

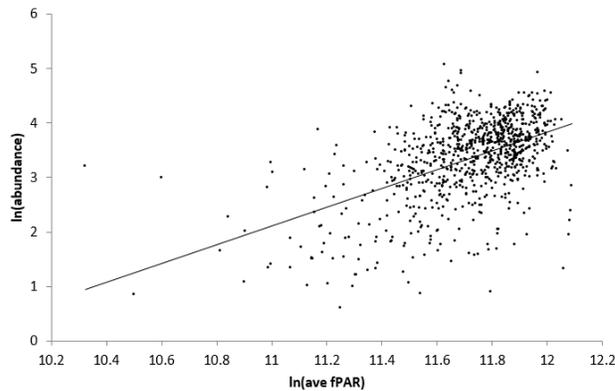
**Title of Study:** Accounting for potential ecosystem capacity in predictions of realized avian diversity: combining species-energy theory and anthropogenic pressures in modeling geographic and temporal shifts in avian community structures.

**Need/Rationale:**

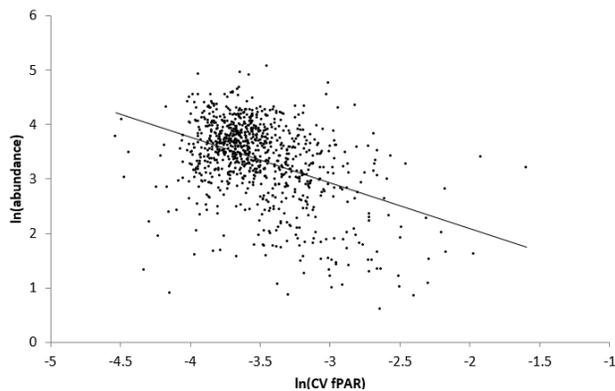
A fundamental question of ecology is what factors govern the distribution and abundance of species across the earth (Ricklefs and Schluter 1993)? Our basic premise is that global climatic patterns (solar radiation, precipitation, temperature) and their complex interactions with local topography and land use history are the basic drivers of plant and animal community structure (Rahbek and Graves 2001; Hillebrand 2004; Mittelbach et al. 2007). Within this framework species-energy theory suggests that basic climate and insolation patterns affect energy availability, which in turn influences **the potential capacity** of ecosystems to support the number of individuals and their species-level variety. Specifically, increasing amounts of energy should result in greater numbers of individuals (abundance) as well as a greater variety of different species (species richness) within the assemblage pool. Although relationships between energy availability and species richness are often complex (Mittelbach et al. 2001), the consensus indicates that energy is the main driver of species richness (Hansen et al. 2011). Much of our knowledge about what shapes species distributions generally, and species-energy relationships specifically, is based on range distribution maps and static environmental data (e.g., insolation, topography). For this reason, the relationships reported in the literature may in fact be idealized constructs of what is expected to exist in pristine systems that lack sources of variation attributed to land use histories and other anthropogenic activities. As a result, ecology's current framework for understanding species distributions and abundances may be overly simplistic and based on system potential and average effects. By expanding the framework beyond average effects to evaluate the variance in capacity of ecosystems to support biodiversity we are hoping to refine a core ecological concept, more completely account for biodiversity response to environmental change, and provide a sounder basis for developing management and conservation recommendations.

Environmental variation can be broken into two basic components, natural and anthropogenic. The source of natural variance in species-energy relationships that may play a strong role in the capacity of an ecosystem to support biodiversity is temporal variability (Currie 1991, Rowhani et al. 2008). Precipitation and temperature vary each year not only in their overall amount, but also in their timing. Delayed springs, droughts, and other climatic deviations from long-term averages, have significant effects on the timing and overall productivity of ecosystems (Linderman et al. 2005). It is, therefore, essential to quantify how the temporal variability of ecosystems affects their capacity to support abundant populations and species rich assemblages. In particular, consistent (i.e. stable) ecosystem conditions may lead to fewer extinction events and refined partitioning of the ecosystem niche space, resulting in higher species diversity (Currie 1991). Conversely, unpredictable and severe environmental conditions may have lower richness due to broader niches and higher extinction risks (Slobodkin and Sanders 1969, Pielou 1975). We completed preliminary (proof-of-concept) analyses and confirmed: (1) the expected positive association between total bird abundance with increasing energy (Figure 1a); and (2) the expected pattern of reduced capacity to support individuals with increasing energy variance (Figure 1b) – where energy is measured by photosynthetically active radiation.

a.



b.



**Figure 1. Relationships between bird abundance and the average (a) and variance (b) of photosynthetically active radiation (fPAR) – a measure of energy.**

Anthropogenic factors are another other source of variance that **influences the realized capacity** of ecosystems to support biodiversity. Anthropogenic factors that are known to affect species abundance and richness include land cover and human settlement patterns (Lepczyk et al. 2008, Pidgeon et al. 2007, 2014) with richness and abundance tending to decline (although not always due to oasis effects; Bock et al. 2008) with the conversion of natural ecosystems to novel ones, following the ecosystem stress hypothesis (Rapport et al. 1985). Furthermore, anthropogenic factors are also affected by ecosystem variability as we have demonstrated by showing how interannual energy variability relates to housing density across the conterminous United States (Linderman and Lepczyk 2013). Understanding how human influences on the landscape relate to an ecosystem's capacity to support biodiversity will expand species-energy theory and refine our conceptual framework for understanding faunal community structure, which is critical both for basic ecology and for establishing conservation priorities in a changing world.

### **Objective(s):**

The overarching goals of the research are to improve our measure of ecosystem capacity to support biodiversity by incorporating the contribution of variance in energy as a driver of system potential and examine the manner by which the realized capacity is altered under the human footprint. Our specific objectives are:

- 1. Climate predicts potential:** Estimate the potential capacities of ecosystems to support individuals and a variety of species based on mean and variance of energy-

related predictors.

**2. Land use predicts realized:** Determine the degree to which anthropogenic drivers (e.g., land use) explain the deviation from the potential – what we are calling the realized – number of individuals and variety of species.

The set of models developed for these two objectives will provide a sequence of analyses that will allow us to assess the effects of different climate futures (changes to ecosystem potential) and land use projections (changes to realized). Thus, our third objective is:

**3. Bird biodiversity response:** Project how bird communities (abundances and variety of species supported) are likely to respond to changes in the energy profile (derived from climate projections) and anthropogenic land use intensities (derived from land use projections).

### **Study Approach:**

*Study Area and Species* – To address our research objectives we will consider the ecosystems of the conterminous US where bird species data have been collected (see *Avian Data* below). Aside from a large variation in the types of ecosystems present, the continental area being investigated varies markedly in temporal variability of energy, has data on species richness and abundance, land use/cover, and expands the geographic scale of analysis beyond previous studies with these data.

*Avian Data* – Breeding bird data from the North American Breeding Bird Survey (BBS) will be used as the main species database. Initiated in 1966, the BBS annually surveys breeding birds along roadsides on permanently established 39.4 km long routes. Currently there are >3500 routes across the conterminous US. At each route, a skilled volunteer conducts an annual survey during the breeding season (May through June), carrying out 50, three-minute point counts per route at 0.8 km intervals. At each point count, the observer records all birds seen or heard within 0.4 km (Bystrak 1981). The BBS provides data on avian abundance and is commonly used for assessments of avian community response to energy availability, land use/cover, housing density, and climate extremes (Flather 1996, Lepczyk et al. 2008, Albright et al. 2010, Hansen et al. 2011, and Wood et al. 2015). We will use all acceptable BBS routes from 1981-2015 across North America to match with remotely sensed imagery. Any routes flagged as unacceptable by the BBS coordinator will be removed, along with routes run by first year observers (Erskine 1978).

*Climate and Vegetation Data* – Interannual climatic data will be derived from available databases and image products. First, the North American Land Data Assimilation System (NLDAS) data provides hourly 0.125 deg climate drivers and estimates of land surface parameters for North America (25-53°N) based on land surface models that are decoupled from atmospheric models (Rodell et al. 2004). Land surface measurements available from the Advanced Very High Resolution Radiometer Long Term Data Record (AVHRR LTDR) version 3 and MODerate resolution Imaging Spectroradiometer (MODIS) provide nearly daily global coverage of earth surface from 1981 to present. We will derive estimates of absorbed Photosynthetically Active Radiation (fPAR) from daily AVHRR and MODIS Normalized Difference Vegetation Index (NDVI) products (Myneni et al. 2002; Yang et al. 2006). Annual summaries of fPAR, as well as 30 year averages and Coefficients of Variation (CV) of fPAR, will be calculated. Summaries and change metrics (as in Linderman et al. 2005) will be subset to correspond to domain and province level ecoregions as defined by Bailey (1994) and individual BBS survey routes.

*Anthropogenic and Protected Area Data* – We will estimate anthropogenic drivers based upon land cover, nighttime lights (a measure of intensive urban development), and human population, each of which has demonstrated impacts on biodiversity (Sanderson 2002). We will also use the protected areas boundary information from the Protected Area Database, which delineates actual land holdings and includes private inholdings within public land administrative boundaries (<http://gapanalysis.usgs.gov/padus/>). All public lands (state, federal, Native American, regional agency, local government, non-governmental organization, and private conservation lands [land trusts]) will be included in the analyses to consider how different types of land protection relates to ecosystem variability.

*Analysis* – Following established protocols developed by CHF and LAC we will analyze data at 3 spatial scales around BBS routes. The finest scale (400 m buffer) is based on the detection distance specified by the BBS protocol; moderate (~5 km) and large scale (~ 20 km) observation grains will be tied to allometrically defined footprints based on the median and maximum natal dispersal distance (Sutherland et al. 2000), respectively, thus capturing landscape effects that have been shown to occur over tens of kilometers (Tittler et al. 2009). The databases and derived products described above will be integrated to address the main research objectives at each of the scales mentioned.

**To address objective 1**, we will map the mean and variance of interannual change metrics (interannual change in ifPAR and timing of fPAR) across the coterminous U.S. and model them in relation to bird abundance and diversity using quantile regression of observed individuals/species under the assumption that more pristine systems would be located at the outer frontier (upper 95<sup>th</sup> or 99<sup>th</sup> quantile) of that scatter. These models will be fit for each ecoregion and will define the relationship between an ecosystem's capacity to support individuals and variety of species based on abiotic environmental attributes suggested by species-energy theory.

**To address objective 2**, we will measure the deviation of each route's current estimate of total individuals (i.e., total abundance) and species diversity (i.e., species richness) from the frontier estimated under objective 1. That measured deviation will become the response variable in a second sequence of model estimation that will attempt to explain the magnitude of the deviation as a function of current land use/cover, nighttime lights, population density, and protected areas.

**To address objective 3**, we will use the climate, land use, and human population projections developed by the RPA Assessment team to construct predictive outcomes of bird community response across the coterminous United States. Climate projections will drive objective 1 model predictions of spatial and temporal shifts in ecosystem capacity to support bird communities. Land use and human population projections will drive objective 2 model predictions of spatial and temporal shifts in realized bird community structure.

#### **Anticipated Benefits:**

Provide the U.S. Forest Service with a projection tool for anticipating how bird abundance and diversity is expected to respond to both changing climate (by modifying ecosystem capacity) and anthropogenic disturbances (by modifying the realized abundance and diversity relationships).

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