PROJECT SUMMARY

Overview:
Global climate change has resulted in shifts in the timing of life history events in many plant and animal species. As a result of such shifts, the phenology of some species has become mismatched with the phenology of other organisms on which they depend, in some cases resulting in declines in fitness and abundance. In this proposal (Causes, consequences, and cross-scale linkages of climate-driven phenological mismatch across three trophic levels) led by Dr. Morgan Tingley of the University of Connecticut, we propose to examine the fine-scale causes and regional consequences of such phenological mismatch at a semi-continental extent for foliage gleaning birds, their insect prey, and the vegetation on which those insects depend. We have assembled an interdisciplinary team of experts in avian and Lepidopteran biology, remote sensing, demographic modeling, and statistics from Georgetown University, University of North Carolina, University of Florida, Pennsylvania State, Evergreen State College, and the Institute for Bird Populations. In addition to answering critical research questions on phenological mismatch we will extend the impacts of our work through both specific training opportunities and broad-based education and outreach efforts.

Intellectual Merit:
Understanding how and why the diversity and abundance of organisms varies non-randomly across the face of the globe is one of the fundamental goals of both basic and applied ecology. Birds and butterflies are the groups for which the most expansive and detailed macroecological datasets on distribution, diversity, and demography exist over space and time. Our proposed research will be the first attempt to examine phenological mismatch across three trophic levels at a semi-continental extent. We will unite these multiple, large-scale citizen science datasets with targeted field data collection, and remotely-sensed climate and vegetation data layers, in order to examine the cross-scale and multi-trophic interactions that connect climate change, phenological mismatch, and fitness consequences. This will be accomplished by: (1) assembling and uniting continental and regional monitoring and citizen-science databases for Lepidoptera and birds; (2) building spatio-temporal models to assess drivers of phenology, calculate direct metrics of phenological mismatch across trophic levels, and evaluate fitness and population consequences of those mismatches; and (3) testing the ability of generated models to predict phenology and population trends for focal birds and Lepidoptera across eastern North America as a function of climate-induced, tri-trophic phenological mismatch. Local studies have documented specific instances of phenological mismatch but fail to inform how mismatches change across spatial, temporal, or trophic scales. Taking a macro-scale perspective on phenological mismatch is critical for understanding the range-wide impacts of climate change.

Broader Impacts:
This proposal addresses Broader Impacts in four key areas. (1) Environmental education for K-18. A key data-generating initiative of this proposal, the citizen science program "Caterpillars Count!", will expand across the eastern United States providing educational opportunities for K-18 students through participation of schools and environmental education centers, and the development of learning activities and programming material. Phenological products, analyses, and visualization of phenology and mismatch will be incorporated into undergraduate teaching at multiple universities involved with the project. (2) Public outreach. A dedicated online portal, promoted by these activities and in publications, will provide exploratory visualization tools for both scientists and the public, while collaborating with the National Phenology Network will assure integration with current phenological data products. (3) Collaborative Science. This proposal will provide training to 4 postdocs and one graduate RA in collaborative science - a skill increasingly recognized as necessary for large-scale inference. (6) Broadening participation. Through integration with existing institutional programs for underrepresented groups, the proposed work will provide opportunities to engage with the science of phenology for such groups at the K-18, undergraduate, and graduate level.

Collaborative Proposal: MSB-FRA: Causes, consequences, and cross-scale linkages of climate-driven phenological mismatch across three trophic levels

1. BACKGROUND AND OBJECTIVES

Shifts in the timing of major life-cycle events (i.e., phenology) such as flowering, fruiting, emergence, and migration are some of the most notable responses of plants and animals to recent climate change (Parmesan 2006). Plants are initiating growth earlier in the spring, resulting in widespread advances in the timing of 'green-up' (Cleland *et al.* 2007). Butterflies are also emerging earlier (Altermatt 2012), while migratory bird species, which respond to both temperature and abundance of insects, are arriving on breeding grounds (Rubolini *et al.* 2007, Hurlbert and Liang 2012) and laying eggs earlier (Both *et al.* 2004). While phenological shifts such as these are widely documented in specific locations across a broad range of taxonomic groups, the degree of advancement or delay varies across taxa, across species within a taxon, and within species across their range. Differential responses to changes in climate conditions can result in *phenological mismatch* between two interacting species (Stenseth and Mysterud 2002). Mismatch occurs when the timing of phenological events has shifted differently for two species resulting in a change in magnitude or outcome of ecological interactions (Miller-Rushing *et al.* 2010a). Phenological mismatch has been documented between plants and their pollinators (Rafferty and Ives 2010, Kudo and Ida 2013), and between predator and prey (Durant *et al.* 2007, Both *et al.* 2009, Reed *et al.* 2013a). A study of 100 bird species in Europe demonstrated that bird species that did not shift their phenology were more likely to have shown population declines (Møller *et al.* 2008). It is now apparent that local-scale phenological mismatch has the potential to be an important, macroscale driver of species' populations.

The majority of mechanistically-informed examples of phenological mismatch come from a few intensive, long-term studies that are local in nature. Foundational work in the Netherlands starting in the 1980s has shown pervasive mismatches between spring leaf-out, caterpillar emergence, and several avian species that rely on caterpillars as a key food resource (Visser *et al.* 1998, Both and Visser 2001, Visser and Holleman 2001, Visser *et al.* 2004, Both and Visser 2005, Visser *et al.* 2006). Critically, Both *et al.* (2006) documented strong population-level consequences for Pied Flycatchers (*Ficedula hypoleuca*) in areas where mistimed migratory arrival resulted in nestling provisioning periods that occurred after peak caterpillar emergence. In another example, non-migratory Great Tits (*Paris major*) in the Netherlands had lower individual fitness in years with greater mismatch with caterpillars, but were resilient to mismatch as their overall population rebounded in the following years due to reduced competition (Reed *et al.* 2013a, 2013b). Lany *et al.* (2016) recently reported on 25 years of monitoring that found Black-throated Blue Warblers (*Setophaga caerulescens*) at a single site in New Hampshire synchronized their breeding phenology to vegetation to maximize fecundity, but that this timing had little correlation with caterpillar abundance. They hypothesize that caterpillar mismatch is less important for birds breeding in forests with high tree diversity where a greater diversity of caterpillars creates more sustained resource waves rather than a single narrow resource peak (Lany *et al.* 2016).

The contrasting results of long-term monitoring from just a few well-studied locations present a host of unanswered questions. This work has carefully documented the mechanisms by which phenological mismatch across multiple trophic levels can lead to demographic and population-level consequences. It is poorly known, however, how pervasive such processes are and to what extent they are important for all species, in all areas, in all years. *Are some species more prone to phenological mismatch than others, and is this predictable by species traits? Are mismatch consequences stronger in some regions, and can this be explained by their environments? Are mismatch consequences linear or are there distinct climatic or phenological thresholds? How transferable in time and geographic space are phenological relationships across trophic levels?* As important as localized studies are to our understanding of phenological mismatch, they fail to quantify the magnitude of the impact of phenological mismatch over the geographically, climatically, and taxonomically heterogeneous systems subject to climate change impacts.

To address these questions and knowledge gaps, a true macrosystems approach, synthesizing and uniting

temporally-extensive datasets across large geographic areas, is required (Figure 1). **Here, we propose to examine the patterns, drivers and consequences of phenological mismatch at a semi-continental scale for foliage gleaning birds, their Lepidopteran prey, and the vegetation on which those species depend.**

Foliage-gleaning birds are perhaps the best taxonomic group for studying the biogeography of phenological mismatch and its impacts (Visser *et al.* 2006, Miller-Rushing *et al.* 2010b). No other group has such detailed and large-scale datasets on distribution, diversity, and demography in space and time. Our previous work has taken advantage of these data to establish that phenological shifts are variable across avian species, and across geographic regions within species (Hurlbert and Liang 2012, Mayor *et al. in revision*). We will extend this to develop a biogeographic dataset of avian resource dynamics to complement existing datasets. Eighty-nine percent of North American bird species are primarily or partially insectivorous, and even species typically thought of as granivores like sparrows and finches rely heavily on insect prey when feeding young (Capinera

Figure 1. Multi-scale depiction of tri-trophic system. Measured quantities (circles) give rise to cross- and within-scale patterns. Inspired by Heffernan *et al.* (2014).

2011). Lepidoptera larvae in particular represent an important and often primary food source *(Holmes et al.* 1979, Holmes and Schultz 1988, Sillett *et al.* 2000, Jones *et al.* 2003) known to influence avian density (Graber and Graber 1983), reproductive success (Rodenhouse and Holmes 1992, Visser *et al.* 2006), clutch size (Perrins 1991) and number of broods raised (Nagy and Holmes 2004, 2005).

Lepidoptera are an ideal group for characterizing avian resource availability over broad geographic extents. Like most insects, Lepidoptera are known to be extremely sensitive to climate, and climate-based phenological shifts have been shown for many species, including in North America (Diamond *et al.* 2014, Cayton *et al.* 2015). Butterflies and moths are the second-most monitored taxa globally after birds, with several large-scale monitoring networks of citizen scientists collecting fine-scale spatio-temporal data replicated over many years. These data represent an untapped resource for estimating the spatial and temporal variability in an important food source over a broad geographic extent.

Several meta-analyses have suggested that higher trophic levels are slower to adapt to climate change, leading to increases in mismatch propagated up trophic ladders (Parmesan and Yohe 2003, Thackeray *et al.* 2010). With the dataset we are assembling, we will examine phenological mismatch across three trophic levels at a semi-continental scale for the first time. We will do this by integrating multiple large-scale citizen science datasets with targeted field data collection and remotely-sensed climate and vegetation data layers in order to examine the cross-scale and multi-trophic interactions that unite climate change, phenological mismatch, and fitness consequences. Specifically, we have four aims:

(1) **to establish the patterns and drivers of spring phenologies for three trophic levels over time and space across east-temperate North America;**

(2) **to quantify phenological mismatch using improved yardsticks, and develop a predictive understanding of where and when mismatch will be greatest;**

(3) **to test demographic and population-level consequences of phenological mismatch across a tri-trophic system; and**

(4) **to evaluate the role of both scale and spatio-temporal transferability in the potential to predict future tri-trophic phenologies and mismatch**
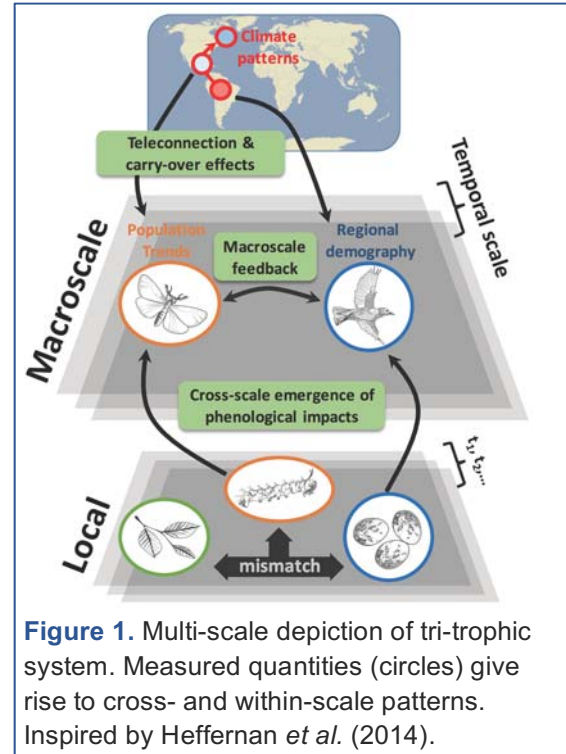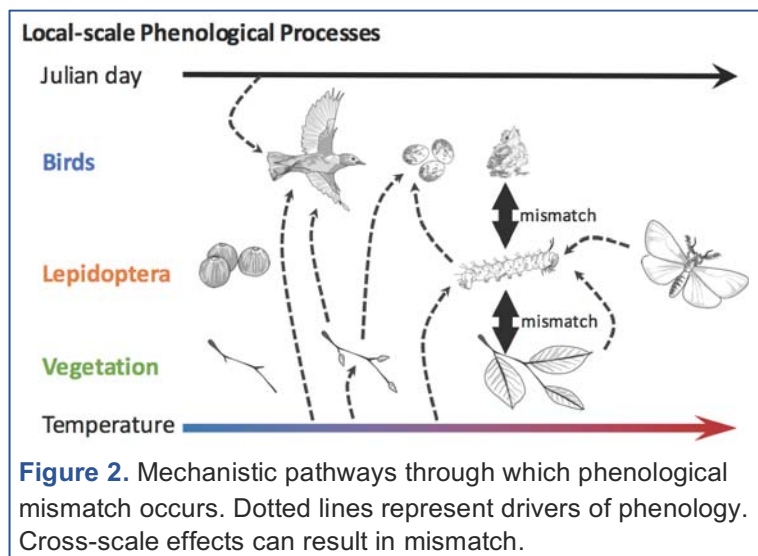
1.1. Expected Significance

Understanding how and why the diversity and abundance of organisms varies non-randomly across the face of the globe is one of the fundamental goals of both basic and applied ecology. This work will take advantage of the wealth of macroecological and monitoring datasets on birds and adult Lepidoptera to provide the first test of the idea that phenological mismatch between one trophic group and its resources can explain broad-scale patterns in demography and population trend. While the link between phenological mismatch and reduced reproductive success or population decline has been established for a handful of species and locations, these fine-scale, local studies fail to inform how phenological mismatch changes across space, over time, for species with different traits, and across trophic level. This missing macro-scale perspective on phenological mismatch is a critical obstacle for understanding the range-wide impacts of climate change (Fei *et al.* 2016). Our proposed research program provides a bridge between traditional ecological studies which involve intensive sampling of a single local area and traditional macroecological studies that examine communities at many locations but are restricted to explaining patterns using coarse, remotely sensed proxies rather than the specific ecological variables of interest. In doing so, we draw strength from computational and statistical advances and an interdisciplinary team of experts (see Project Management Plan), to tackle the explicit challenge of scaling temporally and spatially local patterns and processes to broader scales to understand macroscale climate change impacts.

2. DEFINING A MACROSYSTEMS APPROACH

We evaluate each of our specific aims with respect to three main axes of scale (Figure 1): (a) *trophic scale*, where birds, insects, and plants may show similar or correlated phenological responses; (b) *geographic scale*, where local patterns of mismatch may or may not scale up to present emergent regional patterns; and (c) *temporal scale*, where patterns of mismatch may be stationary or non-stationary in time. The consequences of phenological mismatch for the demography of birds and butterflies will depend greatly on the extent to which fine-scale patterns are correlated in time and space, necessitating a macrosystems approach. Under strong spatial autocorrelation, an individual bird arriving on its breeding ground might have few options for avoiding mismatch should it arrive late relative to the optimal timing for the region. Alternatively, if phenology is strongly influenced by local variation in land cover, then fine-scale habitat selection could potentially allow a bird to minimize perceived mismatch. Finally, because the phenology of migratory birds depends in part upon environmental cues on distant wintering grounds (Cotton 2003; Zuckerberg *et al.* 2015), important teleconnections in time and space may exist with respect to how avian populations respond to climate change.

Our study spans the entire Eastern Temperate Forest biome, and we will use data from 2005-2018—the period with highest data density—as a model building period to predict phenological patterns at each trophic level. We will successively hindcast back in time over three time periods spanning a century to evaluate and refine our model, and then forecast phenological dynamics into the mid- and end-century using Global Climate Models (GCMs). Our grain of analysis varies from 50-km wide grid cells (~2,500 km², a scale set by limits of data density) to entire ecoregions (~1,000,000 km²), nearly 3 orders of magnitude. If phenologies or mismatches show large-scale correlations across any of these three axes, then we would expect cross-scale

Figure 2. Mechanistic pathways through which phenological mismatch occurs. Dotted lines represent drivers of phenology. Cross-scale effects can result in mismatch.

emergence of ecosystem consequences, such as region-scale, long-term, or community-wide phenological shifts. Together, multiple macroscale phenological patterns can feed back, resulting in regional or long-term demographic consequences or population declines. By taking a multi-scale, multi-axis approach to phenological mismatch, we will be able to test and evaluate these macroscale interactions across the tri-trophic system while also predicting their likely impact into the future.

2.1. Inferential and modeling framework for macroscale questions

Our questions and models are framed around a tri-trophic ecological system with well-described mechanistic linkages (Figure 2). Climate can directly drive populations of plants and insects because temperature determines how much energy is available for growth for these ectothermic organisms. Further, insect emergence can be triggered by the presence of host plant material and so is impacted by climate both directly and indirectly through action on hostplants (Altermatt 2012, Kharouba *et al.* 2014). Bird arrival can depend on migratory distance, wintering location, and other species-specific traits (e.g., diet, body size, flight efficiency) but arrival on breeding sites is sensitive to spring climate (across the migratory range) and plant phenology (Palm *et al.* 2009, Saino *et al.* 2011). Clutch incubation (and thus the beginning of provisioning) is ultimately limited by arrival phenology plus the time necessary to find a mate, build a nest, and lay a full clutch. However, birds can flexibly delay incubation in response to local conditions, such as delayed green-up or food phenology (Lany *et al.* 2016).

Connecting and uniting these mechanistic linkages requires a cohesive modeling framework. We will combine data across dozens of different data sets, each with its own spatial and temporal resolution and density. While we restrict inference to the Eastern Temperature Forest ecoregion (Figure 3a), within this broad, semi-continental extent we intend to model phenological events and their mismatch across the
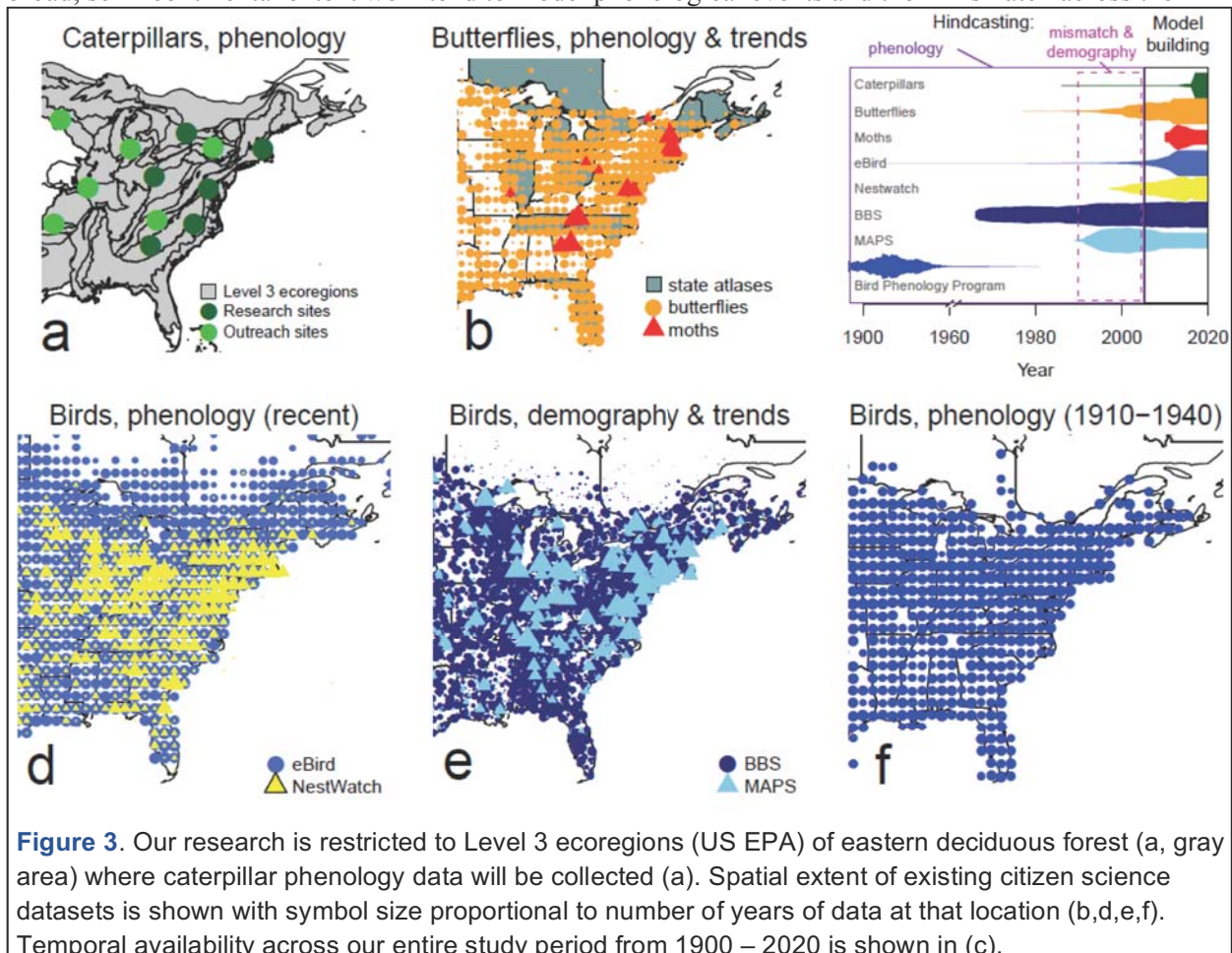

Figure 3. Our research is restricted to Level 3 ecoregions (US EPA) of eastern deciduous forest (a, gray area) where caterpillar phenology data will be collected (a). Spatial extent of existing citizen science datasets is shown with symbol size proportional to number of years of data at that location (b,d,e,f). Temporal availability across our entire study period from 1900 – 2020 is shown in (c).

entire spatial extent. To accomplish this, while accounting for variable sampling density, our general approach will be to fit *Bayesian spatio-temporal hierarchical models* that draw strength from areas or times with dense sampling and allow the fitting of models to similar or neighboring areas or times with poorer sampling, all while robustly accounting for uncertainty. The general framework for this model would be, response $= f(\text{predictors} + \phi_j + \eta_i)$, where: f is an appropriate linear or non-linear function—including the hierarchical use of latent variables—that models the response variable; $\phi_{j,t}$ is an auto-regressive term per jth ecoregion (Figure 3a) that links processes temporally; and η_i is a spatially auto-correlated error term, modeled as, $\eta \sim N(0, \Sigma_\eta)$, where Σ_η is an appropriate parametric covariance term. While the specific form of the relationships will vary, this general approach to spatio-temporal hierarchical modeling will be implemented in each of the following aims.

BOX 1: PHENOLOGICAL DATA SETS (*see §Data Management for further details***)**

Climate. We will calculate growing degree days (GDD) from daily, gridded climate data at a 1-km^2 resolution from **Daymet** (Thornton *et al.* 2014), available from the Oak Ridge National Laboratory Distributed Active Archive Center. We use the **WorldClim** climate dataset to characterize January-March temperature and precipitation on non-US avian wintering grounds at 1-km^2 resolution.

Vegetation. We will estimate green-up using data from the satellite-derived **MODIS** product MCD12Q2 Land Cover Dynamics V005, which provides the date of "onset of greenness increase" based on the Enhanced Vegetation Index (EVI) at a 500 m resolution.

Lepidoptera larvae. PI Hurlbert has been involved in the collection of caterpillar density and phenology data throughout the southeastern US since 2010, and in 2015 launched the citizen science project **Caterpillars Count!** (http://caterpillarscount.unc.edu/), which allows interested participants to submit their own standardized observations of caterpillar phenology using established methods (Holmes and Schultz 1988). We will collect data on caterpillar phenology at 24 sites distributed across 6 regions, varying in latitude from Atlanta to Toronto. Expansion of this citizen science project via workshops described under Broader Impacts is expected to result in caterpillar data from 10-20 additional sites.

Lepidoptera adults. We make use of both continental and regional scale citizen science programs dedicated to monitoring adult butterflies and moths. Most prominently these include the North American Butterfly Association (**NABA**), Butterflies and Moths of North America (**BAMONA**) and **e-Butterfly**. We also will use data from more intensively monitored regional transects where volunteers do weekly or biweekly surveys using a standardized protocol at hundreds of sites across IL, OH, MI, IA, DC and TN. A full list of data sources is in the §Data Management Plan.

Birds. Spring arrival phenology for birds will be examined using data from **eBird**, a citizen-science data-set curated by the Cornell Laboratory of Ornithology. We also use data from **Project NestWatch** (Bonney *et al.* 2009), which includes over 100,000 records on the timing of nesting of birds throughout North America. Finally, we use the historical Bird Phenology Program (www.pwrc.usgs.gov/bpp) dataset which provides information on bird phenology from across the continent over the period 1900-1940.

3. AIM 1: PATTERNS AND DRIVERS OF SPRING PHENOLOGY

Prior to being able to model and forecast phenological mismatch across trophic levels and spatial scales, it is necessary to understand the drivers of phenology of each trophic level in isolation, and how each of those phenologies has shifted over time and space. Thus, while this aim is in large part descriptive, we will provide the most comprehensive test to date of the following predictions derived from the literature about how phenological responses are expected to vary with geography, trophic level, and other traits.

- *Phenological shifts will be greater at lower latitudes where the growing season is longer.*
- *Phenological shifts will be greater for lower trophic levels which depend most directly on climate.*
- *Phenological shifts will be greater for short distance compared to long distance migrants.*
- *Phenology of consumers will be better predicted by the phenology of their resources than by climate.*
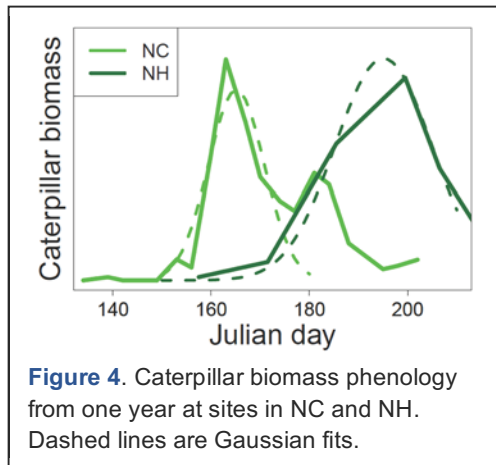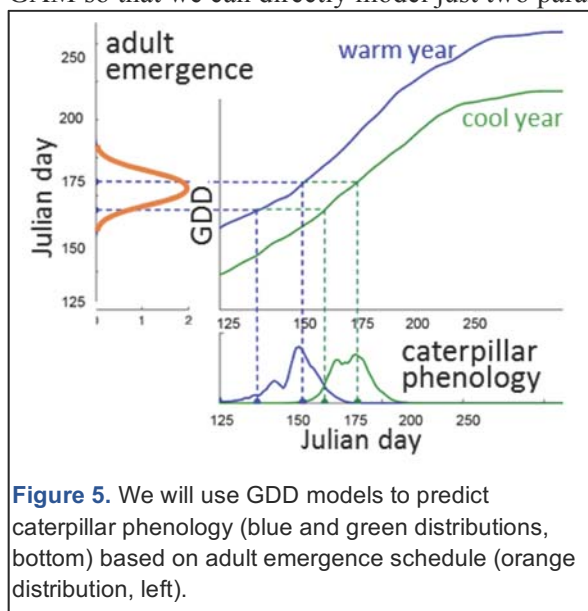
3.1. Analytical approach

<u>Vegetation.</u> To account for temperature impacts on growth, we will use the Biome-BioGeochemical Cycles model (BBGC, White *et al.* 1997) which was found to slightly outperform a pure growing degree day (GDD) model within deciduous broadleaf forest (Fu *et al.* 2014). According to the BBGC model, woody plant green-up begins after the running sum of average daily soil temperature exceeds a critical threshold that is a function of mean daily average temperature (*Tavg*) as: $Tcrit = \exp(a + b*Tavg)$, where *a* and *b* are fitted parameters (White *et al.* 1997, Fu *et al.* 2014). We will use the daily Daymet climate data (Box 1) to develop predictive models of remotely sensed green-up, which will be validated with on-the-ground vegetation phenology data provided through collaboration with the National Phenology Network (see letter of support).

<u>Adult Lepidoptera</u>. We will model flight dates for common species using generalized additive models (GAMs) which allow for complex functional forms which often arise from multivoltine species (Rothery and Roy 2001, Hodgson *et al.* 2011; Figure 4). We will model the full phenological profile of adult Lepidoptera and compare first flight and peak flight in order to understand both phenology of adult Lepidoptera (most clearly distinguishable in spring emergence), and resource availability to birds during the nestling provisioning period. In addition to modeling the phenology of individual species for which sufficient data exist, we also model the phenology of all species in aggregate using joint species distribution models (e.g., as in Thorne *et al.* 2006) in which species with shared ecological traits (e.g., overwintering stage) are modeled as distinct subgroups.

<u>Caterpillar phenology – direct metric.</u> We will model caterpillar biomass phenology during the avian breeding season (within 10 weeks of green-up) based on our observations at ~30 sites in six regions along a latitudinal gradient (see Figure 3a) throughout eastern North America in each of Years 1 and 2. We will do this by fitting Gaussian curves in which the peak biomass date and standard deviation are functions of GDD, latitude, and green-up date. Based on our own pilot data and those from Hubbard Brook, caterpillar density and biomass usually shows a clear peak (Figure 4). We use a parametric function rather than a GAM so that we can directly model just two parameters (μ and σ). In our spatiotemporal model, we will use these estimates of biomass phenology as direct, observed response variables.

Figure 4. Caterpillar biomass phenology from one year at sites in NC and NH. Dashed lines are Gaussian fits.

Figure 5. We will use GDD models to predict caterpillar phenology (blue and green distributions, bottom) based on adult emergence schedule (orange distribution, left).

<u>Caterpillar phenology – indirect</u>. The phenology of adult butterflies and moths will be used to infer the phenology of caterpillars over regions and years where caterpillar data are absent but adult records are plentiful (Figure 3b-c). We will focus on adult Lepidoptera whose larvae feed mainly on woody vegetation, the primary foraging substrate of foliage-gleaning birds. Although most of our data will come from surveys of adult butterflies, comparisons of adult butterfly and moth data from similar locations in the same years shows that the phenology of the entire forest community is similar between these groups. We rely on two types of information to infer caterpillar phenology from adults. **First**, the amount by which to project forward or backward will be determined by a combination of models that derive

emergence and death schedules from adult flight patterns (Zonneveld 1991) and developmental models using generic GDD thresholds. The former is necessary because most adults live for several days or weeks so the presence of an adult does not translate directly into an emergence event. This model, which has since been modified to use more realistic distributions (Calabrese 2012) will be used to estimate the number of adults emerging each day during the season based on the flight curve of adult individuals (Figure 5). Although GDD thresholds (minimum temperature needed to initiate growth) vary between species, a database currently being compiled by co-PI Ries' lab shows they are highly conserved, and similar between moths and butterflies (moth: 10.6°C, SD = 3, n = 25; butterfly: 10.7°C, SD = 2, n = 10). This growing database will allow us to use species-specific data where possible, but reasonable estimates otherwise. We will use Daymet data to estimate at 1km resolution the number of GDD accumulated either backward or forward until we reach the critical larval stages (following Nail *et al.*, *in prep*). **Second**, species-specific overwintering stage determines whether we should project caterpillar presence backward from the observation of an adult (e.g., if the species overwinters as an egg or early-instar larvae) or forward (if it overwinters as later-instar larvae, pupae, or adult). Overwinter stage for North American butterfly species are well-known, but not moths. However, both moths and butterfly species are known to overwinter at all stages, and overwinter stage is highly conserved among clades making it possible to reasonably infer overwinter stage when unknown (Ries, unpublished data). Together, this mechanistic model of adult-derived caterpillar phenology will be validated using both our own caterpillar data as well as high-quality external data collected on monarch (*Danaus plexippus*) adult and juvenile stages. *However*, should the mechanistic modeling of phenology perform poorly, we will use the phenomenological relationship between our own empirical peak caterpillar dates and spring flight date of adults in those same regions. Temperature impacts the development time, and hence the lag between life stages, and so will be included in this model as well. This simpler model will allow us to predict caterpillar phenology curves in other regions and years based on adult butterfly phenology and latitude, although presumably it would have poorer spatial or temporal transferability than the mechanistic model (Kearney 2006).

Bird phenology. As in our previous work (Hurlbert and Liang 2012, Mayor *et al. in revision*), migr-ation arrival phenology will be modeled as a logistic function of the proportion of eBird checklists reporting a focal species as a function of Julian day (Figure 6a), and then spatially smoothed (Arab *et al.* 2016). We will mod-el all foliage gleaning species breeding in our study region with sufficient data (~30-40 species). On-set of egg incubation is minimally limited

Figure 6. (a) Logistic modeling of bird arrival phenology from empirical observational data. Provisioning phenology will be modeled as a translation of arrival phenology. (b) Mean trend in arrival time for 27 bird species, 2001-2012, from Mayor *et al.* (*in revision*).

following arrival by the amount of time to make a nest (n_k, a species' trait) and lay eggs (e_k, 1 day per egg)—both well-documented quantities in North American birds (Rodewald 2015)—but can be flexibly delayed, f_k, in response to local conditions (Lany *et al.* 2016). Incubation length, i_k and total provisioning time show low plasticity within and among species (M. Tingley, unpublished analysis), and will be taken from published accounts (Rodewald 2015) and verified using Project Nestwatch data. We will evaluate predictor parameterizations of increasing complexity for avian phenology (both arrival and incubation onset) as well as different functional forms (Arab *et al.* 2012) by sequentially including spring climate phenology (GDD), vegetation green-up date, peak caterpillar date, and winter-range climate.
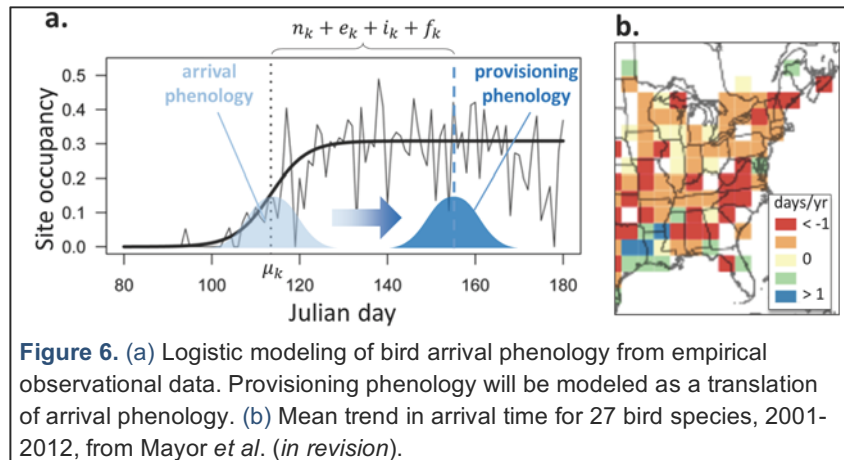
3.2. Summary

In this aim we assemble the largest known datasets to date on phenology across three trophic levels, and establish the primary drivers of phenology for each, as well as how phenological shifts vary across trophic level, taxonomic level, geographic region, and climate change context. The outcomes of this aim, which include novel modeling for describing spatio-temporal variation in both caterpillar and avian phenology, will be critical components used to quantify and predict mismatch between trophic levels (Aim 2).

4. AIM 2: QUANTIFYING AND PREDICTING MISMATCH

Most research to date on phenological shifts has simply documented how the timing of phenological events has varied over time (e.g., demonstrating earlier budburst in more recent years), or as a function of climate (e.g., early bird arrival in warmer springs). While a reasonable starting point for documenting change, such relationships provide no benchmark for judging how an organism *should* be responding, i.e., if it were adapting perfectly to changes in climate and/or phenology of key resources. This realization prompted Visser and Both (2005) to call for a better "yardstick" based on the phenology of resources upon which an organism depends. Here, we develop direct and indirect yardsticks for evaluating phenological mismatch in Lepidoptera and birds, and test a number of hypotheses regarding the geographic context and traits expected to increase species' susceptibility to mismatch. Specifically:

- *Mismatch will be greater in regions with stronger warming trends*, as species' inability to keep up with shifting phenologies are expected to accrue linearly with warming temperatures.
- *Mismatch will be greater for univoltine than multivoltine Lepidoptera*, as multivoltine species respond more strongly to GDD than univoltine species (Cayton *et al.* 2015).
- *Within Lepidoptera, mismatch will be greater for host plant specialists versus generalists*, as generalists will have multiple resource options regardless of their phenology in any given year.
- *Mismatch between birds and Lepidoptera will be greater in systems with simpler Lepidopteran communities*, as resources will be more narrowly pulsed.
- *Within birds, mismatch will be greater for long distance migrants*, as they rely on migration cues that are less strongly correlated with breeding ground conditions compared to short distance migrants.
- *Mismatch will propagate across trophic levels*, such that avian-Lepidopteran mismatch will be greater in years with high Lepidopteran-vegetation mismatch.

4.1. Analytical approach

Lepidopteran mismatch. We will assess the mismatch between Lepidoptera and their host plants in two ways. First, we use a variance partitioning approach which tests whether climate (e.g. GDD) has any explanatory power for predicting Lepidoptera phenology above and beyond its effect on green-up. If the unique variance component attributed to climate is close to 0, then Lepidoptera must be tracking interannual variation in climate in the same manner as vegetation. The greater this variance component, the greater the potential for mismatch.

Our second approach examines phenological shifts of the consumer over time (butterflies and caterpillars) relative to shifts in the resource (vegetation or green-up) at a given location (Both *et al.* 2009, Mayor *et al*. in revision). Figure 7 highlights three possibilities, although others exist. First, under perfect resource tracking, an advance in green-up of *x* days would result in an equal advance of *x* days in butterfly phenology (*blue line*). Second, butterfly phenology shifts might always lag shifts in green-up by some fixed number of days (*green*). Finally, of most concern would be if shifts in butterfly phenology do not occur at an equal rate to shifts in vegetation phenology (*red line*), implying that as the climate
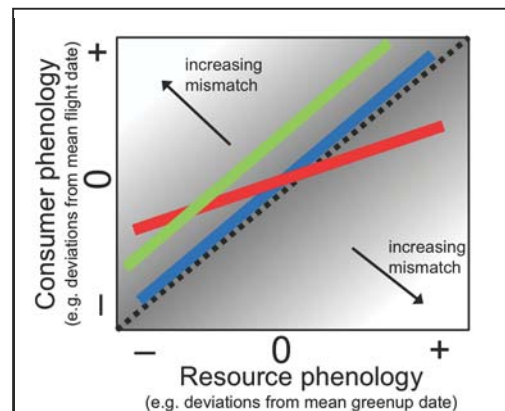

Figure 7. Phenological shifts by consumers in relation to shifts by their resources provides a measure of mismatch (see text).

changes phenological mismatch will get progressively worse. Across spatial scales, we will calculate mismatch trend as the slope of the line relating consumer shifts to resource shifts. We will model species-specific mismatch trends as a function of key life history traits such as voltinism and diet specialization, as well as latitude.

<u>Avian mismatch.</u> We can calculate phenological mismatch between birds and their resources using both relative and absolute yardsticks. The relative yardstick examines deviations in mean avian arrival date as a function of deviations from mean spring flight date of butterflies or mean green-up. Preliminary work by our group (Mayor *et al. in revision*) has also calculated relative yardsticks of mismatch between birds and green-up and found strong trends across broad geographic regions (Figure 6b).
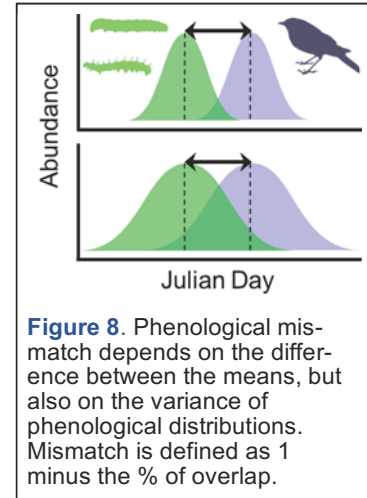

Figure 8. Phenological mismatch depends on the difference between the means, but also on the variance of phenological distributions. Mismatch is defined as 1 minus the % of overlap.

Absolute yardsticks provide more mechanistic estimates of mismatch which we expect to be better predictors of population-level impacts (Aim 3). Using our derived products (Aim 1), we will translate regional butterfly phenograms for a given year and location into expected caterpillar phenograms which provide an absolute yardstick for when birds should be raising their young. We calculate absolute mismatch based on the overlap of the normalized caterpillar phenogram ($c(t)$) and the normalized avian provisioning phenogram ($p(t)$), both derived from Aim 1, as: $m = 1 - \sum \min(c(t), p(t))$, where $m = 0$ if the curves do not overlap at all, and $m = 1$ when the two curves are identical (Figure 8). As noted by Miller-Rushing *et al.* (2010), this type of measure takes into account how the variance of the respective phenograms impact mismatch as well as the difference in means. By using Bayesian statistical models, uncertainty in phenograms will be easily propagated through to mismatch estimates. Absolute mismatch will be calculated for each bird species in each grid cell, and summarized within each eco-region, for a given year, but trends and patterns in mismatch can be modeled spatially and temporally. Mismatch will be modeled as a function of migratory distance, species traits, and latitude.

4.2. Summary

Building on the work done in Aim 1, we will create spatiotemporal maps of phenological mismatch between Lepidoptera and vegetation, birds and vegetation, and birds and Lepidoptera. In the latter case, we will provide the first analysis of absolute rather than relative phenological mismatch over a semi-continental extent, identifying the traits and geographic context that make species more or less susceptible. These measures of mismatch will be used as inputs to the demographic modeling in Aim 3.

5. AIM 3: DEMOGRAPHIC CONSEQUENCES OF MISMATCH

Recent calls have highlighted the needs for demographic analyses in an effort to better predict the effects of changing climate and the mechanisms that underlie those population-level effects (Post *et al.* 2009, Franklin 2010, Schurr *et al.* 2012, Normand *et al.* 2014). Dynamic models that integrate across multiple populations and species will be especially useful in understanding the range dynamics of individual species and meta-communities as they respond to climatic variability in real time (Yackulic *et al.* 2014). A demographic approach will be especially valuable in our case where we will have available time-series of annual climate, mismatch, and food availability and can examine how year-to-year variation corresponds with demographic variation for both birds and butterflies. Analyses will directly link annual measures (e.g., caterpillar abundance and degree of absolute mismatch) to demographic measures (λ, recruitment, survival) using hierarchical modeling approaches that account for state uncertainty in individual observations, link data across populations and species through the use of hyper-parameter structure, and integrate analyses across data sets to maximize our analytical efficiency. Specifically, we predict:

- ***Regions with greater mismatch will exhibit more negative population trends** (butterflies, birds)**, and lower fecundity, recruitment, and survival rates** (birds only)*.

- *Mismatch will explain more variance in fecundity than survival, recruitment, or population size.*
- *Absolute mismatch metrics will explain more variance in demography than relative metrics.*
- *Mismatch will have a weaker effect on demography at lower latitudes with longer breeding seasons.*

5.1. Analytical approach

We will employ three general approaches to modeling demographic rates. The approaches represent a gradient of increasing resolution regarding demographic processes but decreasing data availability. In each case we will estimate the relationship between demography and mismatch and determine how these relationships vary spatially and within and among species. Bird data will employ all 3 approaches while

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BOX 2: AVIAN DEMOGRAPHIC AND POPULATION-LEVEL DATA SETS

Bird population size and growth. The North American Breeding Bird Survey (**BBS**) is a continent-wide avian monitoring network which consists of over 5,000 roadside survey routes, many which have been surveyed for >40 years (Bystrak 1981, Sauer *et al.* 2008). These data have long served as a source of information about regional population trends (Flather and Sauer 1996, Sauer 2011, Bled *et al.* 2013).

Bird demography. The Monitoring Avian Productivity and Survival (**MAPS**) dataset, curated by the Institute for Bird Populations (IBP), has collected data from constant-effort mist-netting at over 1,200 stations spread across North America since 1989. MAPS data provide direct estimation of key vital rates for birds, including apparent adult survival, recruitment, and breeding productivity (DeSante *et al.* 1995, Saracco *et al.* 2010a, 2010b). See §Data Management Plan for more details.

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butterfly data will rely on the first, state-space modeling, approach due to data availability.

Avian Community State-Space Population Models for Count Data. We will analyze BBS data using Bayesian state space models (SSM; De Valpine and Hastings 2002) as extended by Ross *et al.* (2015) to account for variation in population dynamics across multiple locations (and also multiple species in our case). Predictions will take the form of a simple population growth model where $N_{t+1} = N_t * e^r$ (i.e., population size N_{t+1} is a function of the previous population size N_t multiplied by the exponent of the instantaneous population growth rate, r; Note that $e^r = \lambda$). Our goal is to estimate the relationship between annual environmental variables (e.g., climate) and population growth rate in that year, r_t, while at the same time accounting for observation uncertainty and unexplained variation in annual growth. We will fit the hierarchical model by reworking the growth formula into a linear equation where $\log(N_{ti}) = \log(N_{t-1,i}) + r_{ti}$. The growth parameter will be treated as a random variable where the mean is a function of time- and space-varying covariates (i.e., local food abundance and phenological mismatch) and unexplained annual variation captured using random-error terms including site specific effects so that $r_{ti} = \boldsymbol{\beta}*\boldsymbol{X} + \delta_j + \varepsilon_{ti}$. The values of $\boldsymbol{\beta}$ represent the sensitivity of population growth rate to variation in a specific annual driver and thus directly quantify population level effects of change in values of that predictor. We will account for observational error in counts in how we model the relationship between our observed data and the predicted population size. If $\log(N_{ti})$ is the log-transformed population size, we will assume that the log observed count (total number of birds of a given species observed) for a route and year, Y_{ti} is given by $Y_{ti} \sim Normal (\log[N_{ti}] , \sigma^2_{obs})$. Finally, the model structure is easily extended to incorporate multiple species by indexing counts to also include species (s = 1 to $n_{species}$), so that $\log(N_{tis}) = \log(N_{t-1,is}) + r_{tis}$ and modified similarly for other levels of the hierarchical model. This modification will allow us to model the relationship between species traits and the effect of our annual covariates on local population growth rates by modeling $\boldsymbol{\beta}$ as a function of species specific covariates (e.g., migratory distance or foraging guild). This extension is akin to community occupancy modeling approaches (Iknayan *et al.* 2014, Thorson *et al.* 2016) and will provide a synthetic framework for incorporating uncertainty when estimating community level patterns in the effects of mismatch. The approach allows for efficient scaling for data sets given millions of observations across a community.

Lepidopteran Community State-Space Population Models for Count Data. We will use a similar approach for butterflies and moths as for birds, above, except Lepidoptera have the added complexity of being modeled from many different data sets with different spatial and temporal (inter- and intra-annual)

resolutions (Box 1). To account for this, datasets—comprising all available continental and regional Lepidopteran monitoring programs—will be hierarchically combined where N_{tis} is an imperfectly observed, latent variable with detection-specific processes that vary with universal factors (e.g., Julian day, weather) and dataset specific factors (i.e., categorical detection covariates unique to each dataset). The general hierarchical modeling framework otherwise follows as described previously for birds with the addition of density-dependence. To best leverage available data, we will focus analyses where Lepidopteran monitoring data density and quality is greatest (Figure 3b).

Mark-recapture models of avian vital rates. For MAPS data we will estimate the relationship of annual covariates to population growth rate (λ), survival (φ), recruitment (*f*), and productivity (P, an index related to fecundity) building on standard approaches for analyzing the data (DeSante *et al.* 1995, Saracco *et al.* 2010a, 2010b, 2016). The mark-recapture data collected at MAPS stations can be analyzed to estimate demographic parameters while accounting for incomplete detection and for transient individuals that may not belong to local populations, but which are caught at local MAPS stations. We will estimate λ using reverse-time modeling (Pradel 1996, Pradel *et al.* 1997). We will estimate survival using the standard Cormack-Jolly-Seber survival estimator modified using an ad hoc approach to account for transient individuals (Pradel *et al.* 1997, Hines *et al.* 2003). Recruitment will be estimated as the difference of the first two estimates $f = \lambda - \varphi$. We will extend previous modeling of these data sets to incorporate covariates related to annual variation in mismatch and food availability. All models will be run using Program MARK called from the RMark package in R (Laake *et al.* 2013). In addition to the mark-recapture data, MAPS stations provide information about productivity (P) based on the age ratio of birds caught during banding operations (number of juveniles to adults), which will also be modeled as a function of food and mismatch covariates using the hierarchical modeling approach for estimating variation in productivity (Miller and Otis 2010). Effects on P will measure initial effects on productivity within years, while mark-recapture estimates of will measure recruitment into the adult population.

Integrated Population Model for avian count and mark-recapture data. Recent methodological development focused on estimating demographic rates in wild populations has emphasized the value of integrated approaches that link multiple data sets to make inferences about demographic processes (Schaub and Abadi 2010, Maunder and Punt 2013). MAPS and BBS provide a natural opportunity to implement an integrated population model (IPM) that links the mark-recapture analysis of the MAPS data with the state-space model for the BBS data via their shared inclusion of the local population growth rate parameter (λ). We will focus only on species that we know to have good data for the MAPS component and which represent a range of ecological traits (~15). We will use a joint estimator, which combines the BBS model (state-space model described above) and the mark-recapture estimator implemented within a Bayesian framework for the MAPS data (Jergenson *et al.* 2014). The primary challenge in jointly estimating parameters is that while BBS routes and MAPS stations co-occur within grid cells used for the phenological analyses they do not directly coincide in location. Thus, we will need to incorporate within-cell variability in population growth rates into the model. We will do this by assuming there is an average growth rate for all populations within a cell λ^{*} and that population growth rates for BBS routes and MAPS stations within a cell come from a random distribution with mean λ^{*}, so that $\lambda_{it} \sim N(\lambda^{*}\sigma_{\lambda})$. We will use the IPM to validate our results from the individual MAPS and BBS analyses, to more efficiently decompose the contribution of reproduction and survival to population change, and to improve precision of estimates.

5.2. Summary

Population and demographic data provide powerful and unique opportunities to estimate the magnitude and variability of the effects of phenological mismatch on bird and butterfly populations and bird demographic rates. Output of these models will be the first large-scale influence on the effects of mismatch on these species, and will provide opportunities for transformative discoveries on how climate change impacts wide groups of species over space and time as well as improvements in the statistical tools available for large scale demographic analyses. Fully parameterized models from Aim 3, along with models from Aims 1 and 2, will form the nucleus for testing spatial and temporal transferability in Aim 4.

6. AIM 4: LINKING PHENOLOGICAL MISMATCH ACROSS SPACE AND TIME

Aims 1 to 3 focus on the mechanistic components that drive phenology and result in phenological mismatch and its demographic consequences. In Aim 4, we will evaluate both how models of phenological shift and mismatch *scale* in space and *transfer* in space and time. We are keenly interested in the spatial scales at which mismatch is strongest across our tri-trophic system. We hypothesize that **if mismatch exhibits strong spatial autocorrelation, then the demographic consequences of mismatch at fine scales may be compounded at coarser scales, while fine-scale geographic variation in mismatch may result in weaker impacts**. We are additionally interested in the transferability of phenology, mismatch, and demographic models. Temporal transferability will be estimated through hindcasting to previous decades and evaluating predictive strength with out-of-sample data. We will also evaluate spatial transferability of models built in one region and predicted to another. In all cases, **evaluating the temporal and spatial transferability of our models is critical for assessing both the generality of our understanding and the certainty with which forecasts can be made into the future based on global climate models.** Thus, given spatially- and temporally-evaluated models, we will then forecast phenology, mismatch, and demography and their uncertainty forward to 2100.

6.1. Analytical approach

Spatial scaling of phenological mismatch. The consequences of phenological mismatch for the demography of birds and butterflies will depend greatly on the extent to which fine-scale patterns (i.e., our 50-km grid cells) of tri-trophic phenology are spatially autocorrelated over large distances. If so, then an individual bird arriving on its breeding ground might have few options for avoiding mismatch should it arrive late relative to the optimal timing for the region. Alternatively, if phenology is strongly influenced by local variation in land cover, urbanization, or habitat, then fine-scale habitat selection could potentially allow a bird to minimize its perceived mismatch. We will directly evaluate the spatial structure of green-up, flight, and arrival dates using spatial correlograms that characterize spatial correlation (e.g. Moran's *I*) as a function of distance. Our own previous work has indicated that arrival date in birds exhibits strong autocorrelation (Hurlbert and Liang 2012, Mayor *et al.* in revision). Utilizing approaches developed for charact-erizing the spatial structure of habitat selection (Mayor *et al.* 2007), we will compare phenological correlograms across trophic levels. We will thereby characterize the spatial structure of mismatch—that is, relative mismatch across the continuum of spatial scale. To the extent that the spatial structure of mismatch exhibits consistent patterns, this approach will facilitate up-scaling of mismatch to scales larger than those observed (beyond Eastern Temperate Forests ecoregion) and downscaling of mismatch to finer resolutions (down to the native MODIS or climate data resolution of 500 m x 500 m).

Complementary to the correlograms, we will use a coarse-graining approach (Mayor *et al.* 2007) to characterize mismatch across hierarchical grains (resolutions at which mismatch is estimated), allowing us to directly compare scales of mismatch to scales of demographic trends. We will use nested grains, using two methods: (i) a focal cell aggregated with the nearest 8, 24, 48, or 80 neighbors (a range in grain of $2,500 – 2022,500$ km^2), or (ii) focal cells aggregated into the nested EPA ecoregions of Level IV, Level III, Level II and ultimately Level I (Eastern Temperate Forests). After evaluating the scale dependence of phenological mismatch, we will examine whether the scales of strongest mismatch exhibit the strongest negative demographic trends. That is, if mismatch is strongest at finer scales, will demographic trends also appear strongest when observed at these finer scales.

Spatial transferability. We will perform two types of spatial cross-validation of our models. First, we will assess overall model performance and degree of overfitting via leave-one-out-cross validation (Arlot and Celisse 2010). Second, we will perform extra-regional transferability analysis by examining the efficacy of models built at smaller ecoregional grains (EPA Level IV and III) in predicting mismatch of neighboring ecoregions. The variability in prediction strength from models developed at small EPA Level IV ecoregions in predicting neighbors within the SAME (nested) larger EPA Level IV Ecoregion, versus

across DIFFERENT (non-nested) Level IV ecoregions will be used to predict the spatial transferability of models to Level I ecoregions neighboring the Eastern Temperate Forests. The transferability to neighboring Level I ecoregions (e.g., Great Plains, Northern Forests) will then be evaluated. As with the hindcasting, models will be assessed based on root mean square error and proportion of variance explained between observed and predicted values, and these cross-validation analyses will be performed on models of phenology, phenological mismatch, and demography. While we expect models generated in one region to perform more poorly outside that region, this analysis will provide further insight into the extent to which phenological models are transferable in time and space.

Hindcasting. We will evaluate our spatio-temporal models of phenology (Aim 1), mismatch (Aim 2), and demography or population size (Aim 3) by using them to hindcast to places in space and time where we have historical data. Our model-fitting time period is 2005-2018; during that period we have access to the greatest data extent and density for all data types (Figure 3). We will hindcast back to previous periods that have progressively sparser data, focusing on historically data rich regions (e.g. MA, OH, IL, Mid-Atlantic). Thus, phenology, mismatch, and demography for all three trophic levels will be hindcast to 1990-2004, a period when we have all data types except direct caterpillar data (so we will rely on indirect estimates, see Aim 3.1). Based on our ability to predict into that time period, we will refine our model parameterizations and then hindcast back to 1982-1990 where we still have remotely-sensed vegetation phenology in addition to avian and Leipdopteran records. Finally, we will use the historical Bird Phenology Program dataset (Zelt *et al.* 2012) to validate hindcasts of bird phenology based solely on climate predictors. This historical dataset—primarily with records <1940—will be used to check our ability to predict into "novel" climates and distant time periods. Hindcasting model performance will be evaluated using both root mean square error and total variance explained. Daily climate data going back to 1915 will be used to parameterize model predictions (Livneh *et al.* 2013; see §Data management Plan).

Forecasting. After revising our models based on hindcasting performance and spatial cross-validation, we will determine our ability to predict different aspects of phenological patterns and mismatch based on climate alone. Importantly, through our hindcasting efforts, we will be able to gauge whether those models can effectively predict into a non-analog climate period (the early 1900s) for at least one variable, bird arrival phenology. Forecasting into the mid- and end-21st century will be done by using the output of Global Climate Models (GCMs) from the Coupled Model Intercomparison Project (CMIP5, http://cmip-pcmdi.llnl.gov/ cmip5) under both "business as usual" and more optimistic emission scenarios (Moss *et al.* 2010) to make predictions about the phenology of each of our three trophic levels, and of our estimates of phenological mismatch. After choosing a subset of models that meet our validation criteria, we will use those models to form an ensemble model for the future. Also, using these coarse projections as surface and lateral boundary conditions for a regional climate model, we will produce a high-resolution climate projection for the ecological applications. We already have the infrastructure to produce these future projections (see Georgetown Facilities statement), including transforming output into relevant metrics such as GDD (Figure 9). The cross-validation provided by the hindcasting and spatial transferability analyses will allow us to reasonably estimate the uncertainty for each prediction. This will allow us to explore the potential impacts in an increasingly altered climate to the magnitude and direction of phenological mismatch and its potential consequences on bird and Lepidopteran demography.

Figure 9. Historical and future projections of spring climate conditions from the CCSM4 model with the most extreme emissions scenario. Maps show accumulated GDD during March–May.

6.2. Summary

In this aim, we capitalize on the macroscale nature of our analysis to explore questions of spatial scaling as well as both spatial and temporal transferability. Together, these
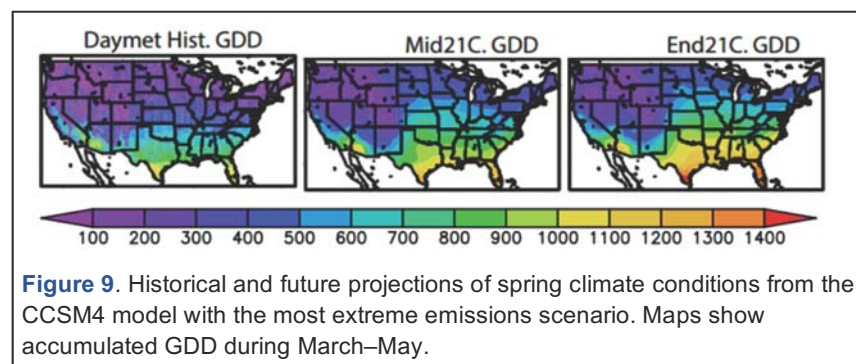
two inferential goals will provide critical knowledge with which to interpret future forecasts of phenology, mismatch, and demography at variable spatial and temporal scales. Differences in predictive ability by region, species, and year will provide critical inference on uncertainty of future predictive work as mechanistic models are increasingly preferred to predict climate change impacts.

7. BROADER IMPACTS OF THE PROPOSED WORK

7.1. Linking K-18 education to citizen science

PI Hurlbert has developed the citizen science project Caterpillars Count! which allows participants to collect data on the phenology of caterpillars and other foliage arthropods. The project website (caterpillarscount.unc.edu) provides learning activities and data visualization opportunities that engage participants beyond data collection in the field. This project has already been implemented at 3 Environmental Education (EE) centers and 1 middle school across North Carolina and Tennessee, and 2 educator workshops were held during the summer of 2016 introducing the project to 38 environmental educators. We will host 6 workshops (3 per year in Years 1 and 2) that introduce Caterpillars Count! to 90 more educators at EE centers and schools throughout eastern North America with a focus on the target regions for our analysis. We have requested resources to support these workshops and the outreach to and recruitment of potential participants by Sarah Yelton, Environmental Education Coordinator at UNC. SP Withey also has experience serving as a teacher/mentor for a different citizen science-based activity ('Schoolyard Birdwatch'), and will also advise on outreach strategies for the Caterpillars Count! team. For undergraduate education, co-PI Leslie Ries will utilize the data resources generated from this proposal to create content on data-intensive instruction in undergraduate environmental and ecology courses and share these resources on the QUBES hub (Quantitative Undergraduate Biology Education and Synthesis, and NSF funded project) and our own online portal (see §7.2). This content will showcase phenology data and walk students through tools to access, visualize and do basic analyses so students can begin to explore phenological asynchronies and also become familiar with data-intensive approaches, database use, and analysis in R. As part of our work to develop classroom content, we will also create a case study on phenological mismatch to submit to the National Center for Case Study Teaching in Science (NCCSTS), where it will be broadly accessible to science educators. Our outreach will be further enhanced by partnering with Science Live (science-live.org) to create short films highlighting how citizen scientist participants in our projects contribute to real scientific discoveries (see letter of support).

7.2. Bringing active research on phenology to the public

Collaborations with other national efforts. We will coordinate our activities with the National Phenology Network (NPN) as a natural partnership given shared interests in monitoring continental scale phenology (see letter of support). In particular, we will leverage NPN data to help better fit plant phenology information from in-situ monitoring, especially aggregated individual and site phenometric data that NPN produces. We will also share results of our analyses broadly with NPN. This collaboration initially will focus on use and sharing of products from both NPN and this effort without further or deeper integration. To continue to grow potential further collaborative efforts, we will invite NPN staff to participate in at least one of our early annual meetings and continued discussions over the course of funding.

Online portal. These same outputs will also be available via a project website that will feature animations and visualizations of our data for use in explaining the links between climate, phenology and trophic levels. We will build a simple set of tools for visualizing phenology change at each level of this tri-trophic interaction and the relationships between levels. These tools will provide users a chance to select a region of interest within the extent of our work and examine aggregated outputs. We plan to build these visualizations by connecting outputs for temporal trends and forecast future trends on CyVerse (see letter of support). Those datasets will be linked to R-scripts and a Shiny app that will provide remote users a chance to explore outputs. We will also coordinate efforts to share these results with key partners, e.g. NPN above, based on further discussions about best methods to make sure these are made available to planners, managers and regional scientists. These applications will also be linked into our undergraduate

classroom modules (see §7.1).

7.3. Training in quantitative modeling and biodiversity informatics

The proposed research team would include graduate students (1), postdocs (c. 4–5 over 6 funded person-years), and a team of undergraduate students (12 over 2 years in field, ~6 more in lab), thus contributing to the field, lab, and statistical training of the next generation of scientists. The graduate student and postdocs will be encouraged to spend 1 week per year in the lab of another PI or team member in order to facilitate progress on research aims between institutions but also to expose them to a greater breadth of research and analytical approaches. In addition, each year these early career scientists will take advantage of national workshops that expand their quantitative toolkit such as NEON's Data Institute. With respect to undergraduate training, MAPS data validation efforts at the University of Connecticut led by PI Tingley in collaboration with SP Siegel will train a cohort of undergraduates (recruited from diverse programs such as the McNairs Scholars program, for which PI Tingley is a faculty mentor) in bird banding (including ageing, sexing, and species identification in the hand) and database management. Over the past 1.5 years, PI Tingley has trained 3 undergraduates (1 female, 1 first-generation college) in bird banding and database structure while developing MAPS data verification protocols. Further, PI Hurlbert has demonstrated a commitment to developing the quantitative skills of ecology students through his organization of 3 Software Carpentry workshops as well as his upper level Biodiversity & Macroecology course aimed at enabling students to work with and analyze large ecological datasets in R.

7.4. Broadening participation in the sciences

In coordination with MAPS training at UConn, IBP will host a regional training event in introductory bird banding and MAPS station protocols at UConn in spring 2017 and 2018. These events provide intensive training in bird handling, mist-netting, and banding and provide important field skills which are hard to train. Participation in the event will be prioritized for undergraduates working on MAPS validation and students from under-represented backgrounds (a particularly strong issue in ornithology). Additionally, upon completion, the trainers and trainees will provide outreach days conducting urban bird banding in downtown Hartford in collaboration with local under-served middle and high schools – providing continuity to a program that has been successfully conducted for many years by a retiring local professor. We will also use best practices (e.g., those recommended by the Strategies and Tactics for Recruiting to Increase Diversity and Excellence) to recruit to open positions associated with this grant proposal. We will recruit from under-represented pools through outreach to target audiences at our universities (e.g., via listserves and boards of campus cultural groups, or through programs like the McNair Scholars), and the broader community such as ESA's Strategies for Ecology Education, Diversity and Sustainability program. Of the three post-docs named in this proposal, one is a women and one other is a minority.

8. Results of Prior NSF Support

Ries: *ABI Development: Access, visualization and statistical tools for the analysis of butterfly monitoring data* (DBI-1147049; 2012-2017; $1,134,740). *Intellectual merit*: To date, this project has produced 3 book chapters and 9 articles in journals such as Ecology (2), Bioscience, and Global Ecology and Biogeography (2). *Broader impacts*: This project supported community building among 30+ organizations that collect and share butterfly data, including building a central location to find monitoring programs (www.monarchnet.org , www.thebutterflynetwork.org) and two web portals to manage, visualize, and share data. The project trained a total of four undergraduates (all women) and four postdocs (three women and one minority). Ries developed data-based modules for two undergraduate courses (Gedan et al. in prep). **Hurlbert:** *SG: Distinguishing between core and transient species: new insights into the determi-nants of species richness* (DEB-1354563; 2014-2017; $149,843). *Intellectual merit*: Preliminary results were presented at ESA and three manuscripts are in prep. *Broader impacts:* Two graduate students have received training and summer support, two Software Carpentry workshops (65 participants) have been conducted to train graduate students and postdocs in computational skills, and two environmental educator workshops (40 participants) were held to promote the Caterpillars Count! project.

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Data Management Plan

1. Description of data

All data compiled for this project are publically available via repositories sharing remote sensing products, interpolated climatologies, or directly from each citizen science program. Below we further provide information on these sources of data. The PIs and Senior Personnel are directly involved or work closely with the producers of much of these data, and will assure that all data rights and licensing are respected. However, we expect no issue with the download, storing, aggregation, or analysis of any data product listed below for the purposes of this proposal. In all cases, data will be stored in raw, native formats, utilizing a set of computing resources available across the collaboration, often leveraging cloud-based resources.

Climate

We will use daily, gridded climate data at a 1-km^2 resolution for our study area known as '**Daymet'** (Thornton et al. 2014), available from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC). The downloadable data products include continuous surfaces of maximum air temperature, minimum air temperature, and precipitation derived from meteorological station data by interpolation and extrapolation algorithms (Thornton et al. 1997). These data products are currently available from 1980 through 2015, with data through 2018 expected to be processed by the third year of our proposed research. For daily climate data prior to 1980 we will use the Livneh dataset (Livneh et al. 2013), available at 0.06-degree horizontal resolution (roughly 7km) from 1915 through 2011. Daily maximum and minimum temperature values from this dataset will be used to calculate GDD from 1915-1940. We use the WorldClim climate dataset (Hijmans et al. 2005) to characterize January-March average temperature and precipitation on avian wintering grounds at 1-km^2 resolution as the other sources are unavailable for South America.

Vegetation

We utilize two sources of vegetation green-up data. The first is satellite-derived **MODIS** product MCD12Q2 Land Cover Dynamics V005 and in particular the "onset of greenness increase" which is derived from an Enhanced Vegetation Index (EVI), for each year, at a 500 m pixel resolution. We will assemble a time series of these data spanning 2001-2016. Derived products will include a coarse-grain estimated date of green-up in 200 km grid cells by aggregating the dates in all pixels using GIS to determine the mean date of onset of greenness each year across all MODIS pixels. In order to ground-truth and potentially assimilate with remote-derived metrics, we will utilize both raw and (recently) gridded **National Phenology Network** data being produced (https://www.usanpn.org/data/spring) as a validation dataset. All derived data built in downstream models will have proper provenance as described below.

Lepidopteran data

Caterpillars. The caterpillar phenological dataset is a new and developing dataset, "**Caterpillars Count!**", begun in 2015 by Co-PI Hurlbert (http://caterpillarscount.unc.edu/), that will be expanded geographically through this proposal as a publically-available citizen science project. The core observation for estimating caterpillar abundance is a foliage survey, which entails examining a sample of 50 leaves (and associated petioles and small twigs) at breast height, identifying arthropods to order, and recording body length to the nearest mm (Holmes & Schultz 1988). Each site is characterized by 40 surveys on a weekly basis from leaf out through mid- to late July. All data can be submitted directly to a MySQL database hosted by Caterpillars Count! via existing smartphone apps. For validation, we use data from another citizen science program, the **Monarch Larvae Monitoring Program** (www.mlmp.org).
Adult Lepidopterans. We are working with data from a network of butterfly monitoring programs, both regional and continental (Table DM1). Co-PI Ries has been instrumental in uniting, standardizing and centralizing data or information about data access from these diverse monitoring efforts.

    Continental programs: The oldest and most geographically expansive butterfly program in the world is The **North American Butterfly Association's** (www.naba.org) Count Program. This program was

started in 1975 and continued by NABA which still collects data, currently at ~500 permanent sites each year. In addition, the **Butterflies and Moths of North America** (www.butterfliesandmoths.org) launched a program in 2006 – building off a historical database of sightings – where users could upload photos of butterflies or moths. Also, in 2011 **eButterfly** launched and has recently partnered with iNaturalist to provide a platform for butterfly sightings. In 2010, a project started by Discover Life (discoverlife.org/moth) has volunteers photograph all specimens at a light source (**Moth Photo Project**) up to 365 days per year providing unparalleled phenological data using a standardized protocol.

Regional programs: There are several regional programs that collect butterfly monitoring data. One network of programs uses standardized protocols called Pollard Walks (Pollard 1977). These programs set up permanent transects and have a volunteer assigned to individual transects to monitor them several times per season. Although many programs started surveys 10 or 20 years ago (Table 1), most of these programs called Butterfly Monitoring Networks (**BMNs**) have recently begun using a central portal for data entry, quality control, curation and access. All North American BMNs either use or plan to use this portal, called PollardBase (www.pollardbase.org). This site was developed and is managed by co-PI Ries' lab. There are several other regional programs that use a variety of protocols and have collected tens or hundreds of thousands of records over the past several years (see Table DM1).

Table DM1. Lepidopteran data sources

Data source	Years of data*	~# Records
Continental-scale data		
- North American Butterfly Association (3 programs)	1975 – 2018	700,000
- e-Butterfly	<1980 – 2018	300,000
- Butterflies and Moths of North America	<1980 – 2018	625,000
- Discover Life Moth Photo Project	2010 – 2018	360,000
Regional surveys and atlases		
- Iowa BMN	2007 – 2018	7000
- Illinois BMN	1987 – 2018	120,000
- Maine Butterfly Survey	2005 – 2015	25,000
- Massachusetts Butterfly Club Trip program	1993 – 2018	150,000
- Maritimes Butterfly Atlas	2010 – 2018	16,000
- Virginia Occoquan Survey	2001 – 2017	13,000
- Michigan BMN	2011 – 2018	8400
- North Carolina Butterfly Atlas	1994 – 2018	143,000
- North Carolina Moth Atlas	1993 – 2018	80,000
- Ohio BMN	1996 – 2017	200,000
- Ontario Butterfly Atlas	1991 – 2018	221,000

*We expect most of these data to be available through 2018 (unless noted) by the beginning of year 3 of the project – and we will update preliminary analyses with those data as needed.

Avian Data
Migratory phenology: **eBird**, a citizen-science dataset curated by the Cornell Laboratory of Ornithology represents one of the largest actively growing datasets in ecology, with between 5-10 million bird observations added per month (Sullivan et al. 2014). eBird's strength lies in the fine-scale spatial and temporal resolution of data, and ability to infer absence, providing day-to-day updates of bird occurrence, including migratory dynamics. We have already requested and downloaded from eBird data for all breeding bird species occurrences in recent years (2000-2015), and new records will be downloaded and

updated as curated and checked forms become available (expected prior to the beginning of project timeline). We also make use of data from the **Bird Phenology Program** which includes historical bird phenology information across North America over the first half of the 20th century (Zelt et al. 2012). Senior Personnel Arab has worked extensively with these historical data.

Demography: Here, we will utilize two extensive databases. First, the North American Breeding Bird Survey (**BBS**) is a continent-wide avian monitoring network which consists of over 5,000 roadside survey routes, many of which have been surveyed for over 40 years (Bystrak 1981, Sauer et al. 2014). These data have long served as a source of information about regional population trends. To corroborate BBS-based trends and provide explicit mechanistic links, we will also use the Monitoring Avian Productivity and Survival (**MAPS**) dataset, curated by the Institute for Bird Populations (IBP). Since 1989, MAPS has collected data from constant-effort mist-netting at over 1,200 stations spread across North America, collecting more than 2 million captures (DeSante et al. 1995, 2001). MAPS stations band birds once every 10 days for 8-12 consecutive 10-day periods from early May through mid- to late August, identifying birds to species and sexing and aging them when possible. MAPS data provide direct estimation of key vital rates for birds, including apparent adult survival, recruitment, and breeding productivity. Although the MAPS database continues to grow in size, with over 300 independently-run stations per year distributed across the US and Canada, maintenance of the database is not funded, so data are not currently available post-2009 due to a need for verification. PI Tingley, in collaboration with SP Rodney Siegel of IBP, are coordinating validation under this proposal of all remaining MAPS station data – through 2016 – east of the 100th meridian using a combination of undergraduate trainees and contract support with IBP. As MAPS is publically available (http://www.birdpop.org/pages/maps.php), this process will unlock important demographic data from recent years, bringing the timeframe of inference from MAPS on par with the rise of large-scale citizen science monitoring databases (e.g., eBird and NABA).

2. Products of research

The main data products of research are as follows: (1) A data resource for internal use only that will hold all incoming data and that can report citation of the data, and linkbacks to the web-based resources; (2) Aggregated spatial data normalized to the same continental pixel size for climate, plant, caterpillar, butterfly and bird phenologies and demographic products utilizing the database as an engine to produce these outputs; (3) A set of pipelines, mostly based on R-scripts, that will take as input harmonized data (2, above), and produce analyses that test the core hypotheses that are presented in the main project descriptions; (4) A set of output analyses per grid cell and potentially including further trend analyses. These outputs, which are spatial and temporal, will be provided both via traditional mechanisms (i.e., on request) and through a website devoted to the project so that others can explore these data.

Additional details on data products

Aggregated raster data will be produced by intersecting grids against monitoring data (as described above). All raw data will be archived as described below, and views of those datasets will be assembled into a Postgres datastore that will serve as the backend storage for derived products developed here. The team has strong experience building such data stores. The Postgres backend will store aggregated views of citizen science input data, along with raster datasets, and will provide means for PostGIS operations to aggregate and manipulate. Data from the database will be immediately queryable via R scripts, e.g. RPostgreSQL. The database will also provide means to track provenance and ownership of all incoming products as part of dataset level metadata captured in needed tables.

When queried via R or python, our team can extract a vector or dataframe describing phenology patterns (and climate conditions or other data products) for a grid cell or multiple grid cells. From these vectors or dataframes, it will be possible to model drivers and relationships based on the proposed hierarchical models. While relatively simple in theory, the efforts to bring these data, with their different inventory reporting bases and with differing ability to infer presence, absence, abundance, or vital rates, and working across a variety of datasets even just for butterflies, is no small feat. We note that one critical product of this research is a consistent set of new gridded products that will be made available that

provides a harmonized view of phenology and relationships to climate. The *tools* to develop these harmonized views, already built into R code in parts, but now ready for scaling-up, will provide a critical product of research that will likely have wider utility. We will assure that all phenological products developed have appropriate dataset-level metadata regarding creator, ownership, rights, licensing, and a description of the processes that created those datasets.

3. Data storage and preservation
Local storage and access
Senior Personnel Guralnick has been involved in multiple large-scale data sharing and biodiversity curation projects and has primary responsibility as **Data Management Coordinator** for shorter and long-term strategies for maintaining, curating, and archiving data. He will assure that all products used are stored and available for the rest of the team using both local storage solutions and cloud-based solutions. For short-term storage, Guralnick has set up a dedicated vanilla Linux server with 14TB disk space, which was built specifically with storage in mind. This 20-core machine is bolstered by a 40-core second box with 2TB storage and 32TB available backup drive space soon to expand to 64TB. We expect such archiving to be necessary depending on needs related to model hindcasting and potential forecasting and are planning for 4-20TB of storage to be sufficient for all project data storage needs given our current spatial scales, including the model output, and therefore we do not anticipate needing to further scale storage on this project. Guralnick's servers are easily accessible via VPN.

We recognize that data products will be hard to fully centralize, and that is not the ultimate goal. The goal is to be sure we have (1) kept copies of the raw data downloaded for analyses and (2) produced harmonized data layers that are consolidated in a GIS-database along with other georeferenced datasets available for full use by the team. We expect that team members will be accessing centralized data resources for local analyses, or may even be using local updated resources from citizen science datasets that may not yet be stored in a centralized data store. We have, however, resourced this effort to free the the ecological modelers from having to manage all the data product. Modelers will access resources, utilize central and sometimes decentralized data, and create new products, but will have easy-to-use tools available to make sure products can be pushed back to a single data store. While we appreciate the value of workflow management software to help this process, we prefer to operate with shared code developed and managed using freely available resources (e.g. GitHub).

Archives/data centers for depositing data
We recognize the importance of archiving data and plan to use CyVerse storage and metadata tools for this project (see Letter of Support). We have also already set up phenology data resources on their iRods servers. The value of CyVerse is further scalability, for both storage and analysis. For public archiving, we plan to deposit the cleaned primary (raw data) and secondary (modeled outputs) information from this work in Dryad (http://datadryad.org/), a key data repository. The Dryad publishing timing will coincide with submission and acceptance of peer-reviewed manuscripts that report our findings.

4. Data formats and metadata
We plan to use EML dataset level metadata, as preferred by Dryad, to describe datasets. The incoming data from this project will include pre-formatted data and metadata about those datasets, and those will be stored as well. We plan to ingest these as provided but note that some level of harmonization is required. Rather than try to reduce dimensionality and push data into formats such as Darwin Core, we instead will work out crosswalks where necessary for data from different sources that need to be integrated (e.g. butterfly count data). We do not anticipate needing to do this at the level of individual dataset harmonizations. Much can be done in aggregation steps. We do plan to assure that all steps which generate new data are well documented and with appropriate provenance. In cases where data additions and annotations are made, we will use well-understood standards and ontology such as Prov-O for such efforts. In general, each project has its own spatial, temporal, and taxonomic descriptors along with observation processes. These need to be clearly reported so that they can be integrated properly for a coherent spatial and temporal view. We will finally consider whether an omnibus method for reporting

inventory metadata can be applied. Such efforts are a research specialty of Senior Personnel Guralnick and he will oversee any needed efforts to standardize inventory reporting across the citizen science efforts. All raster map metadata (e.g. grain, extent, production process, etc.) will conform as much as possible to Federal Geographic Data Committee standards, in order to assure full re-usability and clarity. We will include rights and licensing as a key part of reported metadata.

5. Data Dissemination & Policies for Data Sharing and Public Access

Data availability and dissemination
We firmly believe in transparent, open science. Therefore, all derived data products and algorithms developed for the proposed project will be preserved and made publically available. Raw citizen science data will be available through those individual programs. We plan to build R and Python scripts to automate and replicate model runs. Code, including new R packages, will be made available open source and under a gpl v3 licence on GitHub, as those are produced. We expect to write data processing tools in R and Python and will work to achieve reproducible code; the focus here will be on Jupyter notebooks and/or gist outputs on GitHub (see below). Data will be embargoed until manuscripts using those data are published, with the goal of a complete release of all derived data via Dryad at publication. We note a strong preference to develop not just one-off PDF outputs but content that can be placed directly on the Web. Output rasters will be published and made available in native formats for download, but we will also put rasters into interactive frameworks (such as D3 libraries) where they can be further explored.

Publication of data, privacy and intended users
There are no sensitive data from this project. Raw data collected directly by this project, any derived products, and modeling code will be made available as quickly as possible. Data not tied to publication of manuscripts – and thus not likely to be archived in Dryad – will be made fully publicly available by end date of the project at the latest. All requests made during the project will be honored according to agreements with those requestors.

Ethical Issues and protocols
We do not foresee any issues with making derived products available under a license that has few restrictions about their use. We would either consider a Creative Commons 0 (CC-0) license (close to public domain) or CC-BY, which merely requires attribution for data use. We note however that we fully respect licensing on data products coming from our network of citizen science efforts, and we will respect and help promote proper respect of licenses and use of products according to those licenses, so that providers accrue professional credit for their contributions. We commit fully to sharing data after the length of the grant and have archiving mechanisms in place to assure those data stay available.

Code development and licensing
It is now well understood that care in developing, storing, maintaining, and releasing the software related to scientific research is just as important as carefully storing and maintaining the raw data. All analysis code will be developed, stored, and served from GitHub. All individuals involved in writing code for this project (i.e., the PIs, postdocs, etc.) will commit their changes to this central source so that collaborative code development can proceed rapidly, with all individuals having access to the most up-to-date versions of the code. The GitHub code repository will be publically accessible under an open source (MIT) license.

6. Models and model validation
A detailed reporting of the modeling approach and validation steps is provided in the project description. For modeling management, we will generate a clear set of associated and linked R scripts, that can serve the purpose of a flexible process, e.g. that can be batched together and run either on local computing infrastructure at home institutions of the PIs on the project, or run utilizing medium-scale or larger computing resources managed by Guralnick. All modeling results from final outputs will be stored centrally, as will all model validation outputs.

Postdoctoral Researcher Mentoring Plan

Goals: This project is funding one 4-year postdoctoral researcher at the University of Connecticut (UConn) mentored by PI Morgan Tingley, as well as support for existing postdocs at Georgetown University (Elise Larsen and Naresh Neupane, both mentored by Co-PI Leslie Ries) and University of Florida (Stephen Mayor, mentored by SP Rob Guralnick). Our combined goal is to expose and train these postdocs in the skills and tools necessary for successful collaborative research in Macrosystems science while ensuring that the career development goals of each postdoc are met.

Professional Development: At the onset of the project, each postdoc will establish an Individual Development Plan based on the process developed by the Federation of American Societies for Experimental Biology (FASEB). The development plan is designed to help individuals identify their career goals and determine the critical skills they need to attain for a given career path. Based on the outcome of the self-assessment, the mentors and postdoctoral researchers will identify opportunities to provide training in identified areas. Each of our universities provides myriad support and training services for postdoctoral development, such as private career counseling and career-related seminars, panels, and professional development workshops. Additionally, travel money has been budgeted to send each postdoctoral researcher to national-level workshops or career development opportunities (e.g., NSF regional conferences, or statistical, programming, or open-science workshops). In addition to weekly meetings to assess progress and offer feedback, we will hold biannual meetings will be conducted with the respective PIs to specifically discuss career development issues and assess whether career development goals are being met.

Project Management: In addition to training available through their host universities, the postdoctoral researchers will work actively with the PIs on the management of their teams on the grant (see Project Management Plan). The postdocs will receive training from their PI in managing budgets, annual report writing, and research coordination within and between teams. This training will provide each postdoc with an opportunity to reinforce the training they receive from institutional workshops by being an active part of the grant management for the project they are working on.

Research Mentoring in Macrosystems Biology: Macrosystems grants demand high levels of organization, collaboration, and teamwork, and through organization of group products, ideas, and analyses, each postdoc will receive critical skills in collaborative informatics-based science that are increasingly in demand in ecology and evolution. Postdocs will be encouraged to spend at least 1 week per year in the lab of another PI or team member in order to facilitate progress on research aims between institutions but also to expose the postdoc to a greater breadth of research and analytical approaches. Additionally, emphasis in directed instruction will be placed on two topics important to Macrosystems science: 1) the development of statistical tools that allow for investigations of the importance of spatial scale, including Bayesian approaches and hierarchical modeling; and 2) ecoinformatics approaches to working with and integrating large datasets, and developing archivable workflows Postdocs will be encouraged to participate in multi-day workshops on these and related topics (e.g., from the NEON Data Institute, at the International Statistical Ecology conference, etc.). There is a basic expectation that each postdoc will be lead author on at least 1 paper for every year of support and there will also be opportunities for co-authorship on many other manuscripts. Through lab meetings, they will gain experience in preparing presentations and presenting research. The postdocs will further develop these skills by giving a departmental seminar to gain experience preparing and delivering 1-hr talks. Included funding will support postdocs to travel to major conferences (e.g., Ecological Society of America, International Ecological Statistics Conference, American Geophysical Union) and gain experience presenting large-scale collaborate work to broader audiences. Finally, each fellow will also gain experience mentoring undergraduate (e.g., through MAPS validation or Caterpillar Counts! participation) and graduate students at various stages of their research through the active and diverse labs that PIs Ries and Tingley and SP Guralnick currently maintain.

Project Management Plan
Collaborative Proposal: MSB-FRA: Causes, consequences, and cross-scale linkages of climate-driven phenological mismatch across three trophic levels

Team

We have assembled an eminently qualified inter-disciplinary team to carry out this research (**Table 1**). **PI Tingley's** expertise is in the modeling and detection of species- and community-level responses of birds to climate change. **Co-PI Ries** is a butterfly and community ecologist specializing in the informatics related to the management, curation, analysis and sharing of citizen science datasets. **Co-PI Hurlbert** is a macroecologist with expertise in biogeographic analyses of bird communities, and the founder of a citizen science project for measuring resource availability for foliage gleaning birds. The PI team is aided by a number of critical senior personnel: **Arab** is a statistician focusing on Bayesian hierarchical modeling, **Guralnick** is an expert in biodiversity informatics and biodiversity data curation, **Miller** is a quantitative and population ecologist, **Saracco** specializes on capture-recapture and demographic models of birds, **Siegel** is an ornithologist and ecologist, and **Withey** is an ecologist focusing on the spatial modeling of land-use and climate change impacts. We additionally are naming three postdoctoral researchers who are already participating on this work: **Larsen** is a mathematical and statistical ecologist who has worked extensively both on birds and butterfly dynamics, **Mayor** is a spatial ecologist who has been leading a team for 3 years to investigate phenological mismatch in birds, and **Neupane** is a climate modeler with expertise in future predictions. As a whole, our team brings together both long-term collaborators and new team members with a strong plan to carry out the ambitious aims of this proposal and to ensure exemplary training for our next generation of scientists (see Postdoctoral Researcher Mentoring Plan).

Managing Risks

Risk: Collaborations are difficult to start with significant effort spent learning communication styles and building trust.

Mitigation: Most members of our research team have a history of working together. Five of us (Withey, Miller, Tingley, Mayor, Guralnick) began collaboration as part an NSF-funded Ecological Society of America workshop for Early Career scientists (4 as participants, one as a mentor) in 2013 on the topic of "Scaling Up: Continental-Scale Population and Community Ecology" (EF #1241327) and two of us (Ries and Guralnick) already collaborate on other large-scale projects (NSF GoLife ButterflyNet). This group has submitted one manuscript together on phenological mismatch (currently under revision, with 2 others in prep) and participated in monthly conference calls over the past 2 ½ years. In August 2016, six of us (Tingley, Ries, Hurlbert, Guralnick, Miller, and Mayor) met in person for 2 days to lay the groundwork for further collaboration. This strong and successful collaborative foundation, with regular in-person and virtual meetings, is key to future success with larger and more complicated projects. The four other project personnel have all collaborated with one or more other personnel previously, either in the same lab or on publications. Our shared experience on previous projects has helped us to develop robust internal communication and data coordination practices.

Risk: Collaborative projects carry more overhead in terms of organization and understanding how to work within those roles.

Mitigation: All members of the research team have worked on large collaborative projects, and with large datasets from multiple sources. Therefore, we all have experience with managing raw data resources, building derived harmonized data products, and summarized or aggregated data products that feed into analysis pipelines. We all work in a collaborative context where pipelines that are developed are immediately shared and accessible to all group members, such as through common group repositories (e.g., GitHub). In addition, the research proposed involves the development of analyses and models on which subsets of the research team have already had specific experience. Despite the expertise, we have

world experts in pragmatic and large-scale data management that will guide that side of the project, and a clear delineation of responsibilities as outlined below.

Risk: We note a series of risks associated with compiling and analyzing dataset at the regional to continental scale. These risks include: 1) dataset compilation and development may prove more challenging than anticipated, especially managing very large datasets during the course of the project; 2) assembly and harmonization of different datasets and integrating them all into coherent forms for downstream analyses are difficult, especially over a dispersed team; 3) we recognize that uncertainty across all these data products means there is a deep challenge of accounting for such uncertainties and propagating them through to the final analyses.
Mitigation: We have set up a strong framework and believe these risks are mitigated by the strong technical expertise in data management along with a clear set of subteams tasked with data assembly and modeling workflows. Those teams are phased to do work over different time-frames of the grant as described in more detail below under operational strategies. We note that we will leverage the data and code development skills and expertise of this team to overcome such risks. Our strong background in Bayesian modeling frameworks and deep experience working with the data products and modeling frameworks assure credible and rigorous outputs.

Risk: Sustaining projects, in terms of people investments, and investments in technical resources, is challenging over the longer term (past initial funding horizons).
Mitigation: We have leveraged existing technical resources and networks to be self-sustaining. Many of the citizen science-based datasets are well established, using CyVerse for infrastructure is extremely cost effective, and as our workflows become fully developed, the costs of delivering new analyses will decrease dramatically. We have connections to both governmental and non-governmental agencies that have already shown demand and that work directly with phenology and demography of key taxa.

Project Organization
Tools for coordinating efforts: We will use GitHub to manage all code and issue tracking for the development end of this project. We will set up a single repository for the project and will instill discipline for the team to make code commits regularly along with clear assignments for handling issues. We plan to also leverage Jupyter notebooks, which will be used on this project to show examples of how scripts access core datasets and that help explain, step by step, how analyses are implemented. This focus on repeatable and reproducible science is not only useful for the broadest consumers of our knowledge products but for sharing approaches and techniques among our collaborators.

We recognize that there is also a need for collaborative workspaces in order to share ideas, key manuscripts, figures generated by team members or from new publications, analysis issues, and to more fully coordinate efforts, outside of systems more geared for code and issue tracking. We plan to use Wikispaces as a mechanism to support such collaborative workspaces, and we plan to use Slack for more real-time messaging and coordination. For audio and video-conferencing we will use free audio conferencing services and common platforms such as Google Hangouts or Skype.

Annual Meetings: We plan multi-day annual meetings among all the PIs and senior personnel, recognizing that 100% participation from all members may not be possible. The timing will fall near annual meetings of the Ecological Society of America or the American Geophysical Union, to piggyback on meetings many will already be planning to attend. The annual meetings will be a chance to bring in key partners, including the National Phenology Network and CyVerse partners. We are planning two meetings in Year 1 to ensure the rapid resolution of any problems that arise with project workflow or organizational structure.

Organizational Structure - Team Organized by the Lead PIs: Our Macrosystems proposal has both a critical set of data products and outputs from those products that are encapsulated in Aim 1 of the

proposal. Aims 2, 3 and 4 use initial analyses to build more fully synthetic knowledge products. Rather than propose there is a monolithic 4 year set of "hubs" that persist for the life of this product and past the end of funding, we instead focus on more agile development, where teams persist for certain time periods, and have specific goals, milestones and outcomes, with flexibility to adjust the model as we learn from outcomes. Each team will have appointed leads, as well as additional key personnel (Table 1) and will function for certain lengths of time (Table 2). Three data products and initial analysis teams focused on Aim 1 will spin up in Years 1-2 where most of the work is concentrated, and with more limited efforts in Years 3-4 to update products. The first is **Team Lepidoptera** (LEP, led by Co-PIs Ries and Hurlbert) and will include experts in seasonal phenology of moths and butterflies and assemble key phenology summaries, as well as oversee the collection of new caterpillar phenology data. **Team Birds** (BRD, led by PI Tingley and UConn Postdoc) will assemble bird migratory arrival data and produce initial arrival patterns over time along with assembling bird demography data, all at harmonized spatial and temporal resolutions. **Team Vegetation and Climate** (VCL, led by SP Withey**)** will assemble the remotely sensed vegetation data needed for describing green-up trends spatially and temporally, and the climate data at similar extents and resolutions. The **Data Management Team** (DMN, led by SP Guralnick and UConn Post-doc) will also spin up in Year 1 and work with the data product teams through all phases and across all 4 Aims to assure that data products are produced and managed in parallel. In years 2-4, five teams that are focused on the cross-cutting analyses needed to link trophic levels and evaluate transferability across spatial and temporal scales will perform their work. Focused on Aim 2, **Team Mismatch** (MIS, led by Co-PI Hurlbert), will produce results of mismatch analyses across all three trophic levels, documenting mismatch trends. Focused on Aim 3, **Team Demography** (DEM, led by PI Tingley and SP Miller) will determine the impact of mismatch on demography and population trends in both birds and butterflies. Three teams will work on different aspects of Aim 4: **Team Hindcasting** (HND, led by SP Arab) will assess how well the models developed for Aims 1-3 perform at predicting phenology, mismatch, and demography from historical datasets. In addition, **Team Scaling** (SCL, led by Co-PI Hurlbert) will evaluate how phenology and mismatch vary with spatial scale, while **Team Forecasting** (FOR, led by Co-PI Ries and post-doc Neupane) will use all model results to that point for forecasting phenology and mismatch to future climates. Finally, we will also have a team devoted to Broader Impacts, **Team Education & Outreach** (EDU, led by SPs Guralnick and Withey), that will focus fully on training imperatives, developing phenology outputs that are accessible and understandable to the public, including simple to use tools, and efforts to design scalable outputs such as videos and more traditional materials in high flow areas such as museums or natural areas.

Team meeting and Reporting: Teams will meet or talk by videoconference biweekly to monthly to discuss current tasks, progress and deadlines. Teams will all use similar tools mentioned above to capture content and team leads will also talk approximately monthly to report on efforts and make sure that needed information is passed across the collaboration effectively.

Coordination of Activities over course of project**:** We recognize the coordination burden on a project such as this is high. PI Tingley, as lead, will be explicitly responsible for chief project coordination. He will be aided by a postdoc at UConn (to be named) who will focus 80-90% of her or his effort on science-related questions but 10-20% will cover coordinating efforts and helping to organize team meetings and calls. The postdoc will join PIs on monthly to bimonthly calls, inviting the leads of other teams that are active at the time, to ensure progress and coordination across the project as a whole.

Sustainability: Sustainability is a key aspect of project management, especially with goals to produce longer-term data and knowledge products. We have strong skills dealing with large datasets and infrastructure, and the use of CyVerse as a platform for archiving data and building tools lowers long term costs. We also note that our efforts, if successful, will lead to novel next steps and phenological knowledge products that are in active demand both in the sciences, and for NGO and government

agencies. We are therefore confident in both interest in, and our preparation for, continued work with our models and products.

Expectations: We lay out our expectations for all team members clearly at the outset. All personnel are expected to contribute to data gathering and analysis as defined by their team roles (Table 2), to travel to annual project meetings, to participate in their team's more frequent videoconferences, to give presentations on the research from this project at national meetings, and to contribute to the writing of manuscripts as appropriate.

In addition, PIs are expected to provide mentorship and training to the project graduate student and postdocs (as outlined in the Postdoctoral Mentoring Plan), and to communicate clearly and effectively in the event that team members are not performing to expectations. PIs and team leads will be responsible for leading the writing of manuscripts, or designating alternative lead authors where appropriate. We will create and maintain a table of manuscripts in preparation that includes the lead author, title or short description, the key next steps towards publication, and expected completion dates. Finally, data organization is a key issue in this project and it is expected each team works collectively to use shared infrastructure as described in the Data Management Plan.

Table 1. Teams, Members and Effort. An organization structure showing teams and their composition, along with committed effort over the period of the project. "X" marks indicate team leads. Team abbreviations: DMN, Data Management; BRD, Bird Phenology; LEP, Lepidoptera Phenology; VCL, Vegetation and Climate; MIS, Phenological Mismatch; DEM, Demography Modeling; HND, Hindcasting; SCL, Spatial scaling; FOR, Forecasting; EDU, Education and Broader Impacts.

Personnel	Role	DMN	BRD	LEP	VCL	MIS	DEM	HND	SCL	FOR	EDU	Y1	Y2	Y3	Y4
Morgan Tingley	PI		X				X					4.5	4.5	4.5	4.5
Leslie Ries	PI			X						X		1.5	2.5	1.5	1.5
Allen Hurlbert	PI			X		X			X			3.5	3.5	3.5	3.5
Ali Arab	SP							X				1.5	1	1	1.5
Robert Guralnick	SP	X									X	1	1	1	1
David Miller	SP						X					2	2	2	2
John Withey	SP				X						X	2	2	2	2
James Saracco	SP											0	1	1	0
Rodney Siegel	SP											0.5	0.25	0	0
Elise Larsen	Postdoc											6	6	6	0
Stephen Mayor	Postdoc											6	3	0	0
Naresh Neupane	Postdoc									X		6	3	3	6
UConn Postdoc	Postdoc	X	X									12	12	12	12
UNC Grad RA	Grad											12	12	12	0
Database Dev	Other											1	1	2	2
Sarah Yelton	Other											3	3	0	0

Table 2. Activity timeline by main Aims and teams. Abbreviations of team names used below are described in Table 1. We divide activities by quarters starting in summer 2017 and extending to Spring 2021, but we anticipate the activities persisting past the end of the grant.

Task	2017			2018				2019				2020				2021
	Sum	Fall	Win	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win	Spr
Aim 1																
Vegetation phenology	VCL	VCL	VCL													
Caterpillar Counts! data collection	LEP	LEP		LEP	LEP											
Butterfly phenology	LEP	LEP	LEP	LEP	LEP	LEP										
Caterpillar phenology modeling				LEP	LEP	LEP	LEP									
Bird arrival & nesting phenology	BRD	BRD	BRD	BRD	BRD											
Aim 2																
Vegetation-Lepidoptera mismatch					MIS	MIS	MIS	MIS	MIS							
Caterpillar-bird mismatch							MIS	MIS	MIS	MIS	MIS					
Aim 3																
Butterfly demography modeling									DEM	DEM	DEM	DEM	DEM			
Bird demography modeling									DEM	DEM	DEM	DEM	DEM			
Aim 4																
Hindcasting veg phenology			HND	HND	HND											
Hindcasting Lep phenology						HND	HND	HND	HND							
Hindcasting bird phenology						HND	HND	HND	HND							
Hindcasting mismatch											HND	HND	HND	HND	HND	
Spatial scaling of phenology & mismatch													SCL	SCL	SCL	SCL
Forecasting with GCMs												FOR	FOR	FOR	FOR	FOR
Broader Impacts																
Caterpillars Count! workshops/outreach	EDU	EDU			EDU	EDU										
Musuem exhibits										EDU	EDU	EDU	EDU			
NPN coordination				EDU	EDU			EDU	EDU							
MAPS validation & education	EDU	EDU	EDU	EDU	EDU	EDU	EDU									
Data Management & Curation																
Database development and curation	DMN	DMN	DMN	DMN	DMN	DMN	DMN	DMN	DMN	DMN	DMN	DMN	DMN			
Pipeline assembly				DMN	DMN	DMN	DMN									
Product delivery							DMN	DMN	DMN				DMN	DMN	DMN	DMN
Writing Manuscripts						All	All	All	All	All	All	All	All	All	All	All

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