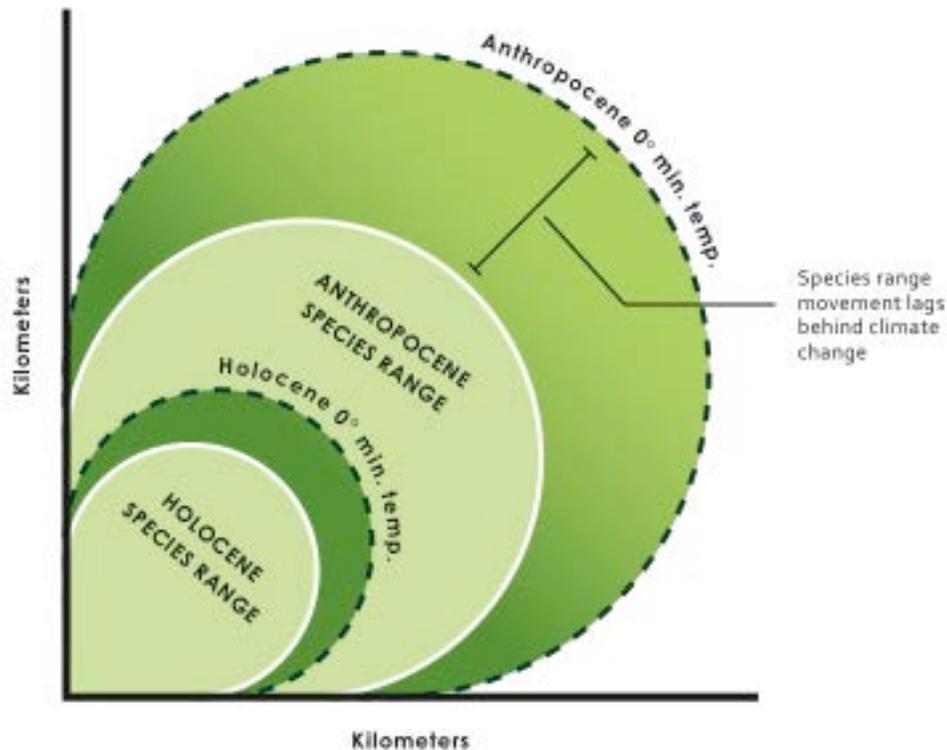


Figure 3. Conceptual model of transient niche responses to climate change, inspired by LaDeau et al 2011. The figure illustrates a hypothetical species whose range ends at the 0° minimum temperature isotherm. The species is initially, in the Holocene, near equilibrium with temperature across its range and a climate envelope estimated here would allow the temperature dimension of species' niche to be inferred. The Anthropocene contour shows the species' distribution at a sample point in time before it reaches equilibrium with new temperatures. As temperatures change, the species' range will lag its climate constraints and at any snapshot in time will still be moving towards steady state. At any point within or along the species temperature limit, non-climatic factors (disturbance, competitive interactions between species) can cause population dynamics so the species need not occupy the entire range at any specific time.

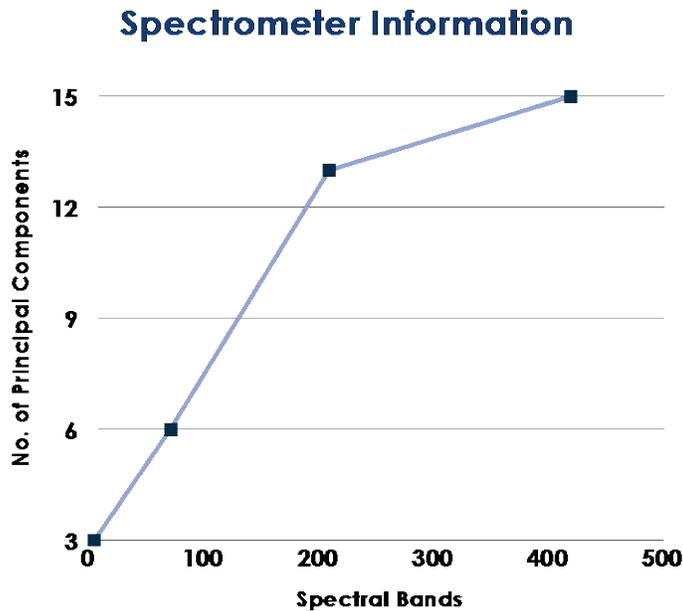


Figure 4. The information content of spectral data. This figure illustrates the impact of spectral resolution on the information content of remote sensing data, by computing the Principal Components of the image. The number of independent components is less than the number of spectral channels because the underlying spectral features are often broader than a single channel and many plant constituents have spectral features in multiple parts of the spectrum, reducing the amount of independent information. We used a 420-band hyperspectral image (380-2510 nm range; 5 nm increments) of closed-canopy forest taken by the Carnegie Airborne Observatory (CAO). These data were degraded to simulate the spectral resolution of other sensors while holding spatial resolution (2 m) and signal-to-noise constant. The simulated sensors included NASA's AVIRIS classic (210 bands; 400-2500 nm; 10 nm increments), the commercially available instrument, CASI (72 bands; 400-1050 nm; 10 nm increments), and Landsat ETM+ (6 bands; 400-2200 nm; 20 nm increments). The dimensionality of information in any given scene will vary with diversity, plant chemistry and canopy structure, but follows this relative scaling of information content.

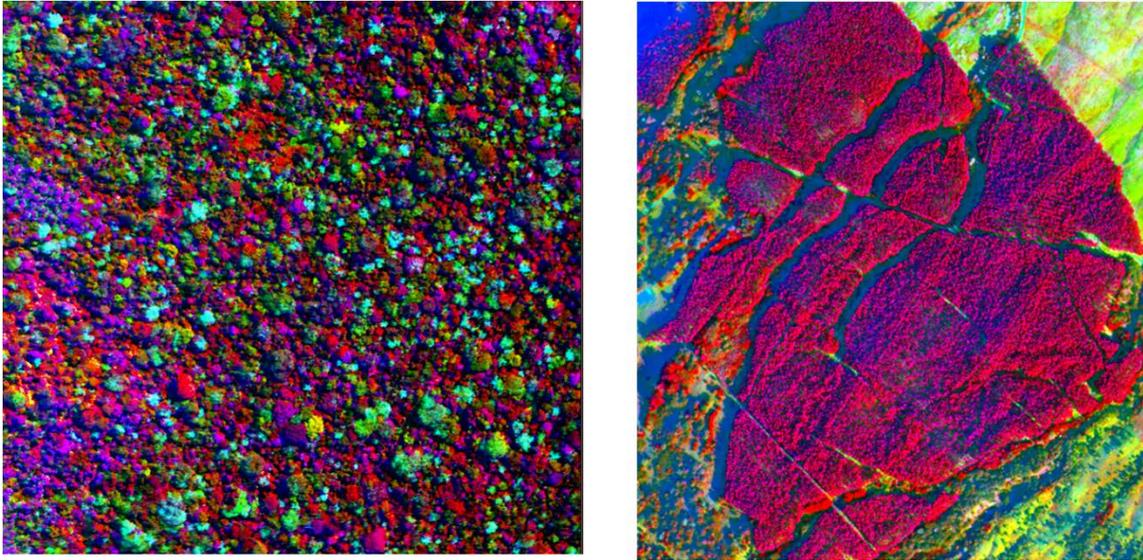


Figure 5. Airborne remote sensing images of ecosystems with high and low plant diversity, obtained by retrieving combinations of growth, longevity and defense compounds including nitrogen, ligno-cellulose and polyphenols. The area on the left is a high diversity canopy in the lowland Peruvian Amazon; the area on the right is a mono-specific eucalyptus plantation on the Island of Hawaii. High species and chemical diversity is expressed as a kaleidoscope of colors in Peru, while low diversity is shown as near constant color in the Hawaiian plantation ecosystem. These detailed maps of functional diversity were obtained using airborne imaging spectroscopy from the Carnegie Airborne Observatory (CAO).