ABSTRACT

Title of Dissertation: THE ECOLOGICAL VELOCITY OF CLIMATE CHANGE

Donal Seán O'Leary III, Doctor of Philosophy in Geographical Sciences, 2020

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Vegetation productivity and distributions are largely driven by climate, and increasing variability in seasonal and interannual climate is both changing the spatiotemporal patterns of resource availability across the landscape, and driving species' migrations towards climate refugia. Climate and vegetation dynamics take place along the time dimension (e.g. earlier snowmelt and arrival of spring in temperate mountains), but they also occur throughout space, where changes in climate can be expressed as a movement across the landscape (e.g. warm temperatures and migratory animals moving uphill in spring, or tree species distributions moving uphill and towards the poles under climate change). Here, we present new methods to track the movement of climate and vegetation, quantifying the ecological velocity of climate change at the landscape scale. Our focus is on national parks of the USA, which are important study areas because of their great conservation and social value, protection from anthropogenic disturbances, and longstanding research and monitoring records. First, we explore the spatio-temporal relationships between snowmelt timing and vegetation phenology in Crater Lake National Park. We find that snowmelt timing is closely linked to spring greenup, but has far weaker influence on later season phenology, such as the senescence or growing season length. Second, we extend our comparison of snowmelt timing with vegetation phenology across space and time together as we track the speed and direction of receding seasonal snowpack (snowmelt velocity) with the 'green wave velocity' of spring greenness that follows. We find that snowmelt velocity has a moderate predictive power for green wave velocity in areas with steep slopes, where both phenomena are controlled by strong spatial gradients relating to elevation. Third, we extend our analysis into the future as we forecast the climate velocity of air temperature and precipitation in and surrounding national parks from 2019-2099. Here, we identify possible corridors and velocities of future climate migration across park boundaries, highlighting locations of ecological concern and climate vulnerability.

THE ECOLOGICAL VELOCITY OF CLIMATE CHANGE

by

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Dissertation submitted to the Faculty of the Graduate School of the
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Dedication:

To Mom and Dad,

two teachers who convinced me to stay in school *for as long as possible*.

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List of Abbreviations

Bureau of Land Management (BLM)

Crater Lake (CRLA)

Day Of Year (DOY)

Endangered Species Act (ESA)

Environmental Site Potential (ESP)

Global Climate Model (GCM)

Forage Maturation Hypothesis (FMH)

Land Use/Land Cover (LULC)

MODerate Resolution Imaging Spectroradiometer (MODIS)

National Park Service (NPS)

Representative Concentration Pathways (RCPs)

Snowmelt Timing Maps (STMs)

United States Forest Service (USFS)

United States of America (USA)

Chapter 1: Introduction and Motivation

In order to flourish, vegetation depends on environmental inputs for water (rain, snowmelt), energy (light, ambient temperatures), and nutrients (carbon, nitrogen, etc.) (Stephenson, 1990). As these climate inputs change across days, seasons, and years, vegetative species and communities respond in turn by changing their productivity, phenology, and distributions, respectively (Billings and Bliss, 1959; Huntley and Webb, 1989; Albon and Langvatn, 1992; Craighead Jr., 2001). Our world's climate is highly spatially and temporally heterogeneous, and the spatial patterns of vegetation life cycles and distributions are closely linked to these changes in climate across space and time (Hopkins, 1920; Holdridge, 1947). Vegetation provides valuable food and other resources for higher trophic levels within the ecosystem, therefore variability in vegetation distributions and productivity causes cascading effects throughout the ecosystem (Hebblewhite et al., 2008). Many researchers within the scientific community seek to identify the linkages between climate and vegetation across spatial and temporal scales to understand better how changes in climate affect vegetation communities and the ecosystems that depend on them (Aikens et al., 2017; Emmett et al., 2019).

Climate Variables

The variables of air temperature and precipitation are principal controls on ecological processes across spatial and temporal scales (Richardson et al., 1975; Huntley and Webb, 1989; Nolan et al., 2018). At coarse scales, the combination of annual mean air temperature and total annual precipitation controls biome type, and often predict the existing ecological communities within a region (Holdridge, 1947). Seasonal variation in air temperature and precipitation drive phenology cycles for countless organisms, particularly for communities outside of the tropics (Craighead Jr., 2001). Interannual variability in air temperature and precipitation controls vegetation productivity (Emmett et al., 2019; Notaro et al., 2019), which in turn controls resource availability for the organisms that depend on the ecosystem's vegetation stocks (Cornelius et al., 2013).

In locations with seasonal snow cover, the timing of snow's disappearance (henceforth - *snowmelt timing*) is a third dominant control on spring phenology (Billings and Bliss, 1959). Seasonal snowpack serves two important controls to the energy balance at the Earth surface; snow's high albedo reflects the majority of incoming solar radiation (Roesch et al., 1999), while snow's high insulation value maintains a soil surface temperature close to 0°C (Lundquist and Lott, 2008). Snowmelt timing initiates a dramatic change in energy balance at the Earth surface (Swenson and Lawrence, 2012), when the highly reflective snow surface disappears, allowing for the (often) darker soils and vegetation to absorb solar radiation, a critical input for vegetation productivity (Billings and Bliss, 1959; Cornelius et al., 2013; Harte et al., 2015). Snow provides >70% of the annual water budget in many parts of the western USA (Hall et al., 2012), therefore, snowmelt releases water to allow the highest soil moistures levels of the year (Harpold et al., 2015). In these ways, snowmelt timing is an essential and important part of climate seasonality in temperature ecosystems.

Seasonal-Scale Ecological Responses to Climate

At the seasonal scale, the ecological processes that occur in spring are vitally important for the organisms within that ecosystem (Craighead Jr., 2001), and these processes have been changing in response to climate pressure (O'Leary et al., 2017b), challenging species that depend on spring resources for food and shelter (McKinney et al., 2012; Mayor et al., 2017). Spring vegetation phenology includes the production of biomass, including leafy vegetation and reproductive structures such as flowers and fruits, all of which provide important food resources for resident and migratory animals (Albon and Langvatn, 1992). The location and abundance of these resources are spatially and temporally heterogeneous and change over time (Denny et al., 2018). Studies have shown that animals change their locations throughout the season, and often migrate throughout the year, in order to maintain position with the most valuable vegetation resources (Van der Graaf et al., 2006). Researchers call this effect 'surfing the green wave,' where animals track ('surf') the pace and direction of the 'green wave' of spring as it moves across the landscape (Bischof et al., 2012; Merkle et al., 2016; Aikens et al., 2017). However, some migratory species travel long distances in anticipation of finding the usual resources along the way or at their destination, and climate change has been disrupting these routines by changing the timing of resource availability, leading to trophic asynchronies which harm dependent species (Harrington et al., 1999; Post and Forchhammer, 2008; Post et al., 2008; McKinney et al., 2012). Seeing as many animals migrate in coordination with vegetation resources, and those plants are themselves responding to climate forcing, there are many direct and indirect links among air temperature, precipitation, and snowmelt timing and animal migration. Considering these mechanisms and important relationships, the seasonal spatial patterns of vegetation responses to climate have serious implications for animal success and migrations.

There are broad networks of instrumented and remote observation systems in place to track climate change and the resulting ecological responses. Satellite-based remote sensing platforms have been making daily observations of snow cover and vegetation greenness for decades, with the landscape scale MODerate Resolution Imaging Spectroradiometer (MODIS) sensors producing science-grade images since 2000 (Hall et al., 2002; Huete et al., 2002). These observations have been developed into extensively validated daily maps of many Earth surface characteristics, including vegetation dynamics (Zhang et al., 2003) and snow cover (Maurer et al., 2003; Huang et al., 2011; Crawford, 2014; Hall and Riggs, 2016). By incorporating the time dimension, researchers have distilled these daily observations into annual maps showing the timing of a particular state change. In particular, researchers are interested in the timing of when vegetation transitions from dormancy to productivity (i.e. spring phenology), which lead to the development of the MODIS-based vegetation phenology maps (Zhang et al., 2003; Ganguly et al., 2010; Friedl et al., 2019). Seeing as snowmelt timing is a dominant control on a number of Earth surface processes including vegetation phenology (Inouye and McGuire, 1991; Inouye et al., 2000; O'Leary et al., 2017b), O'Leary et al. (2017a) developed a set of snowmelt timing maps to correspond with the existing phenology maps (O'Leary et al., 2018). These satellite-based observations, and their resulting higher-level datasets, provide an important data record that has been used in countless studies into the interactions between climate and ecosystems, from local case studies to global analyses.

Decadal-Scale Climate Velocity

Scientists broadly agree that climate will continue to change at the decadal scale into the coming century, with widespread consequences for ecosystems around the world (IPCC, 2014; Nolan et al., 2018). Decadal or century-scale climate change leads to species redistributions (Huntley and Webb, 1989; Pearson, 2006; Nolan et al., 2018), and occasionally local (Beever et al., 2016) or global extinctions (Ceballos et al., 2017). Plant and animal species are known to move across the landscape as they redistribute to maintain position within their preferred climate niche (Huntley and Webb, 1989). Species redistribution requires migration, which typically happens along latitudinal and elevational gradients, such as following the last glacial maximum in the Eastern United States, when tree species migrated northwards and uphill in response to rising temperatures (Davis, 1983; Huntley and Webb, 1989; Davis et al., 2015). Identifying the speed of such movement is important, as climate may move faster than a species' dispersal ability, leading to increased stress and potentially extinction (Corlett and Westcott, 2013; Sittaro et al., 2017). While these migrations have occurred many times in the geological record, current rates of climate change are expected to be much greater than previous episodes, presenting an additional challenge to slow-migrating species (Jump and Peñuelas, 2005). Furthermore, there are impediments to movement such as a mountain range, desert, or human-disturbed area (Iverson et al., 2004). Therefore, there is a need to identify the speed and pathways for expected climate-driven migration so that land managers and conservationists can identify at-risk species and manage their conservation accordingly. To do so effectively, researchers need climate projections with relatively high spatial resolution. Fortunately, NASA has recently generated monthly predictions of air temperature and precipitation at a 1km spatial resolution from present to 2099 under four emissions scenarios across the conterminous USA (NASA, 2017), allowing for detailed spatial analysis of climate velocity at the landscape scale.

At the decadal scale, climate velocity is a concept that estimates the speed and direction of climate variable movement by comparing a location's temporal rate of change with its surrounding spatial gradient (Loarie et al., 2009). For example, in considering mean annual temperature, if a 0°C isotherm exists at a location that will experience an increase of 1°C over the next 10 years (temporal rate of change), and the closest location that is 1°C cooler is 10 km away (spatial gradient), that isotherm will travel 10 km over 10 years, resulting in a climate velocity of 1km/yr in the direction of the cooler location. If there were a particular species at that location which could only grow at a mean annual air temperature above 0°C, that species could then expand its range to follow the isotherm. Conversely, if a species were to require a mean annual air temperature below 0°C, that species would need to travel at least as fast as the isotherm to avoid unfavorable climatic conditions, and perhaps, local extinction (Moyer-Horner et al., 2016; Wilkening and Ray, 2016; Stewart et al., 2017). In this way, climate velocity can predict an upper or lower bound for a species' movement, particularly in the context of climate-driven migrations and redistributions.

Climate velocity is highly dependent on topography and local climatology (Dobrowski and Parks, 2016; Carroll et al., 2018; Loarie et al., 2009; Dobrowski et al., 2013; Carroll et al., 2017). Different landforms, such as canyons, valleys, ridges, and peaks, generate different patterns of climate velocity. For example, valleys experience fast climate velocities along their long axis (up river) and slow climate velocities up the steeper gradients of their surrounding hillsides, whereas mountain peaks can act as 'climate sinks' that attract climate variables (such as isotherms) until they 'disappear' off the top of the mountain (Dobrowski et al., 2013). The ecological result is that a species can extend its range long distances along the valley floor, or short distances up the surrounding hillsides, to find appropriate climatic conditions (Carroll et al., 2015). However, once it reaches the mountain peak it has nowhere else to travel (Carroll et al., 2015; Dobrowski and Parks, 2016), so it may experience a local extinction when encroached upon by untenable climate conditions (Stewart et al., 2017). Furthermore, different climate variables may experience different climate velocities. For example, temperatures may move uphill, while precipitation levels move downhill, resulting in 'niche splitting' which can lead to novel climates (Ordonez et al., 2016). These locations may experience a reorganization of the ecosystem rather than system movement *en masse* (Both et al., 2009a), and identifying particular locations of novel climate is a new area of interest for land managers seeking to understand how climate change will affect their lands (Hansen et al., 2014; Monahan and Fisichelli, 2014; Gonzalez et al., 2018).

Ecological Velocity

The ecosystem responses to climate velocity are described here as *ecological velocity*. Ecological velocity consists of two main factors: the spatial and temporal patterns of ecological responses to changes in climate. It also must consider the lags between a change in climate and a response in ecology to best capture the dynamics of the system. Table 1 describes examples of the spatial and temporal dimensions of ecological velocity.

Table 1 - The spatial and temporal dimensions of ecological velocity. These examples are not exhaustive, as ecological velocity as a concept can be applied to an unlimited variety of ecological processes.

Spatial/Biological Scale	Ecological Response	Time Scale (processes and lags)	Variables of Interest
Cell	Photosynthesis	Seconds	Oxygen, CO_2
Leaf	Leaf Economy	Hours/Days	Nutrients, ET
Organism	NPP	Hours/Days	Nutrients, ET
Stand	Phenology	Days/Months	Forage, Habitat, Cover
Population	Migration	Years	Habitat, Carbon
Community	Reorganization/Migration	Decades	Biodiversity
Ecosystem	Reorganization/Migration	Centuries	Land Cover, Biodiversity

An important consideration for ecological velocity is the lag between a change in climate and the resulting ecological response (Alexander et al., 2018). These lags may take many forms, and depend strongly on the ecological process involved. For an example of a short lag, photosynthesis may increase rapidly as a function of incoming solar radiation. Conversely, a tree species may have substantial lags to migrate in response to decadal-scale climate velocity depending on that species' reproductive and dispersal strategies (Davis, 1983). Furthermore, some species may not respond to a change in climate if that change results in an environment that is still suitable for that species. Simply put, why move if you don't have to? Additionally, many species occupy physical niches that are not influenced strongly by precipitation and air temperature for parts or all of the year (Millar et al., 2016), and genetic variation within a population may result in differential responses to changes in climate (Castillo et al., 2016). Anticipating and accounting for these lags will be an important part of managing change for landowners, and may require consultation with a species expert, especially for sensitive species with legal conservation requirements (Moyer-Horner et al., 2016).

Ecological velocity has the capacity to describe the speed and direction of ecosystem changes in response to climate change (Merkle et al., 2016). Taken further, in a geographical setting ecological velocity can indicate potential migratory corridors, and describe the speed/timing of the associated ecological changes, in the past or the future (Burrows et al., 2014). Identifying potential migration corridors is highly beneficial for conservationists as they manage their natural resources across space and time, a challenge that is being escalated by increasing climate variability (Monahan and Fisichelli, 2014). Climate change is a problem, but it's the ecological responses to climate change that are the pressing issue for land managers. Here, we offer new tools for analyzing and anticipating ecological responses to climate change in a land management perspective.

Management Relevance for National Parks of the USA

While one can make generalized assumptions about a region's ecological future based on the overall climate projections and these idealized topographic rules, a detailed analysis of local geophysical and ecological conditions is essential to generating a quality prediction of ecological velocity (Carroll et al., 2018). The national parks of the United States are important locations to quantify ecological velocity because of their great value and visibility to the global public (NPS, 2017), their strict protections from human interference, and the presence of hundreds of long-running ecological studies (Craighead Jr., 2001; National Park Service, 2016b, 2016a, 2016c). National parks of the USA are at the extreme limits of their historical climate variability (Monahan and Fisichelli, 2014), and the combined forces of climate change and land use change are threatening to alter permanently their ecosystem functions and compositions at the landscape scale (Hansen et al., 2014, 2016; Guay et al., 2016). Identifying likely ecological changes is of intense interest, particularly within the National Park Service (NPS), where land managers are actively planning adaptation strategies to preserve cultural and ecological resources for an uncertain future with unprecedented climates (National Park Service, 2010). Current approaches generally consider net changes in climate variables (e.g. 2°C warmer, 15% more precipitation) to model ecological changes such as tree species redistributions (Guay et al., 2016; Hansen et al., 2016), however, such approaches cannot account for the rate of change, nor the likely pathways of climate and ecological migration across park boundaries (Hansen et al., 2016). Recent advances in spatial climate analysis have shown that topography and surrounding landscapes have a substantial impact on the local expression of climate and ecological change (Dobrowski and Parks, 2016; Carroll et al., 2018). By including information about a park's geophysical surroundings, we can greatly improve our understanding of how changes in climate – on seasonal, annual, and decadal time scales – have and will manifest in ecological changes within a park at the landscape scale (Carroll et al., 2018).

The US National Park Service and US Forest Service have already begun to shift their management focus from preservation to adaptation (National Park Service, 2010; Kerhoulas et al., 2013; Gonzalez et al., 2018) as it is increasingly apparent that these lands are likely to experience unprecedented climates within decades (Monahan and Fisichelli, 2014; Guay et al., 2016), leading to changes in ecosystem composition and function (Gonzalez et al., 2010). Furthermore, many US national parks are in mountainous areas with an increased risk of climate change (Rangwala and Miller, 2012), making them more vulnerable than other parts of the USA (Gonzalez et al., 2018; Panetta et al., 2018). Seasonal snowpack, which is a principal climatic control on the ecology of such mountainous systems (Billings and Bliss, 1959), is rapidly depleting (Pierce et al., 2008; Stewart, 2009; Margulis et al., 2016b; Sproles et al., 2017; O'Leary et al., 2018), affecting hydrology (Hall et al., 2015), phenology (Inouye, 2008; O'Leary et al., 2017b), and wildfires (Westerling et al., 2006; O'Leary et al., 2016; Westerling, 2016; Holden et al., 2018; Littell, 2018). While there is a growing body of literature that identifies climate's controls on vegetation and ecosystem dynamics (Huntley and Webb, 1989; Harte and Shaw, 1995; Nolan et al., 2018), there is less understanding of how changes in climate will affect the ecosystems that are currently present in and around national parks of the conterminous USA (Hansen et al., 2016). Of particular interest is locating climate and ecological migration corridors that cross land-cover classes or political boundaries, because these can identify locations of likely ecological change such as biome shifts or exotic species invasion (Marra et al., 2004; Francl et al., 2010; Bischof et al., 2012; Middleton et al., 2013; Merkle et al., 2016; Aikens et al., 2017; Jesmer et al., 2018; Flanagan et al., 2019). Using the ecological velocity framework, we can identify the beginning (present) and end (future) points along a path of climate velocity (Dobrowski and Parks, 2016; Carroll et al., 2018), locating climate migration corridors surrounding and within national parks. We can then compare the Land Use/Land Cover (LULC) of those lands to the ecological quality of migration access for each park, including regions of unencumbered ecological migration (natural lands), likely sources of invasive species (agricultural lands), or barriers to migration (urban/developed lands) (Carroll et al., 2018).

Research Objectives

In this dissertation, the concept of ecological velocity is established. Ecological velocity is expansive in its scope; therefore three studies (chapters 2-4) are conducted as real-world examples of ecological velocity to improve the connection of this theoretical concept with real-world management applications. These three examples of ecological velocity provide a foundation for further work in this field, as well as actionable results for land managers and conservation scientists to apply in their own work.

First, in Chapter 2 the interaction between snowmelt timing (climate driver) and vegetation phenology (ecological response) is investigated at Crater Lake National Park (CRLA). This chapter builds upon the work of David Inouye and others who have established that snowmelt timing is one of the most important climate drivers of spring ecology in seasonally snowy areas, particularly the high elevation mountains of the western USA (Inouye and McGuire, 1991; Inouye et al., 2002; Inouye, 2008; Lambert et al., 2010).

Next, in Chapter 3 the analysis from Chapter 2 is extended into multiple spatial dimensions to compare the climate velocity of snowmelt with the *'green wave'* velocity of spring phenology across an enormous spatial domain spanning much of North America. The work is on the seasonal time scale, but across multiple spatial dimensions, establishing a connection between climate velocity and ecosystem responses at a scale and spatial domain that are, to our knowledge, unprecedented in large size. High-quality and validated MODerate resolution Imaging Spectroradiometer (MODIS) data packages offer millions of observations of the earth surface, from which snowmelt timing and spring greenup are readily derived.

Finally, in Chapter 4 the future on decadal time scales is examined, by identifying the pathways of climate velocity relative to National Park Service boundaries from present until 2100. This analysis focuses on climate movement across space at the landscape scale to identify particular locations in and around national parks that are prone to experiencing substantial ecological responses to climate change. This chapter relies on the established principals of the relationships between climate movement and the movement of ecological responses, found both in the preceding chapters, and throughout the literature. That is because there are no ecological observations from the future. Furthermore, there are no climate *observations* from the future, but rigorously modeled climate projections that have recently been downscaled into the NASA NEX Downscaled Climate Projections (DCP-30), which are 1km resolution projections of monthly air temperatures and precipitation for the conterminous USA from 2006-2100 under four Representative Concentration Pathway climate scenarios (RCP) (van Vuuren et al., 2011). This analysis is relative to national park boundaries, which highlights velocities of management concern – particularly velocities that may suggest the movement of invasive species, or perhaps the exodus of a current park's inhabitants as they emigrate, seeking climate refuge elsewhere.

Taken together, these three chapters span a gradient of spatial and temporal scales of ecological velocity. This work spans the spatial dimension – ranging from the relatively small CRLA to the North American continent. It also span temporal dimensions, ranging from daily/seasonal variability to decadal scale climate change. While these examples are not an exhaustive encyclopedia of dimensions of ecological velocity, this dissertation establishes three points of contact between *ecological velocity* and the real world. Much like the legs of a stool, these three chapters work together to build upon the existing grounds of ecological and spatial sciences, and allowing for future work that continues upwards.

Chapter 2: Snowmelt timing, phenology, and growing season length in conifer forests of Crater Lake National Park, USA

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Abstract

Anthropogenic climate change is having significant impacts on montane and high elevation areas globally. Warmer winter temperatures are driving reduced snowpack in the western US with broad potential impacts on ecosystem dynamics of particular concern for protected areas. Vegetation phenology is a sensitive indicator of ecological response to climate change and is associated with snowmelt timing. Human monitoring of climate impacts can be resource prohibitive for land management agencies, whereas remotely sensed phenology observations are freely available at a range of spatiotemporal scales. Little work has been done in regions dominated by evergreen conifer cover, which represents many mountain regions at temperate latitudes. We used moderate resolution imaging spectroradiometer (MODIS) data to assess the influence of snowmelt timing and elevation on five phenology metrics (greenup, maximum greenness, senescence, dormancy, and growing season length) within Crater Lake National Park, Oregon, USA from 2001-2012. Earlier annual mean snowmelt timing was significantly correlated with earlier onset of green-up at the landscape scale. Snowmelt timing and elevation have significant explanatory power for phenology, though with high variability. Elevation has a moderate control on early season indicators such as snowmelt timing and green up, and less on late-season variables such as senescence and growing season length. PCA results show that early season indicators and late season indicators vary independently. These results have important implications for ecosystem dynamics, management, and conservation, particularly of species such as whitebark pine (Pinus albicaulis) in alpine and subalpine areas.

Keywords: climate change; National Parks; NDVI; phenology; remote sensing; snowmelt

Introduction

The earth's surface has experienced unprecedented warming over the past several decades (IPCC, 2014). However, warming trends are not uniform, with mountain ecosystems experiencing greater rates of change globally (Rangwala and Miller, 2012). Reductions in snowpack and earlier snowmelt due to increasing temperatures in the US Mountain west is altering hydrological systems, forest dynamics, and fire regimes (Barry and McDonald, 2012) which raises significant concern for iconic National Parks and protected areas that encompass montane and high elevation ecosystems of the region (Moritz et al., 2008). Many parks are already at the extreme warm end of their historic range of variation (1901-2012) for climate variables such as mean annual temperature and minimum temperature of the coldest month (Monahan and Fisichelli, 2014). Management agencies are mandated to incorporate climate change into action plans (Burns et al., 2003a), creating significant demands for ecological data at large temporal and spatial scales to make science-based decisions that acknowledge changing conditions and novel futures (Baron et al., 2009).

Ecological monitoring of large, often remote national parks and protected areas is extremely challenging given the complexity of climate change impacts and the limited financial and personnel resources of many units (Fancy et al., 2008). A vital ecological indicator of climate change is phenology, the timing of biological events, which is integral to species reproduction and survival (Forrest and Miller-Rushing, 2010) and is central to most ecological interactions and processes (Parmesan and Yohe, 2003; Walther, 2010). Phenological research and monitoring has become a vital tool for understanding ecological responses to climate change at multiple scales and developing management strategies that reduce vulnerability of natural systems (Enquist et al., 2014).

In ecosystems with seasonal snowpack (Moore et al., 2015) phenology is closely associated with the timing of spring snowmelt, particularly vegetation green-up, senescence, and growing season length (Lambert et al., 2010; Sedlacek et al., 2015). These phenological metrics are central to predator-prey synchrony (Visser and Holleman, 2001; Visser et al., 2005; Durant et al., 2007; Post et al., 2008), recent asynchronous trophic cascades (Harrington et al., 1999; Both et al., 2009b), community dynamics and composition (CaraDonna et al., 2014; Leingärtner et al., 2014), invasion pathways of exotic species (Wolf et al., 2016), pest outbreaks and subsequent tree mortality from Phytophagous bark beetles, frequency and duration of wildfires and the wildfire season (Westerling et al., 2006), and wildfire area burned (Semmens and Ramage, 2012; O'Leary et al., 2016).

Despite the diversity of studies on phenology relevant to snowmelt, much of this research is accomplished through local-scale, ground-based monitoring (Inouye, 2008; Post et al., 2008) and is often focused on individual species and deciduous plants and communities (Lambert et al., 2010; Meier et al., 2015; Sedlacek et al., 2015). Particularly lacking is applied landscape-scale research on snowmelt and phenology of high elevation ecosystems abundant in cordillera of the western United States. These ecosystems are often patchwork mosaics of closed canopy conifer forests, open canopy woodlands, and/or alpine grasslands, which may produce snowmelt/phenology interactions that are complex and unique to these areas. Studying phenology and snowmelt at large spatial and temporal scales through ground-based monitoring may be optimal (Enquist et al., 2014) but is resource intensive and may be beyond the immediate capacity of park budgets and near-term management priorities. Therefore, the use of free, readily-available data from remote sensing satellite instruments such as the Moderate Resolution Imaging Spectroradiometer (MODIS) (Zhang et al., 2003; Pettorelli et al., 2005; Cleland et al., 2007) can be a cost-effective tool for immediately assessing a range of phenological indicator metrics related to climate-driven impacts of snowmelt at large spatial scales, albeit over a limited time period. Again, although seasonal changes in MODIS-derived Normalized Difference Vegetation Index (NDVI) values are commonly used to assess phenological metrics, these efforts have been primarily restricted to deciduous broadleaf, grassland, and agricultural systems (Zhang et al., 2003; Ahl et al., 2006; Fontana et al., 2008) with little application in coniferous ecosystems, despite research indicating the validity and usefulness of NDVI in assessing evergreen conifer phenology (Beck et al., 2006; Knight et al., 2006; Yu and Zhuang, 2006), especially for interannual comparisons (Jönsson et al., 2010).

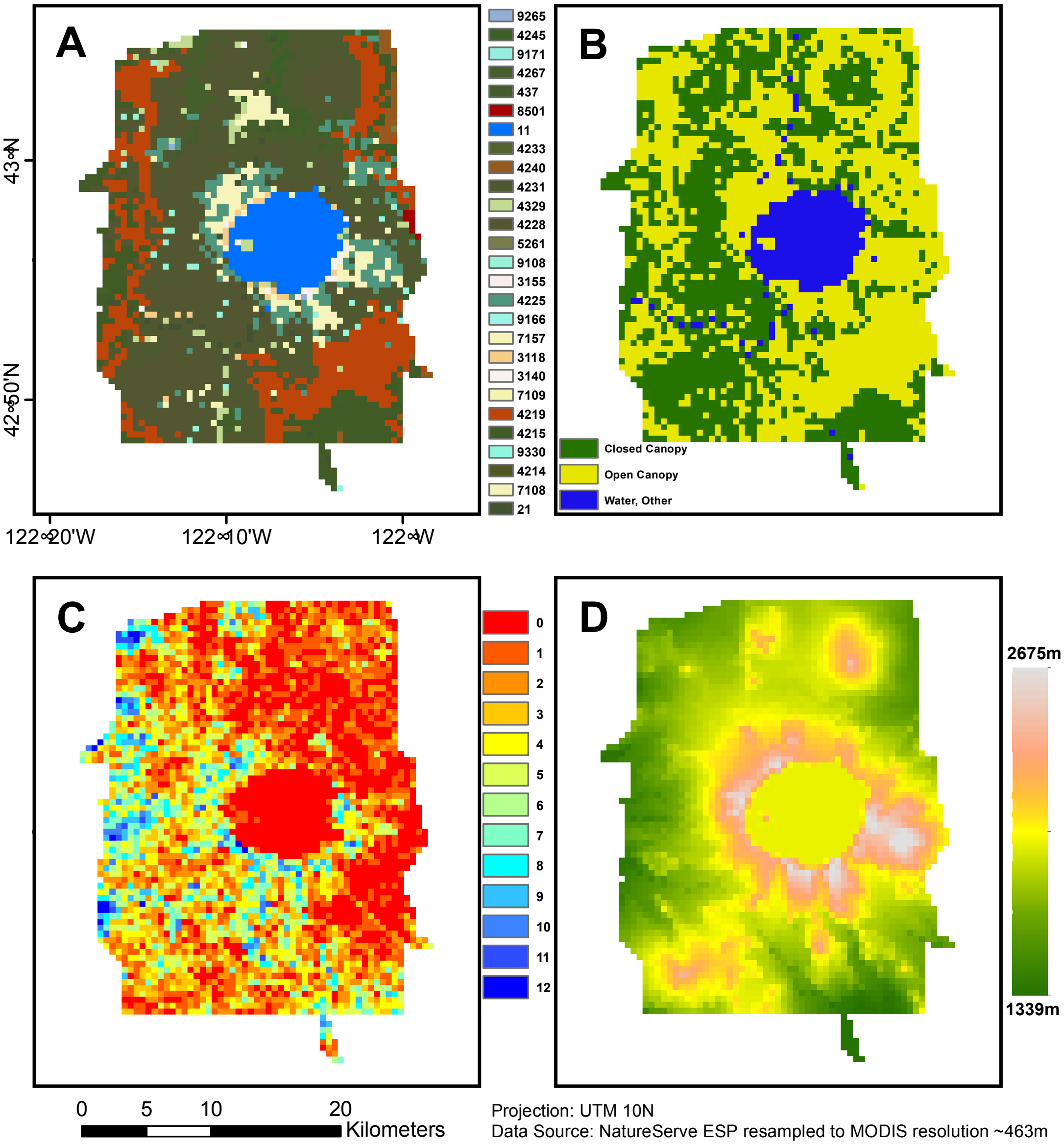
Warmer winter temperatures and reduced snowpack are a significant concern in the southern Oregon Cascades where Crater Lake National Park contributes a significant portion of summer flows to the Klamath, Rogue, and Umpqua. Understanding relationships between forest phenology and snow dynamics is central to many critical ecological and sociopolitical issues in the park and bioregion including plant and animal species conservation from whitebark pine (Keane et al., 2012) to Pacific salmon (Bartholow, 2005), hydrology (Rango and Katwijk, 1990), and human water resources (Levy, 2003; Poff et al., 2003), but lacks large-scale ground-based phenology and meteorological monitoring. Yet, there is immediate demand for insight on climate-driven ecological dynamics to inform management.

Our goal was to assess the relationship of vegetation phenology and growing season length with snowmelt timing in Crater Lake National Park, Oregon (CRLA) using freely available MODIS-derived data products to provide insight of potential climate change impacts on national park resources. Specifically, we examined the relationship of day of year (DOY) of snowmelt timing with onset of green-up, peak phenology, onset of senescence, complete senescence, and length of growing season for CRLA as a whole, and isolating the closed- and open-canopy portions of the park. We then performed a principal components analysis (PCA) to identify the major factors driving variability among climate factors for the years 2001-2012.

Materials and methods

Study Area

CRLA is located in the Cascade Mountain Range of southern Oregon, the encompassing 741Km^2 with over 1350m of elevational difference and a maximum elevation atop Mt. Scott at 2721m (Figure 1, D). Approximately 70% of annual precipitation in the park falls as snow, with average total snowfall of 15m (Adamus et al., 2013). The eastern portion of the park lies in the rain shadow of the Cascade crest and becomes drier moving from the crest towards the semiarid plateau of eastern Oregon. Landcover of CRLA is comprised primarily of a rage of conifer forest types whose distribution is associated with elevation, soil types, and aspect (Adamus et al 2013). We used NatureServe (2009) ecosystem site potential (ESP) classifications to distinguish ecosystem types across CRLA (Figure 1, A). The ESP native resolution is 30m, so we resampled these data to match the scale and registration of the MODIS data (projected as described below), resulting in 27 cover types. We then classified these cover types into three simple categories, closed canopy, open canopy, and water/developed (Table 2, Figure 1, B), as defined in the NatureServe ESP documentation (NatureServe 2009). Common conifer species within these ecosystems include Ponderosa pine (*Pinus* ponderosa), Douglas-fir (*Psuedotsuga menziesii*), white fir (*Abies concolor*), red fir (*Abies magnifica*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), mountain hemlock (*Tsuga mertensiana*), and whitebark pine (*Pinus albicaulis*) at the highest subalpine elevations. Ecosystems details and classification results are shown in Appendix 1.



Projection: UTM 10N
Data Source: NatureServe ESP resampled to MODIS resolution ~463m

Figure 1 - Map of Crater Lake National Park, southern Oregon, USA. Insets show A) NatureServe Environmental Site Potential (ESP) types at the MODIS resolution and registration (with ESP code number in legend, see Appendix 1 for habitat descriptions), B) simplified cover types as defined in our study, C) number of years of complete record by pixel, and D) elevation in meters.

Table 2 - Descriptive statistics for cover class conversion. The NatureServe Environmental Site Potential (ESP) product was reclassified into three major types, open canopy, closed canopy, and water/developed (classes 1,2,3, respectively). Count represents the total number of pixels of that type in CRLA. ESPs represents the number of ESPs combined into each class. Area is calculated by multiplying the number of pixels (Pixels) by the area of each

pixel (0.2147 km2). This area was determined through the MODIS conversion to UTM 10N projection and includes distortion error.

Type	Class	Count	ESPs	Area km2
Closed Canopy Forest	1	1438	5	308.66
Open Canopy Forest	2	1694	20	363.61
Water/Road/Other	3	286	2	61.39

Snowmelt and phenology

To examine relationships between snowmelt timing and vegetation phenology across terrestrial landcover types at CRLA, we used publicly available snow and plant phenology remote sensing data products derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite instruments. We compared Day of Year (DOY) values for each year of record available (2001-2012) for snowmelt and five phenological metrics (see below) within the extent of our study region defined by the boundary of CRLA.

To consider snowmelt DOY, we used the Snowmelt Timing Maps (STMs) derived from MODIS for North America, 2001-2015 (O'Leary et al., 2017a). These STMs are derived from the MOD10A2 500m Grid Maximum Snow Extent product (Hall et al., 2006), which offers 8-day composite images showing the global distribution of snow, filtering out cloud cover when possible. MOD10A2 reports snow presence for the 8-day period when snow is present for at least one day in the time-step, leading to an overestimation of snow presence in some circumstances (Hall and Riggs, 2007; Wang et al., 2008). While the STMs inherit the uncertainties of the parent data product (spatial and temporal resolution, snow presence overestimation, etc.) they provide useful and spatially complete snowmelt timing surfaces which facilitate comparison with other MODIS-based products.

We used the MCD12Q2 data product (Ganguly et al., 2010) to generate vegetation phenology metrics. This phenology dataset is created by fitting Gaussian curves to the time series of the Normalized Differential Vegetation Index (NDVI) values derived from MODIS data (Kriegler et al., 1969; Rouse et al., 1974). The primary limitation of the MCD12Q2 product is that there is a high level of omission of points due to cloud cover obscuring the signal analysis process (Ganguly et al. 2010). After removing grid cells with zero reported phenology values (water, roads, rocks, etc.), only 32% of CRLA has 5 or more years of useful phenology data (Figure 1, C). However, a significant benefit of this product is that it is conveniently co-registered with the MOD10A2 snow data product. Converting from their native date format, we calculated the DOY for four phenological metrics along the annual trajectory of NDVI, 1) the onset of "green up" when vegetation emerges from dormancy (greenness increase), 2) peak phenology when vegetation reaches the fully mature growing season (greenness maximum) 3) the onset of when vegetation begins to senesce (greenness decrease) and 4) when vegetation returns to dormancy (greenness minimum). We then calculated a fifth phenological metric, 5) growing season length by subtracting the greenness increase from the greenness decrease, giving us growing season length in days. Given the limitations of resolution and within-grid spatial heterogeneity for both the phenology and snowmelt timing datasets, we propose that the combination of these methods and products are appropriate for a landscape-level analysis performed here, and may not be appropriate where a more detailed assessment is needed.

Analysis

After preparing the snowmelt and phenology raster products, we projected all gridded data to UTM 10N and extracted DOY values using ArcMap10.2, selecting only the pixels that are centered within CRLA boundary. Therefore, each datum represents an individual MODIS pixel for a single year (from 2001-2012) with an annual DOY value for snowmelt and the phenological metrics. Due to lack of complete snow coverage during some years, difficulty in measuring phenology, and lack of vegetation in many areas including the surface of Crater Lake itself, there are many points that have an observation for some, but not all, phenology metrics (n=41,016). We considered CRLA as a whole, taking the annual mean values for snowmelt and the five phenological metrics within the entire park and for the two vegetated classes: open- and closed-canopy ecosystems. We tested the correlation of the annual mean values of the five phenonological metrics DOY with snowmelt date for all ecosystem classifications and for the park as a whole using Spearman Rank correlations (n=12), giving us an impression of these dynamics at the large scale. We then selected only those data points with a complete record for the point and year (i.e., a pixel containing a DOY value for snowmelt timing and every phenology metric for that year), giving us a sample size of n=9134. This was done to better assess the interplay between these timing indicators at the pixel level. Some locations had better complete coverage than others (Figure 1, C), and coverage also varied between years (Table 3). We compared snowmelt timing and greenness increase with elevation, and we then compared snowmelt timing with each of the phenological variables using linear models to identify trends and variability. To explore sources of variability and covariance within the data we conducted a PCA. We calculated Pearson correlation coefficients for our variables of interest and used the non-correlated ($\rho < 0.7$) variables as inputs to a PCA to identify the driving factors behind the variability within the data. All analyses were performed in program R 3.2.2 (R-project.org, 2016).

Table 3 - Number of pixels with complete data records by year. For a pixel to be considered to have a complete data record it must have a DOY value for snowmelt timing and every phenology metric. CRLA as a whole contains n=3418 pixels.

Year	Complete Pixels
2001	1038
2002	841
2003	865
2004	756
2005	668
2006	722
2007	717
2008	693
2009	683
2010	674
2011	542
2012	935
Total	9134

Results

Annual mean values of the onset of spring green-up (greenness increase) was positively correlated ($\alpha = 0.05$) with snowmelt date for CRLA as a whole (p-val = 0.026, $\rho = 0.650$), and for each of the two vegetated cover classes: closed canopy (p-val = 0.037, $\rho = 0.615$) and open canopy (p-val = 0.019, $\rho = 0.678$) (Figure 2, Table 4). Snowmelt timing and greenness maximum also had a significant positive relationship within open canopy ecosystems (p-val = 0.046, $\rho = 0.594$). All other correlations calculated were not significant, notably those between snowmelt timing and growing season length. The best-fit linear model comparing the spatially-averaged annual mean values of snowmelt timing and greenness increase shows a significant positive relationship with an adjusted R^2 of 0.608 (Table 5 *Mean Increase*).

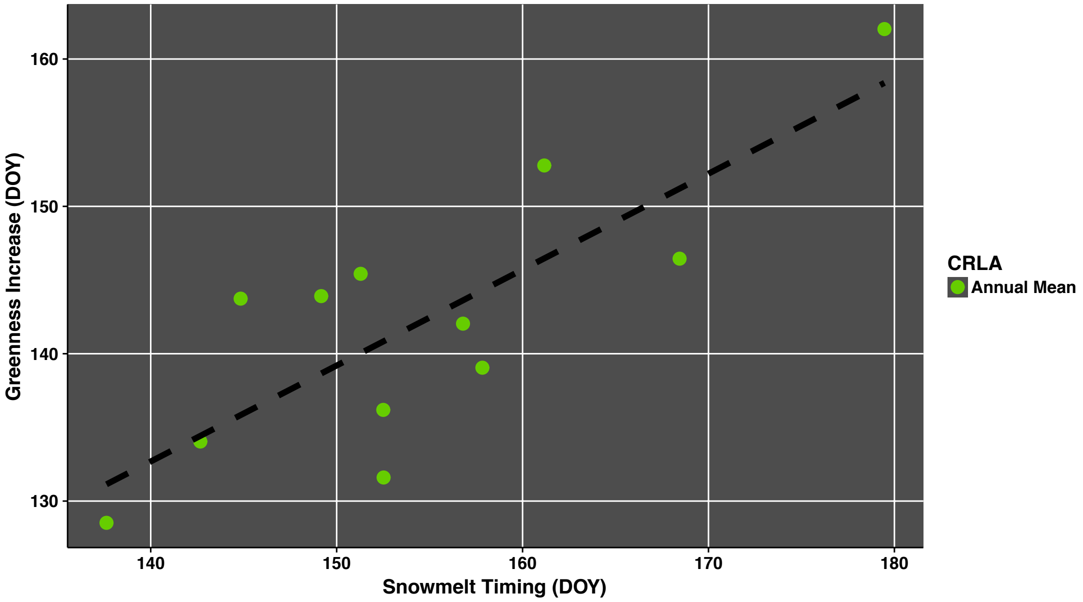


Figure 2 - Correlation of day of year (DOY) of greenness increase with snowmelt date for Crater Lake National Park, OR, USA as a whole (CRLA Full). Each point represents an annual average DOY across pixels for 2001-2012. Significance values from Spearman Rank correlations are in Table 3. Best-fit linear model shown in black dashed line (see Table 4 for model statistics).

Table 4 - Spearman rank correlation results for correlations between annual mean values of snowmelt timing and: greenness increase; greenness maximum; greenness decrease; greenness minimum; growing season length. Significant results (α < 0.05) listed in bold. In general, the two cover classes (open and closed canopy) differ little from CRLA as a whole. For all three cover classes, we see a significant relationship between the annual mean timing of snowmelt and greenness increase. The open canopy class also has a significant relationship between snowmelt timing and greenness maximum. No such relationships were found between snowmelt timing and later phenology metrics, such as greenness decrease, greenness minimum, or growing season length.

		Greenness Increase	Greenness Maximum	Greenness Decrease	Greenness Minimum	Growing Season Length
CRLA Full	S	100	140	148	228	376
	p-value	**0.026**	0.094	0.115	0.528	0.320

	rho	0.650	0.510	0.483	0.203	-0.031
Closed Canopy	S	110	132	172	216	364
	p-value	**0.037**	0.075	0.201	0.444	0.391
	rho	0.615	0.538	0.399	0.245	-0.273
Open Canopy	S	92	116	142	248	404
	p-value	**0.019**	**0.046**	0.099	0.683	0.185
	rho	0.678	0.594	0.503	0.133	-0.413

Linear models show that both snowmelt timing and green up increase with elevation, with an adjusted R^2 of 0.192 and 0.228, respectively (Table 5, Figure 3). Snowmelt timing is also positively associated with greenness increase and greenness decrease, and negatively associated with growing season length, though these models have a much lower explanatory value (adjusted R^2 of 0.131, 0.023, and 0.035, respectively) (Figure 4, Table 5). Linear models comparing snowmelt timing with greenness maximum and greenness minimum had little relationship, and are omitted here.

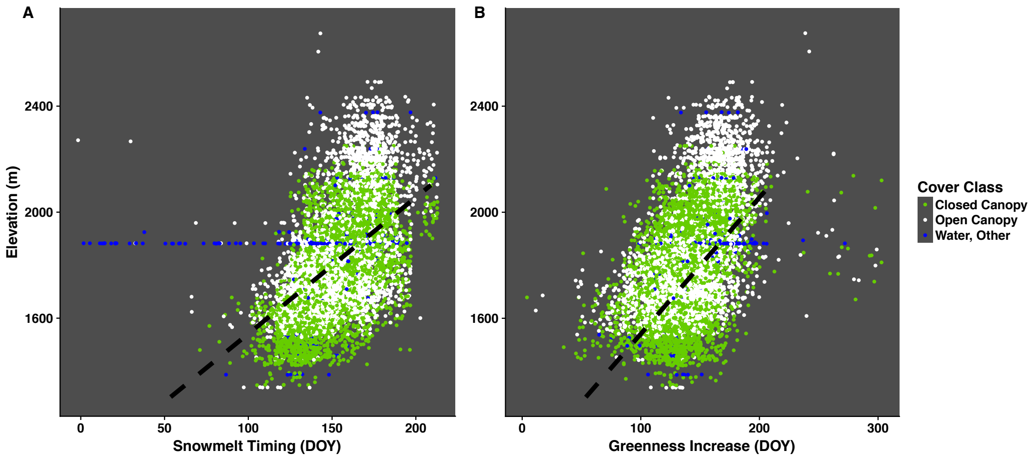


Figure 3 - Per-pixel comparison of elevation vs. A) snowmelt timing and B) greenness increase for all complete pixels on record. Best-fit linear models shown in black dashed line (see Table 5 for model statistics). Each point

represents single pixel for a single year. Point colors represent cover classes as defined by this study. We see a pattern of closed canopy at the lowest elevations, with striations of open and closed canopy at middle elevations, and open canopy at the highest elevations. Both snowmelt timing DOY and greenness increase DOY have a positive relationship with elevation.

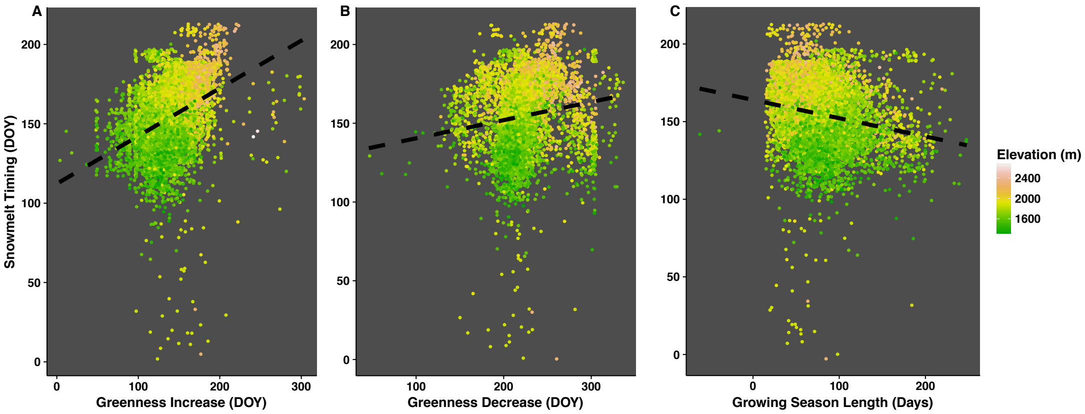


Figure 4 - Per-pixel comparison of snowmelt timing vs. A) greenness increase, B) greenness decrease, and C) growing season length for all complete pixels on record. Best-fit linear models shown in black dashed line (see Table 5 for model statistics). Each point represents single pixel for a single year. Point colors represent elevation. We see a pattern of increasing snowmelt timing and greenness increase corresponding with increasing elevation (A). There is a similar, but weaker, pattern seen in panel B. Panel C has a negative relationship between snowmelt timing and growing season length, indicating a short growing season following a late snowmelt. Higher elevations can be seen to correspond more to later snowmelt timing dates and shorter growing season. Two points indicating negative growing season length are shown, and are obviously errors produced from noise in the MCD12Q2. There is high variability with each of these plots, suggesting that snowmelt timing has a relationship with, but low explanatory power for, each variable of interest. Of the 24 data points with a snowmelt earlier than March 1, 21 of those points come from the shores of Crater Lake itself, possibly resulting from snow-covered lakeshore ice which typically melts out weeks to months earlier than the main snowpack on land.

Table 5 - Results of the linear models relating variables of interest. Significant results (α < 0.05) listed in bold. Mean annual snowmelt timing values are compared with mean annual greenness increase values for CRLA as a whole (Mean Increase). Per-pixel snowmelt timing values are compared with per-pixel greenness increase, greenness decrease, and growing season length, and per-pixel elevation values are compared with per-pixel snowmelt timing and greenness increase values. For mean increase our linear model finds a significant slope, and

a fairly high explanatory power (adjusted $R^2 = 0.608$). For all other comparisons, our linear models found significant slope and intercept, but a low explanatory power with adjusted R2 values ranging from 0.228 to 0.023. The models comparing elevation with snowmelt timing and greenness increase had better explanatory power than the per-pixel snowmelt/phenology comparisons.

	Snowmelt Timing				Elevation	
	Mean Increase	Greenness Increase	Greenness Decrease	Growing Season Length	Snowmelt Timing	Greenness Increase
Intercept	14.02	115.5	129.8	163.988	61.549	25.287
p-value Intercept	0.681	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
Slope	0.989	0.279	0.111	-0.012	0.051	0.063
p-value Slope	**0.002**	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
Degrees of Freedom	10	10904	10263	9177	38650	11112
Adjusted R2	0.608	0.131	0.023	0.035	0.192	0.228

Pearson correlation coefficients for snowmelt timing, the five phenology metrics, and elevation are all under the correlation threshold for inputs to PCA ($\rho < 0.7$) (Table 6), and are therefore included in the PCA below. Elevation has the strongest Pearson correlation with snowmelt timing and greenness increase. Growing season length is strongly correlated with its two components, greenness increase and greenness decrease. Each phenology metric is also moderately correlated with its following metric (e.g. greenness maximum is followed by greenness decrease, with a correlation $\rho = 0.366$), with those correlations decreasing in strength as the season progresses.

Table 6 - Pearson correlation coefficient (ρ) matrix for inputs to the Primary Components Analysis (PCA). All variables have a correlation of less than 0.7, and are therefore retained for the PCA.

	Snowmelt Timing	Greenness Increase	Greenness Maximum	Greenness Decrease	Greenness Minimum	Growing Season Length	Elevation
Snowmelt Timing	1.000						
Greenness Increase	0.375	1.000					
Greenness Maximum	0.173	0.577	1.000				
Greenness Decrease	0.143	0.203	0.396	1.000			
Greenness Minimum	0.006	-0.070	0.022	0.366	1.000		
Growing Season Length	-0.185	-0.634	-0.146	0.628	0.344	1.000	
Elevation	0.527	0.499	0.251	0.261	-0.046	-0.190	1.000

PCA results show that greenness increase and elevation drive most of principal component (PC) 1, while late-season phenology contributes to PC2 (Figure 5), and snowmelt timing dominates PC3 (Table 7). Together, these first three principal components account for 78.1% of the variance in the data.

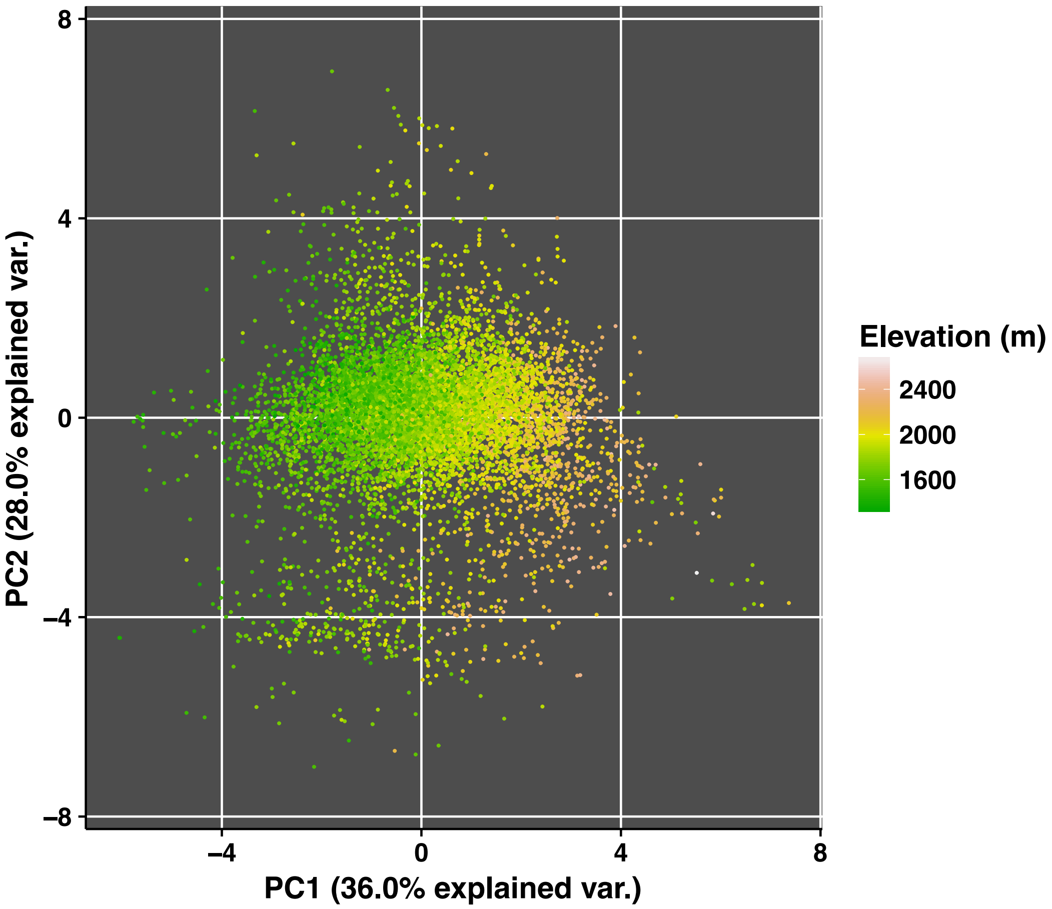


Figure 5 - Plot showing the first two principal components derived from the principal components analysis (PCA) of seven variables. Each point represents single pixel for a single year. Point colors represent elevation. We see a pattern of increasing elevation along the positive PC1 axis, as is to be expected with a positive loading of elevation on PC1 (Table 7).

Table 7 - Results of the Primary Components Analysis (PCA) for the seven variables of interest. The first three primary components (PC) account for 78.1% of the variance in the data. Component loading significance is placed at 0.45. PC1 is driven by a combination of greenness increase (the beginning of the growing season) and the elevation of the location. PC2 is a combination of the late-season phenology metrics (greenness decrease, greenness minimum) and the growing season length (which is the greenness decrease minus the greenness increase, measured in days). PC3 is strongly dependent on snowmelt timing, and is inversely related to the greenness maximum. PC4-PC7 account for little of the variability in the data (21.9%).

	Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Loadings	Snowmelt Timing	0.400	-0.072	**0.610**	-0.067	**0.673**	-0.067	0.000
	Greenness Increase	**0.568**	0.051	-0.261	-0.162	-0.163	**-0.524**	**-0.529**
	Greenness Maximum	0.405	-0.206	**-0.587**	0.142	0.339	**0.561**	0.000
	Greenness Decrease	0.138	**-0.652**	-0.094	0.249	-0.086	-0.449	**0.526**
	Greenness Minimum	-0.077	**-0.451**	0.005	**-0.870**	-0.078	0.163	0.000
	Growing Season Length	-0.342	**-0.555**	0.133	0.325	0.062	0.062	**-0.666**
	Elevation	**0.460**	-0.113	0.434	0.155	**-0.623**	0.418	0.000
Statistics	Standard Deviation	1.588	1.400	0.993	0.871	0.688	0.549	0.000
	Proportion of Variance	0.360	0.280	0.141	0.108	0.068	0.043	0.000
	Cumulative Proportion	0.360	0.640	0.781	0.889	0.957	1.000	1.000

Discussion

Snowmelt timing is expected to occur earlier across much of the western United States over the course of the 21st century (Stewart, 2009). This may have profound impacts on ecosystems where snowmelt timing has a substantial influence on phenology, and land managers are keenly interested in identifying this vulnerability. We found strong associations between some phenological metrics and snowmelt date in Crater Lake National Park in the southern Oregon Cascades. In particular, earlier snowmelt dates were associated with earlier green up across CRLA as a whole, and within both of the vegetated cover classes, indicating the influence of snowmelt timing on spring phenology, likely through the regulation of seasonal temperature accumulation (Sedlacek et al., 2015). Although conifer forests do not show sharp greenness thresholds as in deciduous forests (Jönsson et al. 2010), NDVI does provide a valuable remote sensing indicator of phenophases related to increases in photosynthetically active radiation being absorbed by the canopy. Early season phenophases may be most strongly affected by snowmelt timing, while later phenophases may be driven more by climate factors such as growing degree days (Wipf, 2009).

We also found evidence of longer growing seasons in years with earlier snowmelt (Figure 4, Table 5). It is uncertain what impacts a longer growing season may have on the fitness of conifer forests at CRLA. More growing degree days could increase productivity (Loustau et al., 2001), but hydrological changes that lead to soil water stress could have negative impacts (Harpold et al., 2015). Earlier snowmelt and green up, and increased growing seasons, could have the most immediate impacts on herbaceous plants of the forest understory and open meadow and grassland communities. Earlier leaf emergence can increase risk of frost damage (Inouye 2008), although faster advancement of last spring freeze date than onset of vegetation phenology could reduce this risk (Peterson and Abatzoglou, 2014). Phenological shifts across multiple species can alter plant community composition (CaraDonna et al., 2014) as well as increase vegetative production (Totland and Alatalo, 2002).

Milder winters and longer growing seasons can also increase survival and reproductive output of invasive species facilitating their establishment and range expansion while impacting control strategies (Hellmann et al., 2008). Elevational advancement of native pests and pathogens into previously unsuitable habitats will likely continue, such as the expansion of mountain pine beetle (*Dendroctonus ponderosae*) in British Columbia (Carroll et al., 2004; Sambaraju et al., 2012).

Seeing as earlier snowmelt is associated with an earlier greenness increase, mountain hemlock may present a threat to whitebark pine, a species of significant conservation concern throughout the species range. Whitebark pine populations have declined or been extirpated due to pests, pathogens, encroachment, and changing fire regimes (Keane et al., 2012; Millar et al., 2012) all factors that could be affected by climate-driven phenological ecosystem changes. Earlier phenology of mountain hemlock may encourage its encroachment of whitebark pine stands which are mostly restricted to subalpine habitats around the CRLA caldera rim and its associated peaks where they are adapted to the harsh conditions. Increased competition from mountain hemlock could limit radial growth and seedling regeneration and recruitment of shade-intolerant whitebark pine (Keane et al., 2007). Longer growing seasons could also increase production and accumulation of fuels resulting in larger, more severe wildfires which also threaten whitebark pine (Kendall and Keane, 2001).

Though highly variable, elevation is a substantial control on snowmelt timing and greenness increase (Figure 3, Table 5). The dynamics of snowpack accumulation and snowmelt in a changing climate are complex and vary with geography, elevation, latitude, (Cayan, 1996; Stewart, 2009; Rangwala and Miller, 2012). CRLA lacks the higher elevations of other larger mountain ranges such as the Sierra Nevada or Rocky Mountains. The phenology of more mesic and subalpine elevation forests of CRLA may be particularly sensitive to snowmelt, while more xeric forests at lower elevations may be less vulnerable, at least within the range of variation currently being experienced (Goldstein et al., 2000). While there is no clear single driver for snowmelt timing or phenology, elevation has the strongest association with snowmelt timing and greenness increase – but elevation is not a discrete characteristic. Elevation in this study serves as a geographic indicator, but also as a proxy for temperature and precipitation, which are strongly associated with elevation. Future research should include these variables directly, though they are not a focus of this study which seeks to isolate the influence of snowmelt timing on phenology.

We did not find significant correlations ($\alpha = 0.05$) between the annual means of snowmelt timing with the onset of senescence (Greenness Decrease) or the onset of dormancy (Greenness Minimum) (Table 4). Evergreen conifers do not undergo the level of coloration and foliage loss of deciduous trees that is commonly used to detect senescence through satellite-derived NDVI in deciduous ecosystems (Zhang et al. 2012). The phenology, biology, and ecophysiology of conifer foliage senescence and declining leaf area duration (LAD) across conifer species is poorly studied. Ground-based broadband NDVI could not reliably predict termination of physiological activity during transition to winter dormancy in Scots pine (*Pinus sylvestris*) although onset of green up was consistently determined (Wang et al., 2004). Synchrony of declining photosynthetic activity across conifer species is also not understood, although it varies across species and can be affected by weather and water stress and vary with elevation and latitude (Dougherty et al 1994). This questions our capacity to accurately measure changes in growing season length derived from measures of green up and dormancy onset. The lack of significant correlations for senescence and dormancy with snowmelt suggests these phenological metrics may be more variable among years or across species than green up making it more difficult to detect. Further research into detecting senescence of conifers with remote sensing and its relationship to controls over senescence is needed (Dougherty et al., 1994).

Conducting a PCA provides valuable insight into the variability present within the input data. PC1 is driven by greenness increase (the beginning of the growing season) and elevation, suggesting that topography and the onset of spring (Pearson correlation $\rho = 0.499$) are the main factors driving variability throughout CRLA. PC1 also has fairly strong loadings from snowmelt timing and greenness maximum, showing that the early growing season is critically important for defining spatial and temporal heterogeneity for CRLA. PC2 is a combination of the late-season phenology metrics (greenness decrease, greenness minimum) and the growing season length. The fact that early season and late season metrics define PCs 1 and 2 (which are orthogonal) underscores the fact that the timing of the early and late seasons are driven by different mechanisms (Wipf 2009). These results indicate that the early season timing has little influence on the late season timing within our study area and period. While earlier snowmelt timing may lead to a longer growing season at a coarse resolution (Westerling 2006), our results do not show a strong relationship between the two at moderate resolution in CRLA. PC3 is dominated by an inverse relationship between snowmelt timing and greenness maximum (peak growing season). This may indicate variability in the time it takes to progress from snowmelt to peak growing season, though it is unclear as to which climatic or physiological mechanism may be driving this variability. Together, PCs 1, 2, and 3 explain 78.1% of the variance in the data, showing that the timing of the early season, timing of the late season, and duration from snowmelt to growing season are the major drivers of variability within CRLA. For this analysis, we use PCA as an exploratory tool to identify the driving factors behind the variability within this complex dataset. Results from our PCA collapse variability into understandable and meaningful categories, and help to identify covariance and possibly point towards common mechanisms driving variability for these discrete climate variables. These results will help to guide researchers as they select variables of importance for future climate/phenology analyses.

The use of remote sensing for this application is challenging and limited by available data products. We employed the MODIS-based STMs to identify snowmelt timing across CRLA. These STMs enabled us to evaluate a much greater land area compared to the single snow monitoring meteorological station within CRLA, albeit at the cost of temporal resolution due to the 8-day native temporal resolution of the MOD10A2 parent data. The MCD12Q2 plant phenology product is limited by cloud interference, and the sparse annual phenology readings in alpine regions do not always spatially coincide from year to year, leading to a bias favoring locations with less clouds and vegetation with a stronger NDVI response (Figure 1, C) (Ganguly et al. 2010). MCD12Q2 is also temporally restricted to 2001-2012 which limits our ability to identify long-term trends at relevant time scales of climate change in many regions. Additionally, the phenology signal from conifers and sparse alpine vegetation is subtle and difficult to accurately measure (Jönsson et al. 2010). The MCD12Q2 product relies on a 5°C minimum temperature threshold for phenology calculations, which may not be suitable for alpine and subalpine vegetation (Ganguly et al. 2010). Small alpine plants in particular alter their microclimate to increase productivity on a scale that may be missed by the MCD12Q2 algorithm (Körner, 2016). Finer spatiotemporal resolution of remote sensing data and ground-based observations will improve these methods. Using other indicators of plant phenology could also be advantageous including the modeled spring index presented in (Ault et al., 2015), or including *in-situ* phenology observations from the USA National Phenology Network (Enquist et al., 2014) or other large-scale monitoring programs.

The technical problems inherent in the MCD12Q2 data, described above, lead to irregular patterns of data availability and generate statistical problems that influence this study. As presented here, our work describes relationships within spatio-temporal space. Statistics describing annual mean values eliminate the spatial component by averaging available data across CRLA for each year, describing trends in temporal variability for CRLA as a whole. For all other aspects of this research, we calculate statistics for pooled data, i.e., all available pixels across space and time. This clouds our ability to make distinctions along either the time dimension, or across space, and reduces the confidence of our statistics due to spatial autocorrelation. This approach does, however, have several distinct advantages, and offers insight for the relationships between snowmelt timing and phenology within CRLA. Given the known issues with data quality and availability, it is important to have a large sample size to reduce the influence of noise within the available data. Limiting our research to only those pixels containing a full 12 years of phenology information would reduce our study area to fifteen 500m pixels concentrated along the western border and caldera rim, ~0.6% of the CRLA land area (Figure 1, C). By using pooled data, we greatly improve our sample size, and include pixels from throughout CRLA, improving the representativeness of our sample. During our exploratory analysis, we performed repeated calculations using information from a single year (isolating spatial variability), however the results from these years were not appreciably different from the results from the pooled data. Further research should delve deeper into these challenges, perhaps identifying regions with improved MCD12Q2 coverage, or analyzing individual pixels for phenology patterns within specified ecosystems.

Changing snowpack in the southern Oregon Cascades is partly driven by changes in seasonal climate including increasing minimum winter temperatures (Abatzoglou et al., 2013; Monahan and Fisichelli, 2014). Although the Pacific Northwest has experienced nonsignificant spring cooling trends between 1980-2012, there has been an overarching long-term warming trend in annual mean temperature from 1901-2012 (Abatzoglou et al. 2013). Conservative models of warming rates for western mountains (Leung et al., 2004; Mote and Salathé, 2010) indicate upward elevational shifts in the transitional snow zone where snow alternately accumulates and melts frequently throughout the winter, with increasing sensitivity of spring snow melt and snow water equivalent to temperature (Mote, 2006). This highlights yet another instance of the disproportionate impacts of climate change on high elevation ecosystems (Beniston et al., 1997; Rangwala and Miller, 2012; McCullough et al., 2016). Expected declines in future snowpack may result from a variety of causes. Mote (2006) points out that modeled declines in snowpack due to climate warming (Knowles and Grant, 1983; Hamlet and Lettenmaier, 1999; Miller et al., 2003; Cayan et al., 2008) may be partly characterized by intraseasonal variation with alternating periods of accumulation and melt, potentially due to increased rain-on-snow events (Leung et al., 2004; Payne et al., 2004) and increased lateral energy fluxes with increasing snowmelt (Grünewald et al., 2010). It is unclear how these factors may impact phenology within mid- and high-elevation mountains of the western United States, meriting further investigation.

Changing snowpack in the Oregon Cascades will also have critical ecological and socioeconomic impacts on the larger region. Identifying vulnerability is an important step for resource managers as they work to mitigate the effects of climate change on their lands. Here, we have identified the variability and strength of relationships between snowmelt timing, elevation, and phenology within a highly-visible and well-studied mountain national park. While the relationships between climate, snowmelt timing, and phenology have been studied in different environments, our results distinguish nuances of these relationships within conifer-dominated mid- elevation mountain ecosystems with a complex mosaic of ecosystem types. This work also contributes to our understanding of the benefits and limitations of using remotely-sensed data to conduct ecosystem dynamics investigations. These results will be of interest to land managers, researchers, and other stakeholders who are concerned about protected areas, remote sensing, and the impacts of climate and snowpack changes to temperate mountain ecosystems.

Chapter 3: Snowmelt velocity predicts vegetation green-wave velocity in mountainous ecological systems of North America

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Abstract:

The timing of spring initiates an important period for resource availability for large trophic webs within ecosystems, including forage for grazing animals, flowers for pollinators, and the higher trophic levels that depend on these resources. Spring timing is highly variable across space, being influenced strongly by the departure of snow cover (i.e. snowmelt timing, in locations with a seasonal snowpack), climate, weather, elevation, and latitude. When spring timing occurs along a gradient (e.g. spring arriving later in higher elevations of mountainous terrain), the organisms that rely on spring resources often migrate to maintain an optimal position for spring resources – a phenomenon known as 'surfing the green wave.' While this behavior has been observed by tracking animals, there have been no studies to quantify the green wave as a movement across space and time. Furthermore, considering that snowmelt timing has moderate power to explain green-up timing for a given location, we ask the question: does snowmelt velocity predict green wave velocity? Here, we introduce the first continental maps of snowmelt and green wave velocity for North

America from 2001-2016 as derived from the MODIS MCD12Q2 phenology dataset. We show that both snowmelt and green wave velocities are influenced strongly by topography, including slope and aspect. Furthermore, we quantify the relationships between snowmelt and green wave velocities according to three variables: direction, speed, and distance traveled. We conclude that mountainous ecoregions, such as the western North American cordillera, have the highest correspondence between snowmelt and green wave velocities, compared to flatter regions such as the Great Plains and tundra. This work will be of interest to wildlife ecologists, biologists, and land managers who seek to conserve migratory animals and the ecosystems that support them.

Introduction:

The timing of spring and its associated vegetation phenological indicators initiate an important period for resource availability for large trophic webs within ecosystems, including forage for grazing animals, flowers for pollinators, and the higher trophic levels that depend on these resources (Craighead Jr., 2001). Spatial heterogeneity in spring timing occurs because of many geophysical forces, with long-term climate patterns, elevation, and latitude being principal drivers in the patterns of vegetation (Holdridge, 1947) and phenology (Hopkins, 1920; Richardson et al., 2019). Interannual variability in spring timing challenges the organisms that depend on spring resources for food by altering the timing and locations of available resources. For migratory organisms, there are substantial energetic advantages to migrating at the speed of spring, i.e., maintaining a position along their migratory corridor that maximizes their exposure to essential spring resources (Hebblewhite et al., 2008; Bischof et al., 2012). Tracking a changing greenscape is therefore advantageous for these organisms, and observations of migration behavior show that many organisms closely follow peak spring resource abundance along their migrations (Van der Graaf et al., 2006; Merkle et al., 2016; Aikens et al., 2017). Therefore, the speed and direction of the peak resource availability (a.k.a. the "green wave") is an important control on animal migrations during the spring season.

As plants grow in the spring, their immature leaves and shoots offer high-quality forage to herbivorous animals (Hebblewhite et al., 2008). However, once the plants have matured, they become lower forage quality for animals, as described by the 'forage maturation hypothesis" (FMH) (Fryxell et al., 1988; Albon and Langvatn, 1992). In the past decade there has been increased interest in green wave velocity because migratory animals closely follow ("surf") the onset of spring phenologies ("green wave") to follow peak forage quality during their migrations (Van der Graaf et al., 2006; Sawyer and Kauffman, 2011; Bischof et al., 2012; Merkle et al., 2016; Aikens et al., 2017). This process of following resource availability may even be learned by individuals who are translocated to a new landscape (Jesmer et al., 2018), even if they are introduced from other regions. As climates continue to change, migratory herbivores will be forced to adapt to variation in the timing of resource availability, which makes them particularly vulnerable to anthropogenic climate change (Bischof et al., 2012). With the combined climatic forces of changing snowmelt timing, air temperatures, and precipitation patterns, and peak resource availability, the timing of the "green wave" is likely to change in the coming decades.

In temperate, high-elevation, and boreal ecosystems, one of the principal controls on spring phenology is snowmelt timing (Billings and Bliss, 1959; Inouye and McGuire, 1991; O'Leary et al., 2017b). Snowmelt timing (a.k.a. snow disappearance date; snow ablation timing) is the day of year (DOY) when seasonal snowpack melts away, providing a pulse of liquid water to soils (Harpold et al., 2015), and altering the Earth surface energy balance by removing the insulative snow cover and allowing for increased heat exchange (Lundquist and Lott, 2008), leading to an accumulation of heat at the soil surface (e.g., growing degree days (Richardson et al., 1975; Tuhkanen, 1980)). Conversely, the loss of the insulative snowpack can expose organisms to freezing temperatures, damaging flower buds, killing young animals, and otherwise reducing species fitness (Inouye, 2008). The melt of the primary snowpack moves along latitudinal, elevational, and climatic gradients (Margulis et al., 2016a; O'Leary et al., 2017a, 2018). For example, much like the toe of a receding glacier, one can imagine the movement of the snow/no-snow threshold as seasonal snowpack melts up-valley and into a mountain cirque, where it eventually ends at a glacier, semi-permanent snowfield, or disappears completely. Analogous to the 'green wave' velocity, we will consider this phenomenon to be 'snowmelt velocity.' While there is some evidence that snowpack depletion rates will change into the future (Musselman et al., 2017; Evan, 2018), studies widely expect seasonal snowpacks to melt earlier on average in the coming decades (Stewart, 2009), though with significant spatial and interannual variability in snowmelt timing (O'Leary et al., 2018).

For areas with seasonal snowpack, snowmelt timing is initiates the growing season in terms of water and energy balance, and there is a predictable lag between snowmelt and green-up. This lag has been quantified in several studies as an interaction between snowmelt timing and plant green-up at a single location, or at multiple individual plots (e.g., along one dimension, *time*) (Albon and Langvatn, 1992; Totland and Alatalo, 2002; Cornelius et al., 2013; O'Leary et al., 2017b). However, this lag has substantial spatial heterogeneity (O'Leary et al., 2017b), and it is unknown if the lag between snowmelt timing and vegetation green-up extends into multiple dimensions (*x, y, elevation, time*). Considering the importance of green-wave velocity for ecological processes (especially migration), it could be of great benefit to understand the influence of snowmelt velocity on green wave velocity. If there is such a control, quantifying snowmelt velocity could have power to predict green wave velocity and the cascading ecological processes that unfold therein. Therefore, the goal of this study is to quantify the relationships between snowmelt velocity and green wave velocity to understand better the interaction of these processes in order to answer the question: *does snowmelt velocity predict green wave velocity?*

Methods:

Data: This study focuses on the North American continent, which has broad and varied regions with seasonal snow cover and perceptible spring greenup, as documented by many remotely sensed data products. The North American region has validated MODIS-based datasets which define the DOY for snow departure (snowmelt timing maps (STMs) - O'Leary et al. 2017a) and spring green-up (MCD12Q2 - Friedl et al. 2019, p. 12), spanning the years 2001-2016. However, these data are at times sparse, i.e., there are many pixels where there is no snowmelt timing value, or phenology values, for one or more years. This may be due to any number of factors, including a lack of snow and/or vegetation, cloud interference during the reporting period, or, for the phenology product, occasionally due to small annual amplitude of the input vegetation index. To best investigate the relationships between snow and green-up, we have restricted our investigation to only those areas with >50% of years with a valid snowmelt and green-up identified. For the MDC12Q2 phenology dataset, original values are reported as days since January 1, 1970. For this analysis, we have converted all dates to DOY for the present year, and removed any phenology cycles that begin in the preceding year. Finally, the MCD12Q2 developers note that use of the mid-greenup value is preferred over the initiation of greenup as a more robust and reliable indicator of spring timing, therefore we use this metric in our analysis (Friedl et al., 2019). When upgrading to Collection 6, the authors of the MCD12Q2 updated their phenology detection algorithm, increasing the cutoff for maximum MODIS nadir BRDF adjusted surface reflectances (NBAR-EVI2, hereafter, EVI) amplitude difference, which now generally excludes vegetation classes with low seasonal variation in their EVI values, particularly conifer-dominated ecosystems. To subdivide the North American continent into meaningful ecological groupings, we use the Environmental Protection Agency Level III ecoregions (EPA, 2015). To investigate the influence of topography on these processes, we used the global multi-resolution terrain elevation data 2010 (Danielson and Gesch, 2011), and calculated slope and aspect using the ‘raster’ package in R software (Hijmans, 2016; R Core Team, 2016) (Figure 6).

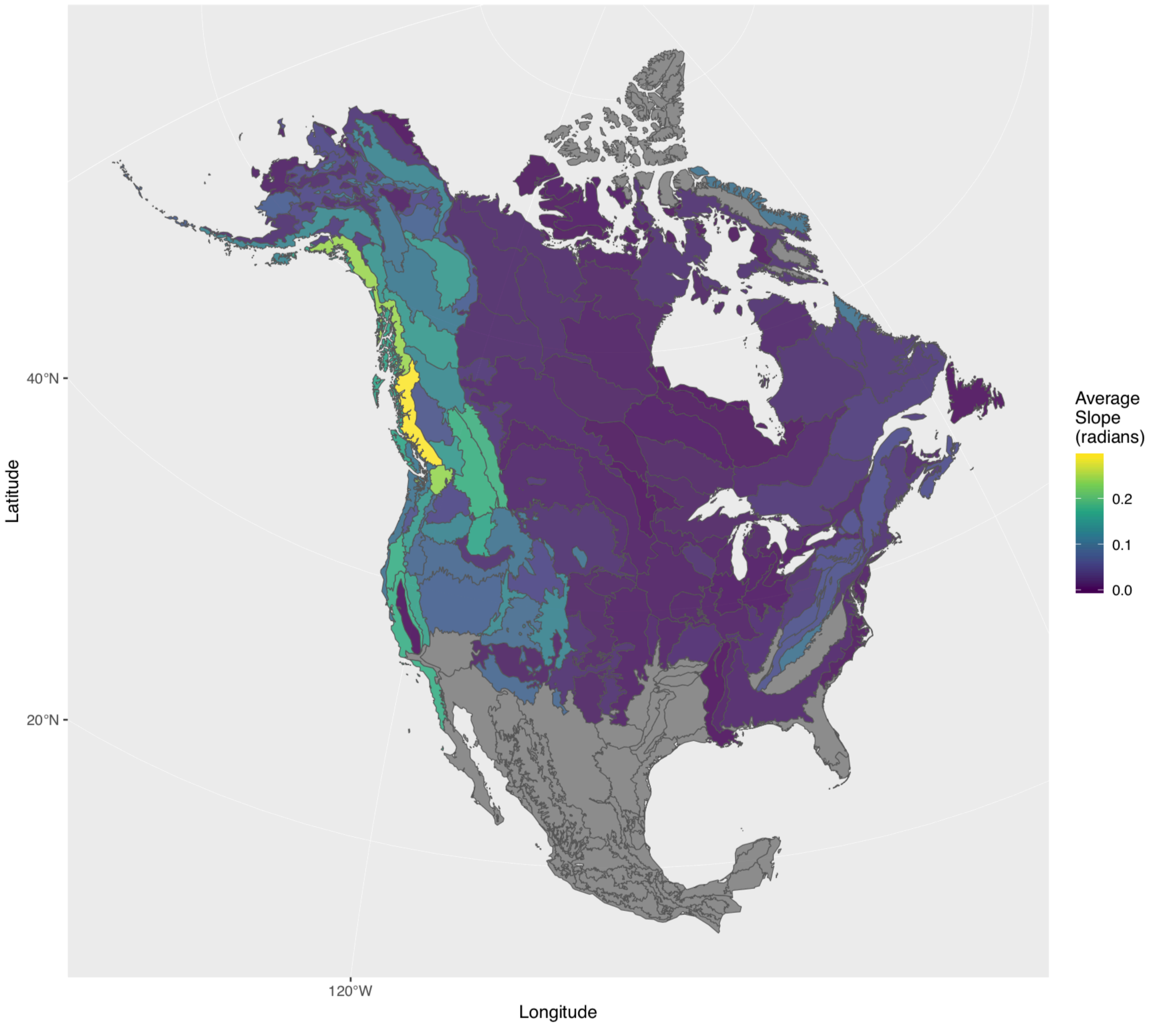


Figure 6 - Average slope in radians for EPA level III ecoregions included in this study. Grey ecoregions are not included because of their sparse snow cover, vegetation cover, or both.

Velocity Calculation: based on the Hamann et al. (2015) method, we use a modified nearest neighbor method for determining the distance and direction between one pixel and the closest pixel with a later resource availability value. This method is computationally intensive, for which the authors recommend rounding input values to reduce processing time. Therefore, we first bin our resource DOY values into 10-day bins to distinguish the spatial gradients of resource availability timing. Next, we limit the search radius for each pixel to 5km, which prevents an apparent resource availability movement of very large, and likely ecologically irrelevant, distances. The two steps above reduced our processing time by orders of magnitude, though it still required several days to process on a 64-core high performance server. Once we have ‘from’ and ‘to’ pixels, we can find the distance, direction, and time difference between those two pixels to determine the velocity for that variable for that year. We first perform these velocity calculations on idealized surfaces to ensure expected behavior and to serve as examples of differing spatial heterogeneity and landforms. We then perform these calculations for both input datasets spanning all of North America for years 2001-2016. Analysis was conducted and figures generated using GDAL (GDAL/OGR contributors, 2019) and the gdalUtils, geofacet, ggplot2, ggpubr, plyr, RcolorBrewer, reshape, rgdal, and sf packages in R (Neuwirth, 2014; Wickham, 2016, 2018; Mattiuzzi, 2018; Bivand et al., 2019; Hafen and Schloerke, 2019; Kassambara, 2019; Pebesma et al., 2019; Wickham et al., 2019).

Statistics: Our objective is to compare snowmelt velocity with green wave velocity across North America from 2001-2016. Our method identifies the destination pixel for each resource wave given an initial starting pixel. Those two points that define the resource wave vector (for that initial location) can be meaningfully resolved into three components: the direction, distance, and speed of the vector. Speed is calculated by dividing the distance traveled by the difference of the destination cell’s snowmelt (phenology) DOY and the starting cell snowmelt (phenology) DOY. Therefore we separated each variable and component into EPA level III ecoregions for each year. We also separated each ecoregion into eight equally spaced aspect classes defined as a 45° arc (e.g. within 22.5° of “North” or “Southeast”) to explore the influence of aspect direction. We calculated summary statistics per ecoregion, including mean and variance for all values within each ecoregion, as well as the mean of annual means, yielding a single value for each component and variable of interest. To compare both variables at the landscape scale, we gathered a sample of pixels from our areas of interest. For our analysis, each ecoregion must have a minimum of 250 valid pixels to sample (as defined below), which defines the minimum sample size. If there are greater than 1,000 valid pixels to sample, a random sample of n=1,000 was taken from the ecoregion (and aspect, if applicable). Using these samples, we conducted the following statistical tests: i) Spearman's rank correlation of snowmelt distance vs. green wave distance per-pixel; ii) Spearman's rank correlation of snowmelt speed vs. green wave speed per-pixel; iii) circular correlation of snowmelt direction vs. green wave direction (Fisher, 1995; Jammalamadaka, 2001; Chen, 2015; Agostinelli and Lund, 2017). We also performed Spearman's rank correlations comparing ecoregion summary statistics with the slope of each ecoregion, allowing us to identify the influence of slope angle on both the velocity of each variable, and the correspondence of snowmelt and green wave velocities.

There are on the order of 10^8 MODIS pixels in North America, presenting certain challenges for interpreting model outputs. We flag pixels that have two or more equal potential destination pixels, which cannot be meaningfully resolved into a distance and direction of movement, and do not include them in our analysis. Another challenge is data sparsity in certain regions, particularly areas with sparse vegetation (e.g., deserts, conifer-dominated stands) and/or snow. To control for data sparsity and its potential artifacts, we also note the number of pixels within the 5km search radius that have real values. We then use this metric to remove pixels with less than 50% of the search radius occupied by real values in order to reduce the influence of data sparsity on the search method. To be included in this study, each EPA level III ecoregion must have 1,000 pixels with a valid snowmelt and green wave velocity value for every year on record.

Results:

Resource velocity of idealized surfaces:

Different topographic features are associated with different gradients of resource availability, and therefore, drive characteristic resource velocity patterns. In these simulated features, the timing of the resource availability (e.g., snowmelt timing and/or green-up timing) is modeled as having a linear relationship with elevation. Therefore, in these examples, the resource wave always moves uphill, and the shape of the topographic feature results in generalizable resource velocities. One simple topographic feature is a round-top mountain where snowmelt timing is 100% explained by elevation (Figure 7 top left). In this scenario, the snowmelt wave always moves uphill, producing concentric rings of snowmelt vectors pointing towards the summit (Figure 7 top middle, right). However, if we simulate vegetation phenology by adding random noise to the same model (Figure 7 bottom left), we see that the resource wave vectors still generally point towards the center of the frame. However, as the spatial gradient decreases (in the center of the plot), the vector directions become more heterogeneous. Examples of two other landforms, a glacial valley (Figure 8 top) and a saddle/pass (Figure 8 bottom) show patterns of movement uphill along the valley floor and up the valley sides, or past the saddle and upslope along the lateral aspects of the topography.

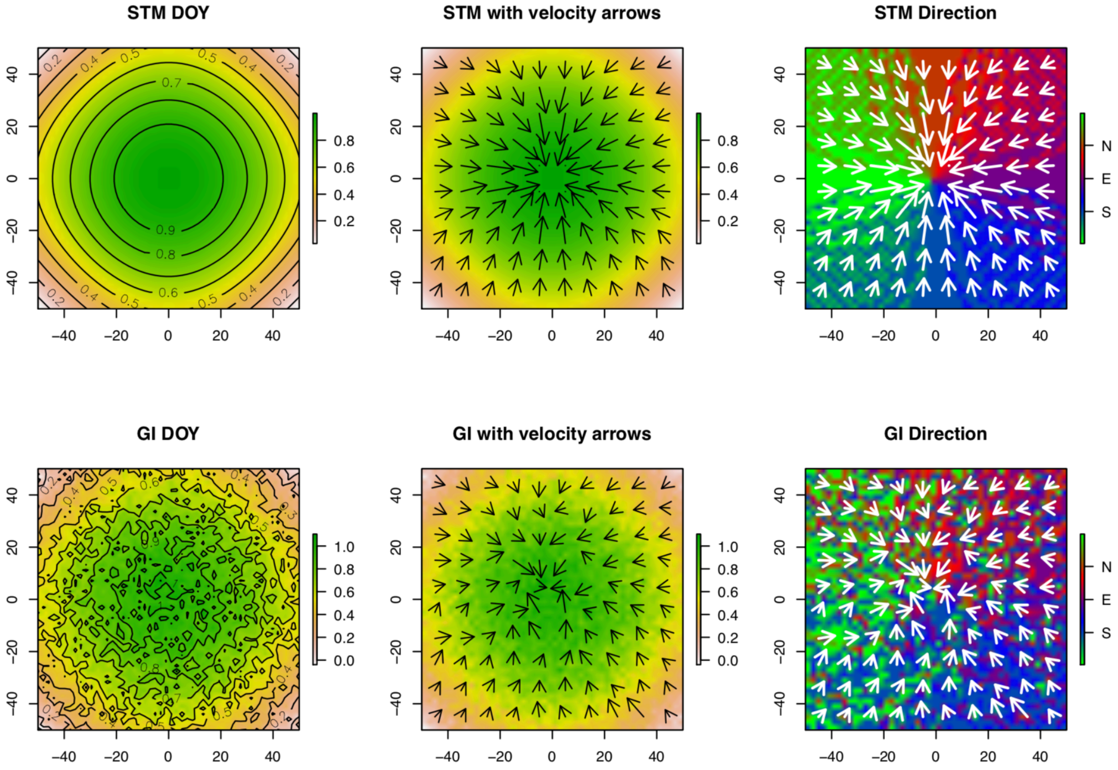


Figure 7 - Examples of idealized topographies and resource timing showing a rounded mountaintop with 100% elevational control on resource timing (top), which symbolizes snowmelt timing maps (STM), and the same with random noise added to the resource timing (bottom), which symbolized 'greenness increase' or the 'green wave'. Resource availability by time is shown in the left panels, with the calculated resource direction vectors shown in the middle and right panels atop the resource timing and per-pixel direction rasters, respectively. Each vector is an aggregate of the direction component of the snowmelt velocity vector, combining a 5x5 pixel window into a single vector showing the mean direction and mean resultant length for the 25-pixel window.

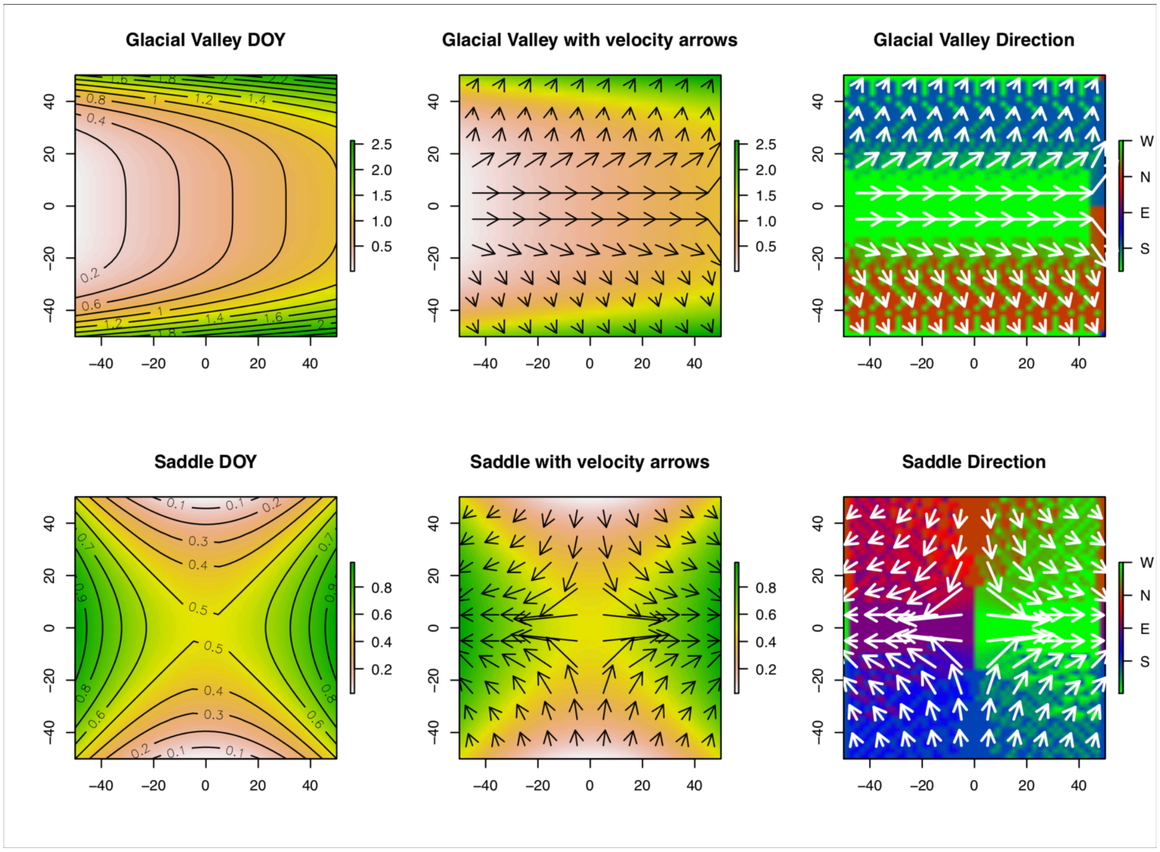


Figure 8 - same as figure 7, except for glacial valley (top) and saddle (bottom) landforms.

Continental Scale Results:

Throughout North America, we found that the mean resource wave velocity direction follows expected latitudinal and elevational gradients, with the resource wave vectors of the flatter regions of the central plains and eastern forests largely moving to the north, while resource wave vectors of the western and Appalachian mountain regions generally point uphill (Figure 9).

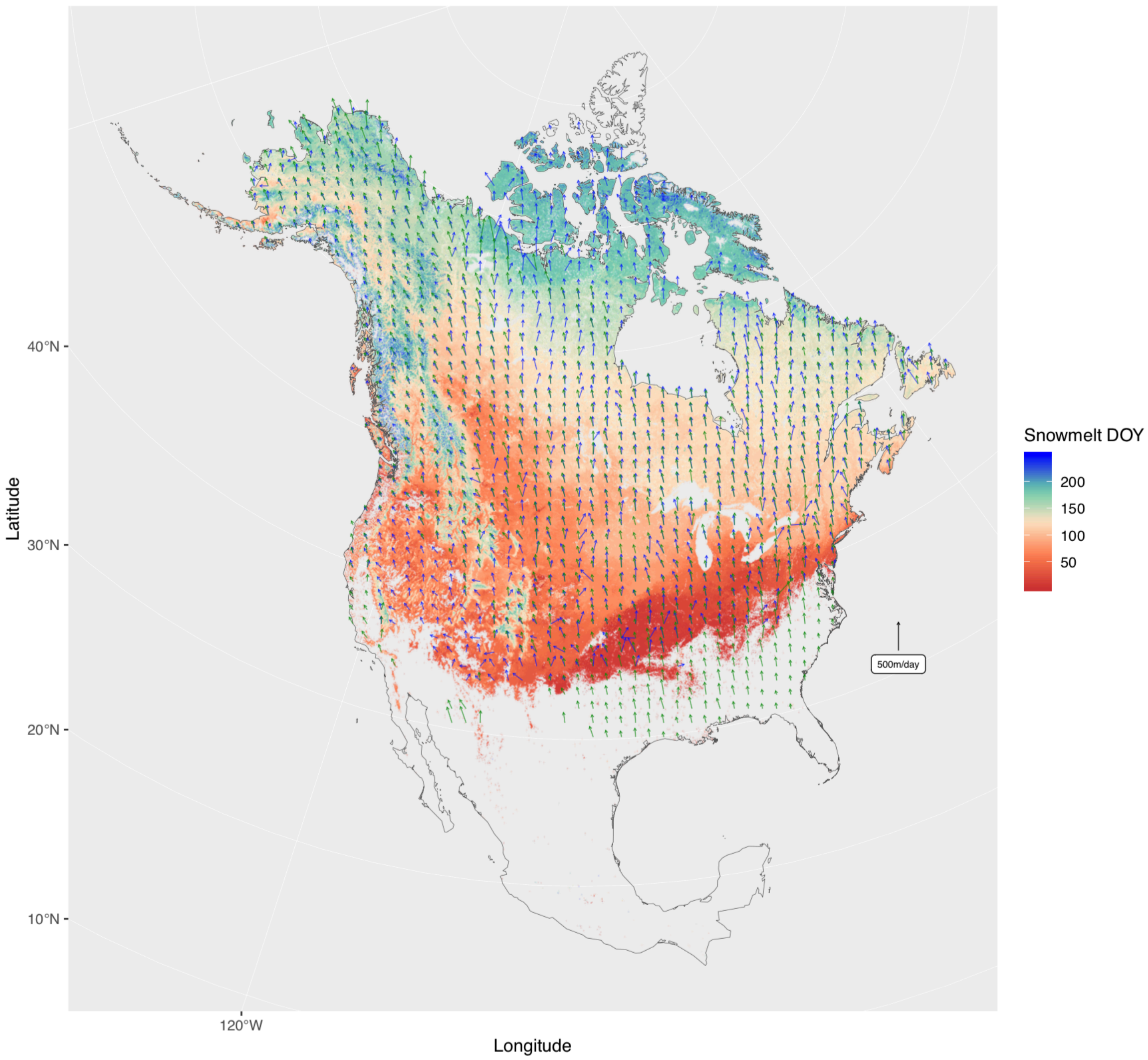


Figure 9 - Map of 2001 snowmelt timing overlaid with resource wave vectors showing direction and speed (length) arrows for snowmelt (blue) and phenology (green) waves. Arrows are mean direction and speed values aggregated from 250x250 pixel windows. Arrows are only shown for aggregated areas with >25% valid data points. 500m/day length arrow shown for reference.

Statistics:

Summary statistics as well as statistical tests were calculated for each EPA level III ecoregion that qualified for inclusion in this study. Each region has different topographic features, green-up and snowmelt patterns, and climatology, which drive different patterns of resource waves. In general, we found that mountainous terrain has higher rates of significant correlations for the direction, distance, and speed of snowmelt and green waves when compared to flatter terrain. Mountainous terrain also has lower speed and distance traveled for both snowmelt and green waves. This is especially true within the western cordilleras of the Rocky Mountains, Cascades, Pacific costal mountains, Alaskan ranges, and the Sierra Nevada mountains.

There are substantial differences among EPA level III ecoregions in terms of their resource wave movement. We calculated mean speed and distance traveled for both snowmelt and green waves for each year, and then calculated the annual mean speed (Figure 10) and distance (Figure 11) for each ecoregion. Annual mean snowmelt distance values ranged from 875m for ecoregion 7.1.6, the Pacific and Nass ranges of British Columbia, to 2,226m for ecoregion 8.3.3, the interior plateau of western Kentucky and Tennessee. Annual mean snowmelt speed ranged from 58m/day for ecoregion 7.1.6, to 226m/day for ecoregion 2.2.4, the Seward Peninsula of Alaska (ecoregion 8.3.3 had the second highest annual mean snowmelt speed at 217m/day). Annual mean green wave distance values ranged from 737m for ecoregion 8.3.6, the Mississippi Valley Loess Plains, to 1,908m for ecoregion 5.3.3, the north central Appalachian Mountains of northern Pennsylvania. The same ecoregions had the lowest and highest annual mean green wave speeds ranging from 61m/day to 354m/day for ecoregions 8.3.6 and 5.3.3, respectively.

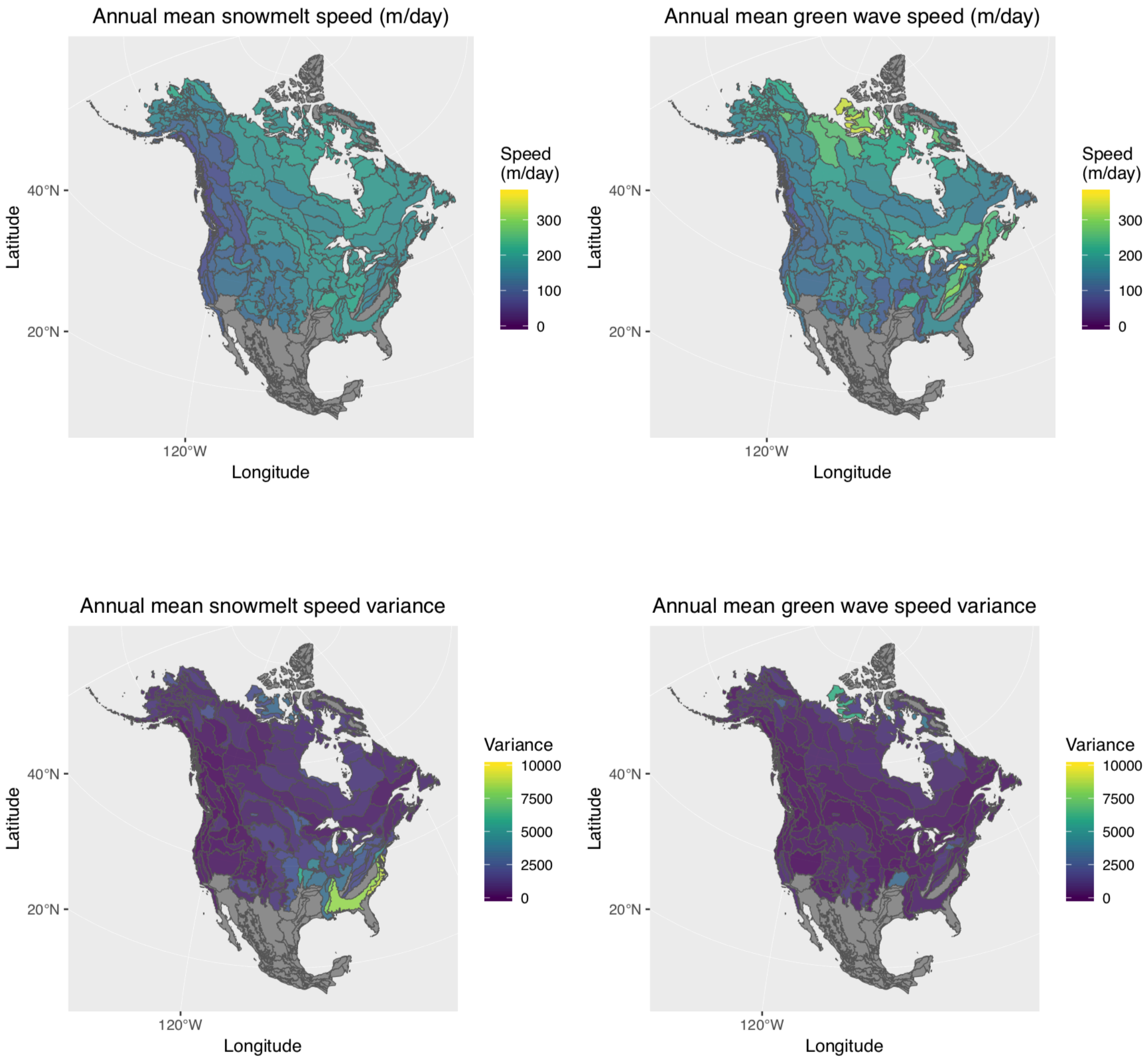


Figure 10 - annual mean values for snowmelt (left) and green wave (right) speed (top) and variance (bottom) for EPA level III ecoregions of North America. Grey ecoregions did not meet our requirements for inclusion in this study. Note how the western cordillera has the lowest speed values for both snowmelt and green waves. The interannual variance of snowmelt speed is highest in southeastern USA, where seasonal snow is sparse and short-lived.

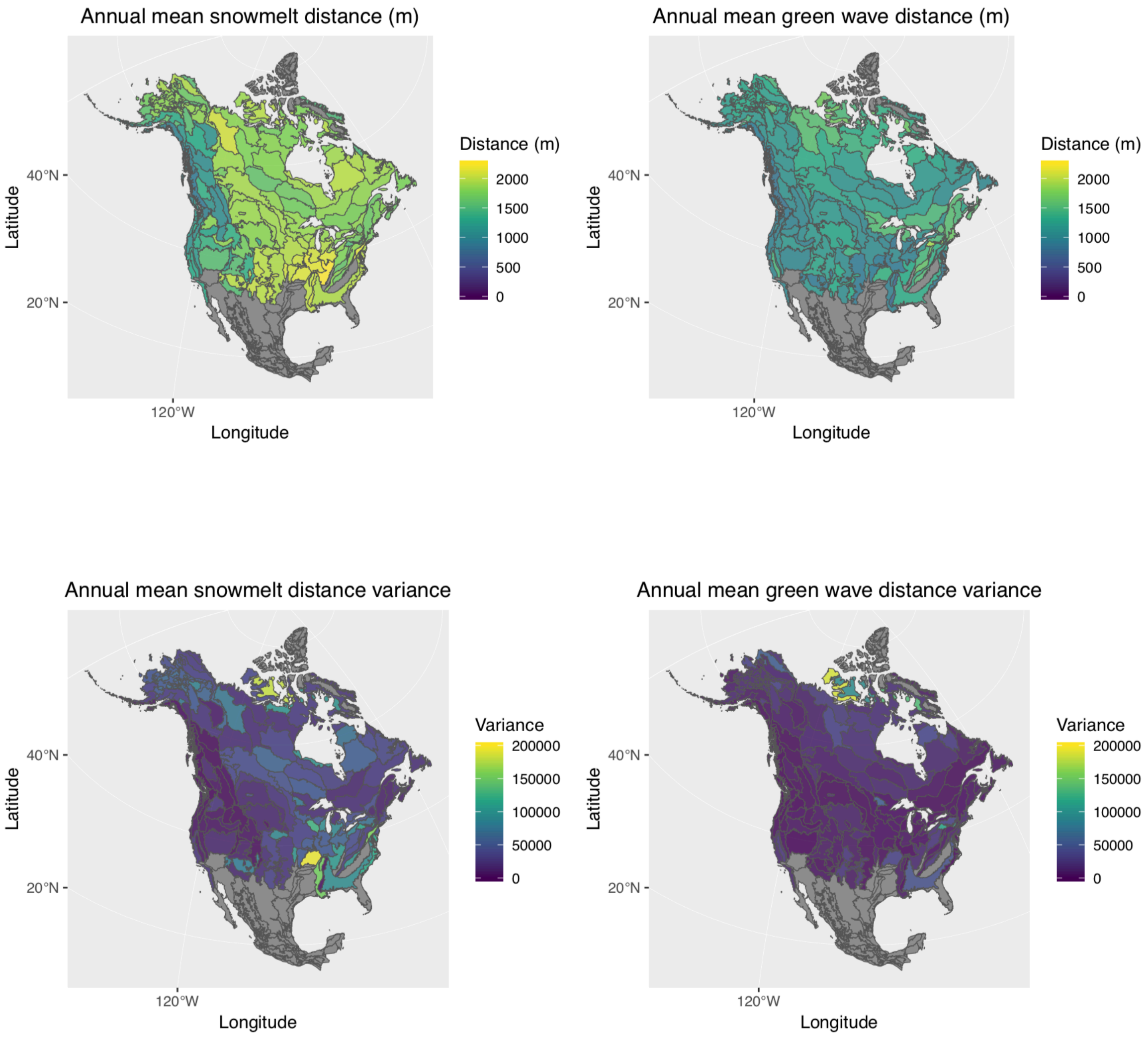
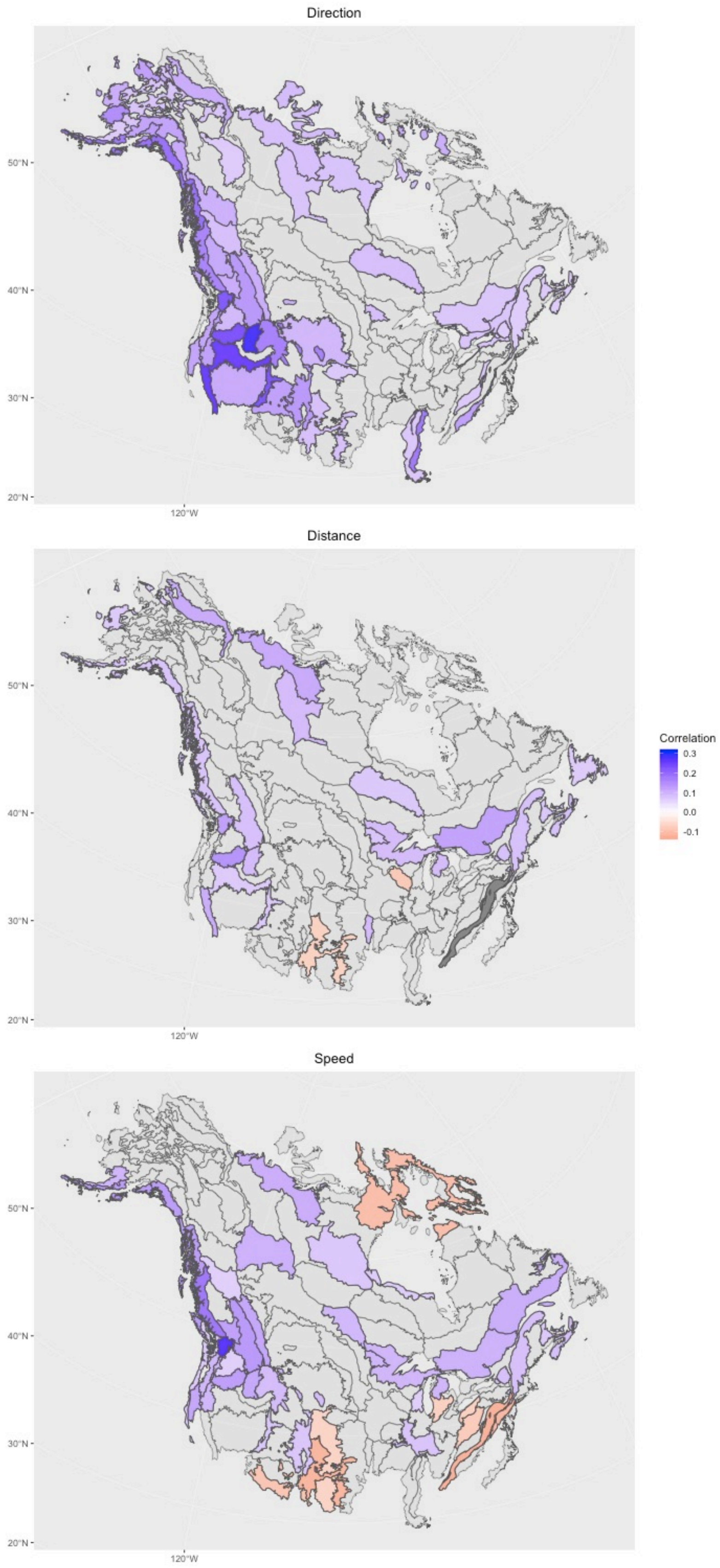


Figure 11 - annual mean values for snowmelt (left) and green wave (right) distance (top) and variance (bottom) for EPA level III ecoregions of North America. Grey ecoregions did not meet our requirements for inclusion in this study. The snowmelt wave consistently travels a greater distance, with higher variance, in flatter ecoregions than in steeper ones. The green wave follows a similar, but weaker, pattern.

When considering all aspects, there are clear geographic patterns to which ecoregions have significant relationships among snowmelt and green-up direction, distance, and speed. Regions with steeper slopes, particularly along the western cordillera, often have significant correlations between snowmelt and green wave velocity components, while regions with flatter topography, and generally those that are further south, have fewer years of significant correlations (Figure 12). There is strong evidence to conclude that ecoregions with higher mean slope have lower mean snowmelt speed and distance traveled than those with lower mean slope (Spearman's $\rho = -.73$ and $-.74$ respectively; $p<<0.01$). However, there is only weak evidence showing that ecoregions with higher mean slope have lower green wave speed (Spearman's $\rho = -.17$; $p=0.055$) and distance traveled (Spearman's $\rho = -.16$; $p=0.074$). Variance decreases with slope increase at the ecoregion level, with variance of snowmelt speed and distance traveled, as well as variance of green wave speed and distance traveled, all having significant negative correlations with mean slope at the ecoregion level (Spearman's $\rho = c(-.64, -.60, -.23, -.27)$; $p=c(<<0.01, <<0.01, 0.002, 0.011)$, respectively). For both speed/distance and their variances, snowmelt velocity has a very strong negative correlation with slope, while green wave velocity has a moderate negative correlation, with p-values that indicate a weak (speed/distance) or moderate (variances) relationship.

Figure 12 - Map of ecoregions colored by correlation coefficient for circular (top), distance (middle), and speed (bottom) correlations for 2001. Grey ecoregions have non-significant ($p>0.05$) correlations. Ecoregional provinces of the western NA continent are most likely to have a statistically significant direction relationship, particularly in mountainous areas.



Direction

Distance

Speed

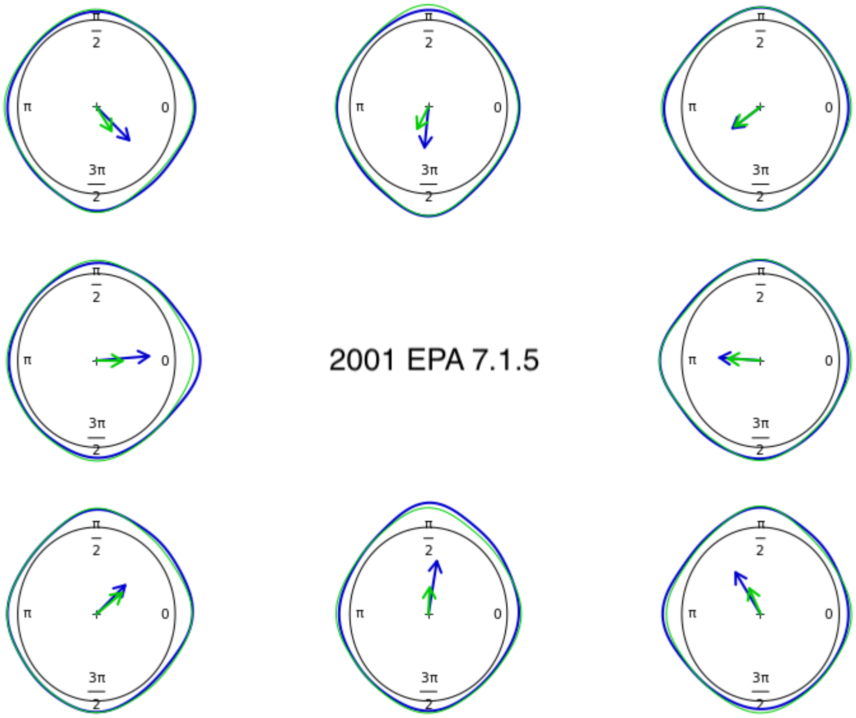


Figure 13 - Distributions of snowmelt (blue) and green wave (green) velocity vector direction densities (blue, green rings, respectively) for year 2001 for EPA region 7.1.5, stratified into eight aspect classes, arranged by their cardinal direction such that uphill is towards the center of the plot. Black circle is the circular axis, with direction shown from 0 (east) counter-clockwise in radians (i.e., 3π/2 = south). For example, the top-left plot shows northwest aspect terrain, with the snowmelt and green wave velocity direction densities modes in the east and south directions, with the resultant vector to the southeast with varying resultant vector lengths according to the overall agreement of resource wave velocity directions in that ecoregion and aspect group. Generally, we see higher resultant vector lengths with the snowmelt velocity than with the green wave velocity, owing to its higher spatial autocorrelation. The multi-modality of each density plot is an artifact of the gridded input datasets.

The ecoregions of North America follow similar patterns in terms of directional relationship when we examine aspects individually. For mountainous regions, we often see strong correspondence in the distribution of directions for each aspect class, with the resultant vector direction consistently uphill. The snowmelt velocity directions are more homogeneous than the green-up directions, as shown by the longer resultant length vector (Figure 13).

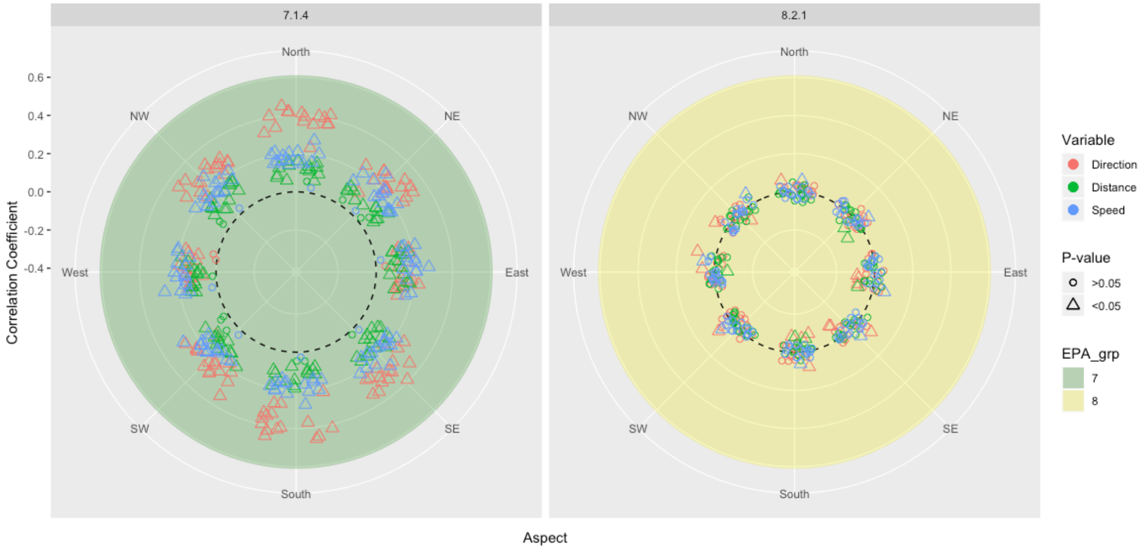


Figure 14 - Diagram showing the test statistic for the circular correlation of direction (red), as well as Spearman's rank correlation statistic ρ for distance (green) and speed (blue) between snowmelt and green wave velocity for the mountainous EPA region 7.1.4 (Pacific costal mountains) and relatively flat EPA region 8.2.1 (Southeastern Wisconsin till plains) for years 2001-2016, stratified into eight aspect classes. Significance (p-value<0.05) is denoted by triangles, with non-significant correlations shown as circles. Each point is given a slight jitter orthogonal to the aspect axis to aid in visually discerning between overlapping points. The black dashed line indicates a correlation coefficient of zero. Background colors for each ecoregion indicate the EPA Level 1 group (EPA_grp). Note how snowmelt and green wave velocity tend to agree in their directions more along the north-south axis compared to the east-west axis.

When we examine the correlations for all aspects across all years of this study, we see the same general patterns as with all aspects combined (i.e., mountainous areas have stronger correspondence). Ecoregions with steeper slopes have stronger correlation coefficients between snowmelt and green wave velocities, for mean values (2001-2016) of direction, distance, and speed correlations (Spearman's ρ = c(.62, .42, .45) respectively; $p<<0.01$). However, there are notable differences among the aspect classes. For some ecoregions, the north-south axis has the strongest correlations, especially for the direction correlation (e.g., ecoregions 6.2.3, 10.1.3), indicating that there are differences in the movement of resource waves for different aspects (Figure 14, left). This is not due to insolation alone, as the least illuminated aspect (north) shows some of the highest correlations in many regions. Compared to the north-south axis, the east-west aspect axis shows fewer strong correlations in these ecoregions. Still, for most of the ecoregions in our study, the correlations between snowmelt and green-wave velocities are insignificant for most aspects and most years (Figure 14, right).

Discussion:

There is a high level of variability in the correspondence of direction, distance, and speed between snowmelt and green wave velocities across ecoregions and aspect classes. Climatic gradients are influenced strongly by regional differences and latitudinal and elevational gradients. Climate is a dominant control on snowmelt and vegetation phenology, so it is not surprising to see that snowmelt wave and green-wave movement are highly related to slope and aspect, and to a lesser degree, latitude. For mountainous regions with steeper slopes, there is a high degree of correspondence between snowmelt and green wave velocity directions, and to a slightly lesser degree, speed and distance. For flatter ecoregions, there is little to no correlation between snowmelt and green wave velocities. These results indicate that snowmelt velocity has a moderate power to predict green wave velocity within mountainous regions of the North American continent.

Considering the three variables of interest: direction, distance, and speed, snowmelt and green waves agree most in their direction, as indicated by stronger positive correlation coefficients, which are more often statistically significant (p-value < 0.05), than the correlations for distance or speed. This makes sense, because, when we consider the spatial gradients that drive these resource waves, the gradients for snowmelt timing and green-up timing often follow local elevational gradients (O'Leary et al., 2018). When these two spatial gradients agree that they are both going uphill, their directions correspond strongly (such as in mountainous terrain). However, this directional correlation is weak or insignificant in many ecoregions and aspects in flatter terrain, such as within EPA ecoregion category 8.2 (central US plains, Figure 14). The distance variable is highly dependent on the spatial heterogeneity of the input resource timing maps. We calculated Moran's i coefficients for several locations, which consistently revealed a higher degree of spatial autocorrelation within the snowmelt timing maps compared to the phenology maps. A close visual inspection confirms this, as the snowmelt timing surfaces contain large areas with uniform snowmelt timing. This may be, in part, because of the 8-day resolution for the input data to the STMs. This may also be a function of true snowmelt patterns, where large areas may melt off rapidly, such as south aspect hillsides following a spring snowstorm, or a wide flat basin that is subjected to warm temperatures and heavy rainfall. Anticipated improvements to the temporal resolution of the STMs should allow for a fair comparison of daily resolution inputs (STMs and MCD12Q2 phenology maps), though it is likely that, even with a daily resolution, the STMs will have a lower spatial heterogeneity than the MCD12Q2 greenup midpoint.

Regional differences explain much of the variability among ecoregions in terms of their correspondence of direction, speed, and distance. Mountainous ecoregions, such as the northwestern forested mountains (group 6.x.x), have a high degree of correspondence between snowmelt and green-wave velocities, whereas flatter regions, such as the Great Plains (group 9.x.x) have low correspondence between resource wave movements. This is likely due to many factors, including the fact that, absent strong climatic gradients generated by steeper slopes, the spatial variability of snowmelt timing is influenced by stochastic events and small-scale processes, such as rain-on-snow events and drifting (Lundquist and Lott, 2008; Beniston and Stoffel, 2016; Berman et al., 2018; Fassnacht et al., 2018). Additionally, snow tends to melt rapidly across large flat areas, and the result is a uniform melt timing across large areas (i.e., the spatial variability of snowmelt timing is within the range of precision for the snowmelt timing maps). Meanwhile, the spatial gradients in vegetation green-up are similarly affected by microclimatic processes, as well as differences in vegetation type and topography (Reed et al., 1994; Barnard et al., 2017; Zhou, 2018). Still, both snowmelt and green-up timing are influenced strongly, and in similar ways, by elevation (O’Leary et al., 2017b; Notaro et al., 2019), and therefore slopes that connect different elevations are likely to have strong gradients in snow and vegetation phenology.

The goal of our research is to determine whether or not snowmelt velocity predicts green wave velocity across North America. However, snowmelt timing is not the only factor that influences green-up timing (Totland and Alatalo, 2002; Ault et al., 2011; Notaro et al., 2019), and therefore, snowmelt velocity alone cannot fully explain green wave velocity. While snowmelt timing is considered to be a critical control on phenology for plants (especially those that are completely covered and therefore thermally insulated by the seasonal snowpack) (Totland and Alatalo, 2002; Cornelius et al., 2013; Sedlacek et al., 2015), many other factors influence green-up. Furthermore, while snowmelt velocity makes for a straightforward calculation using our method, quantifying a velocity for other phenology-driving factors (e.g. accumulation of growing degree days, soil moisture conditions, etc.) may be more difficult or impossible. Therefore, it may be very challenging to quantify a velocity vector for one or more of these important factors, further complicating more sophisticated models for forecasting green wave velocity. Still, our results show that snowmelt timing has a substantial correspondence with green wave velocity among many ecoregions and aspects, and therefore any further investigations into green wave velocity should include considerations for snowmelt velocity.

There is great value in predicting green wave velocity because the green wave substantially influences numerous ecological processes, including animal migrations (Van der Graaf et al., 2006; Bischof et al., 2012; Merkle et al., 2016; Aikens et al., 2017). There is evidence that animals migrate, in part, to maintain their presence in high quality forage, which occurs during peak green-up (Hebblewhite et al., 2008). Therefore, it is possible that by predicting the movement of the green wave, wildlife managers may be able to anticipate the migratory velocities of their animal resources. This could be of great benefit considering the many complications that occur with animal migrations, including exposure of domestic stock animals to diseases (e.g. brucellosis) (Godfroid, 2002) and vehicle collisions (Sullivan et al., 2004). Further research should compare animal migrations (e.g. collared ungulate locations) with the green wave velocity identified here to inquire: do snowmelt and green wave velocities predict animal migration?

Calculating resource wave velocities across large areas is computationally intensive. For this study, the input dataset raster files contain over 200M pixels. Considering the nature of our velocity quantification method, which evaluates pixels within a 5km radius of the source pixel (n=304), and the multiple years of input data (n=16), this analysis required many trillions of calculations. Any changes to the parameters of this model (e.g. expanding the search radius from 5km to 10km), or to the nature of the input datasets (e.g. using a Landsat-based 30m product) could result in a substantial increase in computational demand. We suggest that future investigations carefully evaluate the necessity of such changes if they are computationally limited. Still, changes to our default parameters will be required if researchers are interested in particular flora or fauna that have substantially different migratory velocity, or scales at which they perceive and utilize the landscape.

We determined that the MODIS record and resolution are optimal for this research because of the daily resolution, global coverage, and thorough validation of most MODIS science products. However, there are limitations to the use of this platform. First, the MCD12Q2 dataset collection 6 often does not capture the phenology of many conifer-dominated ecosystems. While there is evidence that conifers do have a phenologically meaningful Enhanced Vegetation Index (EVI) signal (Jönsson et al., 2010; O'Leary et al., 2017b; Emmett et al., 2019; Notaro et al., 2019), the EVI signal for conifer-dominated forests generally has a low amplitude, which does not meet the requirements for the MCD12Q2 collection 6 algorithm, and is therefore not included as an observation for that pixel. This prevents us from analyzing these resource wave dynamics in many conifer-dominated areas. Additionally, the scale of our analysis may not capture the effective scale of investigation for all users. Many organisms that migrate short distances, or utilize a small area of the landscape which is below the resolution of our analysis. For such investigations, repeating our methods using higher-resolution input data will be needed to resolve the level of detail required. This will also necessitate different input data, with resolution equal to or finer than that of their required results. This may present substantial challenges for a number of reasons. First, developing snowmelt and green-up surfaces from satellite imagery at a higher resolution than the MODIS grid is difficult because of the temporal resolution of most satellite-based platforms at those resolutions. Landsat has, at best, a 16-day return period, while Sentinel and VIIRS have relatively short periods of record compared to MODIS and Landsat. Many image fusion methods have the potential to derive such maps (Gao et al., 2006; Roy et al., 2008; Hilker et al., 2009; Berman et al., 2018), however, such methods are subject to various limitations and challenges of their own. Second, collecting and processing imagery using airborne (piloted aircraft and/or 'drones') is expensive and labor-intensive, which may be prohibitive for many research groups. Finally, validating the accuracy of down-scaled (i.e., fusion techniques) or airborne-platform collected data is also costly and labor intensive, resulting in another hurdle for repeating this analysis at a higher spatial resolution. Finally, migratory animals have many constraints, of which green wave velocity is only one. Other factors, such as barriers to migration, or fear of predators, influence strongly their migration routes (Rivrud et al., 2018). Therefore, this analysis may best predict animal movement in locations where complicating factors are minimized, such as open terrain without many predators.

Conclusions:

Here, we created the first ever maps of snowmelt and green wave velocity for North America. We found substantial variability in the correlations between snowmelt and green wave velocity across EPA level III ecoregions of North America, with mountainous ecoregions showing consistent, moderate correlations, and flatter ecoregions showing weak or no significant correlations between the distance, speed, and direction of snowmelt and green wave velocities. This work has applications within resource management and wildlife ecology, where green wave velocity controls animal migrations at many scales (Van der Graaf et al., 2006; Bischof et al., 2012; Merkle et al., 2016; Aikens et al., 2017). Future work should build from these results by considering additional climatic influences on green-up timing, including temperature accumulation, precipitation and soil moisture conditions, and variability among vegetation groups. Additionally, inquiry into the correspondence of resource wave velocities with migratory animal collars will further elucidate these complex interactions. Our methods may also be insightful to compare the movement of various climatic variables across space, such as the possible movement of average annual air temperature and precipitation values under different climate change scenarios. This work defines a new perspective for analysis of spatial patterns of seasonal land cover change, whereby resource wave velocities are quantified, evaluated, and compared, allowing for novel insights into phenologies at the landscape scale.

Chapter 4: Climate Fetch: the coming invasion and exodus of climate space for the national parks of the conterminous USA

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Abstract

Protected areas of the United States are experiencing extreme temperature and precipitation patterns, with some national parks in the USA reporting climate conditions that are unprecedented in the historic record. A primary concern for protected areas is the pace and trajectory of climate changes, and how those differential changes may affect species and ecosystem management within park boundaries. With the conceptual development of climate trajectory, scientists and land managers have a unique mechanism for evaluating the pace and direction of climate changes, both spatially and temporally. In this paper, we calculate climate velocity at a 3km spatial resolution to assess climate changes in air temperature and precipitation between 2019 and 2099 with a particular focus on conservation areas that contain three representative landforms: Shenandoah, Canyonlands, and Badlands National Parks. Our results indicate that mountainous areas such as Shenandoah will be climate sinks that concentrate climate space from surrounding landscapes. Conversely, canyons and valleys, such as those found in Canyonlands, will become climate sources, which experience an exodus of climate space up and out of their lowest elevations. In the Great Plains, Badlands National Park will experience a movement of climate space into, and then out of, park boundaries as a high climate velocity across flat areas results in a movement that completely replaces current with a novel climate. These results identify potential climate-driven migration corridors into, and out of, national parks of the USA, identifying conservation areas at greatest risk for climate disturbance, while also highlighting the need for interagency and public-private cooperation to effectively manage and conserve species that may migrate across political boundaries.

Keywords: climate change; migration; refugia; conservation; protected areas

Introduction

Conservation efforts over the next century must navigate a suite of increasing threats, including ongoing habitat loss, invasive species, and anthropogenic climate change (Maxwell et al., 2016). Given these simultaneous pressures, species are faced with limited options for survival unless land managers provide them additional support. Often under conditions of rapid environmental change, species are forced to migrate, quickly adapt to local conditions, or ultimately face extinction (Hoegh-Guldberg et al., 2008; Dawson et al., 2011; Pacifici et al., 2015; Beever et al., 2016; Hall et al., 2016; Moyer-Horner et al., 2016). Many species are particularly vulnerable to climate change because of a combination of biological traits and vulnerable habitats (Foden et al., 2013). A new synthesis of biogeography and conservation biology is needed to identify those species at greatest risk and plan adequate conservation responses to climate change (Hannah et al., 2002; Ackerly et al., 2010). In recent years, scientists have called for both fine-filter (species-specific) and coarse-filter (ecosystem-specific) conservation strategies that take a diversified approach to adaptive management and reflect varied ecological responses to change (e.g., Tingley, Darling, and Wilcove 2014). Protected areas that have been established or managed to conserve 'representative' ecosystems, may no longer serve this function if these ecosystems no longer exist in future climates (Baron et al., 2009; Langdon and Lawler, 2015; Hansen et al., 2016; Batllori et al., 2017; Holsinger et al., 2019). The national parks of the United States are already experiencing extreme and unprecedented climate conditions (Monahan and Fisichelli, 2014), and are likely to experience substantial climate-driven shifts to their ecosystems in the coming century (Burns et al., 2003b; Gonzalez et al., 2010; Nolan et al., 2018). Moreover, national parks of the USA are predicted to experience a greater magnitude of climate change than the nation as a whole (Gonzalez et al., 2018). Proactively, the U.S. National Park Service has revised its mission and committed itself to a "second century of stewardship" as protected areas worldwide are developing management strategies of their own to better protect their resources in the face of climate change (National Park Service, 2010).

Ongoing and projected climate change will lead to a global change in ecosystems (Nolan et al., 2018), including rapid shifts of species' ranges and ecosystem redistributions (Kelly and Goulden, 2008; Gonzalez et al., 2010), with warming temperatures often leading to species movement upslope (Breshears et al., 2008; Pyke et al., 2016; Brito-Morales et al., 2018) and towards the poles (Davis, 1983; Huntley and Webb, 1989; Nolan et al., 2018). At the intersection of recent efforts to couple conservation biology with biogeography are several climate-integrated assessment tools. Through modeling, these tools attempt to convey the temporal and spatial nature of global change and its impact on species behavior and distribution. Most coarse-filter models are focused on protecting unique environmental characteristics that generally correspond to species' presence, considering protected areas to be the primary management unit (e.g., Tingley, Darling, and Wilcove 2014; Hunter, Jacobson, and Webb 1988). This type of analysis has led to several foundational discoveries about ecosystem migration under rapid environmental change (Gonzalez et al., 2010; Hansen et al., 2014). Changes in species' range and distribution are one of the best-studied impacts of climate change (e.g., Pinsky et al. 2013; Parmesan and Yohe, 2003; Chen, 2015)). While species distribution modeling initially focused on individual species (Nix, 1986), further development of these models has extended to complex statistical techniques and a wide variety of species and communities of interest (Booth et al., 2014). Contemporary research into protected areas of the United States incorporates climate forecasts, bioclimatic modeling, and the combination of species- and community-level models of ecosystem migration (Iverson et al., 2004; Hansen et al., 2016; Rogers et al., 2016). However, these approaches are often agnostic about the speed of movement, and the specific migration corridors that the species of interest will use to move from the present to future ranges.

Many researchers and land managers have recognized the importance of identifying existing and potential migration corridors to facilitate species' climate-driven migrations (Hudgens and Haddad, 2003; Pearson and Dawson, 2005; Williams et al., 2005; Francl et al., 2010; Carroll et al., 2018). This field has taken several approaches to identifying optimal migration corridors, including climate analogue methods (Carroll et al., 2018), ‘least-cost’ surfaces that identify resistance to migration, and mapping strips of mostly undisturbed lands between existing protected areas (Francl et al., 2010; Jantz et al., 2014). Considering that, for many species, climate will be an increasingly dominant driver of migration, there is great potential in identifying the corridors of climate movement in order to predict species’ migration patterns, and their practicability under existing land use. Furthermore, many studies focus on the static beginning and ‘end’ states (i.e., current and projected climate in a given year) without taking into account the velocity of the movement between those states (Svenning and Sandel, 2013). By taking transient movement into account, with an explicit velocity and spatial pathway, researchers may be able to identify the location and timing of climate niche migration, which defines the leading edge of climate-driven species’ migrations (Moyer-Horner et al., 2016; Sittaro et al., 2017), though there may be substantial lags between the onset of climate movement and the subsequent biological migrations (Alexander et al., 2018).

Designing conservation responses to rapid range shifts will require additional information on the rates, mechanisms and direction of change (Hannah et al., 2002). If the pace and direction of climate change are known, strategic management responses would likely include coordination with other protected areas and through public-private partnerships to help species traverse fragmented and diverse land-use matrixes (Tingley et al., 2014). In 2009, Loarie et al. introduced a new index representing the velocity of climate change. As the ratio between the spatial gradient

(C km^{-1}) and the rate of annual near-surface temperature increases (C yr $^{-1}$), the local instantaneous velocity of temperature change (km yr^{-1}) summarizes the speed and direction at which the climate is changing at a given timestep (typically annual) over the next century (Loarie et al., 2009). One primary implication of this study is that species survival is not just contingent on the persistence of viable habitat but also on the species' ability to keep pace with the shifting climate. The strong correlation between topographic slope and velocity from temperature change (correlation coefficient = -0.92), suggests that species within mountainous ecosystems require the slowest velocities to keep pace, as long as their habitats do not disappear altogether (Loarie et al., 2009; Beever et al., 2016; Dobrowski and Parks, 2016). In contrast, flat landscapes such as grasslands and deserts will require the highest migration velocities. The predicted magnitude of these changes is dependent on the Global Climate Model (GCM), IPCC climate scenario, and the period over which the velocity is calculated. Finally, Loarie et al. (2009) calculated climate residence times within protected areas to determine the amount of time it will take current climate to cross park boundaries. The results showed that only 8% of all global protected areas had residence times greater than 100 years.

Building on climate velocity, Burrows et al. (2014) integrated sequential time steps of climate velocity vectors into *climate trajectories*, i.e. pathways of movement implied by climate velocity as spatial and temporal gradients change over time. This extends Loarie et al. (2009) into a useful way to identify not only instantaneous movement, but also pathways of movement implied by climate change. Protected areas have fixed spatial extents and are likely to experience a shift in climate, with some climate niches leaving their boundaries, other novel climates entering, and some climate space disappearing altogether. Given that protected areas are already experiencing extreme climates relative to their historical range of variability, the introduction of climate niches that are unprecedented in the historic record (i.e., 'novel climates') appears to be imminent, if not already present (Monahan and Fisichelli, 2014; Hoffmann et al., 2019). Climate is a primary influence on species distributions and abundance (Huntley and Webb, 1989), and changes in climate can result in major challenges for conservation. For example, current management practices may not be sufficient to protect species whose range shifts will cross protected area boundaries (Peters and Darling, 1985; Hannah et al., 2002; Araújo and Peterson, 2012). While background rates suggest that species have generally been able to track historic climate changes without extinction "spasms" (Roy et al., 1996), recent evidence suggests that we are currently experiencing the sixth major extinction event in Earth's history (Barnosky et al., 2011). Therefore, it may be helpful for protected area managers to use the climate trajectory framework to understand incoming and outgoing climate shifts in order to improve conservation strategies for both species and ecosystems.

In this study we use the climate velocity (Loarie et al. 2009) and climate trajectory (Burrows et al. 2014) methods to track the movement of temperature and precipitation space into, and out of, National Park Service lands, based upon four Representative Concentration Pathways (RCPs) (van Vuuren et al., 2011) and a suite of Global Circulation Models (GCMs). We identify the climate trajectories for air temperature and precipitation within and surrounding 3 distinct national parks in the conterminous USA, and report those findings in a management-relevant framework. Finally, we identify the limitations of our approach, and suggest further research to improve our understanding of climate and conservation interactions.

Methods

Study Area

The National Park Service of the USA was founded in 1916 by President Woodrow Wilson “to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations" (United States Congress, 1916). Today, the National Park Service has 20,000+ employees who care for 400+ protected areas, including parks, reserves, battlefields, and other lands (National Park Service, 2018b). United States Congress designated resource-based national parks (i.e., parks focused around natural features and landforms), in part, to conserve the existing natural resources contained within their boundaries, which are currently exposed to the effects of climate change (Monahan and Fisichelli, 2014). Furthermore, these parks protect diverse ecosystems and topographies, which allow us to investigate the influence of various topographic features on future climate velocity. This study focuses on those lands that are specifically designated as ‘National Parks.’ We exclude parks that are completely surrounded by water (e.g. Isle Royale), because they lack the land-based ‘fetch’ we seek to identify here (see below). We also exclude national parks outside of the conterminous USA due to climate data availability.

Focus Parks

Here, we highlight Shenandoah, Canyonlands, and Badlands National Parks (henceforth, ‘focus parks’) as examples of mountains, canyons, and plains, respectively. While these focus parks may have distinct dissimilarities with other parks of similar landforms, our analysis of all 43 parks (not shown) indicate that there are generalizable lessons to be learned from each landform type, and the results are fairly consistent among different parks of similar topography.

Designated in 1935, Shenandoah National Park is a natural resource-based protected area in the Appalachian Mountains of Virginia spanning 806 km^2. Elevations in the park range from 171m near the northern tip to 1230m at the high point of Hawksbill mountain, and this mountainous park boasts a large relief relative to the many flatter areas surrounding the park. Prior to European invasion, this land was utilized by The Piedmont Siouans, Catawbas, Shawnee, Delaware, Cherokees, Susquehannocks and the Iroquois tribes (National Park Service, 2015). As a major protected area of within the central Appalachian Mountains, Shenandoah National Park is considered to be important for protecting regional natural and cultural resources, including the Shenandoah salamander (*Plethodon Shenandoah*), centuries-old homesteads, and landscape views with high aesthetic value from many wayside vistas on the Blue Ridge Parkway. Situated in the Mid-Atlantic network of National Parks, Shenandoah may be considered a refuge for many species and culturally important resources. The Eastern United States is a highly fragmented ecological landscape due to a history of land degradation and land use change, however it simultaneously includes some of the highest levels of biodiversity anywhere in the temperate world (Highlands Biological Station, 2017). Due to this history of fragmentation, many species are now concentrated within protected areas, such as US Forest Service and National Park Service lands.

Designated in 1964, Canyonlands covers 1,336.2 km^2 of diverse lands including canyons, valleys, plateaus, cliffs as a resource-based national park in southeastern Utah. Canyonlands contains extensive cultural relics – the evidence of the agricultural societies of the Ancestral Puebloan and Fremont peoples stretch back 2,000 years. There is also evidence that the Ute, Navajo, and Paiute peoples utilized these lands as hunter-gatherers as early as 800 CE. However, it is thought that increasing drought and air temperatures made agricultural production increasingly difficult, and forced these residents to flee to other areas as the result of climate change around the year 1300 CE (National Park Service, 2018a). Today, Canyonlands is predominantly covered in desert shrub vegetation. Canyonlands is an interesting case study because it contains a complex landscape of canyons, which rise in elevation from the Green and Colorado rivers, to the overlying Colorado Plateau that they incise. Because of this topographic diversity, Canyonlands has a variety of landforms and micro-habitats that improve the habitability of this harsh landscape.

Designated as a national park in 1978, Badlands National Park covers 982.4 km^2 of sweeping prairie and eroding canyons in South Dakota. Prior to extirpation and colonization by the United States military, the Lakota, Arikara, and Great Sioux Nation peoples utilized these lands for their abundant fresh water and game resources (US-Parks.com 2019). Today, Badlands is managed by the NPS and Oglala Lakota nation as they protect the extensive natural and cultural resources therein (National

Park Service 2016). This park contains moderate topographic diversity within its boundaries, mostly in the form of soft soils that are prone to arroyo-type erosion through weathering. The nearby Black Hills provide the only other notable topographic relief for hundreds of kilometers of sweeping prairies in every direction (USGS, 2006).

Data

For climate data inputs we used the NASA NEX DCP-30 ensemble statistics, which provide monthly values of minimum and maximum air temperatures, as well as precipitation depths, at a 1km resolution from 2019-2099 for four RCPs (NASA, 2017) We then used these data to calculate annual mean air temperature and annual sum of precipitation. Using the technique described in Loarie SR et al. 2009, we produced climate velocity maps at 3km resolution using 5-year annual mean values for temperature and precipitation (details below). We then created climate trajectory surfaces from our climate velocity maps per Burrows et al. 2014. To identify official National Park boundaries, we used a GIS layer produced by the Earth Data Analysis Center at the University of New Mexico. To analyze the influence of surrounding land characteristics for each park, we included land cover (Friedl and Sulla-Menashe, 2015), land ownership (USGS, 2018), and forest fragmentation data (USGS, 2002). These datasets come as rasters, which we projected and re-gridded to a common format to coincide with the NEX climate data using the *raster* and *rgdal* packages in R (Hijmans, 2016; R-project.org, 2016; Bivand et al., 2019).

Calculating Climate Velocity and Climate Trajectory

Following Loarie et al. (2009), we calculated two separate climate velocities based on annual average of monthly mean of the daily-maximum temperature, and the annual sum of precipitation. We averaged these values from 12 months of NEX-DCP30 to create an annual mean for each year from 2019 to 2099, and aggregated them to 3km. We chose 3km aggregation because initial results from our analysis at a 1km resolution found many artifacts (such as extreme velocities) resulting from high spatial heterogeneity (e.g. steep cliff terrain).

The climate velocity vector for either variable $\overrightarrow{V_{x,y,t}}$ at location (x, y) at time t is calculated by following equation:

$$\overrightarrow{V_{x,y,t}} = (\frac{dC/dt}{dC/dx}, \frac{dC/dt}{dC/dy})$$

where dC/dt is the temporal change rate at location (x, y) at time t and it is the linear trend using least squares regression on next 5 years temperature (or precipitation). dC/dx and dC/dy are spatial gradient (longitudinal and latitudinal respectively) at location (x, y) at time t and calculated as follows:

$$dC/dx = ((C_{x+1,y-1} + 2C_{x+1,y} + C_{x+1,y+1}) - (C_{x-1,y-1} + 2C_{x-1,y} + C_{x-1,y+1}))/8S_x$$

$$dC/dy = ((C_{x+1,y+1} + 2C_{x,y+1} + C_{x-1,y+1}) - (C_{x+1,y-1} + 2C_{x,y-1} + C_{x-1,y-1}))/8S_y$$

where S_x and S_y are grid sizes at longitudinal and S_y is adjusted by its latitude. The length and direction of $\overrightarrow{V_{x,y,t}}$ indicates the move distance and direction for species to keep constant temperature (or precipitation).

The trajectory of each grid cell is obtained by updating the climate velocity location every year. The moving behavior of each grid cell is determined by identifying the original and future locations of that cell's current climate variable value. For example, if the grid cell is outside of the park originally, but moves into the parks in future, this behavior is defined as 'move in', and the park's residential grid cells are defined as 'disturbed' if a 'move in' cell moves into those cells. Theoretically, there is no upper limit to the area that may 'move in' to a park, as that climate space may become concentrated (e.g., movement towards a mountain summit), or it may pass through a park (as happens with Badlands, below). Grid cells that are originally inside the park but then move outside the boundaries, are defined as 'move out' and their destinations are defined as 'move out destination.' We are primarily interested in the movement of climate space across park boundaries, therefore, we identify the starting location, pathway of movement, and final destination for all pixels that cross park boundaries in 2099 for each of four RCPs.

Definition of terminology for climate trajectory technique

To describe our results, we first define a few terms for the reader. **Starting location** is the initial position for climate velocity analysis in year 2019. **Ending location** is the final position for climate velocity analysis in year 2099, according to the movement implied by the annual climate velocities. **Pathway** describes the sum of annual climate velocity movement, from the starting location to the ending location for that starting location's **climate trajectory**. **Climate Fetch** describes the sum of land area starting locations that have pathways that move across a park boundary. The term 'fetch' is borrowed here from the sailing lexicon, where it describes the surface area of the water across which wind blows before it reaches one's sails. **Climate**

throw (i.e., the opposite of 'fetch') describes the sum of land area ending locations - these are the locations that are predicted to be impacted by the climate movement.

Results

Over the next century, there will be substantial movement of climate space into and out of national parks in the conterminous USA (Table 8). In general, temperature trajectories move uphill at a velocity proportional to the magnitude of climate change (e.g., RCP 8.5 has the fastest velocities), while precipitation trajectories show either little movement (Shenandoah) or converge upon locations of high precipitation (Canyonlands and Badlands) (Figures 15-26). The move-in climate fetch and move-out climate throw for both climate variables highlight the importance of the surrounding lands for each park – with the relatively disturbed lands surrounding Shenandoah contrasted with the nearly pristine lands surrounding Canyonlands and Badlands (Figures 27-30). Our results also vary widely depending on the park in question, highlighting the variable nature of climate impacts to protected areas depending on topography, existing vegetation types, regional climate, and surrounding lands.

Table 8 - Proportion of park land area that originates outside of the park and crosses into the park boundary (move in), or that begins within the park boundary and leaves the park (move out), for four RCPs, from 2019-2099. While 'move out' cannot exceed 100%, 'move in' potential is only limited by the forces driving climate velocity. The high 'move in' values for Shenandoah National Park are the result of intense climate space concentration among the local high points of the Blue Ridge crest, while the high 'move in' values for Badlands National Park are the result of climate space traversing the park by first moving in, then passing through, the park.

Park	RCP	Move in Temp	Move in PPT	Move out Temp	Move out PPT
SHEN	2.6	15%	5%	5%	7%
	4.5	97%	5%	26%	7%
	6.0	215%	5%	50%	13%
	8.5	315%	6%	57%	28%
BADL	2.6	95%	207%	86%	83%
	4.5	164%	166%	93%	76%
	6.0	197%	183%	93%	87%
	8.5	206%	132%	93%	81%
CANY	2.6	4%	11%	10%	13%
	4.5	11%	7%	27%	7%
	6.0	24%	36%	41%	25%
	8.5	25%	24%	51%	16%

Shenandoah National Park

Shenandoah has substantially different climate trajectory patterns for its temperature and precipitation spaces, where temperature has potentially very large areas of climate fetch moving into the park under high emissions RCPs (but not in the low-emissions RCPs), and very minor changes to the park's precipitation space across all four climate projections. Under high emissions RCPs, the climate trajectory of temperatures moving into the park suggest that the majority of existing temperature niches will be displaced by the year 2100, with the majority of novel temperatures coming from the relatively flat lands to the southeast of the park, which stretch from the Blue Ridge crest of the park down towards the Atlantic coast (Figure 15). Moreover, the temperature climate fetch for Shenandoah under RCPs 6.0 and 8.5 encompasses a much larger area than the park itself, with upwards of 315% of the park's land area moving into the park (Table 8), and 100% of the park interior being disturbed by incoming climate fetch – implying a concentration of temperature space moving from the areas within and surrounding the park towards the mountain peaks of the Blue Ridge. However, this is not the case for move-in temperature in the low-emissions RCPs, or for the precipitation climate trajectories in general. For these cases, the climate fetch is relatively small, and concentrated along the edges of the park boundary in the northern half of the park (Figures 15-18), with few ecological implications due to the low levels of disturbance and small move-in precipitation fetch (Figure 17). Further investigation into the temperature fetch of Shenandoah shows that there are a variety of land cover types represented in the possible pathways of incoming temperature movement. All of Shenandoah's temperature fetch consists of non-federal lands (Figure 27). In spite of the lack of federal protections, the land cover for the majority of the temperature fetch for all four RCPs consists of non-fragmented forests, primarily deciduous broadleaf, savannah, and woody savannah land cover types. There are areas of urban, cropland, and crop-natural lands in the temperature fetch for each of the four RCPs for Shenandoah, highlighting that these human-modified landscapes may be contributing temperature space into the park by the end of the century, increasing the threat of potentially detrimental species movement into the park from these disturbed lands.

When we consider the move-out temperature trajectory for resident park grid cells, we see a similar pattern to the move-in temperature trajectory – the existing temperature space moves towards the highest peaks (along the eastern border of the park) (Figure 16). Due to the climate trajectory method employed here, annual variability among the predicted temperature surfaces may lead to small movements around mountain summits for climate parcels that are concentrated at these summits. Because of this artifact, the trajectories for these parcels may wander into and out of the park boundary for mountain summits that are close to, or define, the park boundary. We see this phenomenon in Figure 16 (e.g., in the southern half of the park), where climate space that is interior to the park arrives to the high peaks along the park boundary, but only leaves the park for a very short distance as it moves around the summit (Figure 28). Considering the move-out potential for precipitation in Shenandoah, we again see that there is little movement shown in our climate trajectory method, with small, slow departures among a few locations along the park perimeter (Figures 18, 30).

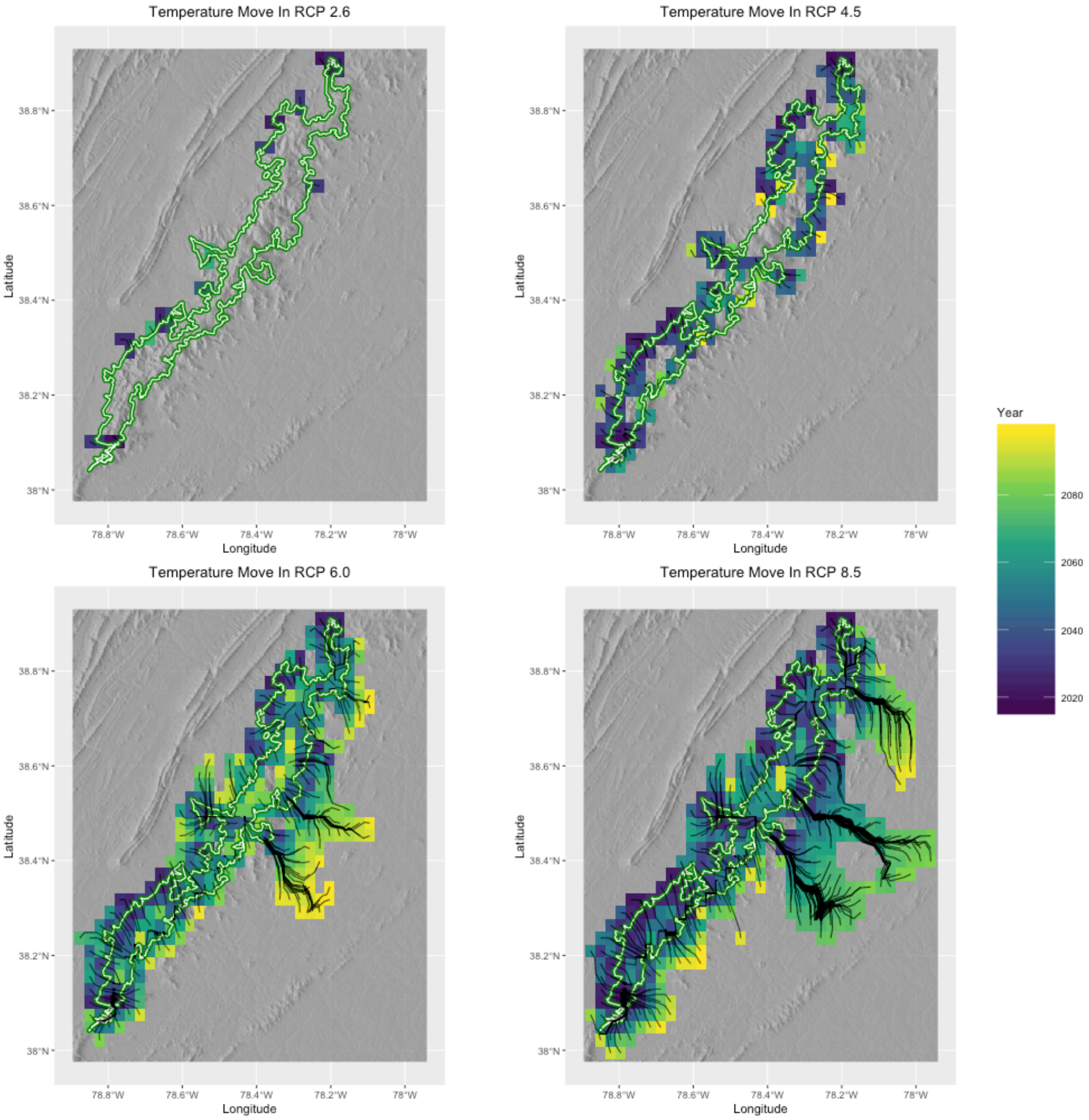

Figure 15 - Temperature move-in fetch for Shenandoah. Highlighted pixels are the 3km climate trajectory grid. Colors represent two dimensions – the climate fetch (i.e. the present day locations) that move into the park are colored by the year that they cross into the park boundary (white/green line). The highlighted pixels within the park are colored according to the year that they are first disturbed by location that has crossed into the park boundary. Thin black lines show the climate trajectory for that starting location. Here, we see many surrounding lands moving into the park, with some converging into migration corridors along ridgelines moving into the park.

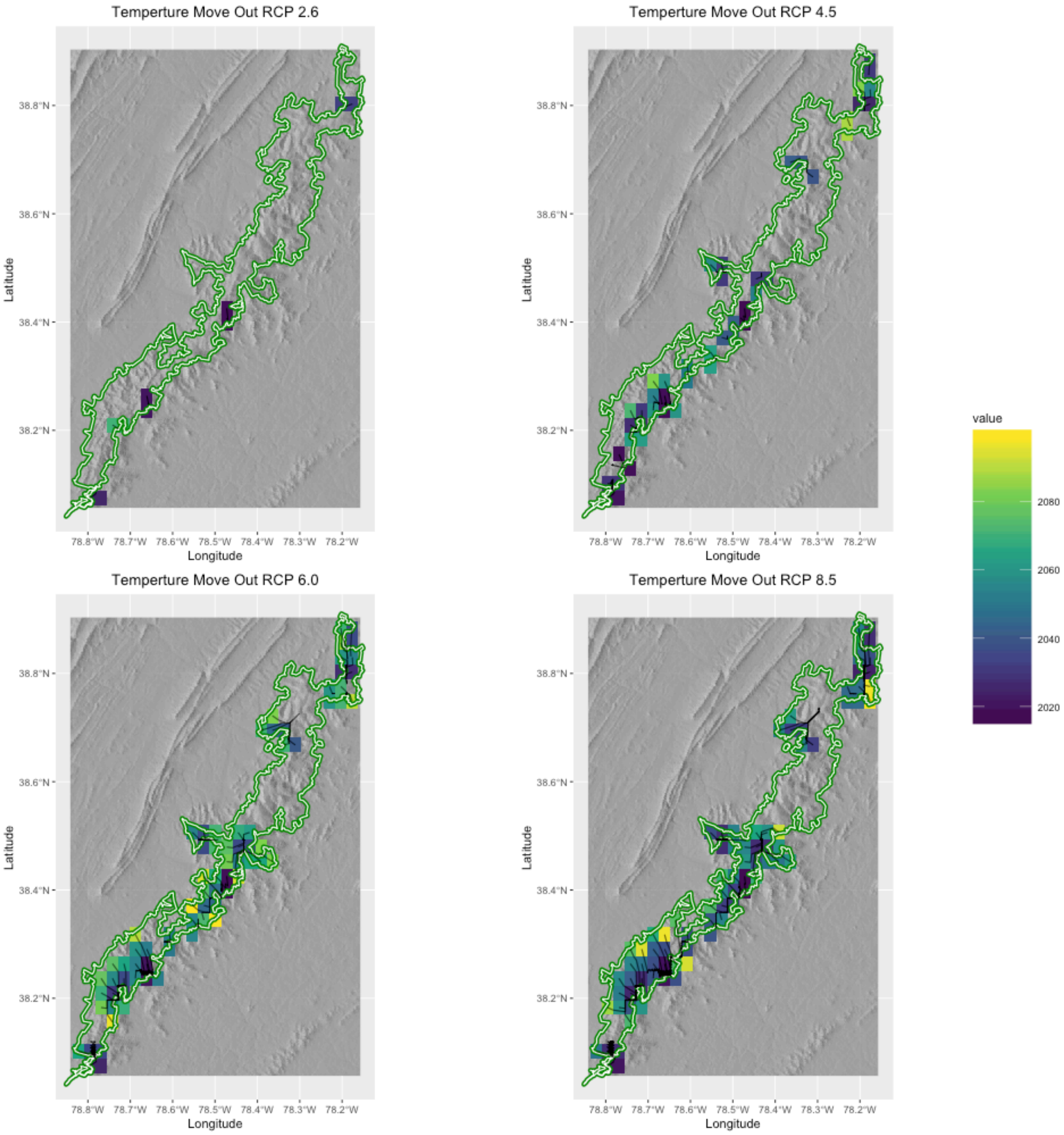

Figure 16 - Temperature move-out throw for Shenandoah. Highlighted pixels are the 3km climate trajectory grid. Colors represent two dimensions – the highlighted pixels within the park are colored according to the year that they first leave the park boundary. The climate throw is the combined highlighted area outside of the park, which is colored by the year that they are first disturbed by pixel movement that leaves the park boundary (white/green line). Thin black lines show the climate trajectory for that starting location. As seen here, Shenandoah has a very small temperature throw, with temperatures that currently exist within Shenandoah only leaving the park boundary for a short distance, or along the southern boundary of the park where the boundary crosses many high peaks.

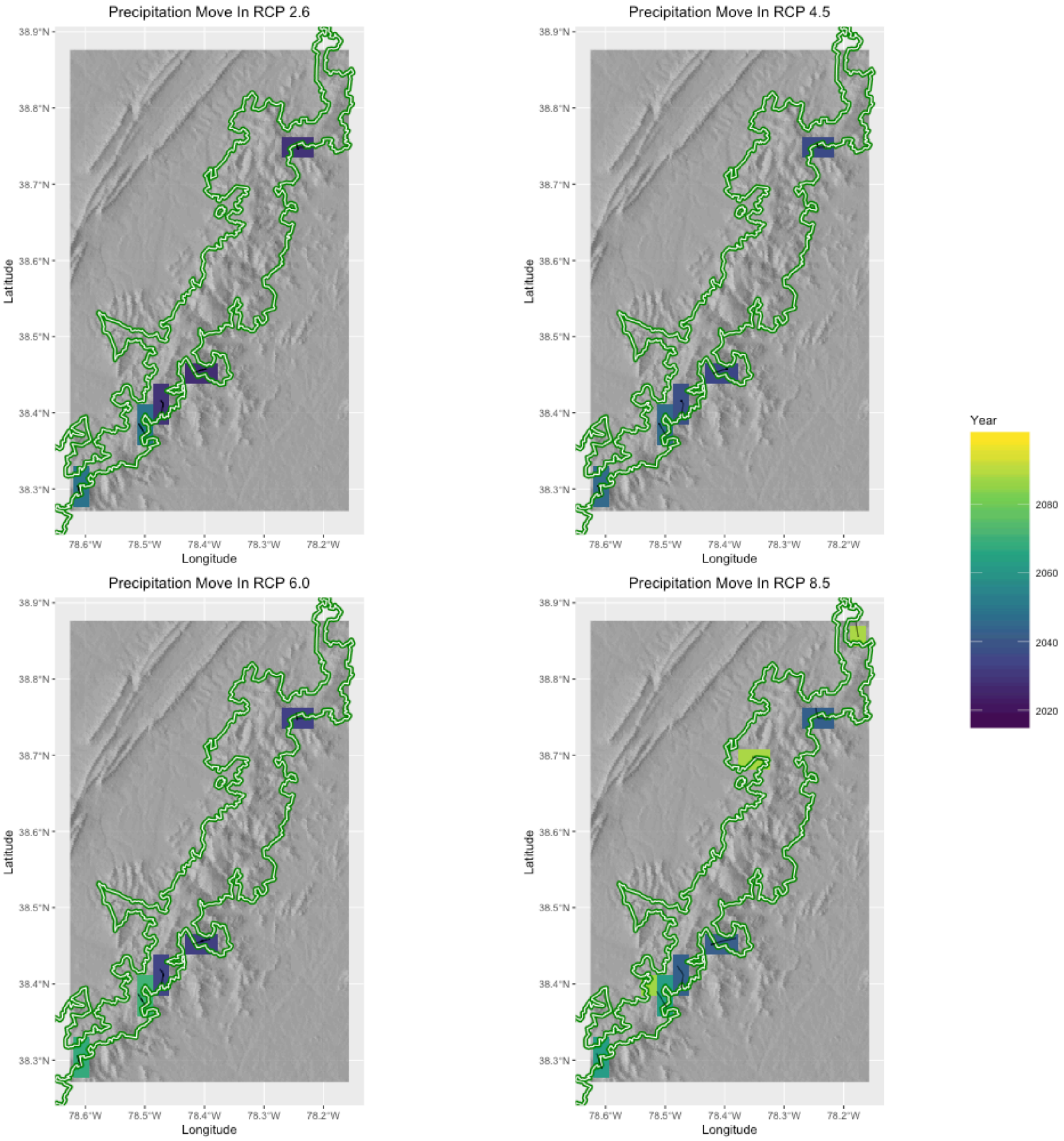

Figure 17 - Precipitation move-in fetch for Shenandoah. Same as Figure 10, but for precipitation.

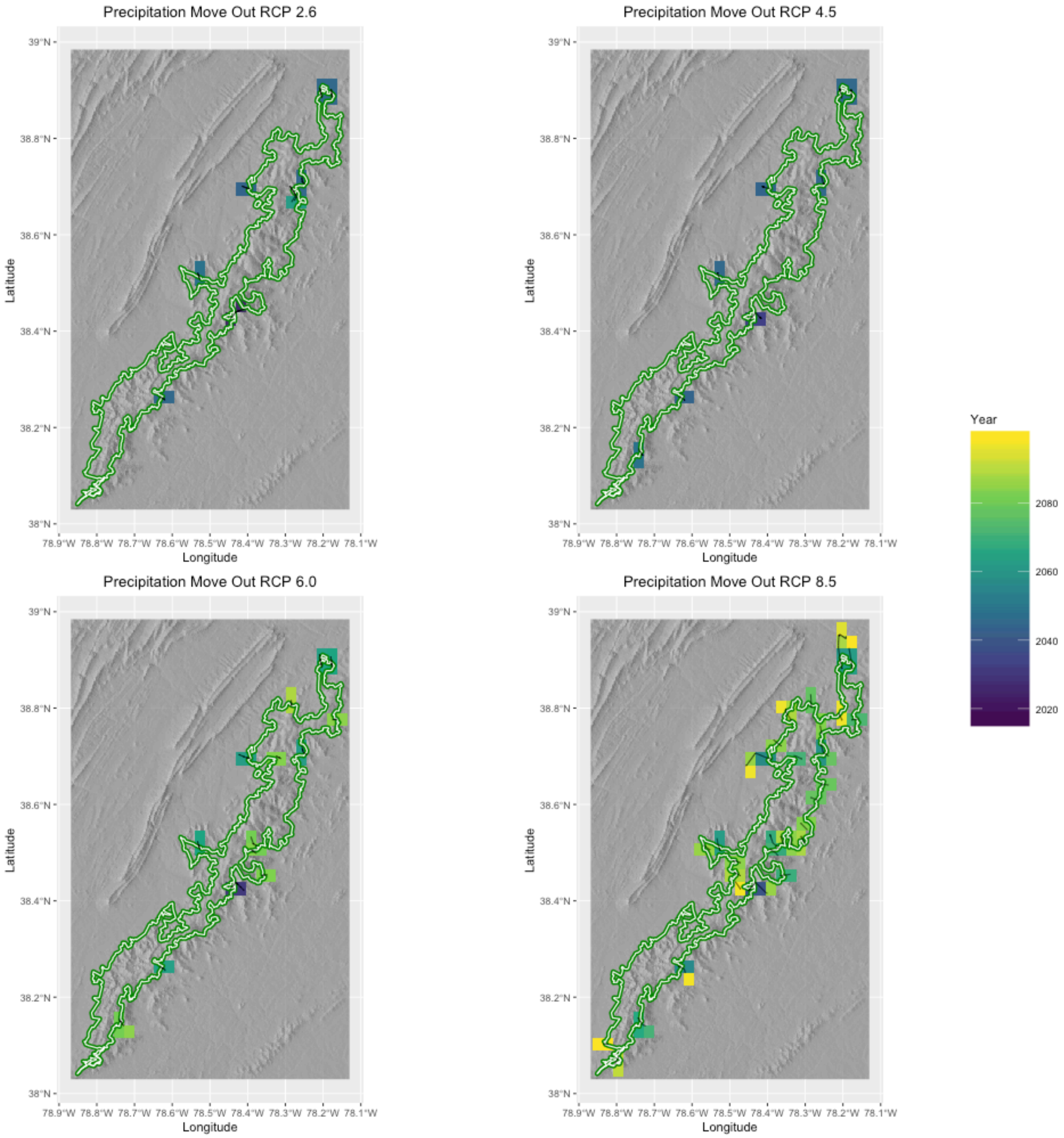

Figure 18 - Precipitation move-out throw for Shenandoah. Same as Figure 11, but for precipitation.

Canyonlands National Park

A landform characteristic of the canyons of the Colorado Plateau, the topography of Canyonlands National Park is the dominant influence on the climate velocities calculated in our methods here. Unlike Shenandoah and Badlands, Canyonlands shows relatively small climate fetch areas (Table 8) and short trajectory distances. This may be due to the fact that Canyonlands has many steep cliffs with abrupt transitions between warmer temperatures below, and cooler temperatures above the cliffs, leading to a high spatial gradient in climate along these landforms. The temperature move-in and move-out temperature trajectories for this park show a general movement up and out of the park, with the exception of the move-in trajectories travelling into the park from the north, towards the Needles District entrance in the southeast part of the park (Figures 19, 20). There are short trajectories around the fringe of the park boundary, but the longest temperature trajectories occur in the small Horseshoe Canyon Unit parcel of the park to the northwest of the main districts, as well as along the southern boundary of the park in the Needles district. The temperature fetch for Canyonlands is much smaller in area than that of our other parks. Due to its position among a broad landscape of fairly homogeneous vegetation cover, the temperature fetch and throw cover lands that that have very similar vegetation types to those currently established within Canyonlands (Figures 27, 28). Furthermore, this temperature fetch and throw areas enjoy the highest degree of federal protection, with the majority of the fetch area under BLM protection, along with a small area designated as a National Recreation Area (Figures 27, 28), which may allow for organized protection efforts in support of species movement into, and out of, Canyonlands National Park.

Both the move-in and move-out precipitation trajectories show the most movement around the Big Spring overlook area slightly north of the Needles District entrance on the eastern side of the park, where there is a moderate convergence of precipitation trajectories near the park boundary (Figures 21, 22). Interestingly, the area of convergence is not a topographic feature itself, though it is ~5km to the southwest of the Needles Overlook prominence, which produces orographic uplift for the dominant weather pattern of storms arriving from the west. Apart from this feature, the precipitation trajectories that cross Canyonland's park boundaries have short travel distances along the fringe of the park boundary, impacting relatively small areas within the precipitation fetch and throw (Figures 29, 30) and are therefore unlikely to have substantial ecological impacts.

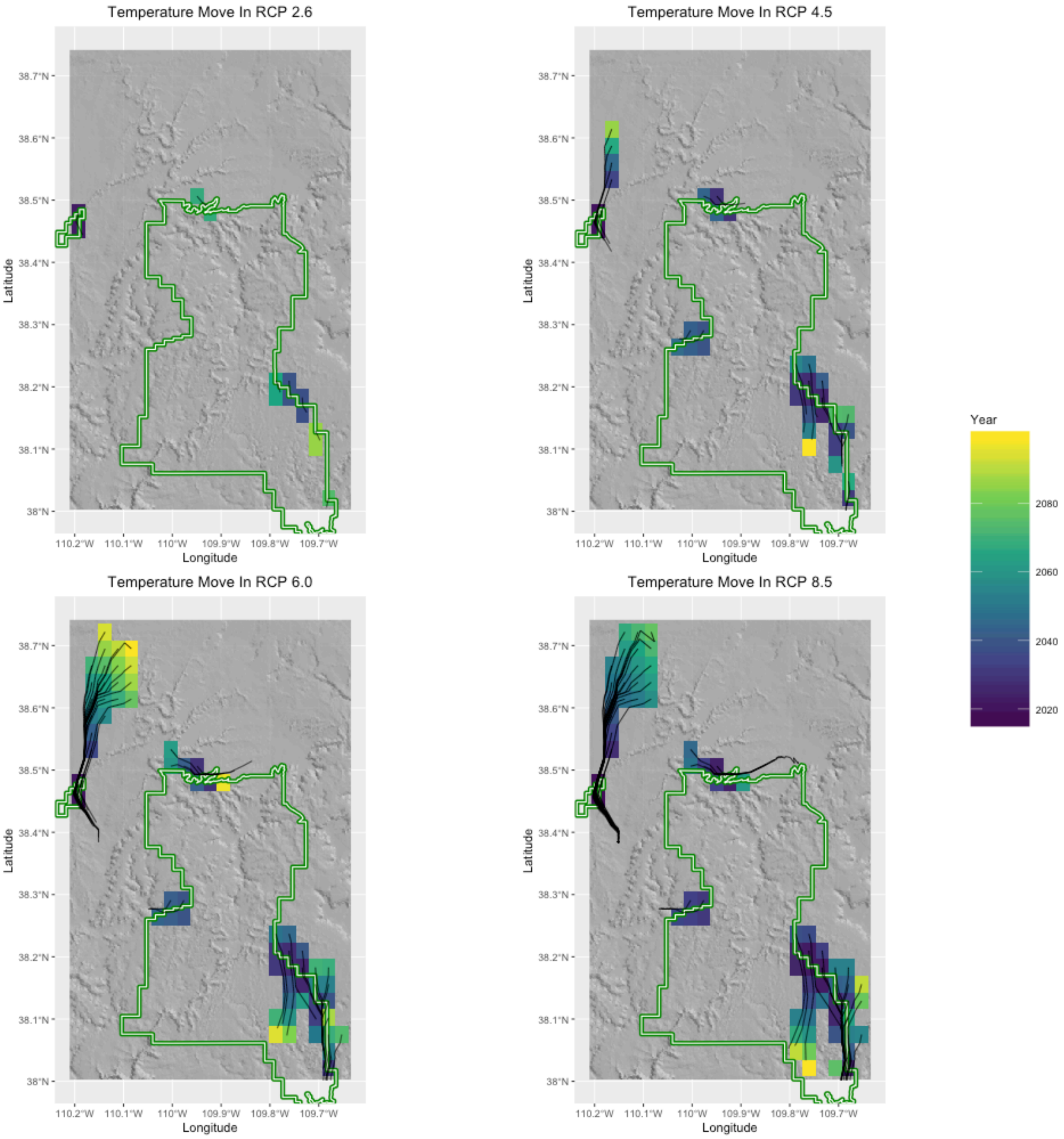

Figure 19 - Temperature move-in fetch (same as Figure 10) for Canyonlands. Here we see a substantial area in the northwest of the plot that travels into the small Horseshoe Canyon, and a smaller area in the southwest (Needles District) part of the park.

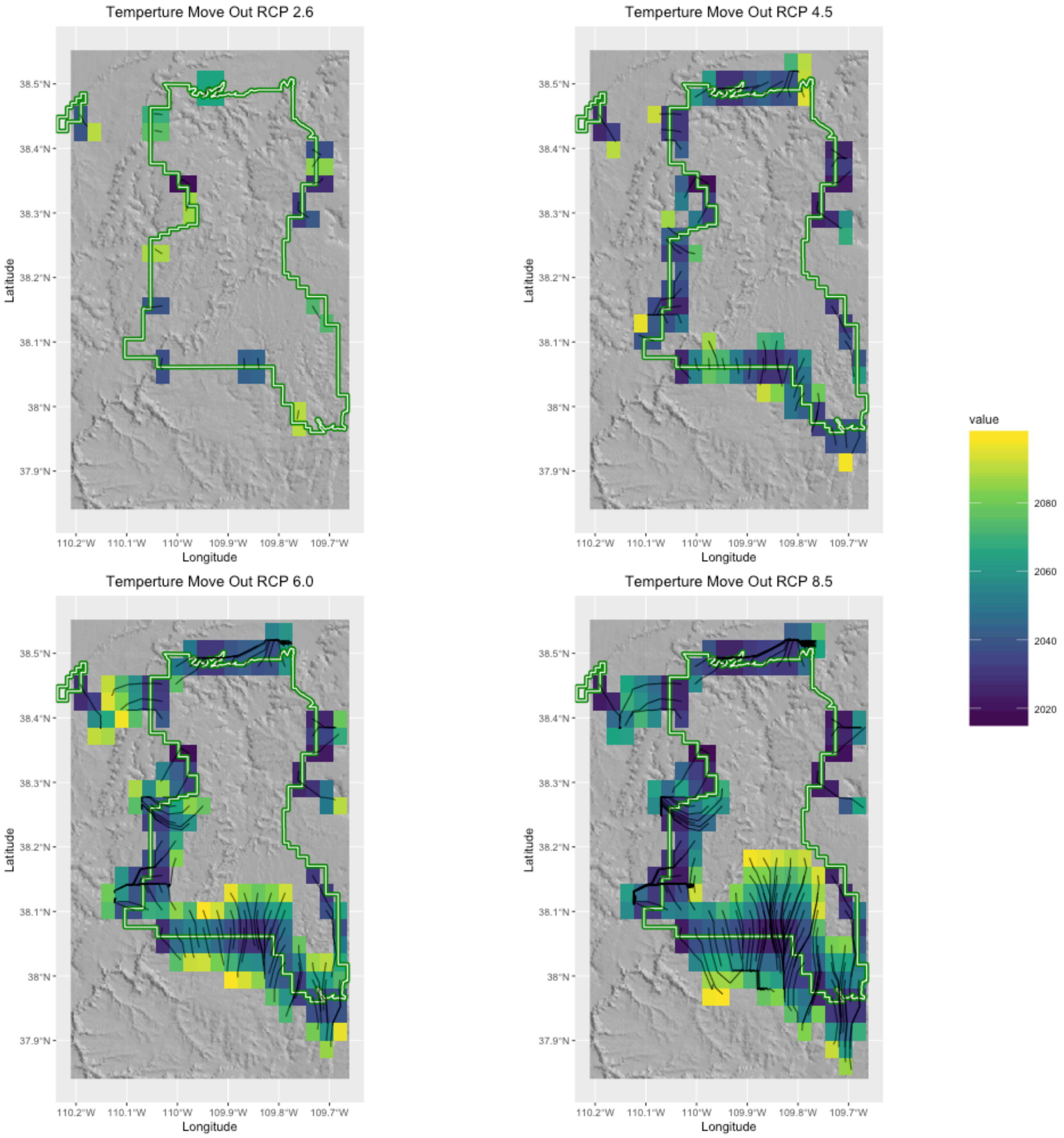

Figure 20 - Temperature move-out throw (same as Figure 11) for Canyonlands. Here, we see the exodus of temperature space as increasing air temperatures lead to a climate velocity up and out of the canyon formations of this park. The temperature fetch in the Needles District shown in Figure 14 continues its movement to the south, which is notably also a former human migration corridor along the salt creek drainage.

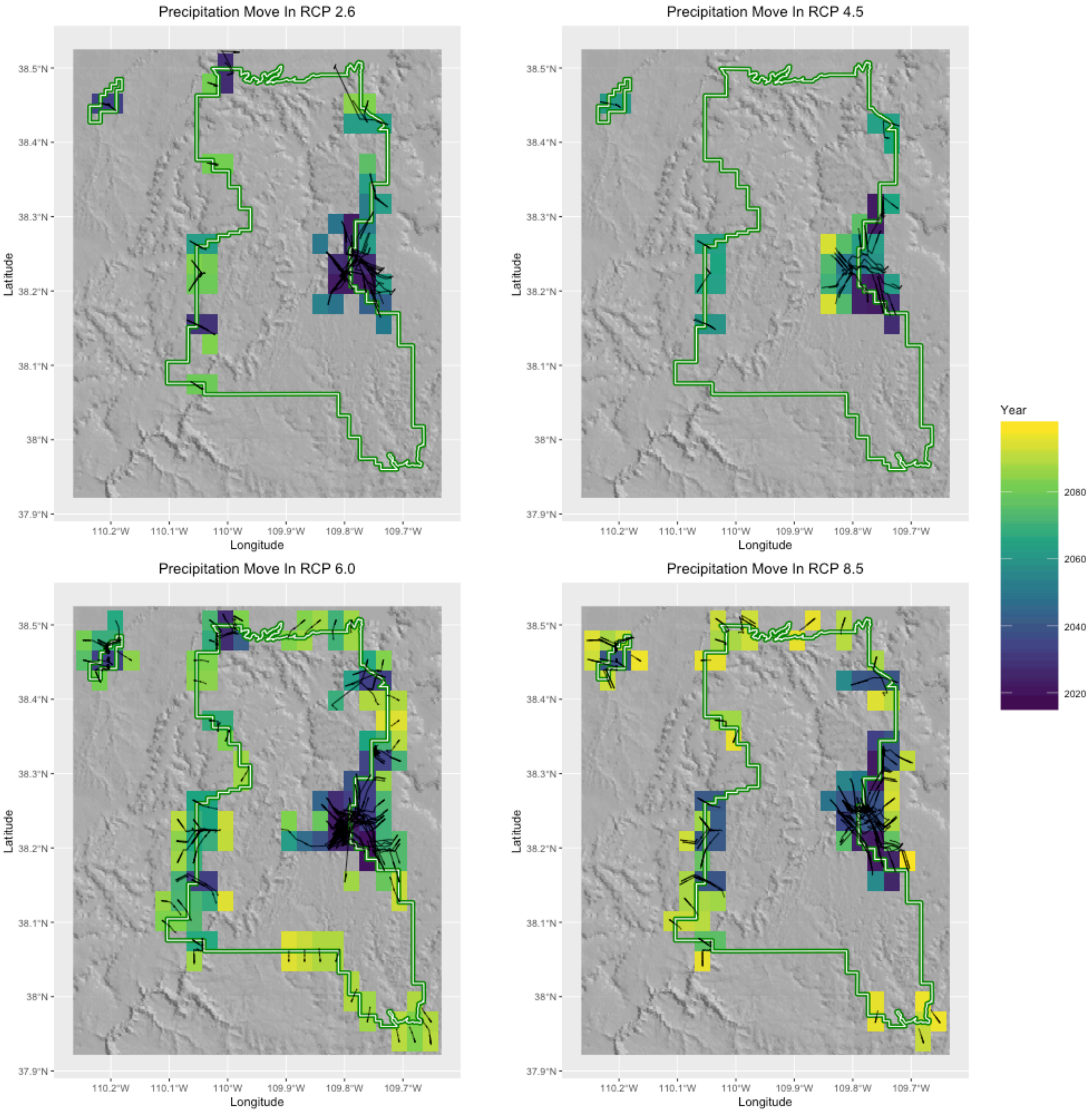

Figure 21 - Precipitation move-in fetch (same as Figure 12) for Canyonlands. We see a fairly strong convergence of precipitation climate velocity along the eastern boundary (Needles District entrance) of the park. Still, the climate velocities that we see have short distances and low apparent disturbance.

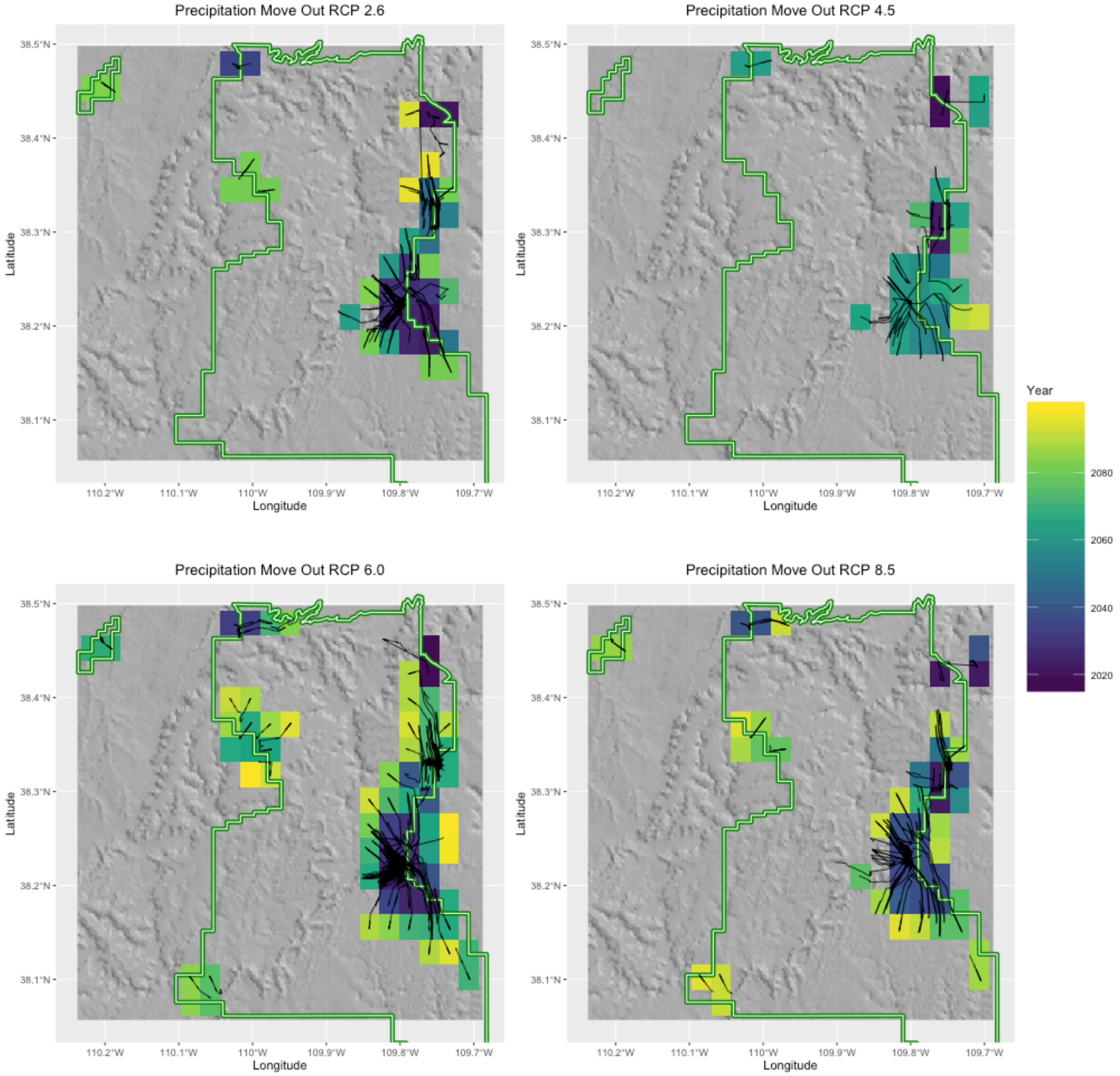

Figure 22 - Precipitation move-out throw (same as Figure 13) for Canyonlands. Here, we see similar patterns to Figure 16, largely due to convergence and subsequent 'jitter' of the location as interannual variability drives the short, sporadic movements of climate along the eastern boundary.

Badlands National Park

For this example of flatter terrain with a few prominent hills, surrounded by the relatively flat and climatically variable northern Great Plains, our method predicts that Badlands National Park is expected to experience dramatic move-in and move-out potential for both temperature and precipitation variables. For all four RCPs, Badlands experiences a near-complete exchange of existing climate space, with >75% of all current resident temperature and precipitation moving out (Table 8). Furthermore, the temperature and precipitation fetches for Badlands show areas greater in size than the park itself moving into, and often across and out of, the park. This is true for all four RCPs and both temperature and precipitation, with a single exception for RCP 2.6, which has a temperature fetch of 95% (Table 8).

The temperature trajectories across all four RCPs in Badlands show a general movement to the northwest, and towards some of the local high points with large swaths of land to the southeast contributing to the temperature fetch. The temperature climate throw shows a similar pattern, though with a greater concentration of temperature space moving into the local high points and a few ‘break out’ climate trajectories that extend well into the lands northwest of the park boundary (Figure 24). Much of the land within the temperature and precipitation fetch and throws for Badlands enjoys federal protection from the United States Forest Service as National Grasslands, though the majority is non-Federally protected lands (Figures 27-30). The land cover map shows that the lands surrounding almost exclusively grasslands, and therefore are designated “non-forested” and are not considered within the forest fragmentation qualification (Figures 27-30). The precipitation trajectories for Badlands tend to converge upon local high points, particularly near the Highway 44 pass southeast of the town of Scenic, South Dakota. Their movements of both the move-in and move-out precipitation trajectories are characteristic of the familiar convergence patterns that we see with temperature in Shenandoah (Figures 25, 26).

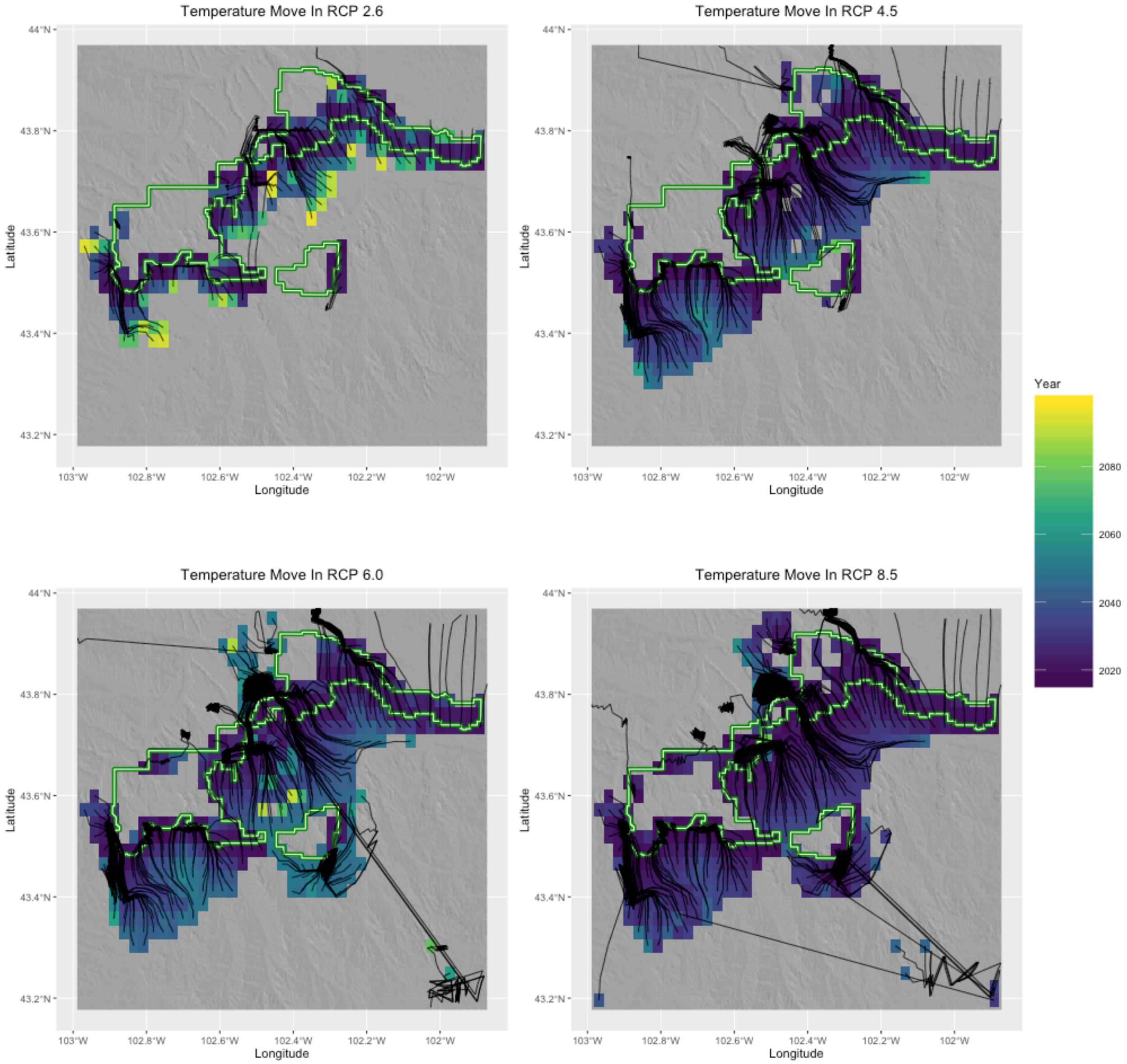

Figure 23 - Temperature move-in fetch (same as Figure 10) for Badlands. Here, we see large areas south of the park that have temperature velocities that cross the southern park boundary. Interestingly, the southwestern part of the park has little apparent temperature space invasion, as temperature trajectories converge upon local high elevation locations along the souther boundary of the park. Conversely, the northeastern portion of the park has

higher incidence of temperature invasion and disturbance, as shown by the colored pixels inside of the park boundary.

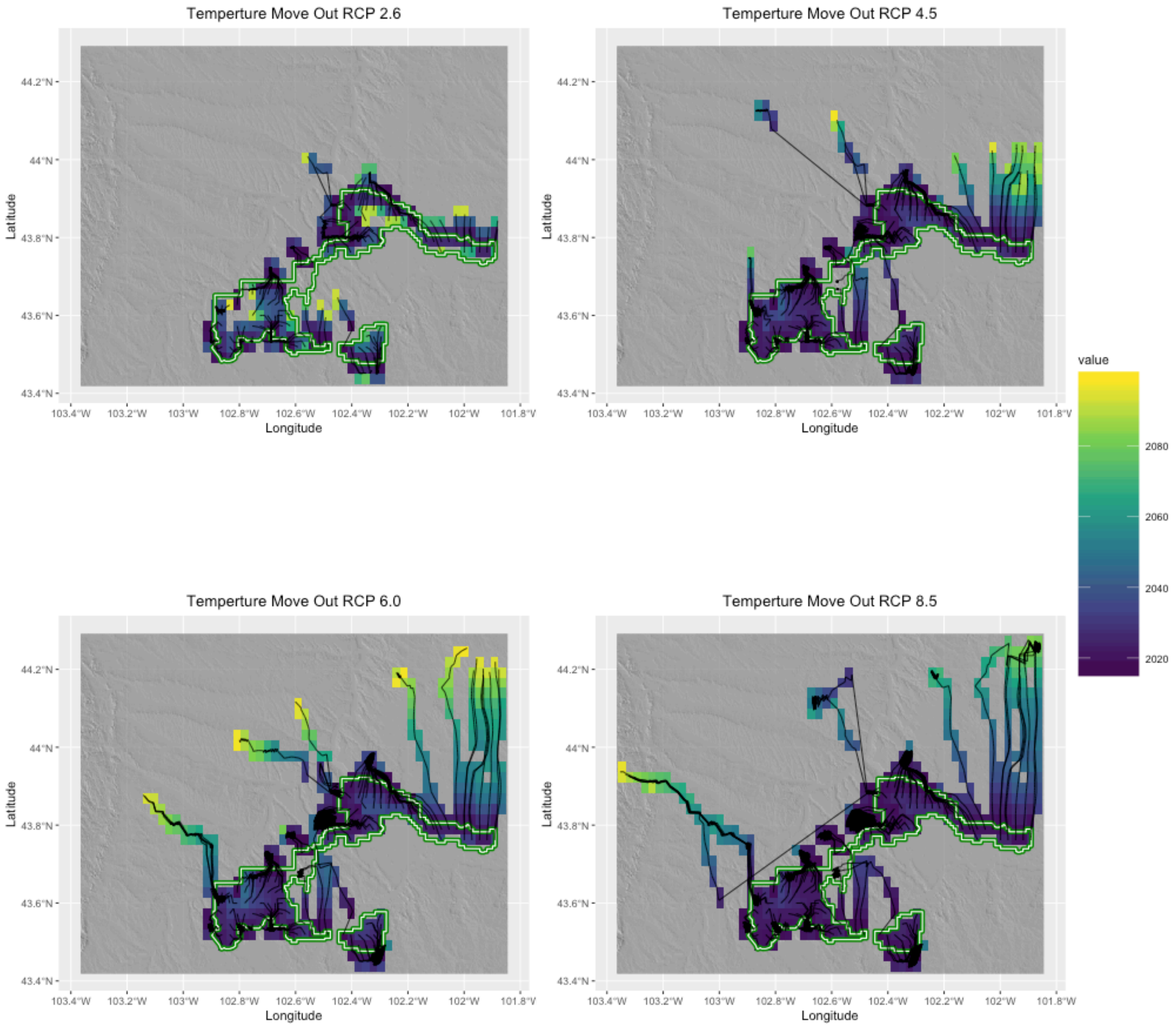

Figure 24 - Temperature move-out throw (same as Figure 11) for Badlands. Here, we see that almost all of the existing temperature space within the park leaves, crossing the park boundary either to converge upon local high elevations along the southern border of the park, or travelling longer distances towards the northwest.

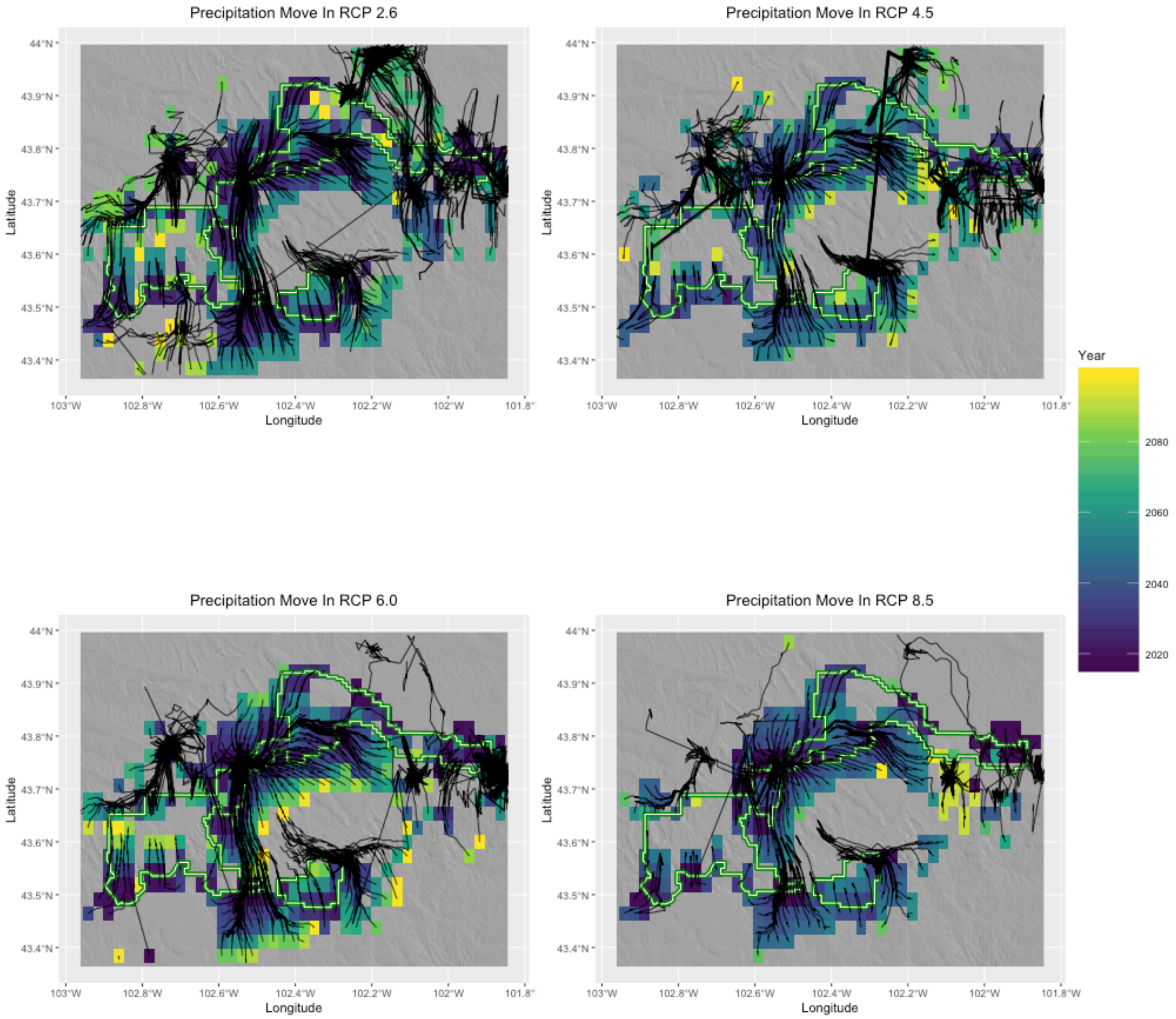

Figure 25 - Precipitation move-in fetch (same a Figure 12) for Badlands. Here we see a particularly striking example of convergence, as precipitation space crosses park boundaries from all directions to converge upon the highway 44 pass near Scenic, South Dakota.

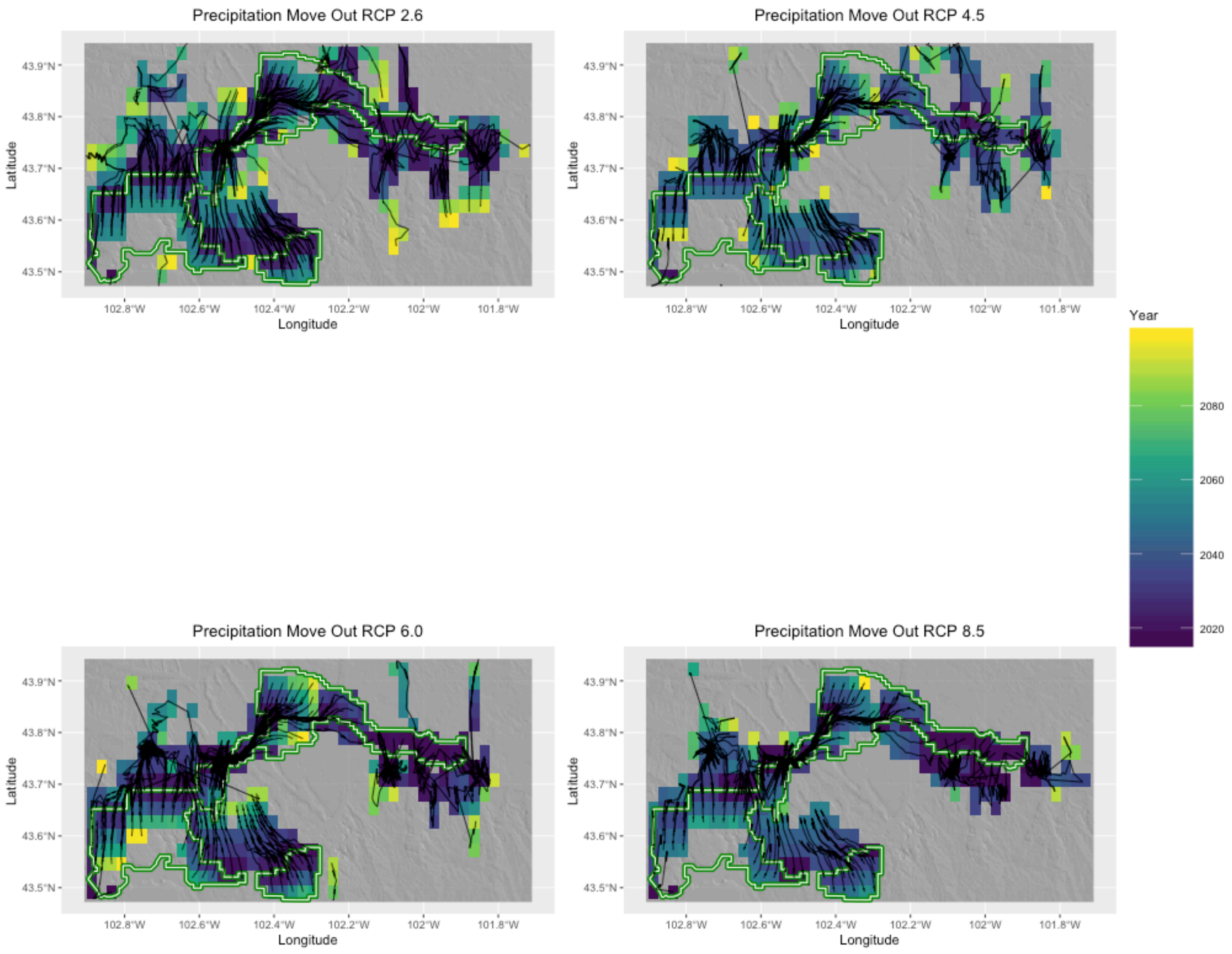

Figure 26 - Precipitation move-out throw (same as Figure 13) for Badlands. Much like we see in Figure 20, the precipitation space that is currently within the park largely moves to converge upon the Highway 44 pass near Scenic, South Dakota, while some locations also have precipitation trajectories that travel north, similar to the temperature throw in Figure 19.

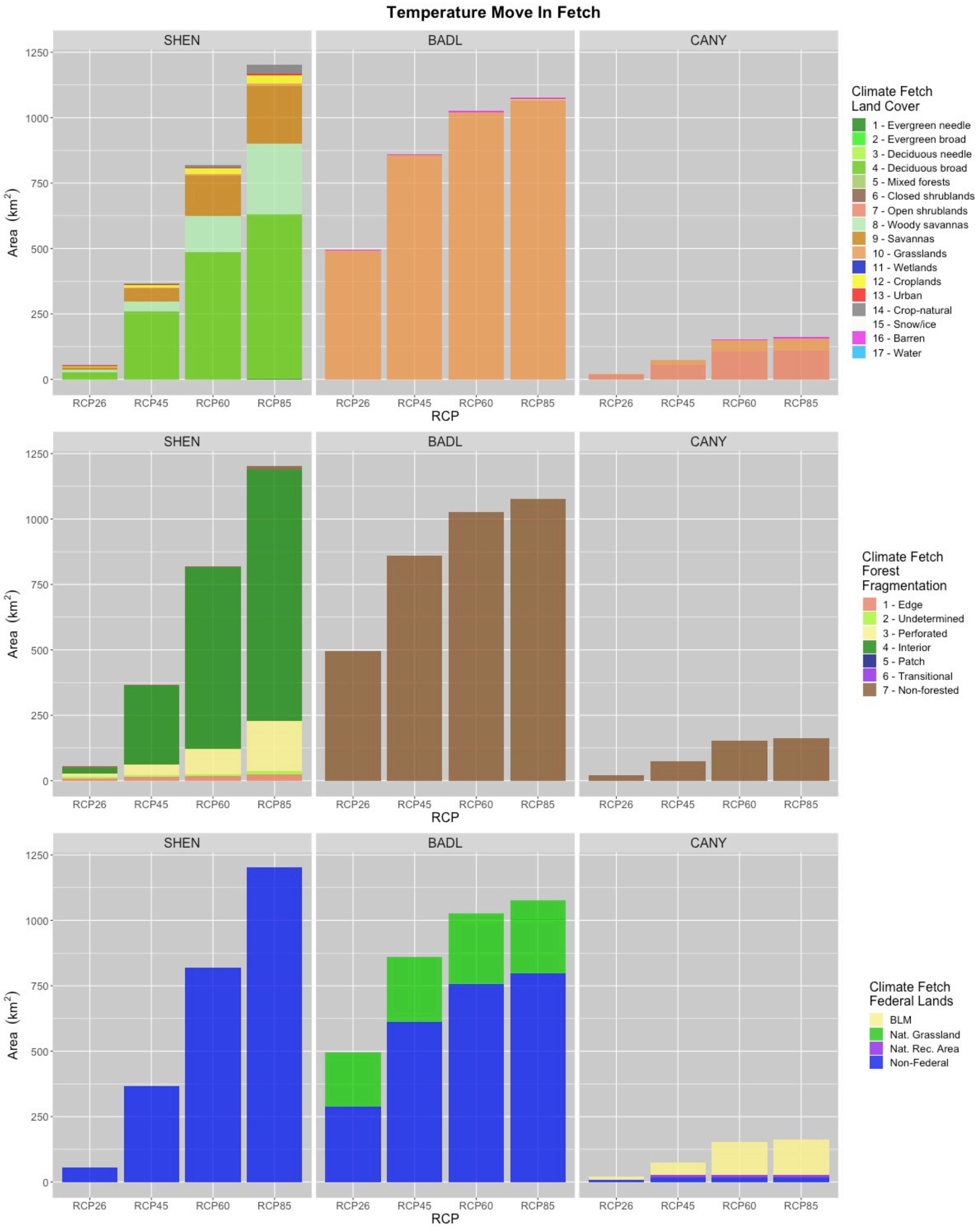

Figure 27 - Temperature move-in fetch land cover (top), forest fragmentation (middle), and land ownership (bottom) for focus parks. Note that Shenandoah has an appreciable fraction of temperature fetch coming from

disturbed areas, such as urban, crop, and crop-natural lands (top), as well as edge and perforated forests (middle) from non-federal lands (bottom). Badlands and Canyonlands have far lower land cover diversity in their temperature fetch lands, with a higher percentage of federally protected areas.

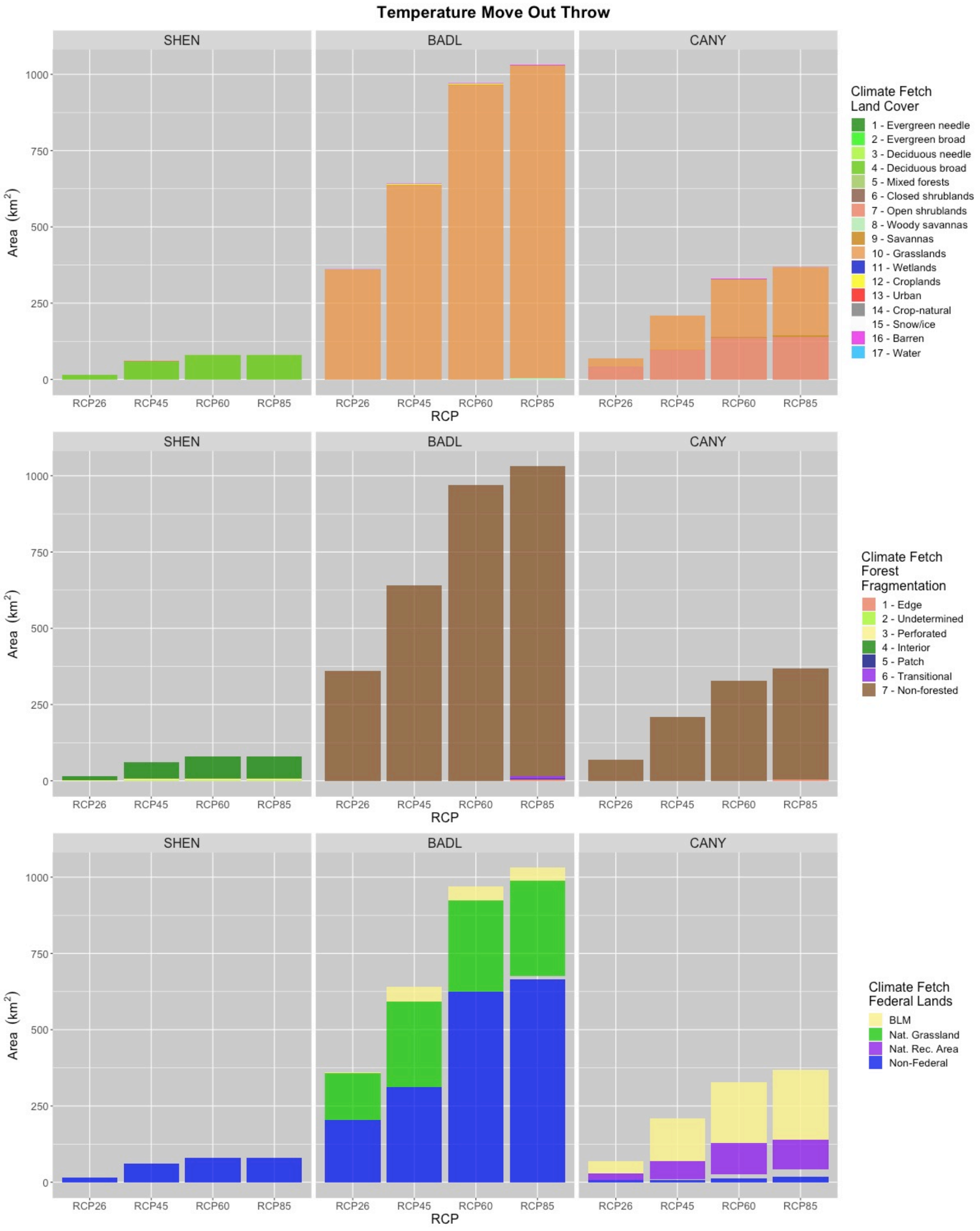

Figure 28 - Temperature move-out throw land cover (top), forest fragmentation (middle), and land ownership (bottom) for focus parks.

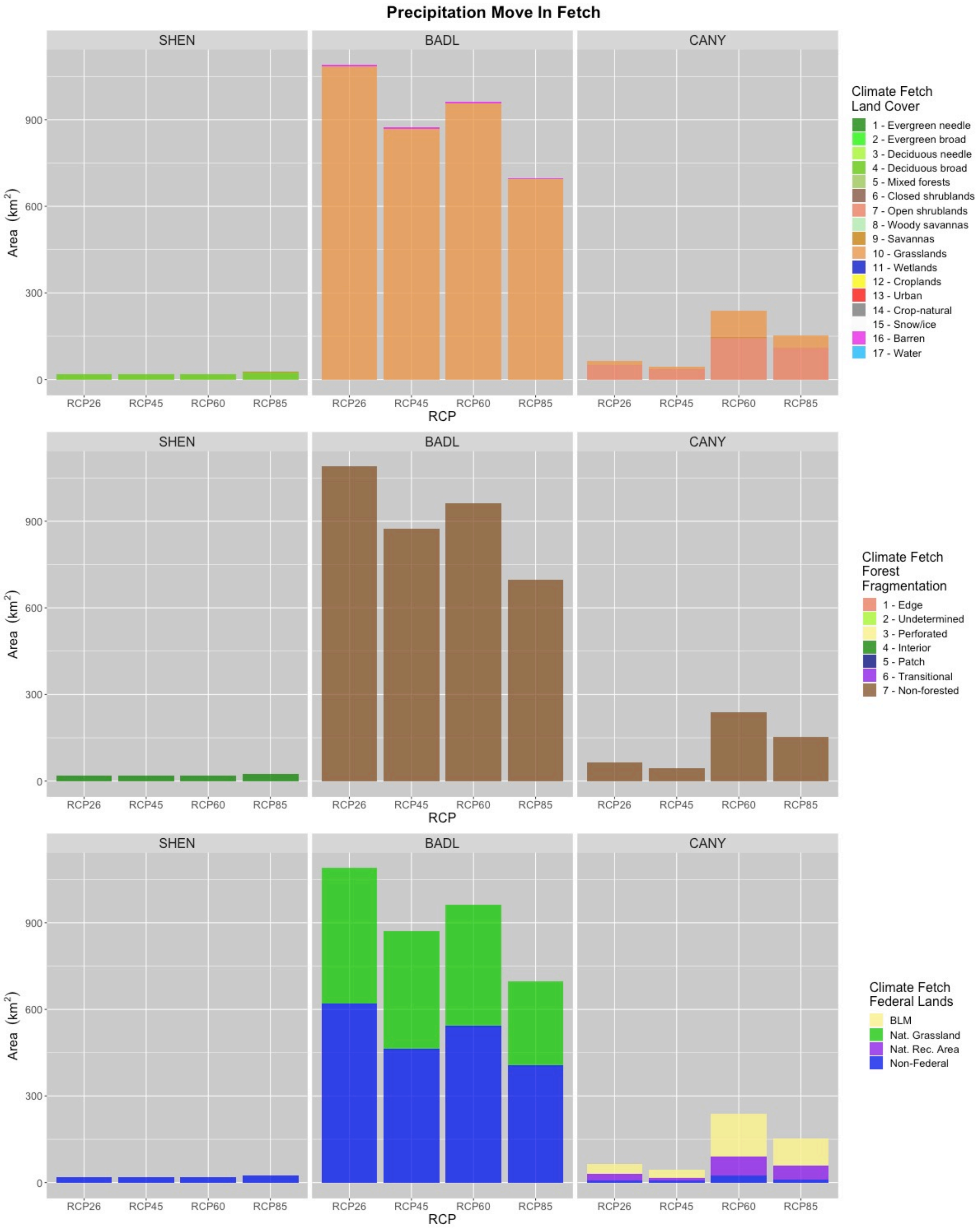

Figure 29 - Precipitation move-in fetch land cover (top), forest fragmentation (middle), and land ownership (bottom) for focus parks.

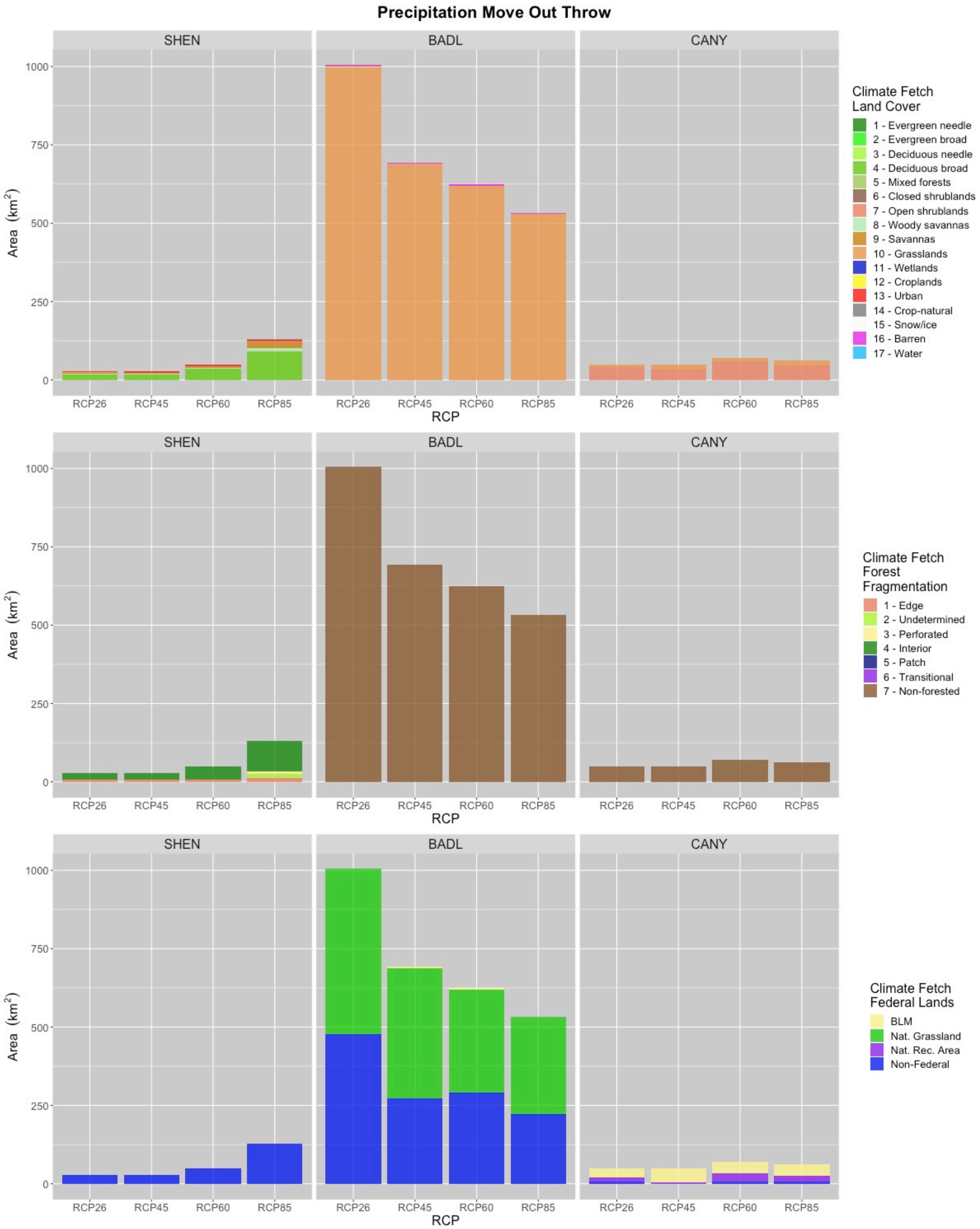

Figure 30 – Precipitation move-out throw land cover (top), forest fragmentation (middle), and land ownership (bottom) for focus parks.

Discussion

The results of our climate velocity analysis identify climate exposure to Shenandoah, Canyonlands, and Badlands National Parks across geographical and climate spaces**.** Our application of the climate trajectory method (Burrows et al., 2014) finds that topography dominated the spatial patterns of climate trajectory, with temperature isotherms moving uphill into (Shenandoah, Badlands) or out of (Canyonlands) these national parks. We find that, in topographically diverse parks, such as Shenandoah and Canyonlands, there is much greater movement of temperature than precipitation (Table 8). However, for the flatter Badlands National Park, both temperature and precipitation experience a nearly complete displacement with upwards of 93% and 87% of existing temperature and precipitation, respectively, moving out of the park, and >100% of the park's land area moving in (and often passing through) as temperature and precipitation fetch.

Our results identify the leading edge of potential climate-driven migration for species that are currently at the limit of their preferred climate niche for average annual air temperature and/or annual sum of precipitation. There is broad evidence that species migrate along latitudinal and altitudinal gradients in response to long-term climate change (Davis, 1983; Huntley and Webb, 1989). Considering that national parks of the conterminous USA are at the extreme ends of their historic climate ranges (Monahan and Fisichelli, 2014), and as air temperature and precipitation patterns change beyond historic extremes, it is likely that these changes will drive species migrations (Gonzalez et al., 2010; Holsinger et al., 2019). Many ecosystems have shown evidence of climate-driven migration and ecosystem changes within the past 30 years (Moyer-Horner et al., 2016; Pyke et al., 2016; Wolf et al., 2016), and by incorporating the climate trajectory method to investigate explicitly the geographical limits of species' migrations we can improve our estimates of potential migration pathways (Burrows et al., 2014; Brito-Morales et al., 2018). Still, depending on species' lifecycles and dispersal potential, migration response will have some duration of lag between the climate pressure and migration itself (Alexander et al., 2018), and major changes to the ecosystem such as a complete change in forest type or land cover often require a disturbance to catalyze such shifts (Dolan et al., 2017; Parks et al., 2019). Therefore, it is important for future research and management planning to understand this limitation and to carefully the factors that may contribute to lags in species' migration responses.

If a species is already at the limit of its temperature or moisture tolerance, and climate change brings increasingly inhospitable conditions, that species may respond by migrating in accordance with the climate velocity. Therefore, identifying the climate fetch area will be important for clarifying where species will be leaving, and the climate throw is the areas will highlight where species will be migrating towards. For the move-in analysis, the climate fetch is of interest because of the species that may move into the park, however the importance of those species depends on their nature. Some species are of interest because they are federally protected, and therefore, the park has a mandate through legislation such as the Endangered Species Act (ESA) to support those species to persist on their lands (United States Congress, 1973, 197). If such a species migrates naturally, that may require a legally mandated change to existing management strategy (e.g. the identification of critical habitat under the ESA) in order to support that species. Natural migration may be prohibitive for a variety of reasons, including physical and chemical barriers, competition from other species, inadequate corridors, and inhospitable climate conditions in the corridors linking the home and destination ranges (Renton et al., 2013). In these cases, assisted migration may be appropriate to introduce protected or desirable species into the park (Hoegh-Guldberg et al., 2008). However, if a species in the move-in fetch is not desirable to have in the park – such as non-native vegetation that may outcompete protected or sensitive native species, the park may decide to take action to prevent invasion by that species (Hansen et al., 2014). Many parks currently fight actively against such species invasions, and therefore, this analysis may aid land managers in identifying sections of their park boundary most at risk for species invasion. It might also spur further cooperation with the adjoining land's owners to prevent the spread of those species. Similarly, the move-out climate throw identifies areas to which species may migrate. If there are species that are driven into these areas due to climate pressure, collaboration with those neighboring lands may be important to maintain continuity of management actions for the preservation of protected species.

Considering the importance of the climate fetch and climate throw lands surrounding each park, an analysis of the conservation-related properties of those lands may provide insights into the potential complications that species may experience while undertaking a climate-driven migration into and/or out of a national park. A clear first step is to determine if those lands are already under federal control, and if so, what is their level of conservation management. Shenandoah has no lands in its climate fetch or climate throw that are under federal ownership. This may complicate cooperation strategies for mitigating the influx of unwanted species, especially from private lands where landowners may find that cost and time of aggressive noxious species management activities are prohibitively expensive. Conversely, Badlands and Canyonlands have move-in climate fetch lands that are primarily designated as National Grasslands and Bureau of Land Management (BLM) lands, respectively. Though these are not National Park Service properties, the BLM is a fellow Department of the Interior agency, and National Grasslands are managed by the United States Forest Service (USFS) in the Department of Agriculture, which similarly has a mandate to conserve national natural resources. In both cases, management collaborations may lead to continuity of management strategy for sensitive and protected species as they response to climate pressure with migration across park boundaries (Monahan and Theobald, 2018).

Shenandoah has large potential temperature fetch areas (Figure 15), especially in the higher-emissions RCPs. The majority of the park's area is affected by intrusion from outside lands, and we see that many of these outside areas move in and concentrate among the highest peaks within Shenandoah. Even many of the temperature move-out areas travel to nearby summits. However, Dobrowski and Parks (2016) have shown that climate velocity methods fail to identify the loss of climate space within mountainous terrain compared to their climate analogue approach, therefore, land managers should be especially concerned about climate space concentration among these summits. While there may be climate refugia that maintain small areas of viable climate space for sensitive species that prefer cooler conditions (Wershow and DeChaine, 2018), such upwards migrations may lead to increased interspecies competition and decreased plant/pollinator synchrony (Pyke et al., 2016), and those stresses combined with the overall loss of habitat area at higher elevations may be enough to drive some species to extinction without human assistance.

With projected climate change, each of our focus parks will be subjected to increases in air temperature similar to the transition from the Pleistocene to today's climate. The temperature trajectory patterns for Shenandoah suggest potential climate-driven migration uphill towards the mountain summits. There is evidence for such movement in the Appalachians as climate has changed since the last glacial maximum ~11,700 years ago (Butler et al., 2015). In many high-elevation areas of the Appalachian Mountains there are ecosystems and forest types that are the last traces of colder-climate forests that were previously widespread throughout the eastern USA (Davis, 1983). The temperature fetch and throw for Canyonlands tells an interesting story reminiscent of the human history in this area. With projected climate change, an increase in air temperatures leads to a movement up and out of the lower canyons – similar to the exodus that the Ancestral Puebloan and Fremont peoples experienced ~700 years ago (National Park Service, 2018a). While the specific drivers of the previous human exodus from Canyonlands remain unclear, our results provide additional evidence of the spatial patterns of climate space migration out of Canyonlands National Park, which supports theories about the human history within this region. Badlands National Park, which resides in the northern Great Plains, is in an area that is widely expected to experience rapid changes to its climate space

(NASA 2017), resulting in high climate velocities. One of the main implications of the climate velocity method is that large, flat areas that experience climate change often have very high climate velocities due to their small spatial gradients (Loarie et al., 2009). In Badlands, we see the largest spatial shifts in temperature and precipitation (Table 8), and the longest travel distances into and out of the park. While this will certainly present migration challenges for any species that has a short dispersal distance, many of the species of that region are well adapted for long migrations, such as deer, bison, migratory birds, and some plants (Alexander et al., 2018). While this may promote long-distance migration across this broad, and fairly homogeneous, landscape, other factors may limit successful responses to climate change. In particular, human disturbances such as highways and agriculture may prevent species movement, and vehicle-wildlife collisions present a substantial risk of fatality to animals travelling across these impediments (FHWA, 2008). Seeing as humans have produced these impediments relatively quickly (in comparison with previous long-term changes in climate), and that predicted climate change will incur rapid shifts in climate across time and space, such human disturbances may present novel challenges for species as they migrate in response to climate change.

The elimination of particular climate niches may have important implications for climate-sensitive species living within those climates, as they may be forced to retreat to refugia within topographically complex mountain habitats (Mclaughlin et al., 2014) despite the higher cost of migration to mountainous regions due to high spatial heterogeneity (Dobrowski and Parks, 2016). If the desired conditions are unavailable due to geographic, competitive, or climatic restrictions, sensitive species may face extinction (Beever et al., 2016). For example, the Shenandoah Salamander (*Plethodon shenandoah*) is endemic to Shenandoah National Park and is listed as a federally endangered species by the US Fish and Wildlife Service (IUCN 2004). This species prefers north aspects on the highest mountains in the range, and will very likely face continued pressure from competitors such as the native Eastern Red-backed Salamander (*P. cinereus*), which has excluded *P. shenandoah* from forested habitat in lower elevations within the park. This species is already a high priority for Shenandoah National Park (Grant et al., 2014), and our findings contribute further evidence that this species faces increasing risk of extinction due to climate change. Failure to retain viable populations of *P. shenandoah* may require intervention, such as captive breeding or assisted migration (Hoegh-Guldberg et al., 2008).

Evidence shows that species are shifting their ranges in accordance with climate velocities, but their ability to keep pace is limited and highly dependent on a range of biological, ecological and climatic factors (Dobrowski et al., 2013; Sittaro et al., 2017). Forecasting the pace and direction of climate change is vital for ensuring future conservation success and climate velocity provides a very useful methodology for doing so (Tingley et al., 2014).

Applications for management

This is the first paper to identify specific patterns of climate variable movement into and out of protected areas at the 3km resolution, leading to potentially novel insights for land managers. Public officials throughout the National Park Service and other federal agencies are interested in understanding the risks that their lands face due to climate change. With unprecedented climate conditions already present in many protected areas (Monahan and Fisichelli, 2014), native species will be forced to acclimate, migrate, or become extinct without management intervention. Recent evidence suggests that native species retreat into mountain refugia, possibly due to a loss of competitiveness at the edges of their established ranges (Muhamed et al., 2013; Mclaughlin et al., 2014). Additionally, invasive species (native species from nearby regions, or introduced from other continents) are known to sometimes 'win' over stressed native species as a result of climate change (Wolf et al., 2016). The negative effects of climate change cannot be adequately managed or anticipated without including species responses to these changes within strategic frameworks (Pecl et al., 2017). Our findings identify the specific locations that will be contributing climate, and therefore potentially species, to national parks throughout this next century.

Climate velocity (and its velocity counterparts) can also be explicitly used in conservation area and corridor planning to determine which direction the majority of species are likely to move (Tingley et al., 2014). Climate velocity research also has the potential to identify protected areas that can function as stepping stones for species that colonize as they move between patches of intact natural habitat (Beale et al., 2013). Considering these factors, future efforts may seek to protect conservation areas by implementing policies that allow the conservation area boundaries to move along with the resources under protection. Mandates such as the Endangered Species Act may lead to a *del-facto* implementation of such conservation areas, as endangered species require conservation actions as they move into previously unprotected lands. The wide range of future climate scenarios calls for using all IPCC RCPs to determine the magnitude of projected velocities and to identify the most strategic conservation site networks (Bagchi et al., 2013). Given the existing organizational structure of the National Park Service's Inventory and Monitoring Networks, this type of analysis could aid the Service in determining high-risk species and opportunities for collaboration within and beyond their own networks (Monahan and Theobald, 2018).

Limitations

There are numerous limitations associated with our methods. As noted in the introduction, the two different climate movement methods used here, climate velocity and distance-based climate trajectory, result in different information, and should be used to interpret different aspects of climate variable movement. Uncertainty surrounding the details of changing climates, particularly at high spatial resolutions, contributes uncertainty to our products. Additionally, species do not always follow climate directly, as there are various other physical, chemical, and other barriers that may prevent free and immediate species movement in response to climate (Burrows et al., 2014). Still, by identifying the movement of fundamentally important climate variables, we can shed new light on potential migration pathways that cross conservation area boundaries into the next century.

Conclusions

Climate change is driving changes in species' distributions and demographics throughout the globe. Protected areas serve as bastions of safety for many populations and often harbor high levels of biodiversity. Our work identifies future climate trajectories into and out of Shenandoah, Canyonlands, and Badlands National Parks. Our methods may be reproduced and applied to additional protected areas such as other management units in the National Park System given the availability of gridded climate information at the appropriate spatial and temporal resolutions. Additionally, elaborating upon this work with additional climate variables would hone the robustness of this approach. As climates continue to change and species are subjected to greater pressures through habitat loss, habitat fragmentation, competition, and climate concentration, assuring the long-term suitability of topographically diverse protected areas will be critical for conservation efforts.

Chapter 5: Conclusions

Here, three distinct research products are presented that explore the theme of ecological velocity. The overarching results are that spatial gradients in climate (primarily topography) drive the direction and spatial patterns of climate velocity across multiple time scales – while the total climate displacement (i.e., the distance of movement along the climate velocity pathway) is determined by seasonal variation at shorter time scales, and by climate scenario at longer time scales. National parks of the USA are designated by congress for a number of reasons, but one common theme is that they protect lands with many types of diversity, including ecological and topographical diversity. This topographical diversity, along with seasonal and decadal scale climate change, drives characteristic patterns of climate velocity. For the studies that had observations of ecological activity (Chapters 2 and 3), the results show that the ecosystems respond in similar patterns to the climate velocity driving those changes. Taken together, there is considerable evidence that national parks of the USA are likely to experience substantial changes to their climates that will result in ecological velocities that will reshape the phenology and distribution of the current, and future, resident species.

These big picture findings are supported by the many incremental results that we found throughout this dissertation. Chapter 2 investigates the spatiotemporal relationships between snowmelt timing and vegetation phenology within the mountainous and relatively high-elevation Crater Lake National Park. This found that snowmelt timing controls spring greenup, but has little to no influence on later season phenology. These results demonstrate that, while snowmelt timing is an important factor for spring phenology, further research should focus on the interactions between snow and the early growing season. Chapter three found that the speed and direction of snowmelt velocity are correlated with the speed and direction of green wave velocity under certain circumstances. In particular, this relationship is strongest in high-gradient regions (i.e., mountainous areas with steep hillsides). However, there is little to no relationship between snowmelt velocity and green wave velocity in many environments, particularly those with flatter topography. Still, the results show that the spatial patterns of both snowmelt and green wave velocity predominantly drive these velocities upslope towards mountain peaks, and generally towards the North Pole. These elevational and latitudinal gradients in vegetation responses to climate are seen in both seasonal phenology, and long-term climate change, which drives our next research objective. Chapter 4 extends upon the finding in Chapter 3 and looks towards the future to investigate the spatial patterns of climate movement relative to the national parks of the USA. This found similar patterns of the climate velocity of air temperature moving uphill, however the spatial patterns of precipitation velocity varied highly. These results indicate that climate niches (i.e. the combination of climate variables at a given location) are likely to move and change into the future, with some regions experiencing ‘niche splitting’ where temperatures go one direction, and precipitation goes another, leading to novel climate space within some national parks. Furthermore, there is substantial evidence of climate variables crossing park boundaries, suggesting possible species’ migrations into and out of national parks in the decades to come. Finally, this chapter highlighted the specific corridors of climate (and potentially, species') movement across park boundaries, which emphasize the management implications of our work.

This dissertation explored multiple time scales at a moderate resolution, which was specifically designed to maximize the potential for management applications using our results. Still, there are barriers to management consideration of this work, and to that end the authors suggest the following as next steps. First, future work should identify the various stakeholders who are interested in these facets of natural lands. Wildlife biologists, ecologists, botanists, rangeland agriculture practitioners, land managers, and others may all have different interests in this work, and elaboration or 'translation' into their lexicon will benefit information retention and adoption. Second, the multiple time scales of analysis in this dissertation will be of interest to various parties, and therefore identifying the relevant temporal scales for stakeholders will further benefit information transfer. Third, a focus on the most relevant and management-practical aspects of this work will improve information transfer. For example, National Park Service managers may be interested in the migration corridors identified in Chapter 4, however the resolution of this analysis may be too much detail for some, and therefore a practical summary such as "the southeastern boundary of Shenandoah National Park has the highest potential for inbound species migration" could benefit land managers as they devise high-level budgets and goal-setting for climate change mitigation strategies.

The authors also suggest improvements and extensions to these analytical methods. For Chapter 2, repeating this analysis with the latest several years of data will extend the data record and improve the statistical analysis by providing additional degrees of freedom. Additionally, the input phenology product has been updated from Version 5 to Version 6, which may substantially change some of the results. Furthermore, analyzing the lag time between snowmelt and phenology green-up will help to constrain the important ‘lag’ feature of ecological velocity. Chapter 3 will be improved by including actual animal migration data, as gathered by GPS collars or other means, to compare the calculated green wave velocity with observed animal movements to understand better the interactions among snowmelt, green wave, and animal migration velocities. Chapter 4 will be improved by extending this analysis to all national parks of the conterminous USA, and perhaps to repeat this analysis for parks of Alaska (given sufficiently high-resolution climate projections, which was a limiting factor in our preliminary analysis of that state). Additionally, finding new way to summarize climate velocities by variable, RCP, and park may distil these results into an easily understandable metric for non-scientists and high-level park managers, rather than bogging them down with the high-resolution details. Finally, high spatial and temporal gradients occasionally lead to extremely high (and likely anomalous) velocities (as seen by the straight lines in Figure 25 RCP 4.5). This effect was particularly worrisome using 1km resolution climate inputs, which lead to our decision to aggregate to 3km (which produced more reasonable results). This should be improved further by implementing a reasonable velocity threshold, and subsequently sensitivity testing the results with and without this threshold.

This research has benefitted greatly from its focus on management-relevant questions and results. While it does address basic science questions, the desire for management-relevance supported the motivation for this work, and advised the tactics for each objective. In particular, this work focuses on the landscape scale using existing moderate resolution observations (MODIS) and high-resolution climate projections (DCP-30). In particular, our results from Chapter 4 are among the first ecology-relevant climate velocity maps, offering a degree of novelty along with their scientific and management relevance. This also benefits land managers, who have long sought to tie high-level climate change predictions (such as global increases in air temperature) to the relevant impacts on their lands. By working in both the climate velocity and landscape management literatures, this work finds synergies that advance both fields simultaneously.

Ecological velocity is a useful framework for conceptualizing changes on the landscape, but some ecosystem responses require a nuanced application of this concept. For example, biogeochemical cycling of elements such as carbon occur on several of these spatial and temporal scales simultaneously (Moorcroft et al., 2001). Whereas some environmental factors may increase the amount of carbon sequestration in the short term (increased temperature and precipitation resulting in increased photosynthesis and net primary productivity) (Birdsey, 1992), these same factors may result in decreased carbon sequestration in the middle and long terms (due to increased disturbances such as hurricanes and wildfires, or a biome shift to a lower density ecosystem i.e., desertification (Dolan et al., 2017)). These dynamics may be further complicated by human activity on the landscape, and other factors as well, challenging the application of ecological velocity to complex phenomena. The same can be said for predicting species distributions using climate velocity; there are many complicating factors. This work has mapped climate velocities, which is a first step of a first order control - temperature and precipitation are known to be a dominant factor controlling species distributions and biogeochemical cycling. These maps, particularly those from Chapter 4, should be interpreted as the prediction of climate velocity, with lags and other factors that will influence further the resulting ecological velocity. Future research should seek to incorporate more complex models to forecast these movements of complex process across the landscape, such as Flanagan et al. (2019) who use an advanced mechanistic model to project biome migrations and the resulting carbon balance in response to climate change, albeit as a coarse resolution. By leveraging today's high resolution ecosystem models (Hurtt et al., 2019), and combining ongoing advances in lateral movement of climate forces and species, there are good opportunities to improve our understanding of the dynamics between today's and a modeled future climate and environmental state.

Finally, there is practically no limit to the number of variables, study sites, and scales that can be used for ecological velocity analysis. These results show that analysis at a moderate resolution (~1km) yields intuitive and management-practical results, though there are also benefits to working at higher and lower resolutions. In particular, computational demand was a challenge for this analysis in both Chapters 3 and 4, however as technologies improve, these limitations will be reduced, opening new doors for novel analysis and deeper insights into these conservation problems.

As technology continues to accelerate the exploitation of natural resources around the world, our global community faces challenges both known and unforeseen. While we as a community are unable to predict the future with certainty, this work builds upon the existing literature to show that potential changes in climate will drive characteristic changes in ecosystems at multiple temporal and spatial scales. These results support a continued allegiance between researchers and land managers as mutually supportive and synergistic professions, as these results here further validate the mutualism between the two. This work offers a step towards sustained conservation, supporting healthy ecosystems and enjoyment for current and future visitors to managed lands.

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