

**Beyond snow leopards:
Leveraging remote sensing datasets to assess alpine
phenology**

**by
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Abstract

Natural ecosystems are increasingly challenged, with more than half significantly degraded since the 1950s due to unsustainable land use, resource extraction, and human-induced disasters. Climate change further exacerbates these pressures on ecological communities, especially in sensitive alpine ecosystems. Detecting ecological change, whether temporary or permanent, requires long-term, multi-modal, and multi-scale datasets, which are particularly scarce in data-poor areas. Focusing on the under-studied alpine landscapes of Kyrgyzstan, where elusive snow leopards (*Panthera uncia*) roam, I examine the potential of remote sensing methods and leveraging wildlife datasets beyond their target use to support ecosystem monitoring.

In Chapter 2, I use satellite imagery to assess landscape-level changes over the past 20 years in areas with various anthropogenic pressures, finding that about 85% of the landscape has remained unchanged. Elevation and northness were key drivers of land cover distribution. While grassland extent contracted across all study areas, bare ground and forest areas expanded, with the least change observed in protected areas. Elevation is a useful proxy for climate-driven change, and intermediate elevations, which showed the most change in land cover, should be prioritized as zones for future monitoring.

Chapter 3 investigates the use of motion-triggered images, originally collected for snow leopard monitoring, to track plant phenology. I show that motion-triggered images can be used to detect the timing of key plant growth periods and produce more accurate peak growth estimates than bi-weekly Landsat data. However, more data are needed to reliably detect seasonal start and end dates and long-term shifts caused by climate change.

Chapter 4 provides the first phenological assessment of the gray marmot (*Baibacina baibacina*), an important prey of snow leopard, showing they are active for only two to three months, which is shorter than typical marmot activities reported in other regions. I also demonstrate the potential to link marmot activity with vegetation phenology using a single camera trap dataset.

Together, these chapters emphasize the value of leveraging existing datasets beyond their original scope to effectively and efficiently fill critical knowledge gaps in ecological monitoring, especially in remote and under-studied areas.

Keywords: ecosystem monitoring; alpine ecosystems; climate change; phenology; camera traps; remote sensing

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Table of Contents

Declaration of Committee	ii
Abstract.....	iii
Acknowledgements	v
Table of Contents.....	xii
List of Tables.....	xv
List of Figures.....	xvi
Entering the snow leopard realm.....	xx
Chapter 1. General introduction	1
1.1. Nature under threat	1
1.2. We are in an era of data abundance.....	2
1.3. Ecosystem monitoring in data-poor areas.....	3
1.4. Alpine rangelands of Kyrgyzstan	4
1.5. Project origin and chapters	6
Chapter 2. Multidecadal changes in land cover across a disturbance gradient in mountain grasslands of Kyrgyzstan	8
2.1. Introduction.....	8
2.2. Material and Methods	12
2.2.1. Study area.....	12
Protected area and mild disturbances: Naryn State Reserve	13
Moderate disturbances: Eki-Naryn	14
High disturbances: At-Bashy	14
2.2.2. Geospatial data	15
ESA land cover map	15
Landsat data source	15
Topographic variables	16
2.2.3. Data processing	17
Plot selection	17
Land Cover Classification.....	17
2.2.4. Analyses	19
The role of topography in current land cover distribution	19
Detection of land cover change	20
2.3. Results	22
2.3.1. Land cover classification	22
Determinants of current land cover distribution.....	22
2.3.2. Detection and direction of land cover change over time	23
How much has changed overall?	23
Land cover change in relation to elevation.....	24
Land cover change in relation to disturbance.....	25
Interacting factors determining trends in land cover change.....	26
2.4. Discussion	29
Role of topography in current land cover distribution	29
Magnitude of land cover changes over two decades	30

Direction of land cover changes over two decades.....	31
Strengths and limitations of our approach.....	32
2.5. Conclusion.....	33
Chapter 3. Wildlife cameras for plants: using motion-triggered wildlife data to monitor plant phenology.....	35
3.1. Introduction.....	35
3.2. Material and Methods	38
3.2.1. Study area.....	38
3.2.2. Geospatial data	39
3.2.3. Landsat data source.....	44
3.2.4. Generate random points.....	44
3.2.5. Quantifying Vegetation Dynamics	45
3.3. Results	48
3.3.1. Quantifying Vegetation Dynamics	48
Estimated timing of growing season phenophases.....	48
3.3.2. Comparison with Landsat imagery	52
Signal detection of Landsat GCC and NDVI	52
Landsat NDVI trends	52
Comparison of Landsat NDVI and camera trap GCC trends	54
3.4. Discussion	55
Chapter 4. Dormir comme une marmotte: tracking activity patterns of the gray marmot (<i>Marmota baibacina</i>) in Kyrgyzstan using camera traps	59
4.1. Introduction.....	59
4.2. Material and Methods	61
4.2.1. Study area.....	61
4.2.2. Camera traps	63
4.2.3. Detecting marmot phenology.....	66
4.2.4. Analyses	67
4.2.5. Linking marmot activity patterns and plant phenology	68
4.3. Results	69
4.3.1. Identifying marmot activity patterns	69
Observed timing of marmot activity patterns	69
Estimating timing of marmot activity patterns.....	70
4.3.2. Simultaneous monitoring of marmot activity patterns and plant phenology	73
Comparison at a single site (Site 9)	73
Comparison across four ‘meadow’ sites.....	74
4.4. Discussion	75
Chapter 5. General Discussion.....	79
5.1. From pixels to phenophases.....	79
5.2. Camera traps as untapped data troves for multi-trophic monitoring	85
5.3. Metadata standards, data accessibility and semi-automated data extraction	87
5.4. Future directions (or what you might get if you hired me for a post-doc)	89

References.....	91
Appendix A. Supporting Materials for Chapter 2	122
Appendix B Supporting Materials for Chapter 3	136
Appendix C Supporting Materials for Chapter 4	139

List of Tables

Table 2.1	Total predicted percentages of browning and greening across areas with various degrees of disturbance (area), the five 5-year time-periods (year), and elevation bands (elevation). The significance of the difference is reported through p-values. Results for each variable are marginalized across levels of the other variable (e.g., the proportion of cells undergoing browning in the core is averaged across years and elevations). To improve readability, we colored cells with percentages significantly higher than their counterpart. Cells with significantly higher browning are colored in red, and those with significantly higher greening are colored in yellow. Cells included percentages that are not significantly different are left blank.	27
Table 3.1.	Summary of camera trap deployments across study sites and years in the Naryn State Reserve, Kyrgyzstan. For each study site and year, the table reports the number of active cameras, the number of cameras in 'meadow' and 'steppe' sites, the total number of images recorded per year and the number of images generated from filtering images the closest to noon used in the phenological analysis. * Removed sites due to insufficient temporal coverage.	42
Table 3.2	Model predictions for the timing of phenophases (start, peak and end; see Methods for definitions) from camera traps deployed in the Naryn State Reserve, Kyrgyzstan, and from Landsat GCC and NDVI values extracted at each randomly selected pixels across the Naryn State Reserve. "All meadow" refers to all meadow sites pooled (n = 4); "Site 9" refers to a single meadow site with the most extensive temporal coverage across years; "Random points" refers to the Landsat data across the Naryn State Reserve. The duration of the growing season is reported in number of days. The timing of phenophases is reported as day of the year (DOY) with associated standard deviation.	50
Table 4.1	Summary of camera trap deployments from 2017 to 2021 in the Naryn State Reserve, Kyrgyzstan. In 2020 – 2022, two cameras were simultaneously deployed at one of the sites. Some sites were removed due to issues with SD card reformatting during the winter and sensor failures. Independent detections represent each marmot detection within 30-minutes of each other.	66
Table 4.2	Summary of camera trap deployments across four 'meadow' sites from 2017 to 2021 in the Naryn State Reserve, Kyrgyzstan. The number of daily green chromatic coordinates (GCC) values collected across the three sites are reported for each given year. The data gap in 2020 is due to the COVID-19 pandemic and the inability to check cameras and change batteries.	69
Table 4.3	Annual first and last days on which gray marmots in the Naryn State Reserve, Kyrgyzstan, were detected across all cameras with the Julian date and reported Day of Year (DOY). The dates in bold coincide with the final set of images received from OSI-Panthera for Site 9 in 2022. Thus, these final dates do not represent the last detection of marmots for that given year. To note that 2020 was a leap year.	69

List of Figures

Figure 2.1	(a) Location of Kyrgyzstan (red) in Middle Asia. (b) The study areas in Kyrgyzstan's Naryn oblast (red) include the Naryn State Reserve, Eki-Naryn Area and At-Bashy areas.	12
Figure 2.2	Location of the core and buffer zones of the Naryn State Reserve.	13
Figure 2.3	(a) Relative importance, expressed as gain, with a higher gain representing greater relative importance of the variable, of five terrain features in explaining the distribution of each land cover class after 1,000 boosted regression tree models. (b) Explanatory variables include A - eastness, B - elevation, C - northness, D - ruggedness (RRI) and E - slope (in degrees).	23
Figure 2.4.	Proportional differences in cover of forests, bare/sparse vegetation and grasslands across elevation bands between 2001 and 2021. The proportion of changed land cover was calculated using the total count of pixels for each land cover class in each elevation band for 2001 and 2021. The difference in number of pixels between 2001 and 2021 was used to determine the area of change. Areal change for each land cover and study area was then divided by the total number of pixels in each band ($n_{band1} = 9370$, $n_{band2} = 15769$, $n_{band3} = 18331$, $n_{band4} = 11808$, $n_{band5} = 1531$) and converted to percentages. The elevation bands include the elevation ranges across study areas and are organized from the lowest (1) to the highest (5). Positive values indicate increases in area over the study period.	25
Figure 2.5	Change in spatial coverage of forested, barren and grassland areas between 2001 and 2021 in each study area. The proportion of changed land cover was calculated using the total count of pixels for each land cover class in each study area for 2001 and 2021. The area of change for each land cover and study area was then divided by the total number of pixels in each study area ($n_{core} = 7997$, $n_{buffer} = 14647$, $n_{eki-naryn} = 23118$, $n_{at_bashy} = 23146$) and converted to hectares.	26
Figure 2.6	Adjusted mean predicted proportions of pixels that transitioned from grassland to barren (browning) and barren to grassland (greening). The transition types are reported in (a) each elevation band at each given time period, (b) each elevation band in each area, and (c) each study area at each given time period. The study areas are ordered along a gradient of anthropogenic pressures, with the least disturbed area on the left (core) to the most disturbed area on the right (At-Bashy). Points represent estimated marginal means based on the model, and error bars represent 95% confidence intervals. Linear regression lines are plotted to better visualize trends.	28
Figure 3.1	(a) Location of Kyrgyzstan (red) in Central Asia. (b) The study area in Kyrgyzstan's Naryn Oblast (red) including the Naryn State Reserve. (c) The location of the core and buffer zones within the Naryn State Reserve.	39
Figure 3.2.	Location of camera traps between 2016 and 2023 within the Naryn State Reserve boundaries (black polygon), Kyrgyzstan. Each location is classified based on the vegetation features, with sites dominated by	

continuous cover of grass-like species classified as ‘meadow’ (green) and sites with exposed bare ground and discontinuous, short, vegetation cover as ‘steppe’ (tan). The size of each circle indicates the number of days recorded at each site, with larger circles indicative of higher sampling effort (see Table 1 for sample sizes). The ‘meadow’ site with the camera facing a boulder, as presented on the left image example, was characterized as a ‘meadow’ based on the type of vegetation observed on the various camera trap field of views throughout the years and other photos from the site from OSI-Panthera. While vegetation is minimal in this field of view, vegetation growth was obvious throughout the years. .41

Figure 3.3	Examples of habitat features targeted by camera traps in the Naryn State Reserve, Kyrgyzstan: (a) open field of view, (b) marking meadow site and (c) steppe marking/ridgeline site. Examples of drawn regions of interest (ROIs) are included as red polygons in each image. The examples also showcase the difference in images captured by Browning (a) and Bushnell models (b,c). Several regions of interest to sample were drawn for areas with discontinued, close to the ground, vegetation cover (c)....42
Figure 3.4	Daily sampling effort across sites and years, presented as the number of days per year the cameras deployed at each site in the Naryn State Reserve, Kyrgyzstan, were triggered. Each row corresponds to a study site characterized as ‘meadow’ (M) or ‘steppe’ (S). Blue shaded areas indicate winter periods (31 October to 1 April), to help visualize sampling efforts during the growing season. The number of days with detections at each site per year is given alongside the corresponding row to indicate the sampling effort. Site 6 (M) was active for 13 days in 2018 and therefore removed from further analyses.....43
Figure 3.5	Predicted timings of phenophases across the four, pooled meadow sites (shaded rows) and a single meadow site (Site 9; unshaded rows) in the Naryn State Reserve, Kyrgyzstan, with their associated predicted distributions from 2016 to 2023 for the four meadow sites, and 2017-2021 for the single meadow site. The daily model predictions of GCC values for each day of available data within each dataset are represented by grey points within the rows. Coloured error bars and points indicate the start (25 th percentile; green), peak (blue), and end (75 th percentile; red) of the growing season and their associated standard deviations. Annual sample sizes are reported in Appendix B, Table B1.....49
Figure 3.6	Annual variation in the predicted timings of the growing season using Landsat NDVI across the Naryn State Reserve (dots), the four meadow sites (squares), and Site 9 (triangles).53
Figure 3.7	Comparison of predicted annual timings of the main phenophases associated with the growing season at meadow sites in the Naryn State Reserve, Kyrgyzstan, between 2016 and 2023 for both NDVI (unshaded rows, bi-weekly samples) extracted from Landsat imagery and GCC (shaded rows, random daily samples) from motion-triggered images by camera traps at the same locations. We report the day of the year (DOY) for the start (25 th percentile - green), peak (red) and end (75 th percentile - red) of the growing season with their associated 95% confidence intervals.54

Figure 4.1	(a) Location of Kyrgyzstan (red) in Middle Asia. (b) The study area in Kyrgyzstan's Naryn Oblast (red) including the Naryn State Reserve. (c) The location of the core and buffer zones within the Naryn State Reserve.	63
Figure 4.2	Location of the 18 sites at which camera traps were deployed between 2017 and 2021 within the Naryn State Reserve boundaries (black polygon), Kyrgyzstan. Each location is colour-coded based on its elevation. The size of each circle indicates the number of days recorded at each site, with larger circles indicative of higher sampling effort than smaller circles. Examples of habitat where cameras were deployed: (a) snow leopard marking sites on ridgelines, (b) open field views, (c) snow leopard marking sites at lower elevations and (d) sheltered 'cave' areas. The red circle indicates the location of a 'meadow' site, Site 9, used in a case study in section 4.2.3, which is also the site at which photo (c) was taken. The black circles around two meadow locations indicate the sites used to compare marmot and plant phenology as presented in section 4.2.3.....	65
Figure 4.3	Predicted timings of gray marmot phenology in the Naryn State Reserve, Kyrgyzstan, across all camera trap locations from 2017 to 2021. The marmot detections for each day of available data within each dataset are represented by points to showcase the annual data distribution. Points and horizontal error bars indicate the start (25th percentile; green), peak (blue), and end (75th percentile; red) of the marmot phenology and their associated standard deviations.	71
Figure 4.4	Predicted timings of marmot activity in the Naryn State Reserve, Kyrgyzstan, based on marmot detections collected by camera trapping between 2017 and 2021 at Site 9. This figure uses the same formatting at Figure 4 to facilitate comparisons.....	72
Figure 4.5	Comparison of estimated timings of the growing season (black lines and upper sets of coloured points and horizontal standard error bars for each year) and marmot activity patterns (lower set of coloured points and horizontal standard error bars for each year) at Site 9 in the Naryn State Reserve, Kyrgyzstan, between 2017 and 2021. The daily model predictions of greenness values (Green Chromatic Coordinates – GCC) and marmot detections for each day of available data within each dataset are represented by points within the marmot activity and plant rows.	73
Figure 4.6	Comparison of estimated timings of the growing season (shaded rows) and marmot activity (unshaded rows) across four meadow sites in the Naryn State Reserve, Kyrgyzstan, between 2017 and 2021. The daily model predictions of greenness values (Green Chromatic Coordinates – GCC) and marmot predictions for each day of available data within each dataset are represented by points within the rows.....	74
Figure 5.1.	Futuristic Archaeology by Daesung Lee. In this work, Daesung Lee showcases the increasingly difficulties faced by nomadic herders to maintain their traditional way of life due to the desertification of Mongolian landscapes. See more photos from this series at www.daesungle.com	81
Figure 5.2	One of the many detections of gray marmots from the dataset provided by OSI-Panthera and used in this thesis. This image is the closest	

representation of what my first encounter with a gray marmot looked like.	
.....	84

Entering the snow leopard realm



Chapter 1.

General introduction

1.1. Nature under threat

Natural ecosystems are increasingly facing disturbances. Globally, 60% of ecosystems have significantly degraded since the 1950s (Watson et al., 2020). The average size of monitored wildlife populations has decreased by 73% since the 1970s, with the fastest regional declines located in Latin America (95%), Africa (76%) and Asia-Pacific (60%) (WWF, 2024). Declines in biodiversity have been observed in Europe, North America and Central Asia prior to the 1970s, but the implementation of conservation initiatives has led to the stabilization and even increase of some populations, resulting in a less drastic biodiversity loss in some regions (WWF, 2024). Habitat fragmentation and overexploitation of resources for food production are the main drivers of biodiversity losses in terrestrial and marine ecosystems (Maxwell et al., 2016; Wang et al., 2025), while freshwater ecosystems are mostly impacted by pollution and changes in sea and land-use (Isbell et al., 2023). Based on palaeobotanical records, the conversion of wild landscapes into agricultural and urban areas over the last 10,000 years has led to the loss of nearly half of the world's forests and two-third of wild grasslands and shrublands, with about half of the loss occurring since 1900 (Ritchie, 2021).

The consequences of habitat and species losses for ecological communities are ever more exacerbated by climate change (Keck et al., 2025; Rubenstein et al., 2023; Shivanna, 2022). Climate change on its own and in interactions with other pressures is a major driver of biodiversity loss, especially in areas experiencing fast warming like the Arctic (García Criado et al., 2025) and alpine regions (Verrall et al., 2023). However, because of its myriad manifestations, its impacts on ecological communities are contrasting. Shifts in temperature and precipitation regimes result in long-term, gradual (press) perturbations, while the increased frequency of extreme events result in sudden (pulse) disturbances (Bender et al., 1984; Harris et al., 2018). Pulse disturbances like wildfires and landslides have obvious, direct impacts on ecosystems. However, most disturbances (e.g., livestock grazing; global warming) press on

ecological communities through long-term, gradual disturbances, making it more difficult to detect change.

1.2. We are in an era of data abundance

Due to the complex nature of ecosystems, detecting change and determining whether it is permanent or temporary requires long-term, multi-modal and multi-scale datasets (Magurran et al., 2010). Field studies are fundamental to obtain baseline assessments of complex evolutionary and ecological patterns. They allow the collection of species- to population-level metrics such as above- and below-ground species diversity, abundance and life traits. Long-term ecological monitoring datasets are ideal to test the local response of communities to specific disturbances. For example, experiments in open-top chambers over the last 30 years have allowed us to gain biome-wide insights of climate warming impacts on tundra (Henry et al., 2022) while long-term (20+ years) herbivore exclosures have revealed the effects of grazing in the High Arctic (Petit Bon et al., 2023). While these datasets are optimal to understand local diversity and dynamics at a specific time and space, they are often taxonomically narrow (Caldwell et al., 2024), geographically limited (Daru & Rodriguez, 2023; García-Roselló et al., 2023), and intensive in terms of person-power. However, over the last decades, technological advances have led to an exponential increase in both quantity and variety of ecological data.

Data from raw sensors are increasingly used due to their breadth of applications (Latifi et al., 2023). High-resolution imagery from satellite sensors generates multi-decadal datasets at various spatial extents (i.e., the total surface area covered by a given dataset) and resolutions (i.e., the total surface area covered by a pixel). Satellite imagery can provide multiple abiotic (e.g., land surface temperature, snow, water, topography) and biotic (e.g., vegetation phenology, land cover distribution) metrics, which are essential for establishing a baseline picture of landscape structure and measuring change over time. The applications of remote sensing methods in ecology has already efficiently assessed dynamics and change in a variety of ecosystems (Bolch, 2007; Ding et al., 2022; Khan et al., 2024; Liu, Fang, et al., 2021; Tomaszewska et al., 2020), including their response to disturbances (Eddy et al., 2017; Goodin & Henebry, 1997; Liu et al., 2016).

Remote cameras are also increasingly used for biodiversity monitoring, especially large mammal and bird communities (Fisher, 2025; Steenweg et al., 2017). These non-invasive devices are used in various contexts, including monitoring species phenology (Hofmeester et al., 2020), wildlife movement (Chen et al., 2022), behaviour (Burton et al., 2022), species interactions (Burton et al., 2015) and tracking changes in abiotic conditions (e.g., snow) (Alison et al., 2024; Breen et al., 2024). Often deployed for a year at time across a geographical grid, remote cameras can capture annual animal movement through motion-triggered sensors and generate near hourly data through fixed time intervals (i.e., timelapse) (Rovero et al., 2013; Swann et al., 2011). Cameras deployed for wildlife monitoring are commonly referred to as camera traps. They differ from PhenoCams, which are cameras specifically designed for plant studies, with no motion sensor (Richardson, 2023). Despite the technological differences between the two, the term ‘camera traps’ has been used interchangeably for both (Meek et al., 2014). Throughout the thesis, the term ‘camera trap’ will only refer to cameras equipped with motion sensors and potentially timelapse features. Camera traps are used throughout the globe to monitor wildlife, especially in remote environments. Their importance was highlighted during the COVID-19 pandemic, when most research was halted but research projects using deployed camera traps continued to passively generate data (Blount et al., 2021).

These methods produce large volumes of data, which provides a myriad of opportunities for ecosystem monitoring over time and space. However, the resources required to manually process these data often limit their use. Improvements in machine learning and the automation of data processing start addressing these limitations (Pollock et al., 2025), but the limited records of local biodiversity and data remain a major challenge in many geographical areas.

1.3. Ecosystem monitoring in data-poor areas

Ecological data are particularly abundant in the Northern Hemisphere, specifically in western countries. Numerous historical and contemporary records of biodiversity, access to long-term, extensive field studies, large temporal and spatial coverage of sensor data and the concentration of expertise have led to an advanced understanding of ecosystem dynamics in these geographical areas (Caldwell et al., 2024). In contrast, many regions do not benefit from the same extensive establishment of scientific experiments, leading to the limited availability

and diversity of data and an imbalance in our understanding of ecosystem dynamics throughout the world (Daru & Rodriguez, 2023).

Data shortages are mostly located in developing countries or areas with historically or actively tense geo-political situations (Isbell et al., 2023; Zhang et al., 2025). Understanding ecosystem dynamics and change in developing countries is crucial as local human populations rely heavily on ecosystem services to provide food security, water, livelihoods, health and culture (Guo et al., 2010). For example, in Central Asia, the critical reliance of people in impoverished communities on a natural environment characterized by harsh climatic conditions has led to the co-evolution of ecological and social systems, resulting in complex, intertwined human and nature interactions (Berkes et al., 2000).

A prime example of socioecological ecosystem is rangelands (Chen et al., 2024). These arid ecosystems include shrublands, grasslands and steppe from low to high altitudes and latitudes, all grazed by domesticated and wild herbivores (Briske et al., 2020). They continue to be shaped by human activities for agriculture and animal husbandry, to which many endemic species and diverse ecological communities have adapted (Milchunas & Lauenroth, 1993). However, climate change and unsustainable land use practices are leading to the degradation of rangelands throughout the world, especially in alpine ecosystems (Robinson, 2016; Shang et al., 2025). Ecosystem degradation is defined by the alteration of ecosystem functioning and structure (AbdelRahman, 2023). The alteration can be temporary (intra-state degradation) or permanent, leading to a new alternative stable state (state conversion; degradation or desertification) (Zhang et al., 2018; Zhao et al., 2023). The latter is clearly of great concern to both people and biodiversity.

1.4. Alpine rangelands of Kyrgyzstan

Kyrgyzstan is the most mountainous country in Central Asia (> 90% of land area is mountain; FAO, 2015). Rangelands constitute most agricultural lands, making Kyrgyzstan a great example of how mountain habitats can economically support local communities through farming and herding. Historically, nomadic herders moved across the landscape, from low elevations in winter to highlands in summer, a migration known as vertical transhumance. Vertical transhumance enabled access to forage for livestock throughout the seasons without

exhausting natural resources (Aryal et al., 2018). Following annexation of Kyrgyzstan by Russia in 1876 and incorporation into the Soviet Union in the 1920s, herders had to shift from centuries of nomadic practices along the Silk Road to the establishment of large-scale sedentary collective farms (*kolkhozes*) at low elevations. Herders maintained seasonal transhumance to high alpine pastures on a more localized scale (Robinson, 2016). Between 1940 to the late 1980s, livestock numbers increased from 3 million to 10 million to support the growing human population and demand (Rozanov 1990), largely exceeding the grazing capacity of Kyrgyz grasslands (Ministry of Environmental Protection 1998). When the Soviet Union collapsed in 1991, the transition from a collective state economy to a private market-based economy resulted in an abrupt decline in infrastructure, resources, and employment (Pankow and Jermakowics, 1995). Between 1989 and 1994, Kyrgyzstan faced a significant population loss, with 7.5% of its population emigrating (CIS Migration Report, 1996, pp. 66-67; Abasov 1999). By 1995, livestock numbers had declined by nearly 60% due to a lack of forage and demand (NSC 2008; Yang et al., 2020), and the land once used for collective farms transitioned to peasant farms and households (Akramov and Omuraliev, 2009). During the first decade of political independence, communities relied on subsistence-based animal husbandry, and this period saw the loss of the more traditional seasonal transhumance (Robinson, 2016). With recent rapid population growth in the 2000s (Avdeev 2021), the number of livestock increased again, reaching nearly 9 million cattle, sheep and goat by 2016 (Kydyshev 2022).

Over the last 25 years, large spatial-scale studies have reported the alteration of rangeland functioning and structure due to the increase in cattle numbers and changes in environmental conditions (Domenech et al., 2022; Eddy et al., 2017; Hoppe et al., 2016; Zhumanova et al., 2018a). These alterations heavily challenge the sustainability of local human populations, as well as ecological communities (Liechti, 2012). Changes in ecosystem functioning have direct, cascading consequences on bottom-up processes through resource depletion, phenological mismatches between plants, predators and prey, changes in species spatial distribution, and alteration of below ground community dynamics (Ripple et al., 2024). Understanding the local drivers of change and the cascading effects on other trophic levels is urgent, but how do we address these issues with little data or limited access to the field? This is the central question I tackle in my thesis.

1.5. Project origin and chapters

This project started in Kyrgyzstan in 2018, designed by local communities, partners and myself, to identify what drives changes in alpine rangelands and the resulting impacts on species such as snow leopards (*Panthera uncia*), Siberian ibex (*Capra sibirica*), argali (*Ovis ammon*) and under-studied marmots (*Marmota* spp). We anticipated being able to use multi-modal datasets from camera traps, satellite imagery, high-resolution drone footage, and conduct vegetation and soil sampling, studies of diet and species identification through DNA metabarcoding, and surveys with local herders and community members. Our goal was to leverage the few existing datasets (i.e., camera traps and satellite imagery) while deploying a holistic, simultaneous monitoring of species dynamics in local alpine ecosystems across time and a disturbance gradient. However, I started my PhD in January 2020 – at the height of the COVID pandemic – which ultimately led to the cancellation of all field opportunities.

Having access only to a 6-year camera trap dataset deployed for snow leopard monitoring in a protected area and satellite imagery, I decided to explore how these two methods could be used simultaneously and beyond their current, conventional (i.e., snow leopard-focused) use to better understand the structure and ecological dynamics of alpine ecosystems in one of the most remote places on the planet.

Chapter 2 provides a big picture understanding of the diverse habitat types, how they changed over 20 years and how the change relates to anthropogenic disturbances. In mountain areas, disentangling the impact of climate change and anthropogenic activities on alpine biodiversity is very challenging due to the complexity of topographic features, resulting in many topo-climates. Using satellite imagery at a fine spatial scale (10 m and 30 m), I first explored the role of topography in driving land cover distribution. Then, I selected four study sites of equivalent surface area and elevation range, including one area protected since 1983, and three sites, each characterized by a different level of anthropogenic disturbance. For each site, I classified and mapped land cover distribution over the last 20 years using contemporary training data, due to the absence of land cover historical records. I then examined how much of the landscape has changed, which land cover types changed, how and where, providing a first picture of recent landscape-level changes in this region.

In Chapter 3, I explore how motion-triggered images generated by camera traps deployed for wildlife monitoring can be used to track the key timings of plant phenology and how these timings differ from satellite observations. To date, camera trap datasets that include time-lapse images in addition to motion-triggered images are used for plant and snow phenological studies. However, most camera trapping projects solely rely on motion-triggered images generated at random by wildlife movement. Here, I highlight how motion-triggered data can be used and analyzed beyond wildlife monitoring to detect and track plant phenology with a semi-automated framework. This study highlights the untapped potential of motion-triggered images to yield ecological data important for tracking the effects of climate change.

In Chapter 4, I assess the main phenological timings of the under-studied gray marmot (*Baibacina baibacina*) using by-catch camera trap data. The gray marmot is one of the largest rodents in Central Asia, and an important seasonal prey for snow leopard. However, little is known about its ecology. Using the same dataset as Chapter 3, I examine marmot activity patterns and how plant and marmot phenologies align to obtain a baseline understanding of local plant-herbivore dynamics and potential synchrony/asynchrony. This study provides a first assessment of gray marmot phenology in the region and highlights the potential of a single camera trap dataset to link plant and marmot phenologies.

Finally, in Chapter 5, I weave the key findings of my three quantitative chapters to reflect on the current use of data in ecology and the direction to take to address the current biodiversity crisis. I emphasize the value of leveraging existing datasets beyond their target species to effectively and efficiently address critical gaps in our understanding of ecological processes, especially in under-studied areas.

Chapter 2.

Multidecadal changes in land cover across a disturbance gradient in mountain grasslands of Kyrgyzstan

2.1. Introduction

Mountains cover up to one-quarter of the Earth's landmass beyond Antarctica. While the definition of a mountain varies depending on local perceptions, conceptions, and culture (Smith & Mark, 2003) the most accepted defining features are ruggedness, vertical atmospheric pressure and temperature gradients (Körner, 2007; Körner et al., 2021). The interaction between such heterogeneous, complex terrain and climate creates a high diversity of land cover, microclimate and therefore habitat types. Approximately one-third of the world's forests and terrestrial biodiversity, including half of the world's biodiversity hotspots, are on mountains (Chape et al., 2008; Gratzer & Keeton, n.d.; Grumbine & Xu, 2021). Mountain habitats also boast high levels of endemic species (Körner, 2021; Noroozi et al., 2018). Considered the world's water towers (Immerzeel et al., 2020; Viviroli et al., 2007), mountains provide fresh water for over half of the global human population (Egan & Price, 2017), as well as myriad opportunities for resource production and extraction, recreation, education, spirituality, and cultural heritage (Bernbaum, 2022; Canedoli et al., 2024). At a smaller scale, mountain habitats support local economies based on farming and herding. Mountain communities, especially in the highlands, are isolated and have few resources, and thus are particularly vulnerable to changes in climate (i.e., extreme events, shifting seasons) and environmental conditions (i.e., habitat degradation, pollution). With unprecedented rates of global human expansion and climate change over the last several decades, people worldwide have observed the rapid pace at which alpine regions are changing.

Mountain ecosystems continue to experience particularly rapid physical and environmental change due to anthropogenic global warming (Gerrard, 1991; Marston, 2008). Warmer temperatures, shifts in precipitation regimes and increased frequency of extreme events seriously challenge the persistence of contemporary mountain habitats and both human and ecological communities (Keiler et al., 2024; Knight, 2022). The reported impacts of climate

change in mountain areas include increased natural hazards (Terzi et al., 2019) and decreasing snow cover, permafrost area and glacier mass balance (Immerzeel et al., 2020). For instance, glaciers retreated in the 2010s at almost twice the pace as they did in the 1980s (Pelto et al., 2020). Retreating and melting glaciers jeopardize water availability for people and ecosystems existing in already arid environments. In addition, while decreases in snow cover and glaciers expose more land with the potential to provide new suitable habitat, these darker areas have lower albedo and thus absorb solar radiation, leading to warmer land surfaces (Zhang et al., 2022). Climate change also drives shifts in ecosystem composition and plant migration (Kelly & Goulden, 2008; Parmesan & Yohe, 2003). Cold-adapted alpine plant communities are highly sensitive to warming (Inouye, 2020), and temperature increases across elevation gradients result in the loss of endemic and cold-adapted species, species movement from low to high elevations, increased competition and overall changes in community composition and ecosystem functioning (Freeman et al., 2018). Finally, climate-change-induced impacts are amplified by the history, intensity and scale of land use practices, leading to accelerated land degradation in a growing number of cases (Orr et al., 2024). While impacts of warming and land use on high-altitude ecosystems are often discussed in general terms at a global scale, it remains a challenge to predict how local and/or regional mountain areas will respond due to the structural heterogeneity and complexity of these vast, remote, and rugged landscapes as well as the political and governance history of the region (Reyer et al., 2017).

The Tian Shan Mountain range, which extends from China to Uzbekistan, provides an example of drastic recent changes in land use, linked to political upheaval. Called the *celestial* or *heavenly mountain*, this extensive system of primarily arid and semi-arid mountain ranges covers approximately 1,000,000 km², including peaks of more than 7,000 m and low-lying areas >150 m below sea level. As part of the Palaearctic steppes (Wesche et al., 2016), the Tian Shan Mountains' arid and semi-arid grasslands provide one of the richest source of livelihood for humans. In Kyrgyzstan, the most mountainous country in Middle Asia (> 90% of land area is mountain; FAO, 2015), rangelands constitute most agricultural lands, making Kyrgyzstan a great example of how mountain habitats can economically support local communities through farming and herding. Historically, nomadic herders moved across the landscape, from low elevations in winter to highlands in summer, known as vertical transhumance. This vertical transhumance enabled access to forage for livestock throughout the seasons without the exhaustion of natural resources (Aryal et al., 2018). These ancient patterns were severely

disrupted in the 1920s following annexation by Russia and incorporation into the Soviet Union, and then again following the collapse of the USSR in 1991, which saw an abrupt decline in livestock numbers (see Chapter 1 – Introduction).

However, over the last 25 years, reduced transhumance and the increasing numbers of livestock across rangelands have led to a growing concern about rangeland productivity. While observations of land degradation are not unanimous throughout the country (Levine et al., 2019), an expanding body of evidence from herders and scientists is raising concerns about pasture degradation (Eddy et al., 2017; Hoppe et al., 2016; Zhumanova et al., 2018a). Land degradation is defined as a temporary or permanent decline in a system's productive capacity and potential to be used, including for economic purposes (Stocking, 2001). The increasing amount of livestock and the loss of movement through transhumance leads to concentrated grazing pressures resulting in pasture degradation, also referred to as browning (Cook & Pau, 2013), which differs from natural seasonal senescence. In 2022, pasture degradation maps showed that 81.5% of winter pastures were severely degraded (vs < 43% in other seasons; Domenech et al., 2022). This alarming degradation rate is forcing herders to supplement feed their herds, jeopardizing the sustainability of local communities already relying on animal herding as a subsistence-based livelihood.

High rates of pasture degradation also pose a major concern for ecosystem functioning. Plant growth depends on nitrogen mineralization and soil organic carbons that increase with rising precipitation (Burke & Rundquist, 2021; Liu, Zhou, et al., 2021; Wilsey, 2018). Arid and semi-arid grasslands have limited, periodic water availability, extreme temperature seasonality and short growing seasons, which has selected for adaptations such as small growth forms, high root-shoot ratio, reduced leaf area, and a more efficient photosynthetic pathway (C3) (Taft et al., 2011). As a result, mountain grassland ecosystems typically have low net primary productivity (NPP) (Wingler & Hennessy, 2016a), are particularly sensitive to environmental change, and recover slowly from disturbances. Significant warming rate in Central Asia over the last 30 years (+0.4 °C; Ma et al., 2021), extreme climatic events and ongoing pressures from land use (i.e., grazing activities) have drastically altered grassland dynamics, structure and functioning (Yang et al., 2023; Zhao et al., 2023), leading to gradual degradation and potentially

permanent state conversion (Zhang et al., 2018; Zhang et al., 2018). Changes in grassland functioning and structure have cascading effects on other trophic levels and species interactions, such as soil dynamics and microorganisms and herbivory through reduced foraging, which can ultimately alter predator-prey dynamics that involve emblematic mammals, such as the snow leopard (*Panthera uncia*), argali (*Ovis ammon*) and Siberian ibex (*Capra sibirica*). It is unclear if degraded pastures are now permanently altered, highlighting the urgency of assessing and restoring grasslands before it is too late.

Given the established importance of mountain ecosystems through the myriads of ecosystem services they provide and the increasing intensity of challenges they face, it is crucial to assess potential patterns of rangeland degradation at the fine scales at which management can be implemented. Using satellite imagery, we i) classified, quantified, and mapped land cover distribution between 1997 and 2021 at fine spatio-temporal resolutions and ii) compared land cover distribution between areas with different conservation statuses in the Naryn oblast, the region with the greatest concentration of grasslands in Kyrgyzstan (Figure 2.1). These adjacent conservation designations offer a gradient of anthropogenic pressures from areas with prohibited herding to areas with intense herding. Then, we investigated the role of (1) topography in driving the spatial distribution of land cover classes in the region and (2) anthropogenic disturbances and elevation (as a proxy for global warming) as drivers of changes in land cover over time. While we expected elevation to be the most important driver of land cover distribution (Han et al., 2024; Schrodtt et al., 2019; Setiawan et al., 2024), we also predicted that the combination of slope and aspect might play a role (Borchardt et al., 2011; Yang et al., 2020) along with ruggedness as a measure of habitat heterogeneity (Jay et al., 2023; Malanson et al., 2023). The widespread use of sensor data with large spatial resolutions (e.g., 500 m or 1 km) often limits the characterization of land cover change within more localized and smaller areas. The fine-scale, high resolution methods used in this study provide a framework to disentangle the roles of topography, anthropogenic pressures and climate change in the distribution of land cover in an area with limited baseline assessment of plant diversity and assemblages.

2.2. Material and Methods

2.2.1. Study area

The study took place in the Naryn oblast, the poorest of the seven administrative regions of Kyrgyzstan (Fig 1; Crewett, 2012). Located south-east of Kyrgyzstan, the Naryn oblast has the largest proportion of agricultural land in the country, with animal herding as the main source of livelihood (Azarov et al., 2020). Home to grassland valleys and tundra plateaux of the Inner Tian Shan, the region has a climate characterized by dry, cold, long winters and short warm and dry summers (Weather Spark, 2025), with daily mean temperatures ranging from -15.8 and 18.2 between January and August along with 290 mm of annual mean precipitation mainly occurring between April and July (Eddy et al., 2017). Naryn, the capital of the region, is considered the tenth largest city in Kyrgyzstan, with 41,000 inhabitants in 2021 (National Statistical Committee of the Kyrgyz Republic, 2023). We selected three study areas, each located in adjacent parts of the Inner Tian Shan range, that present similar topographic and landscape features but that together represent a gradient of anthropogenic pressures based on the history of grazing through local herding.

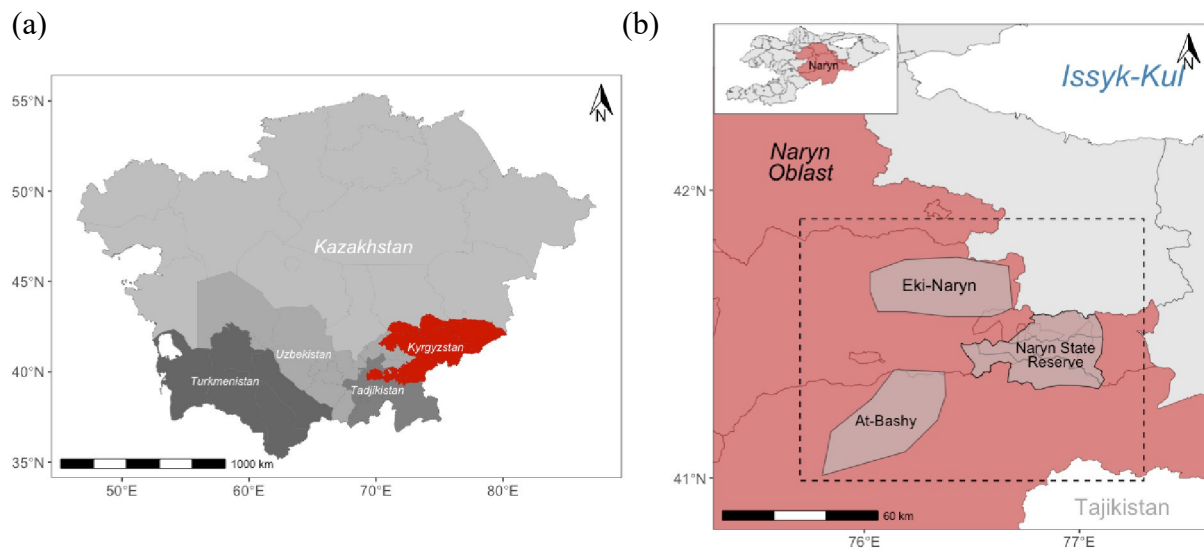


Figure 2.1 (a) Location of Kyrgyzstan (red) in Middle Asia. (b) The study areas in Kyrgyzstan's Naryn oblast (red) include the Naryn State Reserve, Eki-Naryn Area and At-Bashy areas.

Protected area and mild disturbances: Naryn State Reserve

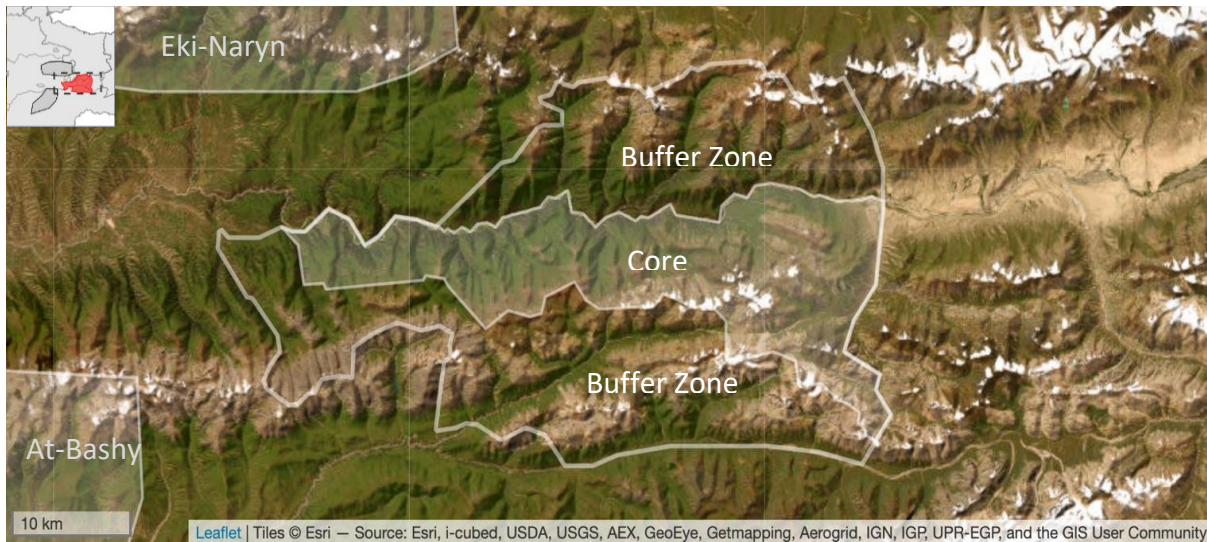


Figure 2.2 Location of the core and buffer zones of the Naryn State Reserve.

The Naryn State Reserve ($41^{\circ}25'50''\text{N}$, $76^{\circ}35'11''\text{E}$) is a 1,080 km² reserve created in 1972 as a multi-use sanctuary (*zakaznik*), with a ban on hunting to protect elk populations (*Cervus elaphus*) (Farrington, 2005). In 1983, the sanctuary became a state nature reserve (*zapovednik*), which further enforced regulations to ensure the preservation, conservation and restoration of the ecosystem while providing research and educational opportunities (Farrington, 2005; Kozhokulov et al., 2021). The reserve presents two types of management: a fully protected core zone located south of the Naryn riverbanks and two large multi-use buffer zones located north and south of the core zone (Figure 2.2). The core zone ranges from 2379 m to 4470 m in altitude, and it is mostly characterized by north-facing slopes only accessible by rangers and research teams. Therefore, the core zone is considered as one end of the disturbance gradient, with minimal to no anthropogenic disturbances over the past 40 years. The buffer zones, however, have historically been shaped by intense grazing and forestry. Signs of degradation and soil erosion from this era were still visible in the early 2000s (Farrington, 2005), and the buffer zones continue to be used for subsistence-based herding to this day (OSI-Panthera, *personal communication*). The Tian Shan Mountain ash and Schrenk's spruce constitute most of the forest cover, along with grasslands, barren lands and glaciers as

main habitat types. Activities in the buffer zones are monitored, and the degree of disturbance is considered mild.

Moderate disturbances: Eki-Naryn

The Eki-Naryn area is characterized by the small village of Eki-Naryn, which results in a moderate degree of disturbances compared to the Naryn State Reserve. Eki-Naryn is a small village located in an area with features like those of the Naryn State Reserve (i.e., surface area, elevation, slope, and aspect ranges), 8 km to the northwest (Figure 2.1b). The Eki-Naryn area ranges from 2314 m to 4422 m in elevation with the same characteristic continental, dry and seasonal climate. Overlapping with the Issyk-Kul region, humans from the time of nomads over 3,000 years used this area for herding and as a travel route. More recently, tourism has been growing in the region because of various exceptional landscape features such as the Eki Naryn valley (41°40'48.43"N, 76°25'27.40"E). Due to the proximity to human settlements and accessibility, this area is considered moderately disturbed.

High disturbances: At-Bashy

The last study area, At-Bashy, represents a “highly disturbed” state. The At-Bashy Mountain range borders south of At-Bashy, one of the major cities in the Naryn oblast and capital of the At-Bashy district. This southern district of Naryn faces more drastic overgrazing than the Eki-Naryn area because of its closer proximity to villages. Recent maps indicate that pastures located in the At-Bashy range are already considered degraded (Domenech et al., 2022). In 2010, the At-Bashy district included 13,300 households (Azarov et al., 2020), from which 72 households were randomly sampled to understand the socio-economic situation of the local population. Each herder owned, on average, 3.85 ha of agricultural land and 15.8 livestock, with a strong preference for sheep, horse and cattle, and goats (Azarov et al., 2020). Despite an overall poor irrigation system, most of the land is used to produce fodder as supplementary feeding for livestock during the winter, which remains nutritionally insufficient. Sheep and horse herds migrate to higher pastures (*jailoo*) from June to September before returning near the settlement for the rest of the year, where cows stay throughout the year. Our defined study area ranges from 2072 m to 4396 m, south of the city of At-Bashy and is considered highly degraded due to the high level of disturbance (Domenech et al., 2022).

2.2.2. Geospatial data

ESA land cover map

To classify and map the land cover in the Naryn region, we used the 2021 v200 European Space Agency (ESA) WorldCover 10 m resolution (Zanaga et al., 2022). The ESA WorldCover is a global land cover dataset that includes 11 land covers derived from the United Nations Land Cover Classification System (UN-LCCS): tree cover, shrubland, grassland, cropland, built-up, bare/sparse vegetation, snow and ice, permanent water bodies, herbaceous wetland, mangroves, moss and lichen. The ESA imagery uses both Sentinel-1 and Sentinel-2 satellite data. This combination of datasets allows mapping areas with frequent cloud cover, which is a common characteristic of high mountain areas. We used Google Earth Engine (Gorelick et al., 2017) to access the ESA imagery, after which we clipped the cloud-hosted tiles to our areas of interest and downloaded them. Then, we used the ESA land cover classification to perform a supervised classification of the Landsat composites (Appendix A: Figure A1).

Landsat data source

To characterize and track changes in land cover between 1997 and 2021, we used the open source 16-day 30 m Landsat Analysis Ready Data (ARD) provided by the Global Land Analysis and Discovery (GLAD) team at the University of Maryland (Potapov et al., 2020). The Landsat ARD provides normalized surface reflectance from 1997 to the present by combining and harmonizing Landsat 5 (TM), 7 (ETM+) and 8 (OLI/TIRS) collection 2 (Table 2.1). We downloaded the Landsat ARD imagery from 1 January 1997 to 18 December 2021, using GLAD Tools, a user-friendly software package developed by the GLAD team to allow users to conduct various analyses and pre-processing steps to the ARD (Potapov et al., 2020). As three ARD tiles straddled our study areas, they were mosaiced together and clipped to the shape of each study area across the disturbance gradient. Land cover assessment and imagery for the 1990s are limited in Kyrgyzstan due to gaps in ground station coverage between the fall of the Soviet Union and the mid-2000s. As a result, imagery for some of this period is missing. Thus, we selected a target year and used the previous years ($n = 4$) annual Landsat imagery to fill in the gaps and create a multi-year composite at the expense of a finer temporal resolution. The aggregation was done for six time periods - 1997 to 2001, 2001 to 2005, 2005 to 2009, 2009 to 2013, 2013 to 2017, and 2017 to 2021, later referred to as 2001, 2005, 2009, 2013, 2017 and

2021 periods - to best classify and quantify land cover change. Each composite pixel represents the median value recorded in each pixel across a given period in each of four spectral bands - near-infrared (NIR), shortwave infrared 1 (SWIR1), shortwave infrared 2 (SWIR2) and red. Using a composite with shortwave bands and a composite with pseudo-natural colors, we compared which composite increases the accurate detection of vegetation cover types. Here, we used multi-year metric composites generated by GLAD Tools composed of NIR, SWIR1 and SWIR2 bands, which is expected to be more accurate in predicting vegetation types due to the presence of both shortwave infrared band (Li et al., 2022; Potapov et al., 2020) compared to our second composite composed of NIR, red and SWIR bands, more commonly used to predict land cover types (Potapov et al., 2020) (Appendix A: Figure A1).

Topographic variables

To quantify the topographic complexity of the region, we used the 30-m NASA Shuttle Radar Topography Mission Global (SRTMGL1 v003) digital elevation model (DEM) (NASA JPL, 2013). The SRTM data was downloaded using the GLAD Tools software ([GLAD TOOLS v2](#); Potapov et al., 2020), thus providing an exact spatial overlap and match in resolution with the Landsat ARD. Slope, i.e., the degree of change in elevation in the direction of the water flow line, and aspect, i.e., the angular direction that a slope faces (Amatulli et al., 2020), are essential in creating topo climates in alpine landscapes. We generated slope and aspect, both in radians, as well as slope in degrees, by using the SRTM DEM rasters for each study area. Due to the aspect being a circular variable, we calculated eastness and northness to provide a continuous measure indicating a site's north/south and west/east position (Amatulli et al., 2020). Northness and eastness are calculated as the sine of the slope in radians multiplied by the cosine and sine of aspect, respectively (Amatulli et al., 2020). To characterize the landscape's ruggedness, we also included the radial roughness index (RRI), as a measure of terrain heterogeneity to predict species distribution across the landscape (Trevisani et al., 2023) (Appendix A: Figure A1).

2.2.3. Data processing

Plot selection

Each study area was separated into five elevation bands based on their respective elevation range, with a fixed width of 414 m (core zone), 428 m (buffer zones), 421 m (NW), and 465 m (SN) (Appendix A: Figure A2). We reclassified the DEM for each elevation band to limit demands for computational power (Appendix A: Table A1). We randomly extracted 1% of the pixels available within each band, with each pixel with a spatial resolution of 30 m ($0.00025^\circ \times 0.00025^\circ$), producing a total sample size of 14,647 pixels for the buffer zones (439,410 m²) and 7997 pixels for the core zone (239,910 m²) of the Naryn State Reserve, 23,118 pixels for the Eki-Naryn area (693,540 m²) and 23,146 pixels for the At Bashy area (694,380m²) (Appendix A: Figure A3, Table A2).

Land Cover Classification

Reference data

We used the 2021 ESA WorldCover to characterize the land cover for each randomly generated sample site. First, we aggregated the 10m resolution of the ESA composite into a 30m resolution composite, defining the most frequent land cover class out of the 3 aggregated pixels as the main land cover. In the event of ties (i.e., 3 different classes), the pixel was removed. Then, we classified each generated sample site, which were used as the training dataset to classify the Landsat multitemporal metric composites for each period at a spatial resolution of ~ 30 m ($0.00025^\circ \times 0.00025^\circ$). According to the 2021 ESA world cover dataset, more than half of our study area is characterized by grasslands, followed by 20% of barren land with sparse vegetation and moss and lichens (Appendix A: Figure A4). Grasslands, bare/sparse vegetation and moss and lichens have similar surface reflectance signatures, leading to separability and characterization issues during the supervised classification. Thus, we decided to remove moss and lichens from the training dataset to improve the classification accuracy. We also removed shrubland, herbaceous wetlands, permanent water bodies and croplands due to their low representation across the region, as well as permanent snow due to the challenges in accurately classifying this land cover (Appendix A: Figure A5). Thus, our reference data includes bare/sparse vegetation (barren), forest and grassland classes.

Supervised classification algorithm

To predict the most probable land cover class at each site for each time period, we used the Classification and Regression Trees (CART) algorithm (Breiman et al., 2017). CART is a machine-learning algorithm that uses decision trees to predict the likelihood of a target variable falling in a specific class. The goal was for the CART algorithm to predict which spectral signature from Landsat corresponds best to the input training dataset, with each internal node limiting the loss function (i.e., the difference between the model's predictions and the data). Every pixel was selected based on its surface reflectance value for that specific band and sent to the subsequent attribute and threshold decision node. We used the Recursive Partitioning and Regression Trees (rpart) package in R (v.4.4.2) to run the decision trees.

Training dataset

First, we merged the reference datasets from each study area into a regional dataset ($n = 57315$ pixels). We masked the pixels belonging to land cover classes other than forest, grassland and barren out of the rasters to limit errors during the supervised classification. To best calibrate the classifier, we balanced the training dataset by selecting the number of pixels found in the least represented land cover class ($n = 3454$) and randomly sampled the same number of pixels in the other, more represented classes. Then, we randomly sampled 30% of the balanced dataset ($n_{30\%} = 3108$). From the sampled sites, we extracted surface reflectance values from both 2021 Landsat multitemporal metric composite, the pseudo-natural color composite (SWIR1, NIR and red) and the double shortwave composite (NIR, SWIR1, SWIR2). Thus, the two obtained input datasets included a sample of pixel coordinates, the associated 2021 composite reflectance values (i.e. NIR, SWIR1, and red or NIR, SWIR1, SWIR2), and the 2021 ESA land covers. The algorithm subset each input dataset and repeatedly classified them until every pixel belonged to a class. We selected 200 observations as the minimum number required in a node to generate a split (Appendix A: Figure A6). Once trained, we used the classifier to classify the entire Landsat annual median composite, which assigned a probability of the likeliest land cover class for each pixel (Appendix A: Figure A7). We selected the land cover with the maximum probability at each site and compared the predicted classification with the observed ESA classification (Appendix A: Table A3).

Classification accuracy estimation

To evaluate the algorithm's accuracy, we calculated the overall accuracy (Alberg et al., 2004), defined as the probability of an individual pixel being correctly classified, as well as the user's accuracy (the number of commissions), the producer's accuracy (the number of omissions) and Cohen's kappa (κ), the measure of agreement between variables (McHugh, 2012) (Appendix A: Table A4). We used k-fold cross-validation, randomly dividing the set of observations into k-folds ($k = 5$) of equal sizes to estimate the accuracy. We used the algorithm to classify Landsat mosaics for the remaining time periods (i.e., the five-year spans ending in 2001, 2005, 2009, 2013 and 2017), selecting the land cover with the maximum probability at each site to detect changes in land cover between time periods.

2.2.4. Analyses

The role of topography in current land cover distribution

To model the role of topography on the distribution of land cover types across space, we used boosted regression trees (BRTs), a machine-learning framework using the XGBoost 1.7.8.1 package (T. Chen & Guestrin, 2016) in R (v.4.4.1). Boosted regression trees use a boosting algorithm and can handle a variety of data types, including non-linear data, as well as missing data and non-collinear data. By fitting many decision trees, BRTs can handle complex interactions while minimizing the loss function (Elith et al., 2008), also known as the error function. We used the results of our land cover supervised classification for each area for 2021. For each pixel ($n = 3105$), we included the elevation, slope (degrees), northness, eastness and radial ruggedness index (RRI) generated during the topography extraction. Pairwise correlations among all variables indicated some correlation between slope and elevation ($r = 0.59$), slope and ruggedness ($r = 0.48$), elevation and ruggedness ($r = 0.41$) (Appendix A: Figure A8). Correlations among the remaining variable ranged from -0.08 to 0.07. All correlations were low enough to not be a concern for this analysis. Using the classified satellite composites, we assigned a presence-absence binary value for each land cover class at each pixel (i.e., barren, grassland and forest). We ran individual BRT analyses for each class using a logistic regression. The first step in running a BRT requires setting hyperparameters to minimize the root mean squared error (Appendix A: Figure A9, Table A5 and A7). These parameters include the learning rate (η), maximum loss reduction (γ), the maximum tree depth

(max_depth), and the subsample ratio of the training sample (sub_sample). We bootstrapped the model using different combinations of hyperparameters, resulting in 81 iterations, and extracted their respective root mean square errors. We then selected the set of hyperparameters that produced the lowest root mean square error (Appendix A: Table A5).

To fit the final model, we split the dataset in an 80-20% training-test set, randomized the data and bootstrapped the models 1000 times (e.g. Sherman et al., 2023; Yan et al., 2021). We calculated each variable's relative importance and effect on the land cover classes occurrence (Appendix A: Table A8). In addition, we subtracted the predicted probability of land cover occurrence by the input binary classification (i.e., land cover with maximum probability at a site = 1, other classes assigned 0) to calculate bias. If the measures are close to 0, the model minimizes the prediction bias (Appendix A: Table A6).

Detection of land cover change

Quantifying change

To quantify the impacts of the sudden decrease of livestock abundance in the post-Soviet crash in the 1990s and its drastic increase by the 2020s, we used the 2001 and 2021 multitemporal Landsat composites generated from the supervised classification to quantify the overall change in each land cover surface area between the two endpoints of the time series. Using the raw data, we summarized the number of pixels found in each land cover class and calculated the differences in surface area and overall change between 2001 and 2021. We repeated the same steps including the study area to understand where changes might be occurring in the region with the expectation to observe a decrease in grassland cover as pressure intensities increase.

Detecting the direction of change

To detect the direction of change, we selected pixels that experienced a change in land cover at any moment between 2001 and 2021 by using the classified multitemporal Landsat composites for the 6 time periods (i.e. 2001, 2005, 2009, 2013, 2017, 2021). We summarized the number of pixels changed between each period, by study area, elevation band ($n = 5$) as

well as the main land cover transitions (Appendix A: Table A9).

To quantify the direction of change in absolute terms, we scored whether the pixel changed in land cover (value = 1) or not (value = 0) between 2001 and 2021. We then binned the pixels by elevation, period, and disturbance intensity, and recorded the total number of pixels in each bin, as well as the number of pixels that had changed in either direction (i.e., from grassland to barren: “browning”; from barren to grassland: “greening”) (Appendix A: Table A10).

To determine the role of elevation, time and disturbance on the proportion of land cover change, we ran a generalized linear mixed-effects model with a negative binomial distribution and log link function using the *glmmTMB* package (Brooks et al., 2017). We modeled the number of pixels that changed land cover type as a function of pressure intensity (i.e., study area), elevation, period, and land cover transition type (i.e., browning or greening; forestation was omitted because of the low sample size), as well as select two-way interactions. We used the logged total number of pixels in each bin as an offset term to allow model outputs to be interpreted as effects on the *proportion* of pixels that transitioned rather than the *number* (Appendix A: Figure A11). We ran a single full model instead of performing model selection, as our sample size was sufficient to include all parameters of interest, and each parameter was associated with a clear hypothesis (Appendix A: Table A11). We evaluated the model fit using the DHARMA package (Hartig, 2016), and the *emmeans* packages (Lenth, 2017) to perform post-hoc pairwise comparisons between transition types. We also calculated the estimated marginal mean for each bin using a Tukey adjustment for multiple comparisons.

2.3. Results

2.3.1. Land cover classification

The overall accuracy of the supervised classification was high (OA = 0.86), with a substantial agreement (κ = 0.78), high probability of accurately classified pixels (PA = 0.86), and classification reliability (UA = 0.86). The reliability of the classification was the lowest for grasslands (UA = 0.76; Appendix A: Table A4).

Determinants of current land cover distribution

The relative importance of each topographic variable in predicting the 2021 distribution of land cover classes varied per class. Elevation best predicted the distribution of barren areas ($RI_{\text{mean}} = 0.82$), followed by slope, ruggedness, and eastness ($RI_{\text{mean}} < 0.1$) (Figure 2.3, Table A8). All topographic variables played a similar role in predicting forest land cover, with a higher relative importance of elevation ($RI_{\text{mean}} = 0.44$) and northness ($RI_{\text{mean}} = 0.24$) than slope ($RI_{\text{mean}} = 0.12$), eastness ($RI_{\text{mean}} = 0.11$) and RRI ($RI_{\text{mean}} = 0.08$). Elevation remained the most important predictor for grasslands ($RI_{\text{mean}} = 0.64$), followed by northness ($RI_{\text{mean}} = 0.14$), slope ($RI_{\text{mean}} = 0.08$), eastness and RRI ($RI_{\text{mean}} = 0.07$). Overall, the best topographic predictor for land cover distribution was elevation. Forested areas primarily characterize lower elevations, while grasslands dominate mid-elevation, and barren areas constitute the main land cover type at high elevations, though they are also present at lower elevations but to a lesser extent (Figure 2.3b. B). Northness and eastness were the second-best predictors of current land cover distribution, with a greater proportion of forested areas located on northern slopes compared to grasslands, which are mostly found on southern slopes (Figure 2.3b. A-C). Ruggedness and slope did not contribute to explaining the distribution of any of the land cover classes (Figure 2.3b. D-E) (Appendix A: Table A8).

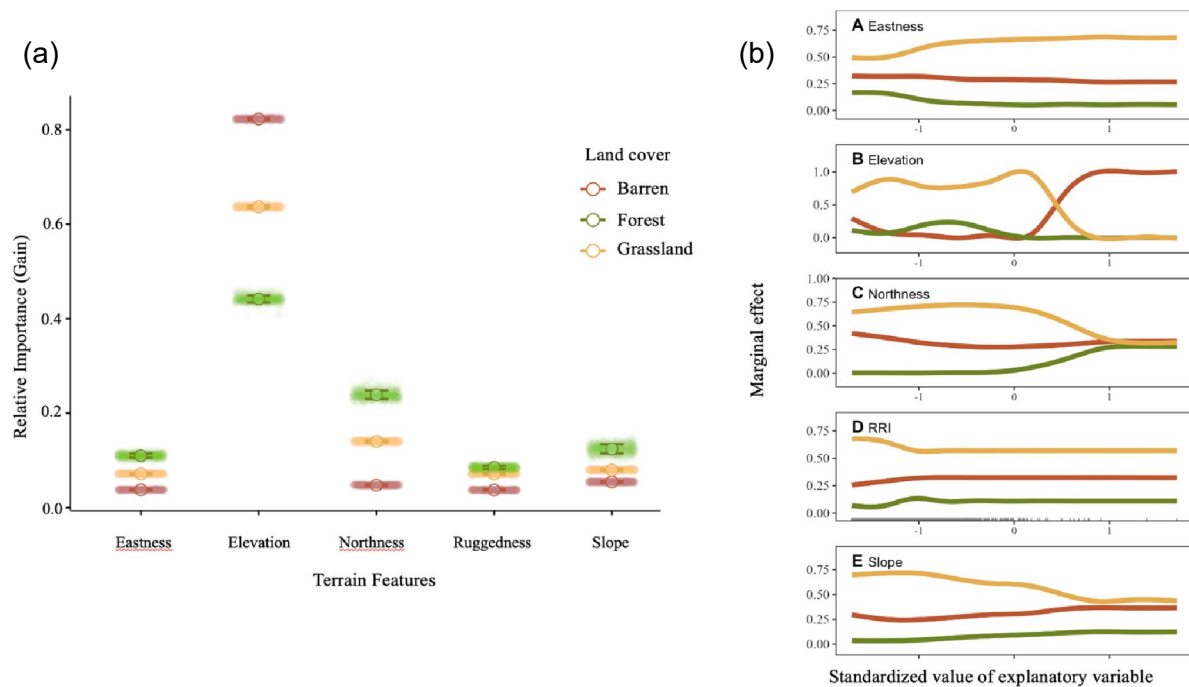


Figure 2.3 (a) Relative importance, expressed as gain, with a higher gain representing greater relative importance of the variable, of five terrain features in explaining the distribution of each land cover class after 1,000 boosted regression tree models. (b) Explanatory variables include A - eastness, B - elevation, C - northness, D - ruggedness (RRI) and E - slope (in degrees).

2.3.2. Detection and direction of land cover change over time

How much has changed overall?

Across all study areas and land cover types, 84.8% of pixels maintained the same land cover class between 2001 and 2021 (Appendix A: Table A9). We found that grasslands remained the dominant land cover type across the landscape, covering 62.7% of the area, followed by barren (32.6%) and forest (4.7%) types in 2021(Appendix A: Figure A10).

Of all pixels that changed between 2001 and 2021, grasslands experienced most change (9.1% of grassland pixels changed), followed by barren areas (4.7%). The proportion of forest cover that changed to another land cover type was less than one percent. Thus, we report the direction of change only for grasslands and barren areas. Of the 9.1% of grassland pixels that changed, the majority (67.7%) transitioned to barren and fewer (32.3%) to forest. Of the

5.4% of barren pixels that changed, 63% transitioned to forests and 37% to grasslands (Appendix A: Table A10). Overall, these figures represent a 339-hectare loss of grassland area, a 274-hectare gain in forest area and a 65-hectare gain in barren area between 2001 and 2021, which were distributed unevenly across elevations and the gradient of anthropogenic pressures.

Land cover change in relation to elevation

Grassland area was lost between 2001 and 2021 across all elevation bands, but the largest area in absolute terms was lost at low-intermediate (144 ha loss) and intermediate elevations (113 ha loss; Figure 2.4). The increase of forested areas mainly occurred at elevations ranging between 2835 m and 3264 m (185 ha gain; elevation band 2), 3264 m and 3693 m (55 ha gain; elevation band 3) and 2072 m to 2835 m (47 ha gain; elevation band 1) (Figure 2.4). We also observed an increase in barren areas across all elevation bands, with the exception of intermediate elevations where 39 ha of barren areas were loss.

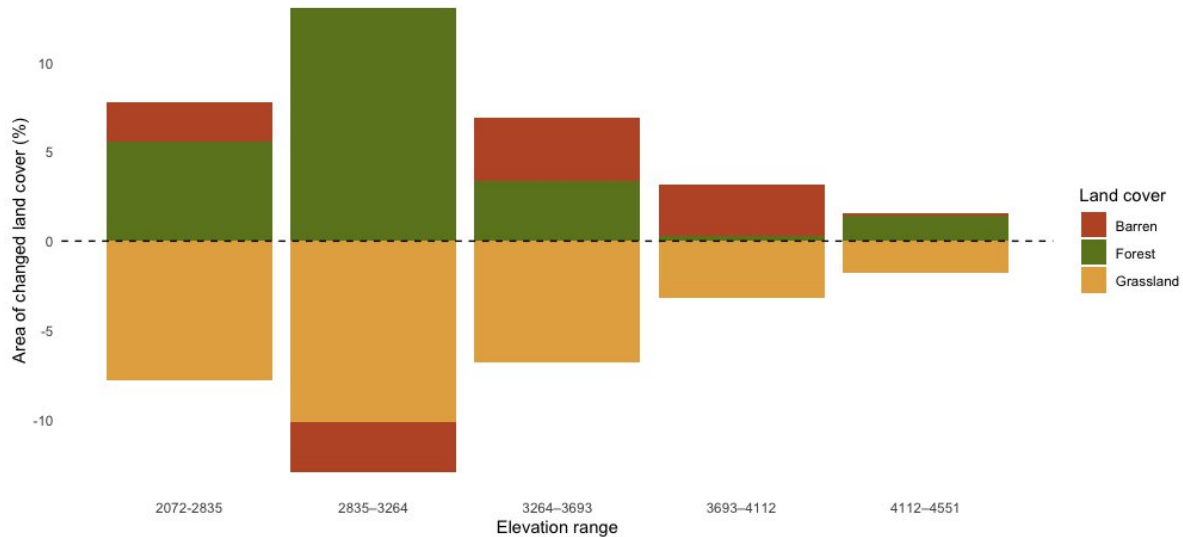


Figure 2.4. Proportional differences in cover of forests, bare/sparse vegetation and grasslands across elevation bands between 2001 and 2021. The proportion of changed land cover was calculated using the total count of pixels for each land cover class in each elevation band for 2001 and 2021. The difference in number of pixels between 2001 and 2021 was used to determine the area of change. Areal change for each land cover and study area was then divided by the total number of pixels in each band ($n_{band1}=9370$, $n_{band2}=15769$, $n_{band3}=18331$, $n_{band4}=11808$, $n_{band5}=1531$) and converted to percentages. The elevation bands include the elevation ranges across study areas and are organized from the lowest (1) to the highest (5). Positive values indicate increases in area over the study period.

Land cover change in relation to disturbance

All study areas were characterized by a net decrease in grasslands and increases in forested and barren areas between 2001 and 2021 (Figure 2.5). These changes appeared to co-vary with increasing anthropogenic pressures. The least disturbed site, i.e. the protected core zone of Naryn State Reserve, posted the smallest decline in grassland cover, which was 2-3 times less in absolute terms than the declines occurring at the two most disturbed sites (Figure 2.5). The patterns of increase in forest and barren cover mirrored each other, being lowest in the Naryn State Reserve and 2-4 times higher in areas with intermediate and high anthropogenic pressures (Figure 2.5).

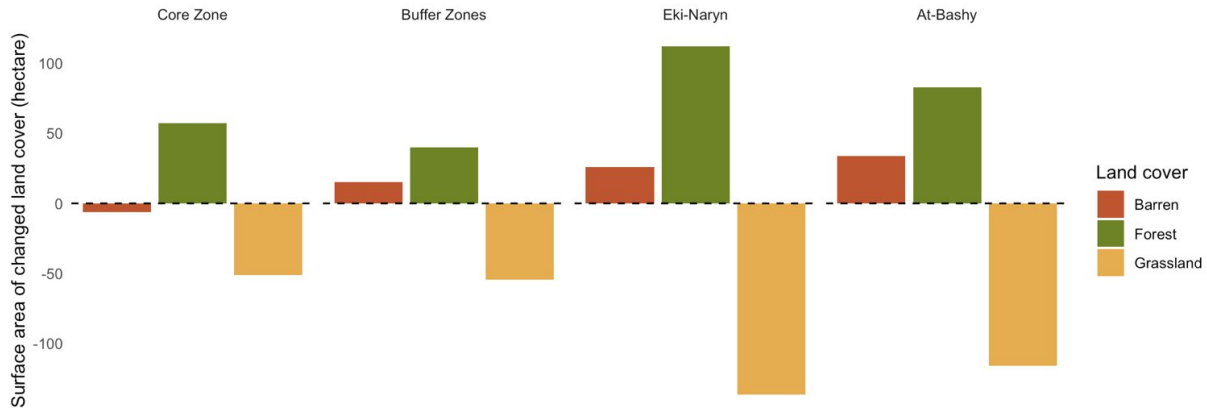


Figure 2.5 Change in spatial coverage of forested, barren and grassland areas between 2001 and 2021 in each study area. The proportion of changed land cover was calculated using the total count of pixels for each land cover class in each study area for 2001 and 2021. The area of change for each land cover and study area was then divided by the total number of pixels in each study area ($n_{\text{core}} = 7997$, $n_{\text{buffer}} = 14647$, $n_{\text{eki-naryn}} = 23118$, $n_{\text{at-bashy}} = 23146$) and converted to hectares.

Interacting factors determining trends in land cover change

Due to the large number of interactions included in the model, individual model coefficients are challenging to interpret and are only presented in Appendix A: Table A11. To facilitate the interpretation of the results, we ran post-hoc pairwise comparisons (using a Tukey adjustment for multiple comparisons) to answer biologically meaningful questions and present the results of these tests here. For each comparison, we indicate which levels of which variable are being compared. Unless otherwise indicated, the estimated effects for each level were marginalized over the levels of the other variables (e.g., estimated effects for different areas are averaged across years and elevations).

In general, more pixels transitioned to barren than to grasslands. Regardless of protection status, all areas experienced significantly more browning than greening when averaged across years and elevations (all pairwise contrasts between amount of browning and greening $p < 0.05$; Table 2.1).

There was no consistent pattern in the relative amount of browning and greening over time. In the five-year periods starting in 2005, 2009, and 2021, there were significantly higher

proportions of browning than greening ($p < 0.01$, $p < 0.001$, $p < 0.001$, respectively), while in the period starting in 2017 there was a shift to significantly more greening than browning ($p < 0.05$; Table 2.1). There was no significant difference in proportions of browning vs greening in the period starting in 2013 (Table 2.1). The relative differences in the amount of browning and greening were driven largely because of inter-period changes in the proportion of browning. The proportions of greening stayed relatively constant across periods in most elevations and areas (Figure 2.6).

Table 2.1 Total predicted percentages of browning and greening across areas with various degrees of disturbance (area), the five 5-year time-periods (year), and elevation bands (elevation). The significance of the difference is reported through p-values. Results for each variable are marginalized across levels of the other variable (e.g., the proportion of cells undergoing browning in the core is averaged across years and elevations). To improve readability, we colored cells with percentages significantly higher than their counterpart. Cells with significantly higher browning are colored in red, and those with significantly higher greening are colored in yellow. Cells included percentages that are not significantly different are left blank.

Variable	Level	Browning	Greening	p-value of pairwise comparison in transition type
Area	Core	3.5 %	2.4%	0.011
	Buffer	2.7 %	1.9%	0.007
	Eki-Naryn	4.1 %	2.5%	0.001
	At-Bashy	2 %	1.4%	0.013
Year	2005	3.7 %	2.3 %	0.001
	2009	4.2 %	1.9 %	< 0.001
	2013	2.3 %	1.9 %	0.155
	2017	1.4 %	2.4 %	0.011
	2021	3.5 %	1.5 %	< 0.001
Elevation	Band 1	3.6 %	2 %	0.003
	Band 2	2.7 %	1.7 %	0.021
	Band 3	3.8 %	2.8 %	0.084
	Band 4	2 %	1.3 %	0.013
	Band 5	0.7 %	0.3 %	0.031

Across most elevations, there was significantly more browning than greening (Table 2.1). However, there was a lot of variability in elevation patterns based on the area (Figure 2.6). For instance, in the core and buffer zones, the proportion of pixels changed peaked at intermediate elevations (pairwise contrasts between elevation band 3 and elevation bands 1

and 5 for both areas: $p < 0.05$; Appendix A: Table A14; Figure 2.6). In Eki-Naryn, the proportion of change was highest at low elevations (pairwise contrasts between elevation band 1 significantly different than elevation bands 4 and 5: $p < 0.001$; Appendix A: Table A14; Figure 2.6). At-Bashy had the lowest overall proportion of change and no consistent pattern across elevation.

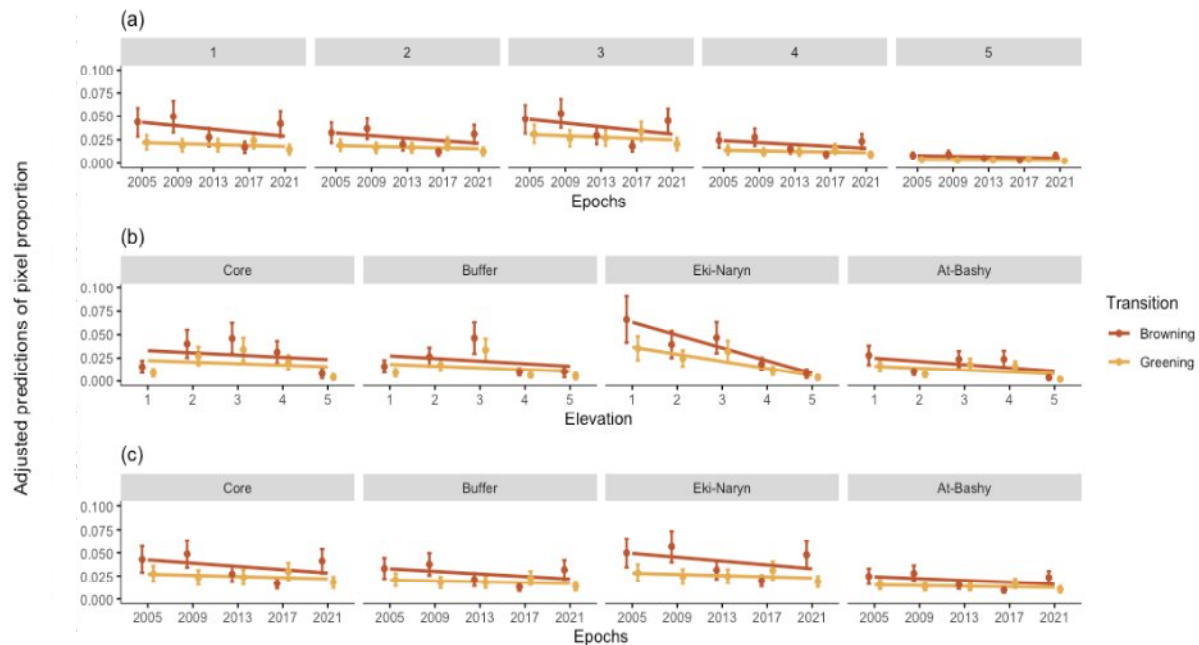


Figure 2.6 Adjusted mean predicted proportions of pixels that transitioned from grassland to barren (browning) and barren to grassland (greening). The transition types are reported in (a) each elevation band at each given time period, (b) each elevation band in each area, and (c) each study area at each given time period. The study areas are ordered along a gradient of anthropogenic pressures, with the least disturbed area on the left (core) to the most disturbed area on the right (At-Bashy). Points represent estimated marginal means based on the model, and error bars represent 95% confidence intervals. Linear regression lines are plotted to better visualize trends.

2.4. Discussion

With unprecedented pressures from anthropogenic activities and climate change directly challenging the productivity and dynamics of mountain habitats, it is crucial to understand localized responses to better inform local management. Yet, we are often limited by the large spatiotemporal resolutions required to characterize the responses. Here, we identified intermediate elevations, high degree of disturbances, and the interaction between the two as the main contributors of recent change in the cover of grasslands, forested and barren habitats, ultimately resulting in a net loss of grassland and increases in forests and barren areas. These findings were revealed by combining Landsat analysis-ready data (ARD) and the European Space Agency (ESA) world cover dataset in a way that is applicable to many data-poor, remote regions of the world.

Role of topography in current land cover distribution

Topography plays a crucial role in the distribution of terrestrial ecosystems (Chiu et al., 2020). We found elevation to be the most important predictor of forest, grassland and barren land cover types, which is consistent with the previously established relationships between elevation and thermal gradients that drive species' niche distribution in mountain ecosystems (Chauvier et al., 2021; Fang et al., 2024; Guo et al., 2018). Indeed, the increase in barren and sparse vegetation surface area as elevation increases directly links to abiotic conditions that limit the establishment of plant communities at altitudes beyond their physiological tolerance range (Körner & Diemer, 1987). While our results also suggest that elevation may explain the occurrence of barren areas at low elevations, we later explore the role anthropogenic pressures play in land cover distribution.

Aspect was also an important determinant of current grassland and forest distribution. Grasslands were mostly found on south-facing slopes with minimal terrain heterogeneity, while forested sites characterized north-facing slopes. Southern slopes are more exposed to solar radiation, providing grassland communities with greater opportunities to grow owing to warmer temperatures and prolonged foraging opportunities for herbivores. Warmer temperature also results in faster and complete snow melt, which improves the release of water at the beginning of the growing period and leads to the full exposure of the landscape to solar radiation

throughout the short growing season. In contrast, northern-facing slopes are less exposed to solar radiation, which leads to less extreme warm temperature and a longer establishment of snowpack that gradually melts through the year. The presence of snowpack provides shaded and moist microhabitats ideal for alpine tree and shrub species with less tolerance to drought (Måren et al., 2015; Verrall et al., 2023), leading to localized increased productivity and thermoregulation opportunities for wildlife.

While ruggedness and slope did not explain the distribution of grasslands, forests and barren areas in our study region, a more complex terrain heterogeneity has been shown to result in diverse topo climates, leading to niche differentiations and the establishment of diverse and highly specialized alpine communities (Antonelli et al., 2018). The evolution of plant traits adapted to a specific set of biotic and abiotic conditions increases the sensitivity of these communities to shifts in environmental conditions and anthropogenic pressures (Adler et al., 2014; Borchardt et al., 2013; Meineri et al., 2020). Thus, the inclusion of terrain heterogeneity and complexity remains important when disentangling the drivers of land cover distributions at more localized spatial scales and to better identify which parts of the landscape is more sensitive to shifts in climatic patterns and increased anthropogenic pressures. Using more accurate land cover classifications and topographic information at finer spatial resolutions may reveal patterns not detected at the current scale.

Magnitude of land cover changes over two decades

Perhaps our most surprising finding was that most pixels (~84%) retained the same dominant land cover between 2001 and 2021. This is contradictory to our prediction following the extensive report of pasture degradation in the area over the last decade (Domenech et al., 2022). The absence of field records limited our ability to evaluate whether grasslands were undergoing intra-state degradation, as highlighted in studies focusing on weed encroachment and the increase of unpalatable species. As such, these results are mostly indicative of a methodological bias.

However, a change of ~15 % in land cover types over 20 years in an arid ecosystem can still be considered important. A small proportion of pixels that changed land cover type

translated into an overall loss in grassland area and gains in forest and barren area. These losses and gains are modest in absolute terms: 339 ha of grassland were lost, while 65 ha of barren area and 274 ha of forest were gained. In general, more grassland was lost, and conversely forest and barren area gained, at lower to middle elevations (i.e. bands 1-3, < ~3,700 m), and along the gradient of increasing disturbance. These findings are consistent with the grassland degradation and desertification (Bardgett et al., 2021; Yan et al., 2023; M. Zhang et al., 2025) and the increase of forested areas observed worldwide (Robinov et al., 2021; Stockdale et al., 2019; Zhang et al., 2022) in montane regions.

A net increase in forested area is of interest because where it is occurring. The largest increases in forested areas occurred between 2835 m and 3693 m (i.e., bands 2 and 3), which coincides with the upper range limit of Schenk's spruce (3500 m; Zhang et al., 2016), the dominant species in Naryn forests. The expansion of Schrenk spruce within and beyond their known upper range limit suggests that warmer temperature may play a role in driving the upward shifts of treelines in the region, as reported in other alpine ecosystems (Dullinger et al., 2004; Hansson et al., 2021; Harsch et al., 2009; Qi et al., 2015; Wang et al., 2006). The sensitivity of Schrenk spruce to warmer temperature supports the hypothesis that higher elevations may be a climate refuge for the species (Qin et al., 2020, 2022; Zhang et al., 2016). Despite forest encroachment being considered negative in the context of grassland conservation, the increase of forested areas can be beneficial by providing new habitats for the local biodiversity and ecosystem services, such as forestry. The increase of forested areas mainly occurred on northern slopes where grazing by livestock was less important. This result highlights the role of grazing in limiting forest encroachment, and therefore grassland contraction in some areas.

Direction of land cover changes over two decades

Pixels that transitioned did so in a relatively predictable way, with most transitions occurring between grasslands and barren habitat types (browning vs greening). Although there was no significant effect of time, disturbance, or elevation, we observed a net increase of barren habitats across all study areas, at the exception of the highly protected core zone, which was the only area with a decrease in barren areas. The core zone was also characterized by the lowest loss of grasslands amongst all study areas, which indicates that, in the absence of direct anthropogenic pressures, grasslands may decline in response to the warming trends in the

country (Guo et al., 2018). Indeed, by including the core zone of the reserve, which does not include any livestock since 1983, we can better compare response to changes across study areas, and understand which changes are driven by grazing and/or shifts in thermal and precipitation regimes. Mild disturbances in the buffer zones yielded to similar loss of grasslands as in the protected core zone but the increase of barren areas indicate that even mild anthropogenic pressures may result in habitat degradation. Moreover, we found compelling evidence that increasing anthropogenic pressures lead to substantial browning, potentially amplifying already existing climate-driven impacts (Yang et al., 2023). However, and to our surprise, we found that areas with prolonged exposure to high degrees of anthropogenic disturbances, such as At-Bashy, were characterized by a lesser magnitude of land cover change and browning compared to Eki-Naryn, which is affected by intermediate levels of disturbances. Our observations suggest that prolonged exposure to high anthropogenic pressures continues to negatively impact grassland habitats, while promoting the expansion of barren and forested area, but less than in areas characterized by lower disturbance pressure. A comparison with recent records of pasture degradation in At-Bashy (Domenech et al., 2022) raises the question of whether the observed patterns align with preliminary signs of a regime shift within grasslands (Zhao et al., 2023).

Strengths and limitations of our approach

Changes in alpine plant communities in response to anthropogenic and climate-induced stressors tend to be subtle and gradual. Detecting and characterizing these changes require long-term and frequent observations at fine spatial resolutions. Our methods showcase the potential of using GLAD Landsat ARD (Potapov et al., 2020) to map and characterize localized land cover distribution and change since the late 1990s. The production of localized mapping and characterization of land cover distribution are particularly important in areas with limited records of plant traits and diversity. Although temporal gaps in Landsat imagery remain the main limitation in areas such as Naryn due to cloud cover and sensor failure (Roy et al., 2016), the GLAD Tools address this issue through gap-filling methods to improve data quality by generating cloud-free, multi-annual Landsat composites. Multi-annual composites can then be used to classify land cover over time, which we did retrospectively using a set of training data from ESA's 2021 land cover (Zanaga et al., 2022). In the absence of ground-truthing data (i.e., vegetation records at recorded locations, high resolution imagery) characterizing local land

cover types and distribution in 2021, the 10 m resolution of the ESA WorldCover provided the most accurate spatial characterization of land cover distribution across the landscape.

Combining ESA imagery, Landsat multi-annual composites and SRTM digital elevation models enabled us to establish a baseline characterization of topographic and land cover within each study area. This baseline then enabled us to dive deeper into the mechanisms and drivers of land cover change in alpine communities.

Nevertheless, there are some caveats to our approach. While we successfully identified the spatio-temporal distribution and variations in grasslands, forests and barren areas, the absence of site-specific environmental, species and community-level information limited our ability to locally validate land cover classification and detect mixed land cover types. To address this issue using remote sensing methods, an analysis including mixed pixels may drastically improve the detection of areas sensitive to change, and provide a more accurate depiction of the landscape dynamics over time and space (Hermosilla et al., 2022; Yang et al., 2017). Moreover, obtaining local maps of the historical and contemporary distribution of pastures based on their seasonal use would help delineate elevational ranges of interest to better map and characterize land cover dynamics based on known seasonal usage of the landscape. When characterizing land cover types in alpine regions, we highlight the importance of recognizing the variation in sample sizes between high and mid-elevations. Indeed, high elevations are characterized by smaller surface areas compared to the intermediate and low elevations, which is directly reflected in sampling effort (Appendix A: Table A2). The variation in surface area can drastically limit the detection, quantification and comparison of dynamics related to change and requires careful interpretation.

2.5. Conclusion

This study aimed to assess fine spatial-scale patterns of rangeland degradation using satellite imagery to classify, quantify and map land cover distribution over multiple decades, evaluating the influence of topography, anthropogenic disturbances and climate change (through proxies) on land cover dynamics. These objectives were successfully met through the development of a robust framework that identified elevation and northness as the primary topographic drivers of land cover distribution, along with the role of protected areas and mild anthropogenic disturbances in mitigating landscape degradation. While the combined used of

harmonized Landsat ARD imagery, ESA global land cover maps and digital elevation models at fine spatial scales provided valuable contemporary and historical landscape and habitat-level insights, future work must integrate a more nuanced pixel characterization, as habitats are often mosaics of vegetation types and land uses with gradual changes that do not conform to discrete categories. Collecting field data, such as comprehensive surveys of plant diversity, information on seasonal pasture types, site-specific disturbances and local weather will also be essential to accurately disentangle and identify the drivers of land cover change.

Chapter 3.

Wildlife cameras for plants: using motion-triggered wildlife data to monitor plant phenology

3.1. Introduction

Rapid shifts in climatic patterns, increasing frequency of extreme events and natural disasters, along with the growing human footprint and overexploitation of natural resources, continue to alter ecosystems around the world (Abbass et al., 2022; Weiskopf et al., 2020). High-elevation ecosystems are particularly sensitive to environmental changes and disturbances (Adler et al., 2024; Gerrard, 1991; Marston, 2008). The high seasonality of these regions results in long winters characterized by extreme temperature lows and prolonged snow cover, limiting foraging opportunities for herbivores, inducing dormancy and hibernation for many organisms while providing a layer of insulation for plants. In the spring, alpine plants rely on thermal cues and prolonged exposure to solar radiation to initiate growth, which will on average last for four months given sufficient precipitation and optimal temperatures (Körner, 2021). Plant phenology (i.e., the timing of seasonal life cycles such as bud break, leaf elongation, senescence), in turn, determines the patterns of activity of alpine herbivores. This synchrony between primary producers and consumers is critical to the persistence of alpine ecosystems (Dainese et al., 2024; Hamann et al., 2021; Richman et al., 2020).

There is a growing body of evidence highlighting the impact of climate change on phenology. For instance, warming temperatures have been associated with earlier starts of the growing season and delays in plant senescence in several alpine regions (Hassan et al., 2023; Möhl et al., 2022; Piao et al., 2011, 2019; Yin et al., 2023). Shifts in the timings of growth directly impact ecosystem productivity, structure and distribution of alpine plant communities (Testolin et al., 2021; Winkler et al., 2019; Zheng et al., 2024) with cascading effects on other trophic levels (Inouye, 2020). Along with shifts in phenologies, temperature increases across elevation gradients result in relative biodiversity loss, species range shifts from low to high elevations, increased competition and overall changes in community composition and

ecosystem functioning (Ding et al., 2022; Dullinger et al., 2004; N. Pepin et al., 2015; N. Pepin et al., 2022; Testolin et al., 2021; Zheng et al., 2024). In mountain landscapes historically and currently used by humans, climate-change-induced impacts are amplified by the history, intensity and scale of land use practices, leading to accelerated changes such as land degradation in a growing number of cases (FAO & UNCCD, 2022; Orr et al., 2024). While impacts of warming and land use on high-elevation ecosystems are often discussed in general terms at a global scale, it remains a challenge to predict how the phenologies of species in local and/or regional mountain areas will respond due to the difficulty in accessing and monitoring these complex, vast, remote, and rugged landscapes across the required spatial-temporal scales.

To date, field sampling and remote sensing are the most used methods to monitor and quantify vegetation responses to climate and land-use-induced changes. Field methods provide detailed information from the individual plant to the population-level at a specific time and location. As such, they are ideal to obtain the timing of specific events, as well as growth rates and other phenotypic traits at the individual level, which can help identify mechanisms and responses to a disturbance or variation in habitat conditions at a species, population or community level (Adler et al., 2014; Bjorkman et al., 2018; Borchardt et al., 2013; Meineri et al., 2020, 2020; Vandvik et al., 2022). However, the main challenge in alpine landscapes is to physically access remote and rugged areas, which directly limits the ability to frequently record localized vegetation and environmental metrics through field methods.

Open-access satellite imagery, on the other hand, provides coarser habitat (i.e., 30 m) to landscape-scale (i.e., 250 m to 1 km) information on vegetation dynamics, especially through tracking greenness as a proxy for plant growth, productivity and overall ecosystem health (S. Li et al., 2021). With the ability to go back in time several decades, depending on the sensor of choice, satellites can also reveal rates of change in the timings of start, peak and end of the growing season, the magnitude of growth and any variation in the spatial distribution of vegetation types at coarser spatial resolutions (e.g., from 30 m using Landsat sensors to 250 m, 500, and 1 km using MODIS sensors) on a weekly to biweekly basis (Cheng et al., 2020; de Beurs & Henebry, 2004; Ding et al., 2022; Eddy et al., 2017; Henebry & de Beurs, 2013; Melaas

et al., 2013; Wang et al., 2015). The combination of remote sensing and field sampling datasets, when available, is clearly optimal to obtain long-term data at the landscape scale while also knowing exactly what is on the ground at a specific time and place. However, when researcher presence in the field is difficult or impossible, there is a need for a tool with long temporal and high spatial resolutions to better track changes in plant phenology.

Camera traps are commonly used for multi-year, remote sampling of wildlife with motion-triggered sensors. To complement motion-triggered sensors, time-lapse imagery (e.g., an image taken at a fixed hourly, daily or weekly interval regardless of motion) is also used to monitor wildlife (Leorna & Brinkman, 2024) and detect when cameras become inactive (Hofmeester et al., 2020). Recent studies have highlighted how time-lapse images from camera traps can be used beyond wildlife monitoring to detect mismatches in species phenology (Hofmeester et al., 2020), simultaneously monitor wildlife activity and vegetation dynamics (Sun et al., 2021) or quantify abiotic conditions such as snow (Alison et al., 2024; Breen et al., 2023). While the production of time-lapse imagery in camera trap projects has become more common (Swann et al., 2011), the majority of past and contemporary camera trapping projects around the world continue to solely use motion-triggered images (Burton et al., 2015). To date, there are more than 68 million wildlife images that have been generated by 160 000 cameras spread across 110 countries (Wildlife Insights February 2025). Finding a way to extract biotic information, such as plant phenology, and abiotic variables (e.g., temperature, snow) from motion-triggered images would lead to an unprecedented data trove that can help document the effects of environmental change.

The aim of our study was to establish the reliability of motion-triggered images as a potential data source to track plant phenology. To do so, we used cameras deployed for snow leopard population assessments in Naryn, Kyrgyzstan (OSI-Panthera, 2016-2023) to quantify the main timings of the growing season in alpine grasslands. We developed a framework to 1) automate the extraction of images closest to noon, 2) extract vegetation indices, and 3) filter the data to optimize the detection of the start, peak and end of the growing season (i.e., phenophases). Moreover, we included steps to compare time-series obtained from camera traps with Landsat imagery to corroborate our observations and evaluate how the simultaneous

use of both methods can help us detect vegetation dynamics in areas with limited to no field studies. We provide a clear step-by-step methodology as well as an overall estimation of the sampling effort required for this method to be successful in quantifying the phenophases and the duration of the growing season, providing a workflow that can then be applied in any ecosystem with already-deployed camera traps.

3.2. Material and Methods

3.2.1. Study area

The Naryn State Reserve in central Kyrgyzstan (41°25'50"N, 76°35'11"E) is a 1,080 km² reserve created in 1972 as a multi-use sanctuary (zakaznik), with a ban on hunting to protect elk populations (*Cervus elaphus*) (Farrington, 2005) (Figure 3.1). In 1983, the sanctuary became a state nature reserve (zapovednik), which further enforced regulations to ensure the preservation, conservation and restoration of the ecosystem while providing research and educational opportunities. The reserve presents two types of management: a fully protected core zone located south of the Naryn riverbanks, and two large multi-use buffer zones located north and south of the core zone (Figure 3.1c). The core zone ranges from 2,379 m to 4,470 m in elevation, and it is mostly characterized by north-facing slopes only accessible by rangers and research teams since 1983. The buffer zones, however, have historically been shaped by intense livestock grazing and forestry. Signs of degradation and soil erosion from the Soviet occupation era until the 1990s were still visible in the 2000s (Farrington, 2005), and the buffer zones continue to be used for subsistence-based herding to this day (OSI-Panthera, personal communication). Tian Shan mountain ash (*Sorbus tianshanica*) and Schrenk's spruce (*Picea schrenkiana*) constitute most of the forest cover, along with grasslands, barren lands and glaciers as main habitat types. The degree of disturbance is considered moderate in the buffer zones (Chapter 2).

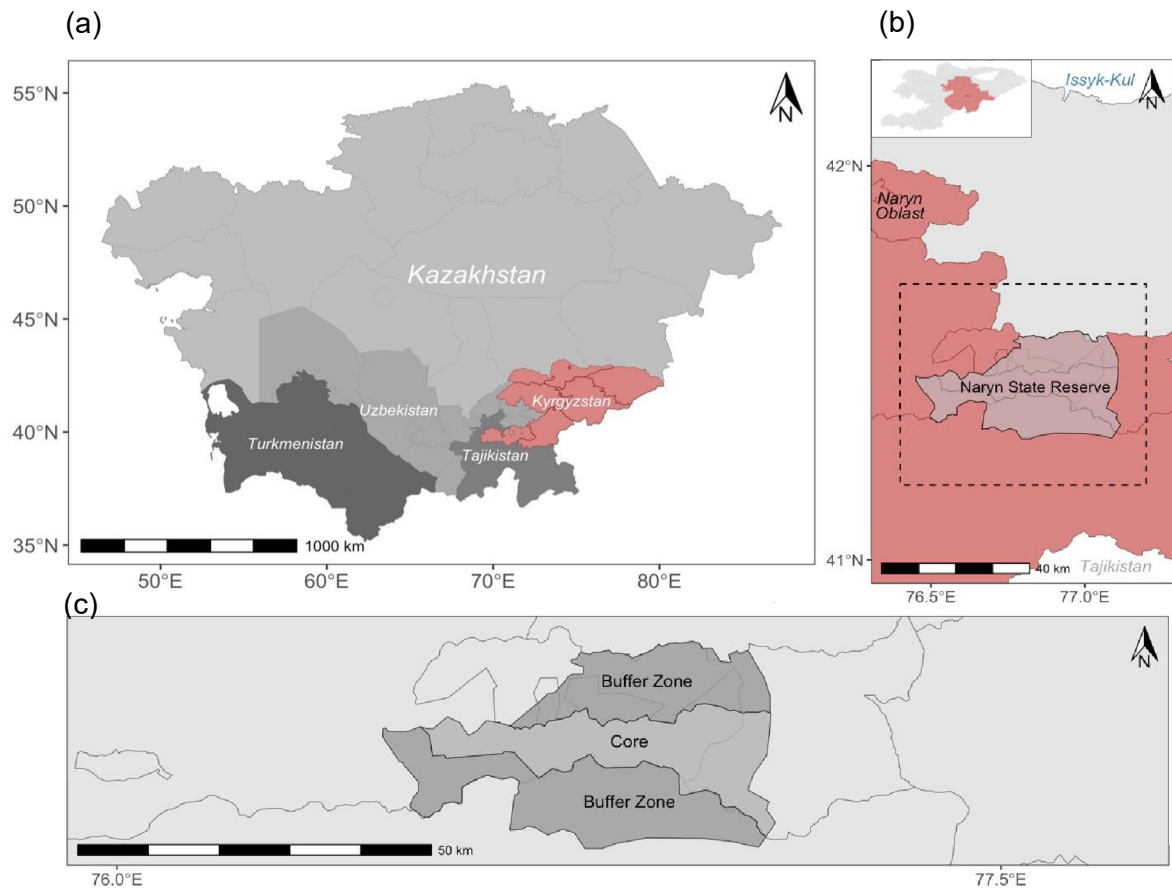


Figure 3.1 (a) Location of Kyrgyzstan (red) in Central Asia. (b) The study area in Kyrgyzstan's Naryn Oblast (red) including the Naryn State Reserve. (c) The location of the core and buffer zones within the Naryn State Reserve.

3.2.2. Geospatial data

Camera traps

To determine the potential use of motion-triggered images to track grassland phenology, we used images generated by 12 Bushnell cameras (E, E2 and E3) and 3 Browning (SPEC)

cameras deployed across 10 locations with vegetation within the Naryn State Reserve (Figure 3.2). Deployed between 2016 and 2023 by the non-governmental organisation Objectif Science International (OSI) Panthera, these cameras were set to detect snow leopards (*Panthera uncia*). With a minimum of one active camera in 2016 to a maximum of nine active cameras in 2021 (Table 3.1), each camera was deployed at elevations between 2,630 m and 4,082 m in optimal snow leopard habitat. All active cameras were at least 5 km apart (Sharma et al., 2014) and attached to rocks between 50 to 150 cm above the ground, depending on the targeted field of view and available landscape features. The preferred field of views to capture snow leopards included open field of views, particularly ridgelines (Figure 3.3a) and marking sites like boulders (Figure 3.3b,c). To address the difference in detecting greenness from tall, grass-dominated vegetation and short, cushion-like vegetation, we differentiated between sites with visually distinct vegetation characteristics. We categorized sites dominated by continuous, grass-like vegetation cover as ‘meadow’ (Figures 3.2, 3.3b), and sites with exposed bare ground, discontinuous, short, vegetation cover as ‘steppe’ (Figures 3.2, 3.3a,c). Due to the absence of available local plant inventories at each camera location, these labels are not intended to represent official vegetation classifications. Once the images were renamed and filtered for metadata issues (e.g., wrong dates; false GPS location), we automated the extraction at each camera site of the three images closest to 12:00 for every available day. We selected 12:00 as our reference time to obtain images with similar sun angles and to allow our dataset to be comparable to other datasets used to track plant phenology (Hofmeester et al., 2020). The extraction of these images was done using R (v.4.4.4) (R Core Team, 2022) (Table 3.1, Figure 3.4; Appendix B: Figure B1). Because the camera traps were triggered by wildlife movement, which often led to obstructions in the field of view, using multiple images per day allowed us to filter out poor-quality data and compute multiple daily greenness estimates to improve data reliability. For each location, we organized the daily images per year and separated images in various deployments. Each deployment started when the camera was initially deployed and ended following shifted fields of view by wildlife or camera controls. Sites with more than one month of temporal coverage were included for phenological analyses, resulting in a total of five ‘steppe’ and four ‘meadow’ locations (Figure 3.4).

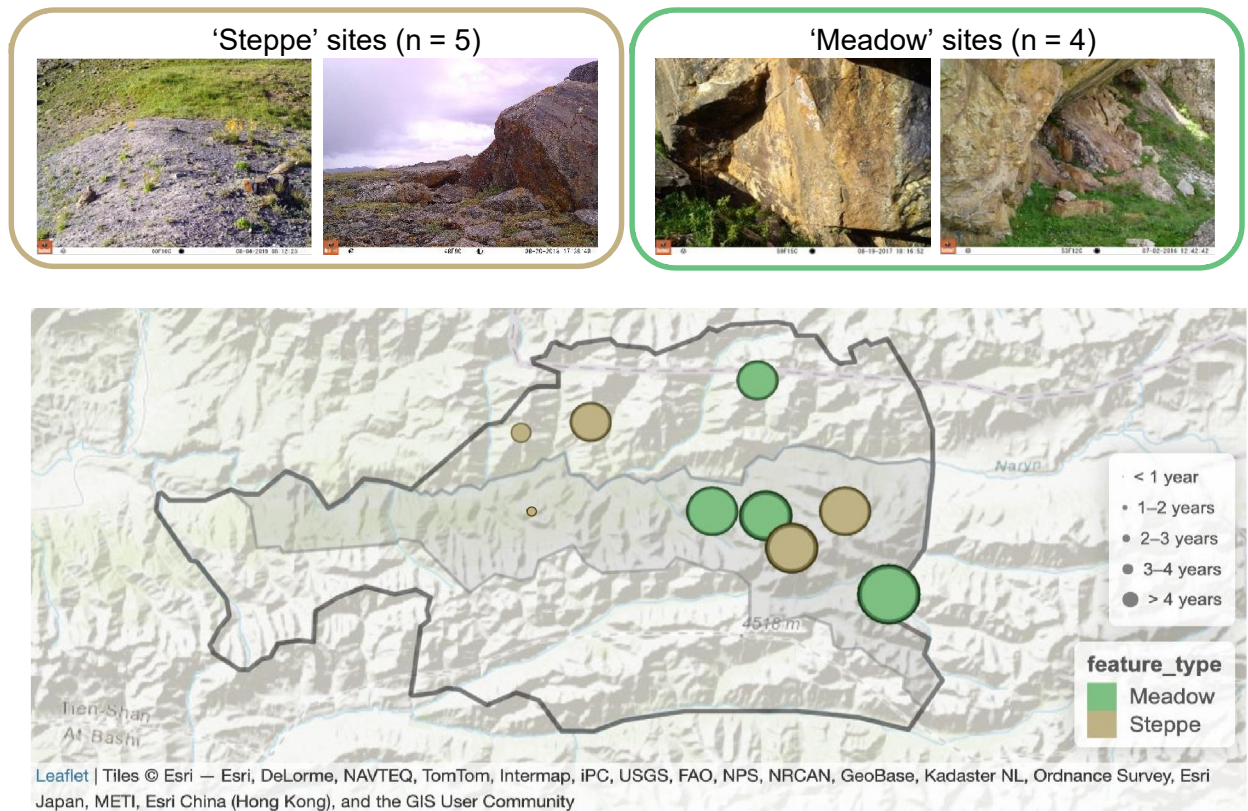


Figure 3.2. Location of camera traps between 2016 and 2023 within the Naryn State Reserve boundaries (black polygon), Kyrgyzstan. Each location is classified based on the vegetation features, with sites dominated by continuous cover of grass-like species classified as 'meadow' (green) and sites with exposed bare ground and discontinuous, short, vegetation cover as 'steppe' (tan). The size of each circle indicates the number of days recorded at each site, with larger circles indicative of higher sampling effort (see Table 1 for sample sizes). The 'meadow' site with the camera facing a boulder, as presented on the left image example, was characterized as a 'meadow' based on the type of vegetation observed on the various camera trap field of views throughout the years and other photos from the site from OSI-Panthera. While vegetation is minimal in this field of view, vegetation growth was obvious throughout the years.

Table 3.1. Summary of camera trap deployments across study sites and years in the Naryn State Reserve, Kyrgyzstan. For each study site and year, the table reports the number of active cameras, the number of cameras in 'meadow' and 'steppe' sites, the total number of images recorded per year and the number of images generated from filtering images the closest to noon used in the phenological analysis. * Removed sites due to insufficient temporal coverage.

	2016	2017	2018	2019	2020	2021	2022	2023
Total number of active cameras	1	5	6	7	6	9	8	5
Total number of sites	1	5	6	7	5	7	7	5
Number of sites removed*	0	0	1	0	0	0	0	0
Number of 'meadow' sites	1	3	3	4	2	2	3	2
Number of 'steppe' sites	0	2	2	3	2	5	4	3
Total number of images	966	5589	16916	21476	10942	25774	35269	11092
Total number of images closest to noon	179	920	2040	2393	1665	2016	2470	1341



Figure 3.3 Examples of habitat features targeted by camera traps in the Naryn State Reserve, Kyrgyzstan: (a) open field of view, (b) marking meadow site and (c) steppe marking/ridgeline site. Examples of drawn regions of interest (ROIs) are included as red polygons in each image. The examples also showcase the difference in images captured by Browning (a) and Bushnell models (b,c). Several regions of interest to sample were drawn for areas with discontinued, close to the ground, vegetation cover (c).

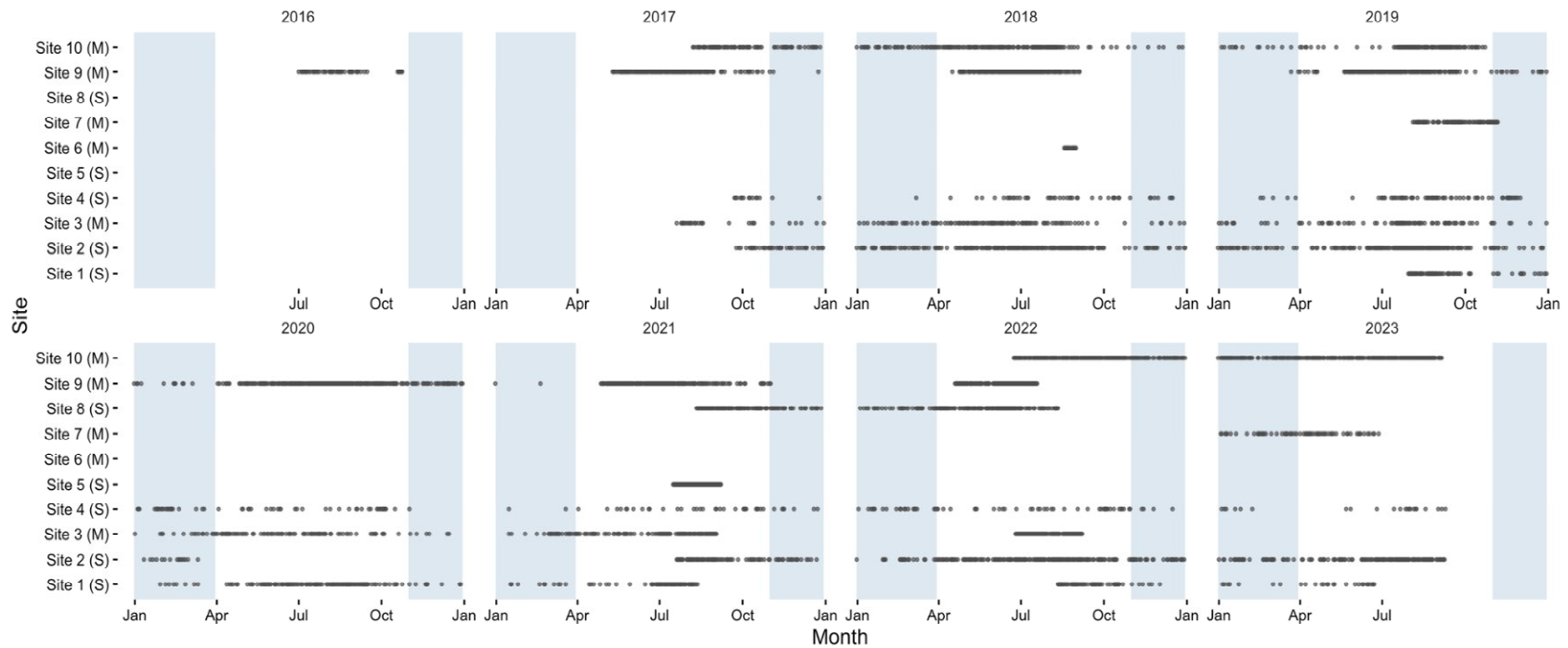


Figure 3.4 Daily sampling effort across sites and years, presented as the number of days per year the cameras deployed at each site in the Naryn State Reserve, Kyrgyzstan, were triggered. Each row corresponds to a study site characterized as ‘meadow’ (M) or ‘steppe’ (S). Blue shaded areas indicate winter periods (31 October to 1 April), to help visualize sampling efforts during the growing season. The number of days with detections at each site per year is given alongside the corresponding row to indicate the sampling effort. Site 6 (M) was active for 13 days in 2018 and therefore removed from further analyses

3.2.3. Landsat data source

To characterize and track changes in greenness at a larger scale (i.e., 30 m x 30 m pixels) and compare these observations to camera trap data (i.e., plot scale, usually 15 m x 15 m unless facing a boulder or an open landscape), we used open-source 16-day 30 m Landsat Analysis Ready Data (ARD) composites provided by the Global Land Analysis and Discovery (GLAD) team at the University of Maryland. The Landsat ARD provides normalized surface reflectance from 1997 to present by combining and harmonizing Landsat 5 (TM), 7 (ETM+) and 8 (OLI/TIRS) collection 2. We downloaded the Landsat ARD imagery using GLAD Tools, a user-friendly software package developed by the GLAD team to allow users to conduct various analyses and pre-processing steps to the ARD (Potapov et al., 2020). We downloaded the Landsat ARD imagery from 1 January 2016 to 18 December 2023 to match the timeframe of the camera trap data. For each Landsat pixel where a camera was located, we extracted the surface reflectance values for the visible (red (R), green (G), blue (B)) and near-infrared bands (NIR).

3.2.4. Generate random points

To obtain a broader characterization of greenness dynamics across the Naryn State Reserve, we selected the minimum (2630 m) and maximum (4082 m) elevations at which cameras were deployed. We then randomly extracted 1% of the Landsat pixels available within this elevation range, with each pixel characterized by a spatial resolution of 30 m (0.00025° x 0.00025°), producing a total sample size of 21,352 pixels (Appendix B: Figure B2).

3.2.5. Quantifying Vegetation Dynamics

Extraction of RGB digital numbers

Using the *Phenopix* package (Filippa et al., 2016), we delineated one or multiple polygons as regions of interest (ROI; Figure 3.4) for each camera trap deployment. The region of interest (ROI) is used by *Phenopix* to extract the RGB digital numbers for each pixel within the defined polygon to provide averaged RGB curves for each ROI per image. We ensured that the surface area covering the targeted landscape features was relatively equivalent between years for sites with limited change in the field of view of the camera. Sites with different field of views from one year to another included different ROIs, leading to further inter-annual variability.

Vegetation Indices

To detect the start, peak, end and duration of the growing season, we converted the RGB digital numbers to a vegetation index at each location. Chromatic coordinates are useful metrics to characterize vegetation and seasonal variation. For instance, the green chromatic coordinate (GCC; Equation 1) is particularly used to directly detect plant phenology and quantify the transition between phenophases (Burke & Rundquist, 2021; Sonnentag et al., 2012; Toomey et al., 2015). Here, we focused on vegetation indices that could be calculated using the visible spectrum (RGB), as camera trap images do not include the near-infrared (NIR) bands necessary to generate the normalized difference vegetation (NDVI; Equation 2) index obtainable from satellite imagery.

$$GCC = \frac{Gdn}{(Gdn + Rdn + Bdn)} \quad (1)$$

$$NDVI = \frac{NIR - Red}{NIR + Red} \quad (2)$$

Moreover, we compared the ability of Landsat imagery to detect greenness dynamics by also calculating the maximum bi-weekly NDVI and comparing the ability of the model to predict accurate key timings between maximum GCC and NDVI (Appendix B: Figure B3)

Analyses and Filtering

To characterize greenness dynamics across the study area using camera traps and Landsat imagery, we used the Phenomix package to predict the annual start (day of year on which 25% of the growing season has occurred), peak (day of year on which 50% of the growing season has occurred), end (day of year on which 75% of the growing season has occurred) and duration of the growing season (number of days between the 25th and 75th percentiles) (Wilson et al., 2023) in R (v. 4.4.4).

Given the temporal sparsity of the camera trap data, we applied the same modelling framework from Phenomix to four different filtered sets of the data to 1) evaluate the type and amount of data required for the model to converge and predict meaningful estimates, and 2) compare the model's ability to detect the main phenological events in the growing season across sites with varying vegetation types and cover, using sparse temporal data. We pooled sites by vegetation type (i.e., meadow vs steppe), generating one GCC time-series per year for all meadow sites combined and, separately, all steppe sites combined. Lastly, we selected one meadow site and one steppe site with the most consistent and extensive temporal coverage across years to assess the feasibility of detecting the key timings of the growing season at individual sites. To enable direct comparison, the same filtering and modelling stages (described below) were applied to Landsat data. While we expected to observe variation in the timings of phenological events across the elevational gradient, we were unable to perform this analysis due to the spatial and temporal sparsity of data across elevations (Appendix B, Figure B4).

Filtering stages

For each GCC time-series generated, we selected the averaged maximum GCC value for each day of the year (DOY). To limit long tails in the distribution of GCC values, we filtered the time-series to include days between early April (DOY ~ 100) and late October (DOY ~ 300) to best capture the growing season and to omit any night image between 19:00 and 7:00. To clearly see vegetation, we also limited noise in the data by filtering any over- or under-exposed images caused by varying solar exposure and sensor issues. We visually compared extreme low and high brightness values extracted from Phenomix with their corresponding image and identified thresholds to target valid images. As a result, we kept images with brightness values constrained between 100 and 580. We selected years with sufficient data quality and data coverage for the entire growing season, resulting in 1,043 observations between 2016 and 2023 across all meadow sites ($n = 4$), 689 observations between 2018 and 2023 across all steppe

sites ($n = 5$), 553 observations between 2017 and 2021 at a single meadow site (Site 9) and 443 observations between 2018 and 2023 at a single steppe site (Site 2) (Appendix B, Figure B5, Table B1). The annual sampling effort using bi-weekly Landsat data at each site ranged between 20 and 23 annual data points (Appendix B: Table B2).

Model

The *Phenomix* package fits data to a hierarchical model with annual and inter-annual levels fit in the maximum likelihood framework to estimate annual (i.e., start, peak, end) and inter-annual (i.e., rate of change) phenology. While we focused on predicting annual estimates of the growing season, the hierarchical model leverages data across years to improve the precision of those annual estimates. The annual level of the model is fit with a single user-selected distribution, error distribution and maximum greenness estimates averaged for each day the camera was triggered, producing an irregular, event-driven time-series at each location. We compared models with four different data distributions (i.e., asymmetric and symmetric Gaussian and Student's t) and two error distributions (i.e., Gaussian and lognormal). We fit GCC data from camera trap and bi-weekly Landsat datasets and prioritized models that produced ecologically meaningful predictions of start, peak, end, and duration for each year, site and site type (i.e., meadow or steppe). Indeed, most models with the lowest Akaike information criterion corrected for small sample size values failed to capture realistic timings of phenophases in the data.

3.3. Results

3.3.1. Quantifying Vegetation Dynamics

Estimated timing of growing season phenophases

Meadow sites

We found symmetric models to best fit the data. Gaussian distribution with lognormal errors statistically best fitted the meadow sites data between 2016 and 2023, but the estimated timings of phenological events for the four meadow sites for 2016 and 2023 were, on average, associated with more uncertainty due to incomplete sampling years (Figure 3.5).

The start of the growing season was predicted to occur, on average, on 16 May (DOY 136 ± 6) across the four meadow sites and on 27 May (DOY 148 ± 2) at the single meadow site (Site 9) (Figure 3.5). The average annual peak was relatively similar between all meadow sites combined and Site 9, with predicted dates of 19 July (DOY_{meadow} 200 ± 3) and 21 July (DOY_{Site9} 202 ± 2), respectively (Figure 3.5). The end of the growing season was predicted to occur, on average, on 20 September (DOY 264 ± 6) across all meadow sites, and 7 days earlier (DOY 257 ± 2) at Site 9 (Figure 3.5). The duration of the growing season ranged from 94 (± 2 days) to 189 days (± 29) across all meadow sites, which is more than a month longer in some years than the duration estimated at Site 9 (94 ± 2 days and $118 \text{ days} \pm 4$). The year 2022 was characterized by an unusually short growing season compared to previous years (Table 3.2). While the modelled predictions from pooling the four meadow sites together highlight a greater inter-annual variation in the timings of the growing season, we did not detect a trend towards a general increase or decrease of the length of the growing season over time. The site-specific analysis at Site 9 showed a consistent increase (Figure 3.5; Table 3.2).

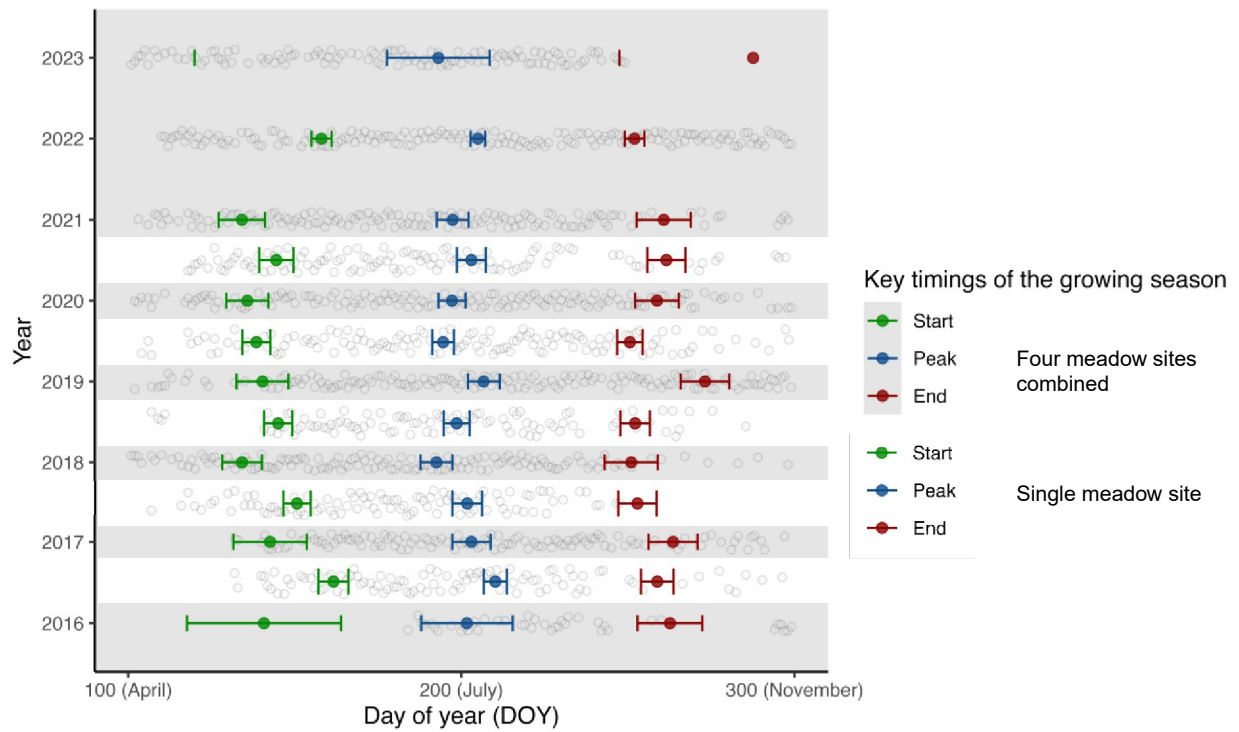


Figure 3.5 Predicted timings of phenophases across the four, pooled meadow sites (shaded rows) and a single meadow site (Site 9; unshaded rows) in the Naryn State Reserve, Kyrgyzstan, with their associated predicted distributions from 2016 to 2023 for the four meadow sites, and 2017-2021 for the single meadow site. The daily model predictions of GCC values for each day of available data within each dataset are represented by grey points within the rows. Coloured error bars and points indicate the start (25th percentile; green), peak (blue), and end (75th percentile; red) of the growing season and their associated standard deviations. Annual sample sizes are reported in Appendix B, Table B1.

Table 3.2 Model predictions for the timing of phenophases (start, peak and end; see Methods for definitions) from camera traps deployed in the Naryn State Reserve, Kyrgyzstan, and from Landsat GCC and NDVI values extracted at each randomly selected pixels across the Naryn State Reserve. “All meadow” refers to all meadow sites pooled (n = 4); “Site 9” refers to a single meadow site with the most extensive temporal coverage across years; “Random points” refers to the Landsat data across the Naryn State Reserve. The duration of the growing season is reported in number of days. The timing of phenophases is reported as day of the year (DOY) with associated standard deviation.

Year	Data Source	Site	start	peak	end	Duration
			DOY $\pm$ sd	DOY $\pm$ sd	DOY $\pm$ sd	Number of days
2016	CT	All meadow	141 $\pm$ 12	202 $\pm$ 7	263 $\pm$ 5	122 $\pm$ 12
	CT	Site 9	-	-	-	-
	Landsat GCC	All meadow	154 $\pm$ 4	213 $\pm$ 4	272 $\pm$ 6	119 $\pm$ 6
	Landsat GCC	Random points	146 $\pm$ 22	226 $\pm$ 20	305 $\pm$ 34	159 $\pm$ 41
	Landsat NDVI	All meadow	185 $\pm$ 6	221 $\pm$ 7	258 $\pm$ 10	73 $\pm$ 8
	Landsat NDVI	Site 9	143 $\pm$ 16	205 $\pm$ 17	266 $\pm$ 22	123 $\pm$ 15
	Landsat NDVI	Random points	92 $\pm$ 10	174 $\pm$ 8	256 $\pm$ 11	164 $\pm$ 13
2017	CT	All meadow	134 $\pm$ 3	193 $\pm$ 2	264 $\pm$ 4	121 $\pm$ 8
	CT	Site 9	162 $\pm$ 2	211 $\pm$ 2	253 $\pm$ 3	98 $\pm$ 3
	Landsat GCC	All meadow	152 $\pm$ 4	212 $\pm$ 4	271 $\pm$ 5	119 $\pm$ 6
	Landsat GCC	Random points	149 $\pm$ 19	222 $\pm$ 17	295 $\pm$ 29	145 $\pm$ 35
	Landsat NDVI	All meadow	183 $\pm$ 5	218 $\pm$ 6	254 $\pm$ 8	71 $\pm$ 7
	Landsat NDVI	Site 9	158 $\pm$ 7	211 $\pm$ 4	265 $\pm$ 8	110 $\pm$ 14
	Landsat NDVI	Random points	138 $\pm$ 7	211 $\pm$ 7	283 $\pm$ 10	146 $\pm$ 10
2018	CT	All meadow	134 $\pm$ 3	193 $\pm$ 2	251 $\pm$ 4	117 $\pm$ 5
	CT	Site 9	151 $\pm$ 2	202 $\pm$ 2	253 $\pm$ 3	103 $\pm$ 2
	Landsat GCC	All meadow	151 $\pm$ 3	211 $\pm$ 3	270 $\pm$ 5	119 $\pm$ 6
	Landsat GCC	Random points	153 $\pm$ 15	218 $\pm$ 14	284 $\pm$ 24	131 $\pm$ 29
	Landsat NDVI	All meadow	181 $\pm$ 4	216 $\pm$ 5	250 $\pm$ 7	69 $\pm$ 6
	Landsat NDVI	Site 9	152 $\pm$ 4	206 $\pm$ 3	260 $\pm$ 5	108 $\pm$ 8
	Landsat NDVI	Random points	123 $\pm$ 6	193 $\pm$ 6	264 $\pm$ 9	141 $\pm$ 9
2019	CT	All meadow	140 $\pm$ 4	207 $\pm$ 2	273 $\pm$ 4	133 $\pm$ 6
	CT	Site 9	145 $\pm$ 2	199 $\pm$ 2	253 $\pm$ 2	108 $\pm$ 2
	Landsat GCC	All meadow	150 $\pm$ 3	209 $\pm$ 3	269 $\pm$ 4	119 $\pm$ 6
	Landsat GCC	Random points	156 $\pm$ 12	215 $\pm$ 11	274 $\pm$ 19	118 $\pm$ 23
	Landsat NDVI	All meadow	180 $\pm$ 3	213 $\pm$ 4	246 $\pm$ 5	67 $\pm$ 5
	Landsat NDVI	Site 9	149 $\pm$ 3	201 $\pm$ 2	252 $\pm$ 4	102 $\pm$ 6
	Landsat NDVI	Random points	130 $\pm$ 7	208 $\pm$ 8	287 $\pm$ 11	157 $\pm$ 11
2020	CT	All meadow	136 $\pm$ 3	197 $\pm$ 2	259 $\pm$ 3	123 $\pm$ 5
	CT	Site 9	139 $\pm$ 2	195 $\pm$ 2	251 $\pm$ 2	113 $\pm$ 2

2021	Landsat GCC	All meadow	144 ± 3	208 ± 3	267 ± 4	119 ± 6
	Landsat GCC	Random points	159 ± 9	211 ± 8	263 ± 14	104 ± 17
	Landsat NDVI	All meadow	178 ± 3	210 ± 3	243 ± 5	65 ± 4
	Landsat NDVI	Site 9	144 ± 4	196 ± 1	248 ± 4	104 ± 7
	Landsat NDVI	Random points	107 ± 10	199 ± 9	291 ± 14	184 ± 15
	CT	All meadow	134 ± 4	197 ± 2	261 ± 4	127 ± 6
	CT	Site 9	145 ± 3	203 ± 2	262 ± 3	117 ± 3
	Landsat GCC	All meadow	147 ± 4	208 ± 3	266 ± 5	119 ± 6
	Landsat GCC	Random points	162 ± 6	208 ± 6	253 ± 10	91 ± 12
	Landsat NDVI	All meadow	176 ± 3	207 ± 3	239 ± 4	63 ± 4
	Landsat NDVI	Site 9	150 ± 3	191 ± 2	231 ± 2	81 ± 3
	Landsat NDVI	Random points	116 ± 11	211 ± 10	307 ± 15	191 ± 16
	CT	All meadow	158 ± 2	205 ± 1	252 ± 2	94 ± 2
	CT	Site 9	-	-	-	-
2022	Landsat GCC	All meadow	146 ± 4	205 ± 4	265 ± 5	119 ± 6
	Landsat GCC	Random points	166 ± 6	204 ± 5	243 ± 7	77 ± 8
	Landsat NDVI	All meadow	174 ± 4	205 ± 4	235 ± 5	61 ± 5
	Landsat NDVI	Site 9	154 ± 2	186 ± 2	218 ± 4	64 ± 4
	Landsat NDVI	Random points	92 ± 12	189 ± 12	287 ± 17	195 ± 18
	CT	All meadow	99 ± 11	193 ± 8	288 ± 20	189 ± 29
	CT	Site 9	-	-	-	-
	Landsat GCC	All meadow	145 ± 5	204 ± 4	264 ± 6	119 ± 6
2023	Landsat GCC	Random points	169 ± 7	201 ± 6	232 ± 7	64 ± 8
	Landsat NDVI	All meadow	173 ± 5	202 ± 5	231 ± 6	58 ± 6
	Landsat NDVI	Site 9	-	-	-	-
	Landsat NDVI	Random points	136 ± 9	223 ± 11	311 ± 17	175 ± 16

Steppe sites

Despite the use of multiple models and selecting years with the most consistent temporal data coverage, all models failed to converge and did not produce reliable estimates of the key growing season phenophases across steppe sites.

3.3.2. Comparison with Landsat imagery

Signal detection of Landsat GCC and NDVI

Modelling the maximum bi-weekly Landsat GCC values (Appendix B: Figure B3) resulted in the prediction of all three phenophases for the four meadow sites and across random points (Table 3.2). The comparison of predicted timings across the four meadow sites using camera trap and Landsat GCC time series camera traps showed the predicted timings to occur within a couple weeks from each other for most years, with the exception of 2023 where the timings were further apart from each other (Table 3.2). Models fitted to Landsat GCC data from Site 9 did not converge. The model generated reasonable predictions of annual phenophases using NDVI as our main response for each of the three datasets by fitting a Gaussian distribution with lognormal errors.

Landsat NDVI trends

Based on the NDVI from random points selected within the Naryn State Reserve ($n = 21,352$), the duration of the growing season increased across the years (from 141 to 195 days) but with moderate to high uncertainty (± 9 -18 days, on average) for all years (Figure 3.6). The duration of the growing season became consistently shorter on average, as the scale of the data decreased (Figure 3.6). For example, the shortest duration was found at Site 9 (109 ± 9 days), followed by the four meadow sites (136 ± 11 days) and the Naryn State Reserve (195 ± 10). Averaged across all years, the start, peak and end of the growing season occurred on 17 April (DOY 117 ± 9), 20 July (DOY 201 ± 9), and 13 October (DOY 286 ± 13), respectively. Although no consistent shifts in seasonal timings were observed, the Naryn State Reserve was usually characterized by earlier start and peak, and a later end compared to the four meadow sites and Site 9 (Figure 3.6). The year 2016 was an exception, with the end of the season for the reserve predicted on 12 September (DOY 256 ± 11) instead of 21 September (DOY 265 ± 8) for Site 9 and 14 October (DOY 258 ± 10) for the four meadow sites combined. The reserve-wide timing of peak in 2016 was also unusually early (22 June, DOY 174 ± 8) compared to the estimated peak times across other years, which usually occurred late July (Table 3.2). Overall,

there was a high degree of uncertainty associated with random points predictions using Landsat data compared to analyses performed on smaller datasets.

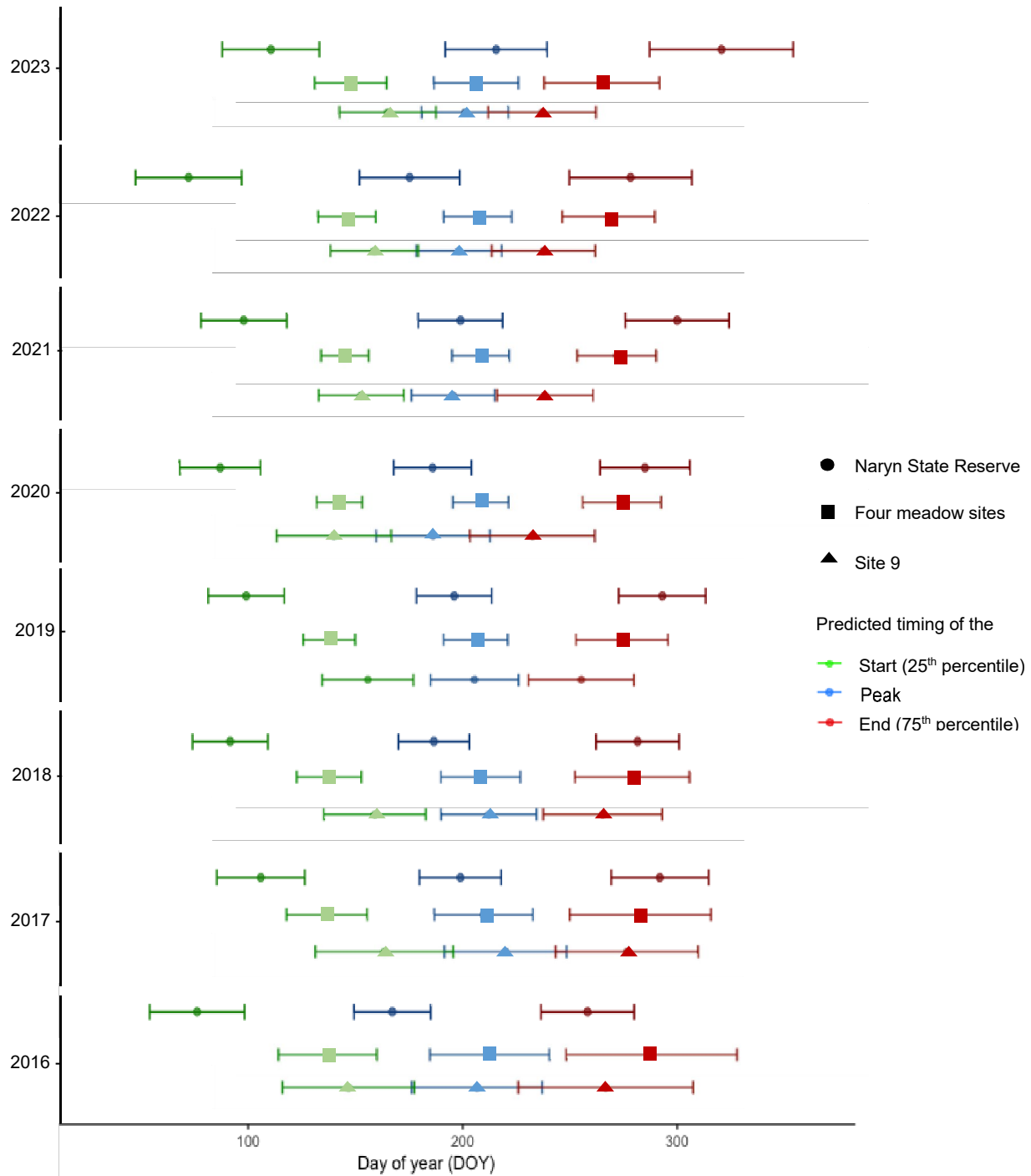


Figure 3.6 Annual variation in the predicted timings of the growing season using Landsat NDVI across the Naryn State Reserve (dots), the four meadow sites (squares), and Site 9 (triangles).

Comparison of Landsat NDVI and camera trap GCC trends

The predicted timings of the start of the growing season modelled from Landsat NDVI usually occurred ~2 months later than the timing predicted by camera traps (Table 3.2, Figure 3.7). In contrast, the end was usually estimated to occur 2-3 months earlier with Landsat data compared to camera traps (Table 3.2, Figure 3.7). Both Landsat and camera trap datasets predicted the peak to occur on an annual basis between 14 July (DOY 14) and August 1 (DOY 213) at meadow sites.

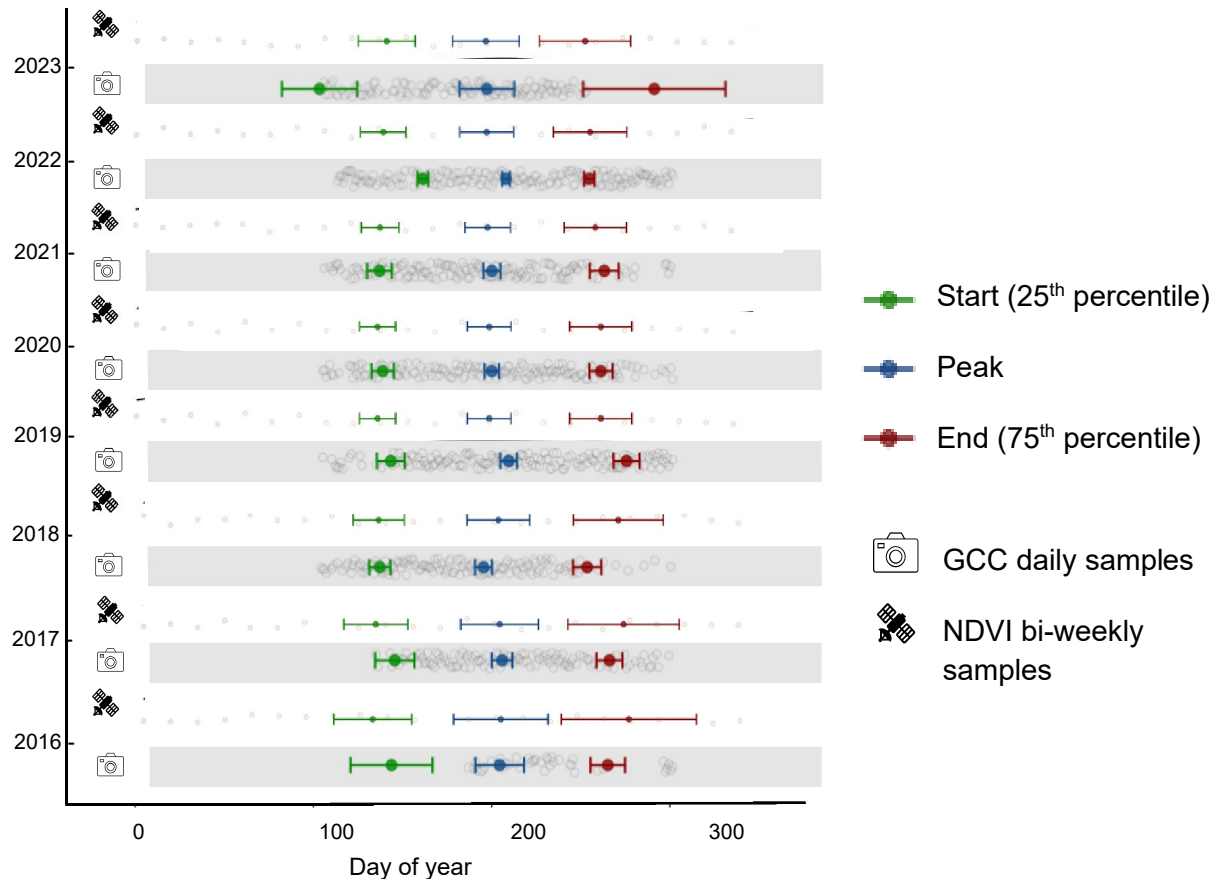


Figure 3.7 Comparison of predicted annual timings of the main phenophases associated with the growing season at meadow sites in the Naryn State Reserve, Kyrgyzstan, between 2016 and 2023 for both NDVI (unshaded rows, bi-weekly samples) extracted from Landsat imagery and GCC (shaded rows, random daily samples) from motion-triggered images by camera traps at the same locations. We report the day of the year (DOY) for the start (25th percentile - green), peak (blue) and end (75th percentile - red) of the growing season with their associated 95% confidence intervals.

3.4. Discussion

Accurately quantifying vegetation phenology in inaccessible rangelands through remote sensing methods is possible. Here, we highlighted the potential usefulness of motion-triggered images generated by camera traps deployed for wildlife monitoring in detecting grassland growing season phenology. Using a dataset with a high data sparsity due to technical issues and non-continuous deployment, we developed a semi-automated framework to extract and analyse the closest representation to time-lapse images, which are often used in phenological studies. We targeted and extracted the closest image to noon for every available day on which the camera was triggered, performed several filtering stages and used a hierarchical model framework developed to detect phenological shifts. As a result, we identified with relatively high confidence the start, peak and end of the growing season for each available year with enough temporal coverage at a remote mountain reserve of Kyrgyzstan. The main limitation lay in estimating the start and end of the growing season for years with incomplete sampling during the growing season.

We demonstrated that motion-triggered images could be used to detect and extract plant phenology with a relatively small dataset. While we observed limited annual variation in the timings of the growing season, using a time-series of eight years across all meadow sites, some incomplete, limited our ability to draw further ecological conclusions, and establish potential trends. We achieved these results by filtering years with at least two-thirds of the growing season captured as well as images captured during daytime and within an acceptable range of exposure to improve the detection of plant-related signals and minimise signals due to artifacts. Our findings highlight the need for longer time-series to confidently detect trends in ecosystem response to climate change. Testing our method on datasets with multi-year camera deployments and a greater number of cameras (> 10 cameras) at vegetated sites will confirm its effectiveness, and such datasets do exist (Burton et al., 2015; Rovero et al., 2013). Increasing the number of cameras would also partly mitigate the problem of data scarcity (see below), but this issue arises both from technical failures and from the type of environment in which the cameras are deployed. In our case, meadow and steppe habitats have low productivity (Shang et al., 2025; Y. Wang et al., 2020; Wingler & Hennessy, 2016). Snow covered the cameras for a large part of the year, and the high seasonality of certain species, especially marmots and birds, led to a consistent but low rate of detections throughout the

spring and summer. Motion-triggered camera trapping projects located in more productive ecosystems, e.g. at lower altitudes and latitudes, may result in better estimates of phenology throughout the year due to greater wildlife abundance and movement without the need to increase the number of camera traps deployed.

Satellite imagery is one of the most common tools used to monitor landscape phenology (Cheng et al., 2020; Melaas et al., 2013; Peng et al., 2021; Tomaszewska et al., 2020; Wang et al., 2015), and we hoped that we could use it to corroborate our camera trap findings. We found that detecting the main seasonal timings using green chromatic coordinates (GCC) yielded more uncertain results at the landscape scale, while the predictions of key timings at a single site or a few vegetated sites were possible using our framework. Due to the uncertainty across the reserve when using GCC time series, we used the NDVI as our main metric and obtained seasonal start, peak and end of the growing season that aligned well with those predicted from motion-triggered images. The use of randomly sampled points within the same elevation range covered by cameras led to better greenness detections that aligned with unfiltered camera trap data. To date, open-access satellite imagery includes high spatial resolutions, such as Landsat imagery, which provides images every 16 days at 30 m, or MODIS imagery, which provides images every 8 days but at 250 m, 500 m or 1 km spatial resolution (Song et al., 2021). To monitor habitat dynamics, Landsat imagery provides the best trade-off between fine spatial resolution and medium temporal scale. However, for plant phenology purposes, we found that a biweekly resolution was not enough to precisely capture the start of the growing season in our system. Other metrics or temporal resolutions for grasslands are needed as the variation in greenness in highly heterogeneous landscapes can lead to misrepresentation of the actual productivity of the landscape.

The main limitations in our study were data scarcity and spatio-temporal inconsistency. Using motion-triggered images, which are opportunistically generated based on movement, at locations with inconsistent camera placement and annual deployment, resulted in sparse data that limited the predictions of the start and end of the growing season. Moreover, sensor failures and reset of SD card due to the cold were common issues amongst Bushnell models used in this study, leading to large data gaps. The COVID-19 pandemic also resulted in cameras being

deployed for a total of two years without changes of batteries and SD cards. Some cameras remained active, but sampling efforts were reduced during that time, which further worsened data scarcity. While several locations remained the same throughout the study, the varying number of cameras deployed per year and the changes in camera placement, which includes changing in the field of view, also led to spatio-temporal inconsistencies, which is problematic when quantifying phenology. Moreover, due to cameras being deployed on unstable rocky features (e.g., cairns) instead of trees as in boreal studies (Hofmeester et al., 2020), each annual camera control resulted in a change in the field of view, preventing the reproducibility of consistent regions of interest (ROIs) for each given year at the same geographical location. The lack of consistency when selecting ROIs within the same site reduces our ability to identify if a change in greenness is a result of the vegetation changing or if the region of interest does not capture the same amount of vegetation. Moreover, predicting the start and the end of the growing season was more challenging than predicting the peak due to long tails on the data distribution and a weak signal detection, which is common in phenological analyses (Wilson et al., 2023). Most sites included rocky features, with limited open fields of view, which increased the presence of shade and limited our ability to properly extract the greenness values of pixels within regions of interest. While the use of this framework on more complete datasets will produce results without manual filtering and trimming, we found that trimming our annual time-series considerably increased model performance in predicting the timings of phenophases.

Studies with camera traps deployed for longer periods and with consistent fields of view may provide an opportunity for more thorough filtering stages to remove noise and detect variations in greenness. The integration of AI tools to detect if wildlife is located within a ROI on each given images would also be valuable to limit the interpretation of the brownness of wildlife coat as plant senescence. While we found the use of green chromatic coordinates to best predict grassland phenology, other greenness metrics such as excess greenness (ExG; Woebbecke et al., 1995) or the green-red vegetation index (GRVI) may also reveal vegetation dynamics, as shown in forested areas (Motohka et al., 2010; Wang et al., 2020). The use of other vegetation metrics may also help define thresholds to filter the data further and focus on detecting greenness by removing pixels corresponding to rocks, snow or wildlife. While our dataset did not provide an opportunity to detect ecological trends due to the short time-series, the framework we present here can be used to achieve this goal with data collected over a longer time frame.

Camera trap studies specifically aimed at quantifying phenology are now likely to use PhenoCams that take time-lapse images of foliage (Khare et al., 2022; Richardson, 2023). However, a large number of older studies using motion-triggered cameras aimed mainly at wildlife have been and are still being conducted (Fisher, 2025). We found that motion-triggered images are a valuable data pool to detect grassland phenology, and we recommend applying our framework to test whether the dataset is complete enough to describe or predict plant phenological patterns. This requirement should be easily met in regions at lower latitudes, which will generally have a greater, more consistent annual temporal data coverage due to greater wildlife abundance and movement. However, our workflow of image selection, filtration and analysis will help to generate better estimates of plant phenology from the more limited datasets that are usually available for arid, semi-arid and boreal ecosystems. Our study highlights the potential of motion-triggered images to reveal and track the health and dynamics of various ecosystems and how the simultaneous use of camera traps, field sampling and satellite imagery can lead to a baseline understanding of contemporary and historical change in ecosystems.

Chapter 4.

Dormir comme une marmotte: tracking activity patterns of the gray marmot (*Marmota baibacina*) in Kyrgyzstan using camera traps

4.1. Introduction

Camera traps have become an essential tool for ecological monitoring. Until recently, species sampling relied on invasive methods (e.g., trapping) or time-consuming and labour-intensive methods (e.g., observer-based sampling), increasing the risk of disturbance to the monitoring targets and often being limited by human and financial resources. The emergence of wildlife-triggered camera traps (hereafter cameras) revolutionized this area of ecology by providing an alternative, non-invasive monitoring method (Shiras, 1906). With continued technological improvements, cameras have become a primary tool globally to monitor wildlife (Burton et al., 2015; Steenweg et al., 2017), especially elusive species located in harsh and remote areas that make prolonged human presence difficult. Usually deployed in groups across a pre-defined systematic grid, cameras vary in deployment duration but are often left for about a year, providing information on species occurrence and spatial distribution (Nawaz et al., 2025; Rich et al., 2016; Wearn & Glover-Kapfer, 2019), behaviour (e.g., foraging, mating, nesting, hunting, alertness) (Burton et al., 2022), phenology (e.g., moulting) (Hofmeester et al., 2020), intra and inter-species interactions (Smith et al., 2020), trophic dynamics and overall health of animals. The focus to date when using camera traps is often on assessing wildlife population densities, dynamics, and responses to direct disturbances (e.g., tourism, forestry, fire) (Burton et al., 2024; Chen et al., 2022; Fennell et al., 2023; Granados et al., 2023; Tjaden-McClement et al., n.d.). However, the implementation of timelapse features has enabled the additional trigger of cameras at fixed intervals, leading to the detection of variation in biotic (e.g., plant phenology, vegetation type) (Hofmeester et al., 2020) and abiotic conditions (e.g., snow cover and temperature) (Alison et al., 2024; Breen et al., 2024). Indeed, recent studies have highlighted the strength of camera traps in simultaneously monitoring plant and mammal phenologies by combining motion-triggered and timelapse images to detect ecosystem changes (Hofmeester et al., 2020).

Shifts in the phenology of hibernating species, such as marmots, are among the clearest indicators of climate changes (Cordes et al., 2020; Falvo et al., 2019). Marmots are highly seasonal, cryptic species. They live in alpine habitats with harsh conditions, to which they have adapted by hibernating through the long, cold winters. These social organisms live in groups through a network of burrows, in which they hibernate. They reproduce on an annual basis right as hibernation ends and primarily forage grasses for 4 to 7 months in meadows, steppes and shrublands, usually located near the burrows. Marmots are particularly sensitive to their environment. Indeed, marmot survival is directly linked to environmental cues, such as temperatures, to initiate and end hibernation at times relatively synchronous to forage availability, which directly reflects on reproductive success (Armitage, 2013; Cordes et al., 2020; Davis, 1976; Ortmann & Heldmaier, 2000; Tafani et al., 2013). Marmots can provide direct evidence of climate change impacts on the environment due to their high sensitivity to warm temperature (Ortmann & Heldmaier, 2000). As such, changes in their phenology (i.e., seasonal activity), body mass and adult survival would indicate that environmental conditions are changing to an extent that requires annual physiological adaptations. However, the difficulty to monitor these cryptic species in remote areas has led to marmots not being fully considered as climate indicators.

Gray marmots (*Marmota baibacina*) are one of the largest marmots found in Asia, but relatively little is known about their population trend and ecology beyond natural history (Batbold et al., 2016). They occur in alpine grasslands in China, Russia, Mongolia, as well as Kazakhstan and Kyrgyzstan. With weights ranging between 4 and 6.5 kg, up to 8kg in some instances, gray marmots become a preferred secondary summer prey for snow leopards and wolves, which usually target mountain goats (Jumabay-Uulu et al., 2014; Weiskopf et al., 2016). Large birds of prey, such as eagles, also feed on juvenile marmots. Despite their highlighted role as secondary prey, gray marmots remain understudied compared to other marmot species and herbivores sharing the same habitat. This knowledge gap is particularly concerning given the significant warming rates impacting alpine grasslands in Kyrgyzstan (Y. Wang et al., 2020; Yang et al., 2023; Zhumanova et al., 2018b), alongside extreme climatic events and ongoing pressures from land use (i.e.,

livestock grazing), which have drastically altered grassland structure, dynamics and functioning (Yang et al., 2023; Zhao et al., 2023). While marmots are directly impacted by changes in forage availability and quality (Armitage, 2013; Cordes et al., 2020), there are currently no known assessments of how environmental change, especially warming, impacts the timing of marmot phenology. Establishing a baseline against which future changes in marmot phenology can be assessed, and how to do so in a relatively data-poor situation, are the first steps in understanding the impacts of climate and human disturbances on mountain ecosystems.

Given the lack of information on gray marmots, our study aims to provide a baseline understanding of the main timings of marmot seasonal activity patterns in Kyrgyzstan. Using by-catch data on marmot detections from camera traps deployed for snow leopards in the Naryn region of Kyrgyzstan between 2017 and 2021, we perform an exploratory analysis to 1) characterize the timings and variation in marmot phenology, and 2) evaluate its synchrony with plant phenology in the same area as presented in Chapter 2. The short time-series limits our ability to detect inter-annual changes and trends. Therefore, our study mainly aims to provide a first description of marmot phenology in the region and their response to annual variation in habitat conditions.

4.2. Material and Methods

4.2.1. Study area

The Naryn State Reserve in central Kyrgyzstan (41°25'50"N, 76°35'11"E) is a 1,080 km² reserve created in 1972 as a multi-use sanctuary (*zakaznik*), with a ban on hunting to protect elk populations (*Cervus elaphus*) (Farrington 2005). In 1983, the sanctuary became a state nature reserve (*zapovednik*), which further enforced regulations to ensure the

preservation, conservation and restoration of the ecosystem while providing research and educational opportunities (Kuskov et al., 2005; Kozhokulov et al., 2021). The reserve presents two types of management: a fully protected core zone located south of the Naryn riverbanks, and two large multi-use buffer zones located north and south of the core zone (Figure 4.1c). The core zone ranges from 2,379 m to 4,470 m in elevation, and it is mostly characterized by north-facing slopes only accessible by rangers and research teams since 1983. The buffer zones, however, have historically been shaped by intense livestock grazing and forestry. Signs of degradation and soil erosion from the Soviet occupation era until the 1990s were still visible in the 2000s (Farrington 2005), and the buffer zones continue to be used for subsistence-based herding to this day (OSI-Panthera, *personal communication*). The reserve is a hotspot for alpine plant species. Tian Shan mountain ash (*Sorbus tianshanica*) and Schrenk's spruce (*Picea schrenkiana*) constitute most of the forest cover, along with grasslands, barren lands and glaciers as main habitat types. The degree of disturbance is considered moderate in the buffer zones.

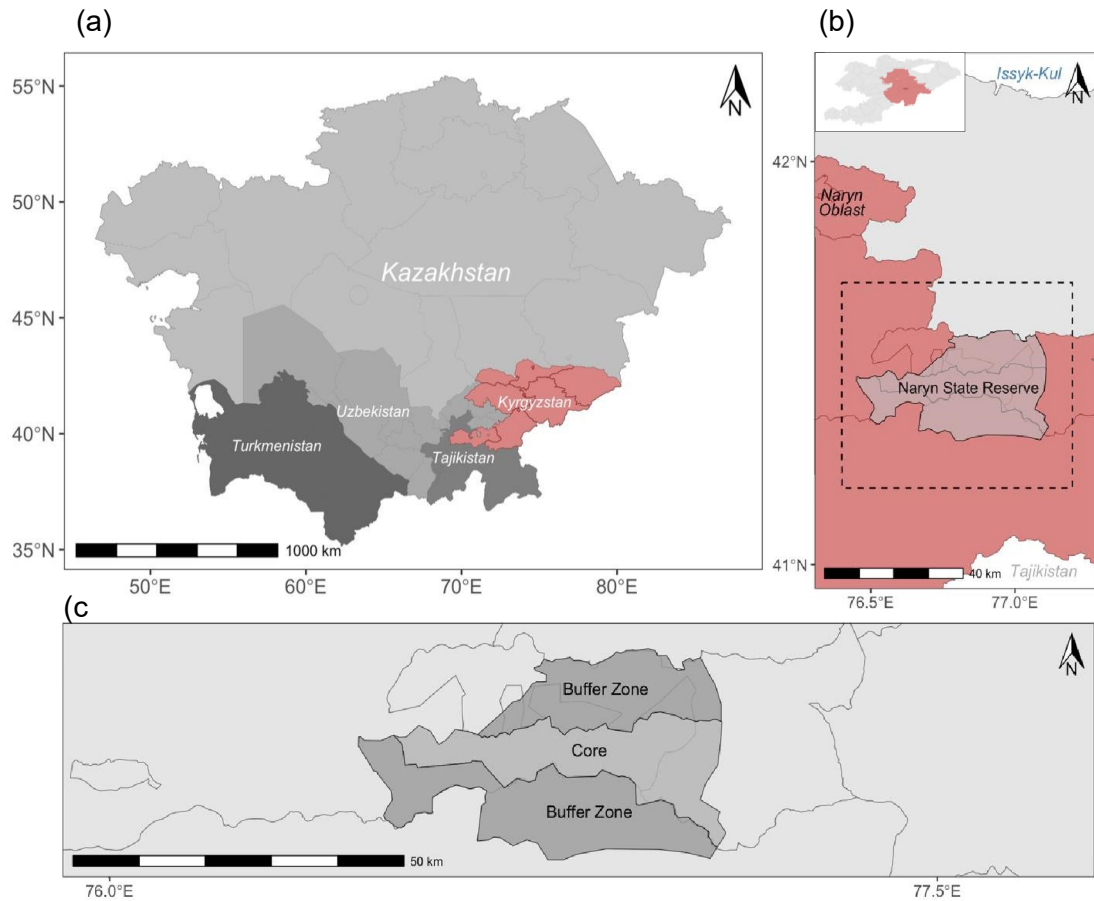


Figure 4.1 (a) Location of Kyrgyzstan (red) in Middle Asia. (b) The study area in Kyrgyzstan's Naryn Oblast (red) including the Naryn State Reserve. (c) The location of the core and buffer zones within the Naryn State Reserve.

4.2.2. Camera traps

To track marmot phenology using bycatch camera trap data, we used images generated by 16 Bushnell cameras (E, E2 and E3) and 3 Browning cameras (SPEC)

deployed across 18 locations within the Naryn State Reserve (Figure 4.2). Deployed between 2016 and 2023 by the non-governmental organisation Objectif Science International (OSI) Panthera, these cameras aimed to detect snow leopards (*Panthera uncia*). Here, we focus on the 2017 – 2021 period, during which cameras were deployed throughout the whole year. With a minimum of six active camera in 2017 to a maximum of 16 active cameras in 2019 (Table 4.1), each camera was deployed at an elevation between 2,630 m and 4,082 m with a field of view optimized to detect snow leopards along ridgelines or marking sites (Figure 4.2). Since cameras were not specifically placed to detect marmots, the resulting by-catch detections of marmots may underrepresent their activity. However, the large number of marmot detections across the dataset justifies the use of these data for exploratory analyses. All active cameras were at least 1 km apart and attached to rocks between 50 to 150 cm above the ground, depending on the targeted field of view and available landscape features. The preferred field of views to capture snow leopards included open field of views, particularly ridgelines (Figure 4.2a,b) and marking sites (Figure 4.2a,c). One camera was in a cave as a potential denning site for snow leopards (Figure 4.2d). We described sites dominated by continuous, grass-like vegetation cover as ‘meadow’ (Figure 4.2c). Due to the absence of available local plant inventories at each camera location, this label is not intended to represent an official vegetation classification.

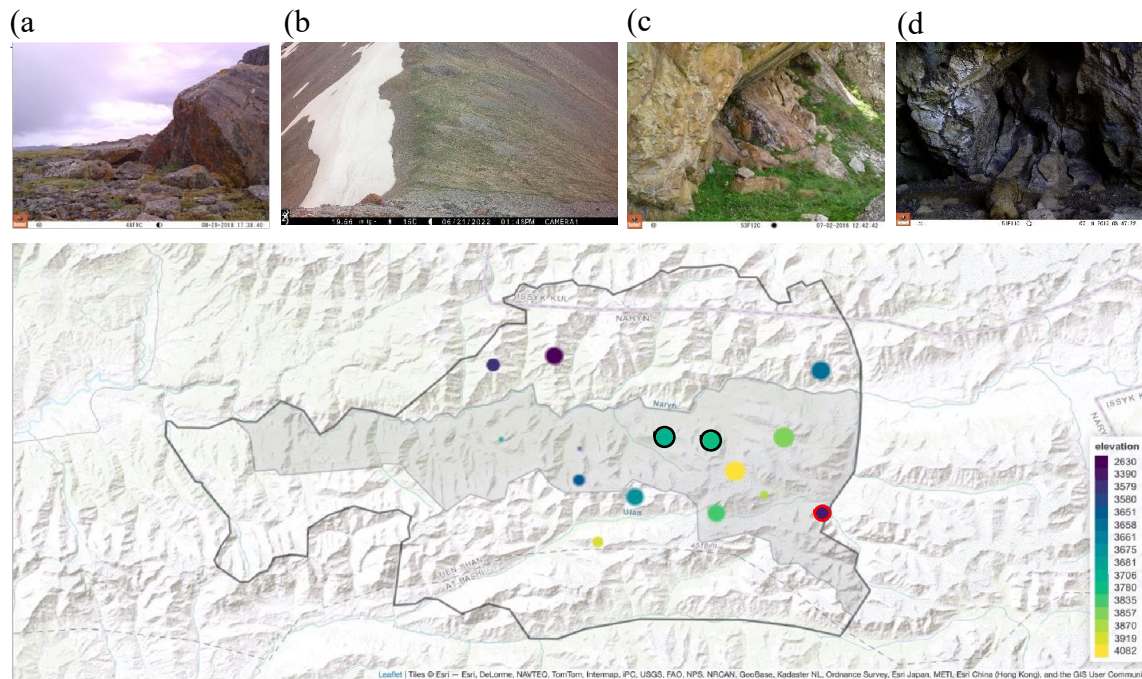


Figure 4.2 Location of the 18 sites at which camera traps were deployed between 2017 and 2021 within the Naryn State Reserve boundaries (black polygon), Kyrgyzstan. Each location is colour-coded based on its elevation. The size of each circle indicates the number of days recorded at each site, with larger circles indicative of higher sampling effort than smaller circles. Examples of habitat where cameras were deployed: (a) snow leopard marking sites on ridgelines, (b) open field views, (c) snow leopard marking sites at lower elevations and (d) sheltered ‘cave’ areas. The red circle indicates the location of a ‘meadow’ site, Site 9, used in a case study in section 4.2.3, which is also the site at which photo (c) was taken. The black circles around two meadow locations indicate the sites used to compare marmot and plant phenology as presented in section 4.2.3.

Table 4.1 Summary of camera trap deployments from 2017 to 2021 in the Naryn State Reserve, Kyrgyzstan. In 2020 – 2022, two cameras were simultaneously deployed at one of the sites. Some sites were removed due to issues with SD card reformatting during the winter and sensor failures. Independent detections represent each marmot detection within 30-minutes of each other.

	2017	2018	2019	2020	2021
Total number of active cameras	6	11	16	12	12
Total number of sites	6	11	16	11	11
Number of sites removed	-	-	2	-	-
Total number of independent detections	83	116	87	105	89

4.2.3. Detecting marmot phenology

The images were renamed and filtered for metadata issues using R (v.4.4.4) (R Core Team, 2022). To reduce the time typically required for image classification, we imported images into the Timelapse Image Analyser (Greenberg et al., 2019), which integrates automated image recognition models provided by Addax AI (van Lunteren, 2023). We applied the *Manas* model, specifically designed to identify Kyrgyz wildlife at the family level (Sornette et al., 2024). Once analysed and labeled, we manually verified marmot identifications to detect false positives and verify classifications with low confidence. For each image, we recorded the presence/absence of gray marmots, the only marmot species observed in the dataset (OSI-Panthera, *personal communication*). We did not record the number of individuals. Marmot detections were exported from Timelapse as a .csv table and imported in R to be analyzed. For each site, we grouped marmot detections into a single, independent detection if they occurred within 30 min of each other (Sollmann, 2018) (Table 4.1). Using a time-to-independence data filter is not usually appropriate to test multi-specific interactions and precise activity patterns (Peral et al., 2022), but the typical 30 min threshold (Holinda et al., 2020; Sollmann, 2018; Sun et al., 2021) used here was based on the time marmots usually spent in front of the camera and aimed to avoid inflating data with multiple events from the same individual (Appendix c, Figure C1). For each year, we reported the first and last Julian day on which marmots were detected (Table 4.3).

4.2.4. Analyses

To quantify marmot phenology across the whole study area and reduce the influence of outliers, we used the *Phenomix* package in R (v.4.4.4). This tool has already been applied to model migration timings of chum salmon and Swaison's thrush (Wilson et al., 2023), as well as plant phenology in Chapter 2. Similarly, *Phenomix* was used to predict the annual start (day of year on which 25% of the total detections has occurred), peak (day of year on which 50% of the total detections has occurred), end (day of year on which 75% of total detections has occurred) and duration (number of days between start and end) of marmot detections (Wilson et al., 2023) in R (v. 4.4.4).

We calculated daily capture rates by summing all marmot detection events (i.e., each independent time a marmot was present, not individual count) per day and per year, which we divided by the total number of cameras active at the time. We thus obtained one annual time-series to gain a baseline understanding of overall marmot phenology at the scale of the reserve. We also evaluated the model's ability to predict the main phenological timings of marmots across four 'meadow' sites (see section 4.2.3), and we did a 'meadow' site-specific analysis of Site 9 (red circle; Figure 4.2c). We focused the single-site analysis on Site 9 based on the continuous sampling effort between 2017 and mid-2022 and its potential as a 'high-fidelity' site due to the recurring and active presence of marmots, potential burrow and grass-dominated 'meadow' vegetation. By comparing marmot detections at a single and across multiple sites, we aimed to evaluate the type of data required for the model to best predict inter-annual marmot activity patterns and how intra-site variations differ from the variation observed across multiple sites.

Model

The *Phenomix* package fit the marmot daily capture rate across cameras (i.e. sites with a detection divided by active sites each day) using a hierarchical model that incorporated both annual and inter-annual variations within a maximum likelihood framework to estimate annual (e.g., start, end, peak) and inter-annual (i.e., rate of change) phenology (Wilson et al., 2023). While we focused on predicting annual estimates, the hierarchical model leverages data across years to improve the precision of those annual estimates. The annual-level of the model was fit with a single user-selected distribution (i.e., symmetric and asymmetric Gaussian, Student's *t* or generalized normal distributions), error distribution (i.e., gaussian, lognormal, Poisson, binomial and negative binomial) and the number of independent marmot detections for each day the camera was triggered, producing an irregular, event-driven time-series at each location. We compared models with two different data distributions (i.e., symmetric Gaussian and Student's *t*). We selected the model with the most ecologically meaningful prediction of duration of marmot activities compared to known records or marmots globally (~130 to ~200 days of activity, Armitage, 1991).

4.2.5. Linking marmot activity patterns and plant phenology

To investigate whether marmots time their emergence of hibernation with the start of the growing season, as well as their peak foraging activity and entry into dormancy align with plant phenology, we compared marmot phenology at the four 'meadow' sites within the Naryn State Reserve (Table 4.2). We selected 'meadow' sites instead of all sites to limit noise generated by limited vegetation at other sites. Motion-triggered images generated by cameras deployed across these three sites between 2017 and 2021 were used to quantify the key phenophases of the growing season (i.e., start, peak, end and duration) across these sites in Chapter 3. Many motion-triggered images generated at these sites resulted from marmot movements, providing sufficient data to do a preliminary comparison of marmot and plant phenologies. Using the analytical framework provided by *Phenomix*, we generated marmot and plant phenology estimates across these three sites as well as Site 9 to evaluate whether individual site-level by-catch datasets contain sufficient data and temporal coverage to yield accurate phenology estimates, or whether integrating a dataset

from multiple sites is necessary (Figure 4.2c). We first compared plant and marmot phenology estimates at a single site by calculating the difference in the predicted start, peak and end dates. We then applied the same approach across multiple sites to evaluate whether patterns of synchrony between marmots and plants were consistent or more detectable than at a single site.

Table 4.2 Summary of camera trap deployments across four ‘meadow’ sites from 2017 to 2021 in the Naryn State Reserve, Kyrgyzstan. The number of daily green chromatic coordinates (GCC) values collected across the three sites are reported for each given year. The data gap in 2020 is due to the COVID-19 pandemic and the inability to check cameras and change batteries.

	2017	2018	2019	2020	2021
Total number of sites	3	3	3	1	2
Total number of marmot detections	82	89	73	94	79
Total number of GCC values across meadow sites	120	143	156	152	143

4.3. Results

4.3.1. Identifying marmot activity patterns

Observed timing of marmot activity patterns

The first detection of marmot activity across all sites was observed, on average, on 29 April (DOY 119) between 2017 and 2021. Across years, the first marmot detections ranged between 15 April in 2018 and 13 May in 2017 (Table 4.3). The last detection of marmots was, on average, around 1 September (DOY 245) (Table 4.3). The timings of last detections occurred earlier over time, ranging from 6 September in 2017 to 22 August in 2021. Similar timings were observed at Site 9, with the first signs of activity occurring ~ 15 days later in 2018 and 2019 compared to the reserve-wide averages (Table 4.3).

Table 4.3 Annual first and last days on which gray marmots in the Naryn State Reserve, Kyrgyzstan, were detected across all cameras with the Julian date and reported Day of Year (DOY). To note that 2020 was a leap year.

	All sites combined				Site 9			
Year	First detection	DOY	Last detection	DOY	First detection	DOY	Last detection	DOY
2017	13 May	131	6 September	249	13 May	133	31 August	243
2018	15 April	105	11 September	254	30 April	120	30 August	242
2019	6 May	126	1 September	244	23 May	143	22 August	234
2020	20 April	111	1 September	245	27 April	118	1 September	245
2021	4 May	124	22 August	234	4 May	124	22 August	234
Average	29 April	119	1 September	245	9 May	128	28 August	240

Estimating timing of marmot activity patterns

Symmetric Gaussian distribution with lognormal errors statistically best fitted the data from all camera traps between 2017 and 2021. The average start of marmot phenology was predicted to occur on 27 May (DOY 147) with a reasonable degree of uncertainty (± 6 days), followed by a peak activity on 28 June (DOY 180 ± 4) and a predicted slow down to the end of activity on 26 July (DOY 207 ± 11) (Figure 4.3).

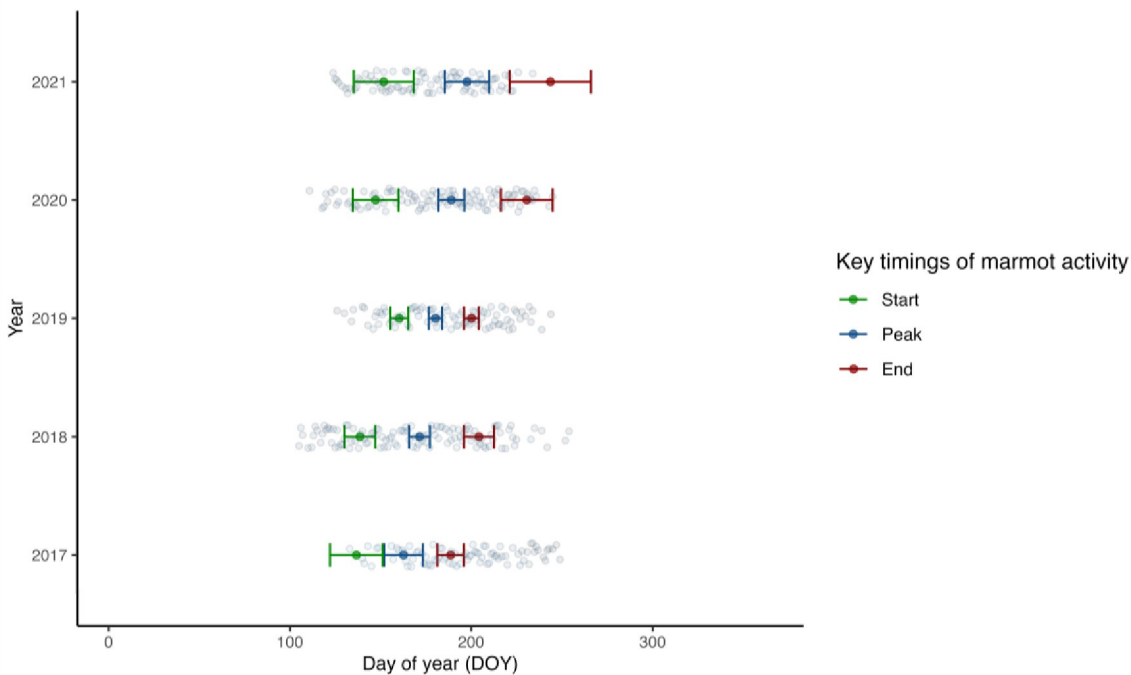


Figure 4.3 Predicted timings of gray marmot phenology in the Naryn State Reserve, Kyrgyzstan, across all camera trap locations from 2017 to 2021. The marmot detections for each day of available data within each dataset are represented by points to showcase the annual data distribution. Points and horizontal error bars indicate the start (25th percentile; green), peak (blue), and end (75th percentile; red) of the marmot phenology and their associated standard deviations.

The timing of marmot activity appeared to vary across years. There was a shift towards later timings of activity from 2017 to 2021 (Figure 4.3). The annual predictions of the main marmot activity duration (i.e., the number of days between the 25th and 75th percentiles) were on average 66 days (± 8). We do not directly compare observed first and last detections with modelled percentiles because observed detections represent single events, while percentiles represent more robust, reliable estimates that reduce the influence of outliers.

To compare the predicted timings across all sites to the timings at a single, grass-dominated ‘meadow’ site with consistent marmot detections, we performed the same analysis at Site 9. The analysis was more challenging due to the intra-annual variation of the raw marmot detections and the absence of a single annual peak per year (Appendix C, Figure C1b). The analysis yielded different results, with annual predictions of marmot activity duration ranging between 58 days (± 12) to 199 days (± 113) days (Figure 4.4). While we expected to observe an increase in predictive accuracy of marmot activity patterns between 2017 and 2021 at a single site with high marmot fidelity, the model did not yield more accurate estimates, as shown by the large standard errors for each predicted timings, especially in more recent years (Figure 4.4). The predicted timings of peak activity occurred increasingly later in the summer, ranging from 24 June 2017 (DOY 175 ± 8) to 8 August 2021 (DOY 220 ± 31) (Figure 4.4). The estimated end of marmot activity within the site occurred later, with predicted timings ranging between 23 July (DOY 204 ± 5) and 15 November (DOY 320 ± 79).

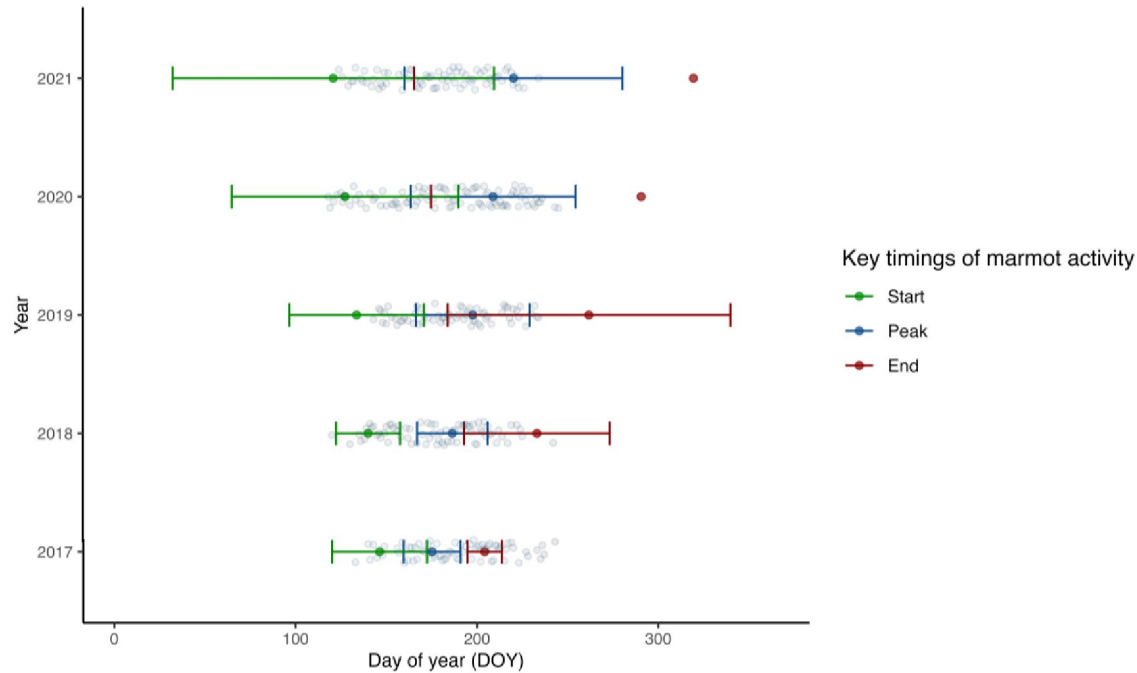


Figure 4.4 Predicted timings of marmot activity in the Naryn State Reserve, Kyrgyzstan, based on marmot detections collected by camera trapping between 2017 and 2021 at Site 9. This figure uses the same formatting at Figure 4 to facilitate comparisons.

4.3.2. Simultaneous monitoring of marmot activity patterns and plant phenology

Comparison at a single site (Site 9)

Comparing marmot activity patterns with the main predicted timings of the growing season at Site 9 between 2017 and 2021 (see Chapter 2 for detailed methods and results) indicated that marmots become active after plants growth begins, reach a peak activity after the peak in plant growth and become less active at least two months prior to the end of the growing season (Figure 4.5).

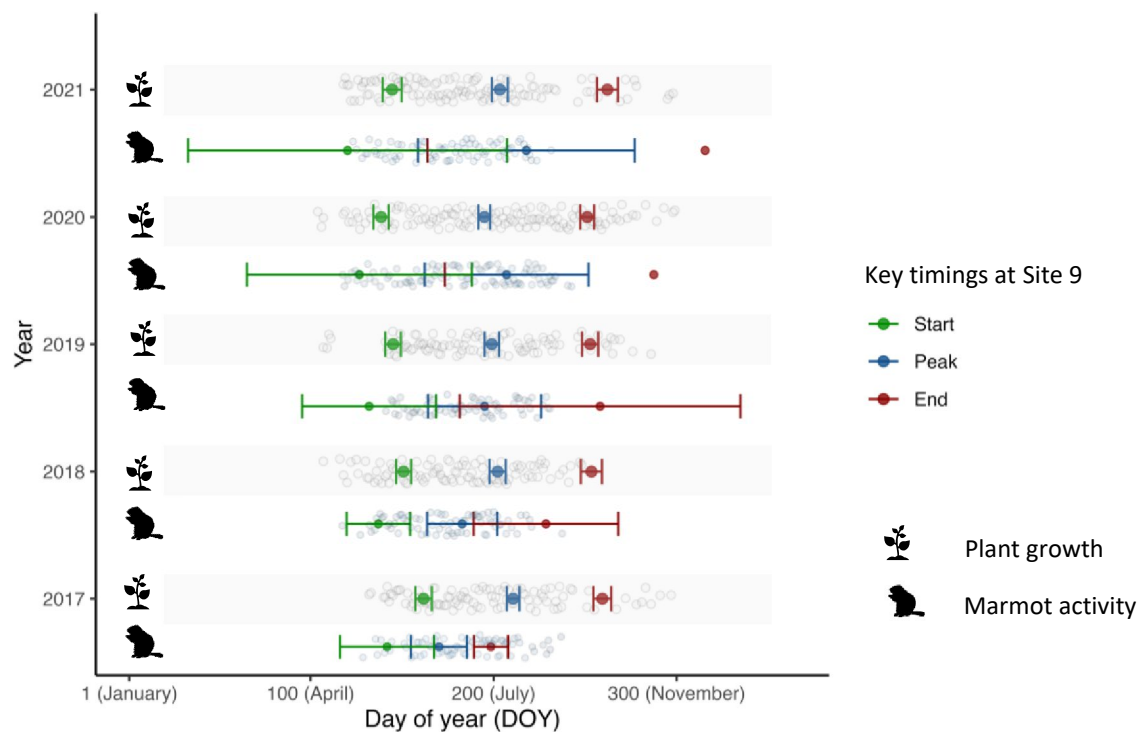


Figure 4.5 Comparison of estimated timings of the growing season (black lines and upper sets of coloured points and horizontal standard error bars for each year) and marmot activity patterns (lower set of coloured points and horizontal standard error bars for each year) at Site 9 in the Naryn State Reserve, Kyrgyzstan, between 2017 and 2021. The daily model predictions of greenness values (Green Chromatic Coordinates – GCC) and marmot detections for each day of available data within each dataset are represented by points within the marmot activity and plant rows.

Comparison across four 'meadow' sites

Limiting the analysis to four ecologically similar 'meadow' sites to evaluate whether patterns between plant and marmot phenologies were more detectable across multiple sites led to smaller standard deviations around the key timings compared to the single-site analysis. The start of marmot activity typically occurred between 26 May and 5 June, which is ~ 3 weeks later than the predicted start of the growing season in mid-May. The timing of peak marmot activity typically occurred before the peak of growth, while gray marmots became less active around peak plant growth (Figure 4.6).

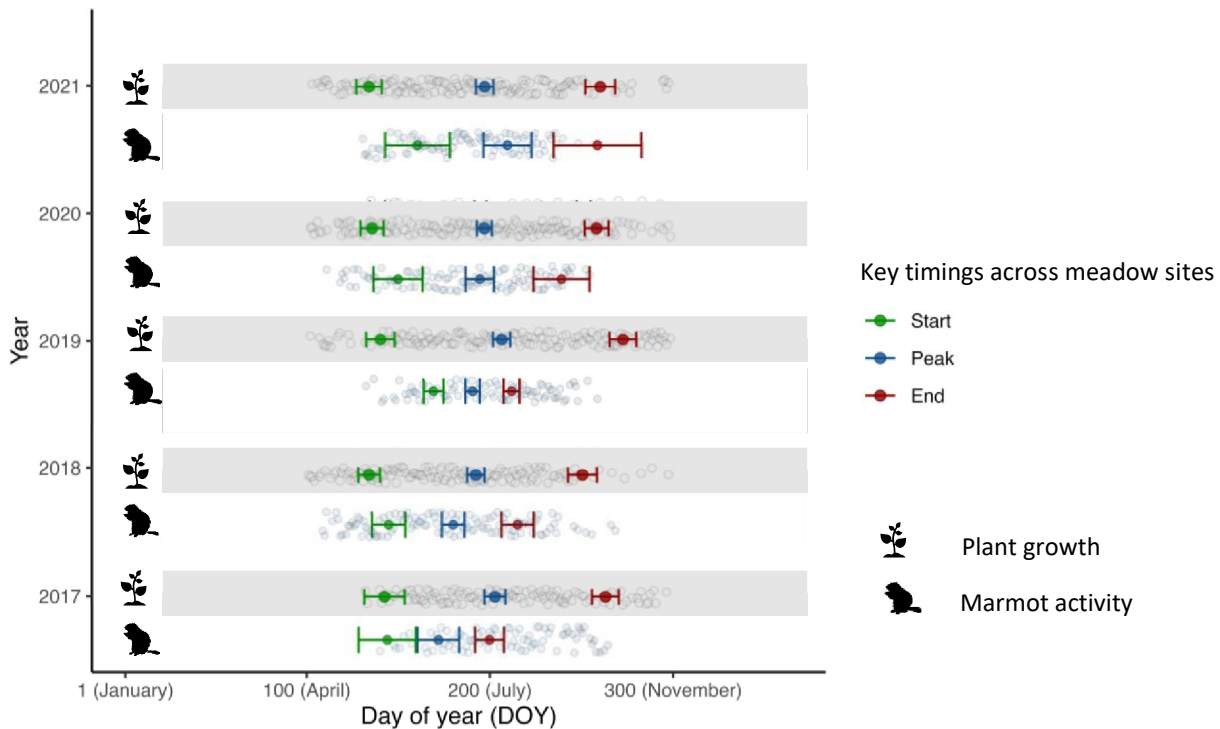


Figure 4.6 Comparison of estimated timings of the growing season (shaded rows) and marmot activity (unshaded rows) across four meadow sites in the Naryn State Reserve, Kyrgyzstan, between 2017 and 2021. The daily model predictions of greenness values (Green Chromatic Coordinates – GCC) and marmot predictions for each day of available data within each dataset are represented by points within the rows.

4.4. Discussion

In this study, we provide a novel, descriptive assessment of when gray marmots become active, and when their activity slows down by reporting the first and last marmot detection *for* each year with *sufficient* temporal data coverage in the Naryn State Reserve of Kyrgyzstan. The short duration of the time-series and the high degree of uncertainty surrounding predicted timings of activity patterns, at the scale of the reserve or at specific sites, prevent us from detecting long-term temporal trends that can be linked, for example, to climate change. Nevertheless, we were still able to identify short-term patterns and link marmot and plant phenologies. Our framework and initial results can serve as a baseline for continued monitoring of the effects of environmental change on remote mountain ecosystems.

Upon emerging from hibernation, alpine marmots rely on accessing forage early in the season to restore depleted energy levels and reproduce (Davis, 1976; Ortmann & Heldmaier, 2000). They accumulate fat throughout the season, which is essential to survive the following winter (Armitage, 1991; Chibowski et al., 2023; Ruf et al., 2023). By leveraging existing by-catch camera trap data, we captured these dynamics with gray marmots showing first signs of activity once vegetation is detected, allowing access to senesced plants at first until plant growth starts ~ two weeks later. While some direct observations recorded the first marmot activities in the presence of snow, modelled predictions suggest that most marmots emerge as forage becomes available, which is consistent with their need to resume foraging and restore metabolic functions after hibernation (Armitage, 2013, 2017; Cordes et al., 2020). During this period, they are particularly vulnerable to predators. Though marmots are adapted to emerge while snow is still present (Ozgul et al., 2010), shifts toward earlier emergence may jeopardize their survival if forage remains inaccessible for prolonged periods they are not physiologically equipped to withstand (Cordes et al., 2020; Tafani et al., 2013). Peak marmot activity occurs prior to the peak in plant growth, which can be consistent with the need to forage early and access high plant quality to support gestation for females, birth timing and accumulate fat as quickly as possible (Ruf et al., 2023). Our results indicate that marmots reach 75% of their total activity duration by the end of July (DOY ~200), even earlier in some years. This indicates the importance of the first couple months of activity. Modelling marmot spatial use of the landscape could help

determine whether the decline in marmot detections after July indicates a bias in marmot detections due to cameras' field of view being optimal for snow leopards, an increase in marmot movements across their habitat that would make them less likely to be captured by cameras, or if their activity levels are diminishing. The detection of marmots also decreases as temperature increases (Ortmann & Heldmaier, 2000), with individuals spending more time in the shade or in the burrows during to avoid high temperatures. Due to their sensitivity to temperature and their limited foraging opportunity during the short growing season, marmots are particularly attuned and responsive to changes in climatic conditions. We recommend future studies to investigate its effects on gray marmot activity. While many camera models record temperature, the Bushnell camera models used in this study did not capture temperature in their metadata, limiting our ability to include temperature in the analysis.

As potential climate indicator species, marmots can help reveal the impacts of climate warming through the timing of their hibernation and peak activity in the summer. Our results do not appear to be consistent with predicted directional effects of climate change. We expected to observe marmot activities to match the duration of the growing season over the study period, but our results did not indicate such a pattern (see also (Cordes et al., 2020; Falvo et al., 2019). The use of such a short time-series is a strongly limiting factor when trying to observe changes in phenological trends. Our results nevertheless provide initial patterns but understanding what drives the seasonal and inter-annual variations in marmot phenology will require the inclusion of longer time-series and abiotic metrics. The latter should include temperature, which drives marmot phenology through hibernation patterns, but also patterns of precipitation and changes in snow phenology, which influence foraging opportunities (Cordes et al., 2020). Changes in snow patterns and seasonal environmental conditions have contrasting effects on marmot survival and seasonal demographic responses based on species and age-classes (Cordes et al., 2020). For instance, yellow-bellied marmot (*Marmota flaviventer*) populations experience an increase in body mass and survival over the summer, with an overall decrease in winter survival (Cordes et al., 2020; Ozgul et al., 2010), while a 20-year study on Alpine marmots (*Marmota marmota*), indicated a decrease in litter size due to the decline in snow cover insulation throughout the winter (Tafari et al., 2013). These findings highlight the importance of species-specific studies, and the need for future initiatives to

focus on gray marmots to understand how this species responds to ongoing climate change.

It is important to appreciate the distinction between observed and modelled activity timings. The observed dates of first and last detections reveal the overall duration of above-ground marmot presence. In contrast, the modelled predictions of key timings show how marmot activity is distributed across the overall above-ground period. The two metrics are complementary. While the former, because its dependence of the timing of snow melt (Armitage, 2013; Cordes et al., 2020), might be a sensitive response to climate change, the latter reveals the periods of most intense activity. Thus, gray marmots are predicted to be active for only the first ~ 2 months of growing seasons that are 200+ days long, which as discussed above highlights the importance of the post-hibernation weeks for adults and pups (Bonenfant et al., 2025). Most of marmot activity is predicted to occur by the end of July but the timing of the last observed marmot detection through our camera trap data is in late August for most years.

Any changes in marmot survival and or distribution across the landscape because of changes in phenologies would have cascading effects on predators, plant community structure and below-ground communities. In Kyrgyzstan, snow leopards, birds of prey and wolves rely on marmots as a secondary prey in the summer (Jumabay-Uulu et al., 2014; Weiskopf et al., 2016). In addition, as ecosystem engineers, marmots play a key role in structuring plant communities through grazing and by moving organic matter through burrows, which can be essential for plant growth in ecosystems with slow nutrient cycling (Armitage, 2017; Ballová et al., 2019). Such interlinked ecological repercussions can only be measured through simultaneous monitoring of multiple trophic levels. Using by-catch camera trap data originally deployed to monitor priority, threatened wildlife, can fulfil this goal and help identify prey phenology and its synchrony with plant resources without needing to deploy new experimental designs. In addition, the presence of other species in the camera trap data, such as snow leopards (*Panthera uncia*), grey wolves (*Canis lupus*), Eurasian lynx (*Lynx lynx*) or Siberian ibex (*Capra sibirica*) and argali (*Ovis ammon*),

expands research and monitoring opportunities by enabling the study of interspecific interactions across multiple levels of the ecosystem.

Chapter 5. General Discussion

5.1. From pixels to phenophases

Monitoring social-ecological systems is more feasible than ever thanks to the myriad of tools now available and the large volume of data they generate. My thesis showcases the huge potential of combining and leveraging remote-sensing methods beyond their target use to explore and describe ecosystem features and responses to our changing world. Being unable to travel to Kyrgyzstan because of the COVID pandemic, my first goal was to generate an overall description of the heterogeneous alpine landscapes of this remote country by mapping and characterizing their topography, as well as the past and current distribution of land cover types and their drivers (Chapter 2). Alpine regions in Kyrgyzstan are primarily monitored for snow leopard population assessments, with a particular emphasis on predator-prey interactions and the human dimension of snow leopard conservation (Davletbakov et al., 2024; Jumabay-Uulu et al., 2014; Khanyari et al., 2021; Rode et al., 2024). However, a critical knowledge gap remains regarding the bottom-up effects of climate change and disturbances on snow leopards (Forrest et al., 2012; Shen, 2020). To address this gap without the need to design new experiments, I used a single set of camera traps deployed for snow leopards to identify the role camera traps can play in monitoring the ecosystem beyond the target species. I showed how wildlife data can successfully be used to detect and track plant phenology and how it compared with satellite imagery (Chapter 3). Then, I used the same dataset to generate the first monitoring and phenology of gray marmots (*Baibacina baibacina*), a seasonal prey of snow leopard, and simultaneously link it with plant phenology (Chapter 4). Each thesis chapter showcases how satellite and camera trap datasets can provide ecological information at species, multi-trophic and ecosystem levels. By offering a semi-automated framework to process data more efficiently and providing baseline assessments of species phenology, my thesis addresses the current urgency to find simultaneous ways to efficiently and effectively monitor biodiversity and explore their response to changing environmental conditions (Pollock et al., 2025).

The idea for Chapter 2 was first born in the pastures of Kyrgyzstan while I was drinking кумыс (kumis), the infamous fermented horse milk, with community members. The growing evidence of pasture degradation was unsettling for those solely relying on herding. Because of the heterogeneous nature of alpine ecosystems and strong variation in the degree of anthropogenic disturbances, both historically and contemporary, there was no consensus regarding whether climate change or human activities drive pasture degradation, and if pasture degradation would ultimately occur homogeneously across the country. Using satellite imagery, I found that about 85% of the landscape remained the same over the last 20 years, which starkly contrasts with the recently published status of pasture degradation across Kyrgyzstan (Domenech et al., 2022). This contrast may simply lie in the way we define pasture degradation. Here, I considered pasture degradation as a state conversion from grasslands to bare areas with sparse vegetation, which is the most extreme, and often the most portrayed outcome an ecosystem can experience. Indeed, photographer Daesung Lee strikingly portrays the impacts of desertification of grasslands induced by climate change and its impacts on nomadic herders in Mongolia (Figure 1). However, pasture degradation is often more subtle and gradual, making it challenging to observe through remote sensing but evident to those who have spent a lifetime in the landscape.



Figure 5.1. Futuristic Archaeology by Daesung Lee. In this work, Daesung Lee showcases the increasingly difficulties faced by nomadic herders to maintain their traditional way of life due to the desertification of Mongolian landscapes. See more photos from this series at www.daesungle.com

Forage depletion through the reduction of forage quality and quantity directly impact herders but is difficult, if not impossible, to measure with remote methods. While the reduction of forage quantity is typically linked to overuse of pastures through year-round or locally intensive grazing (Central Asia Bureau for Analytical Reporting, 2024; Hoppe, 2018; Hoppe et al., 2016; Robinson, 2016), weed encroachments (Eddy, 2016) and the increase

of unpalatable and invasive species (Central Asia Bureau for Analytical Reporting, 2024; Crewett, 2012; Esengulova et al., 2008) directly challenge forage quality. Though not captured in this thesis, differences in pasture composition and responses to disturbances are particularly contrasted, depending on pasture seasonal use (Eddy, 2016; Esengulova et al., 2008; Hoppe, 2018; Liu & Watanabe, 2016). For instance, Domenech et al. (2022) showed that all pastures have experienced a degradation of at least 80% since 2000, with 82% of winter pastures and 43% of summer pastures being severely degraded. Village proximity, intensity and seasonality of use are all key factors to that contribute to pasture degradation. Public access to geospatial data on seasonal pasture use and grazing intensities will be essential to identify the mechanisms and drivers of pasture degradation, and to reconcile herders' observations.

I moved to Kyrgyzstan in 2018 after finishing my M.Sc. in Sweden, during which I explored the role of by-catch camera trap data to simultaneously monitor plant and mammal phenologies (Hofmeester et al., 2020). Prior to my M.Sc., I was primarily interested in working with camera traps because of their main role in snow leopard research, a species living in a socio-ecological system I had long wished to study. Using camera traps through a plant-herbivore phenological lens was not part of the original plan, but it became an unexpected doorway into the snow leopard world and ignited my current fixation with using these tools beyond their common applications. During the 12 months I lived in Kyrgyzstan, I spent numerous weeks looking for snow leopard signs in the rugged, high alpine landscape, to identify suitable sites for camera deployments. (In the spirit of transparency for prospective snow leopard enthusiasts: looking for signs mostly means smelling rocks for snow leopard pee. If you live with a cat at home, you surely have an idea of what wild cat urine smells like, and thus, you can get a glimpse of what fieldwork entails!) When I was not in the field, I spent most of my time looking through motion-triggered-only still images, looking at snow leopard coats and spots to identify individuals. As snow leopards and their associated prey face increasing threats because of poaching, trophy hunting, climate change, diseases and challenges related to human-wildlife coexistence, I became increasingly curious about how camera trap data generated by wildlife movement might also be used to track vegetation and environmental conditions. Obtaining this level of detail could provide the relevant information needed to better inform snow leopard research. However, using camera trap data solely generated by wildlife movement to track

plant phenology had never been done before. Typically, datasets including daily images taken at fixed intervals (e.g. noon; time-lapse images) are used to detect and monitor plant phenology. However, the reality of camera trapping datasets is that most only include images generated by wildlife movement. Using camera traps deployed for snow leopard monitoring over a 6-year period, I developed a semi-automated framework to extract the images the closest to noon and estimate the main timings of the growing season. I confirmed that motion-triggered images could be used to detect plant phenology. Comparing estimated timings of plant phenology with bi-weekly Landsat imagery, which is a more commonly used method, I found that estimating the peak of the growing season was overall more accurate than estimates generated by Landsat imagery. While the temporal sparsity of the dataset and small amount of camera trap data limited the accurate prediction of start and end of the growing season in some years, the findings of Chapter 3 are the most exciting in this thesis as they provide evidence that the wildlife and plant worlds may not always need to be separated and a single dataset can be used to monitor both.

Working in snow leopard habitats means that marmots are not the main species one may actively look out for in the field. At least not in my case. My first encounter with a Kyrgyz marmot led to a near-death experience. While I was staying on guard for bear, wolf or snow leopard encounters, the scariest wildlife moment came from a gray marmot, which jumped out of nowhere onto a rock, right next to my face, and screamed. As previously described, gray marmots are the largest marmot species in Asia (Figure 2). While in size they are like those of a Beagle or a small Cocker Spaniel, the scream of that ~ 9 kg marmot and how large it appeared at that moment left such a lasting impact on me that I devoted an entire chapter of my thesis to them.



Figure 5.2 One of the many detections of gray marmots from the dataset provided by OSI-Panthera and used in this thesis. This image is the closest representation of what my first encounter with a gray marmot looked like.

Using the same camera trap dataset and analytic framework as in Chapter 3, I decided to look at by-catch marmot detections and explore the link between marmot and plant phenology. The wildlife conservation world mainly focuses on big, often charismatic and/or endangered mammals. The gray marmot may not be big or endangered, but it is charismatic (at least in my opinion!). But for some reason, very few studies have looked at gray marmots despite their role as secondary prey for snow leopards and being recognized as under-studied in the snow leopard conservation world. Most camera trap wildlife detections during the summer months were of gray marmots, providing a perfect opportunity to identify the main timings of marmot phenology. As for each chapter, I incorporated a novel, open-source tool to mainstream the data processing. Here, I used the *Manas* AI tool to automatically recognize marmot by-catch detections. The *Manas* AI tool was trained and developed specifically for Kyrgyz wildlife using the same camera trap dataset from this thesis. Comparing marmot and plant phenology indicated that marmots tend to be active for only two to three months, which is shorter than the typical marmot activity reported in other regions. While drawing ecological inferences and detecting inter-annual trends were limited by the short time series, my results further highlight the potential of using camera trap datasets beyond their initial aim. A follow-up study linking marmot and predator dynamics (e.g., snow leopards, wolves) would be a logical next step, especially as this data is already available.

5.2. Camera traps as untapped data troves for multi-trophic monitoring

“No data is clean, but most is useful” – Dean Abbott

Over the last decades, technological improvements have led to the massive accumulation of biodiversity data, deepening our understanding of ecological dynamics faster than ever (Abutaleb et al., 2025; Grémillet et al., 2022; Wig et al., 2025). Efficient experimental designs and surveys, along with an increase in data sharing through open-access frameworks, have facilitated access to high-quality data generated by specialized methods. Given the current *data deluge* and access to specialized methods, why should we consider leveraging datasets designed to capture wildlife to monitor plants or environmental conditions?

The primary reason is the growing urgency to effectively and efficiently monitor rapid ecological changes. Camera trap images provide valuable snapshots of wildlife diversity, habitat features, plant diversity, phenology, and environmental conditions - all of which are critical for understanding multi-trophic dynamics and ecosystem responses to change. However, most projects do not explore their datasets beyond the target species, arguing that (1) time and resources are the main limiting factors, and (2) other methods, such as PhenoCams, exist and should be deployed to answer ecological questions relating to plants and phenology. While it is indeed essential for specialized methods to be deployed to answer specific ecological questions pertaining to plant phenology, habitat composition, and microclimate variation, the by-catch data captured by camera traps represent an underused opportunity for broader ecological monitoring, especially in data-poor areas.

Considering the geographical and taxonomic bias of ecological data (Feeley et al., 2017; Troudet et al., 2017), along with the sudden and unpredictable impacts of climate change, it is unrealistic to expect specialized methods to always be deployed to generate suitable data in a timely manner. Using a single camera trap and satellite imagery dataset, I was able to provide baseline descriptions of poorly documented alpine vegetation and marmot phenologies in an area where ecological monitoring primarily focuses on large, endangered mammals, with methods specifically suited to those species. While drawing ecological inferences was limited in some contexts due to data quality and sparsity, my

thesis highlights how untapped by-catch camera trap datasets can significantly and holistically contribute to both the observation of ecological patterns and the development of ecological inferences.

5.3. Metadata standards, data accessibility and semi-automated data extraction

One of the greatest challenges of this thesis was to navigate large volumes of data that I had no previous relationship to. Despite the pre-existing emphasis on the importance of metadata and metadata standards (Forrester et al., 2016), using data generated by other teams, especially those from citizen science initiatives, becomes nearly impossible without consistent and accurate metadata. Key metadata fields I highlight include accurate *GPS coordinates* for each camera trap, associated with a unique, consistent *camera number* and *site name*, which should match with the name of the folders where the images are stored. When a camera is moved by a few metres or reoriented to capture a different field of view, it is also essential to ensure these adjustments are systematically reflected in the metadata. Moreover, such camera changes should be considered as a different camera deployment. Reporting the *start date* of each camera deployment, along with the *end date* indicating when the camera was controlled or retrieved, is important to calculate active camera days as well as to correct wrong timestamps. Although issues with SD card or camera formatting are common errors found in camera trap datasets, knowing when a camera was deployed, controlled or retrieved can help salvage images with wrong dates and limit data loss. Other key information to include are camera *orientation* and *sensor height*. Sensor height is essential for determining the type of species that are most likely to be detected by cameras. As mentioned previously, camera orientation can be useful to identify cameras located at the same site but with a different field of view. This field also typically indicates which cardinal direction cameras are facing, which can result in drastic differences in data quality depending on light exposure. While other metadata fields (Forrester et al., 2016) should also be populated by camera trappists during deployments, the absence of the key metadata fields emphasized here can lead to completely unusable data. Ensuring the

accuracy of the metadata will effectively improve data exploration, filtering and organization, which can otherwise be time-consuming.

To reduce the time typically required to manually process and extract information from camera trap data, semi-automated frameworks and data management platforms are increasingly being developed and adopted. In each chapter of this thesis, I developed mainstreamed, open-source workflows to demonstrate the accessibility and feasibility of using by-catch camera trap data and long-term satellite time-series, and to encourage their broader adoption in future studies.

As a field ecologist who suddenly had to transition to working with satellite imagery, I designed my thesis with an audience largely unfamiliar with remote sensing in mind. To reduce the sense of overwhelm often experienced when first working with satellite imagery, I deliberately chose user-friendly tools (Potapov et al., 2020; van Lunteren, 2023), and I developed step-by-step workflows with minimal human input required to straightforwardly and readily produce the desired output. On the camera trap side of the thesis, I developed tools to automatically organize camera trap data in specific folder structures based on the structure expected by the analytical framework (i.e., *Phenopix*) and extract images the closest to a set a time for each day of available data without the need for extensive manual labour. Although not included in this thesis due to time constraints, I also developed a method to extract temperature data displayed on camera trap images, particularly for early Bushnell camera models that do not store temperature in the image metadata. While these tools are not considered 'semi-automated', they aim to drastically reduce the time required to manual process large volumes of images.

By definition, semi-automated workflows in ecology include human labeled-images and machine learning to train classifiers (Böhner et al., 2023). Advances in artificial intelligence (AI) are speeding the rate at which data is being processed (Beery et al., 2020; Kellenberger et al., 2020; Norouzzadeh et al., 2021; Schneider et al., 2019, 2020). Because training classifiers require extensive datasets, AI tools are often geographically and

taxonomically biased towards regions with abundant data, typically focused on wildlife. However, the growing appeal of AI tools is driving independent efforts to develop wildlife classifiers in under-studied areas, such as the *Manas* AI (Sornette et al., 2024) used in Chapter 3, openly available through AddaxAI (van Lunteren, 2023) and solely focusing on Kyrgyz wildlife. While these tools drastically reduce the time required for manual wildlife detections and human errors caused by fatigue, expanding their application to identifying vegetation composition, environmental conditions and habitat features could unlock the valuable ecological insights we need to effectively address the current biodiversity crisis.

5.4. Future directions (or what you might get if you hired me for a post-doc)

Given the context of global change and the growing need for long-term, multi-scale data, there is a pressing demand to develop inter-disciplinary frameworks that integrate multiple data types (multi-modal data) and AI tools capable of extracting more than wildlife detections. Building on the technical limitations I encountered in my PhD, I have had many opportunities to reflect on what future research should include. As such, this section not only presents general recommendations, but also outlines what I see as the logical, fundamental next steps I am motivated to pursue in the next stage of my career. Key future directions include developing and integrating AI tools to (1) classify habitat features across various biomes (e.g., vegetation, bare ground, rock), (2) identify plant species and community structure, (3) detect and remove wildlife from images to focus on plant phenology, (4) detect abiotic conditions such as rain and snow, and (5) automatically correct image distortions caused by environmental factors, such as solar exposure, that alter vegetation colour and lead to inaccurate phenological signals.

Considering the large volume of data openly accessible and potentially associated records of species diversity in each area, this extensive data pool constitutes an excellent opportunity to train AI tools to identify plant species or functional groups, plant and mammal phenology, habitat features and abiotic conditions in various ecosystems. Once the tools are developed and adequately trained, they can be used to leverage existing camera trap

datasets and link the output with other metrics generated by camera traps (i.e., wildlife detection, behaviour, intra- and inter-specific interactions), genetic and diet analyses, field, aerial and satellite observations within and across ecosystems. Based on the availability of historical and contemporary records at each given location, there is an additional opportunity to quantify trends in the types of responses of biodiversity to environmental changes across various time scales.

Lastly, while harnessing technological improvements and fully leveraging data are crucial to effectively address the biodiversity crisis, the most important aspect of ecological research remains the meaningful inclusion of communities and community-based knowledge. Coming from a strong community-based background, my transitioning to a remote sensing project on the other side of the world from where my data was collected was challenging. I deeply felt the loss of engaging and working directly with community members, whose knowledge of the land can never be replaced by remote sensors. These experiences reinforced my belief that research is best performed when it is interdisciplinary, collaborative and driven by questions emerging from communities. By combining community knowledge with novel quantitative tools and multi-modal datasets, we can better deepen our understanding of socio-ecological dynamics and global change. I hope this thesis provides evidence that when someone asks, 'Why bother? The data is not ideal', it may be a sign that you should bother. While there may be future opportunities to obtain the ideal data, we should strive to leverage the extensive data that are available and accept to use imperfect datasets. The heavy focus on inferential analyses can sometimes overshadow the value of exploratory and descriptive work, which used to be central amongst naturalists. To date, there is no single method that can address the complexities of the natural world. As such, the best next step we can take to efficiently address the current biodiversity crisis is to truly think outside the box, embrace trial and error, adopt concrete inter-disciplinary approaches, and above all, build and maintain strong relationships with the people, the land, and the data we work with.

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Indicators*, 95, 527–543. <https://doi.org/10.1016/j.ecolind.2018.07.060>

Zhumanova, M., Mönnig, C., Hergarten, C., Darr, D., & Wrage-Mönnig, N.
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Indicators*, 95, 527–543. <https://doi.org/10.1016/j.ecolind.2018.07.060>

Appendix A.

Supporting Materials for Chapter 2

Workflow

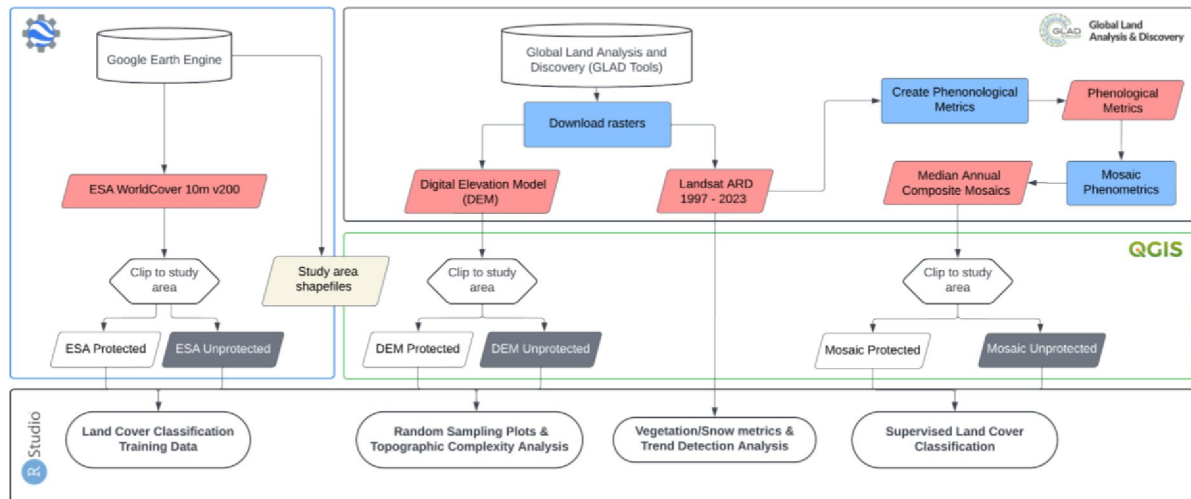


Figure A1. Data sources and preparation flow chart. The GLAD Tools protocol enables the download of the digital elevation models (DEM) and Landsat ARD imagery.

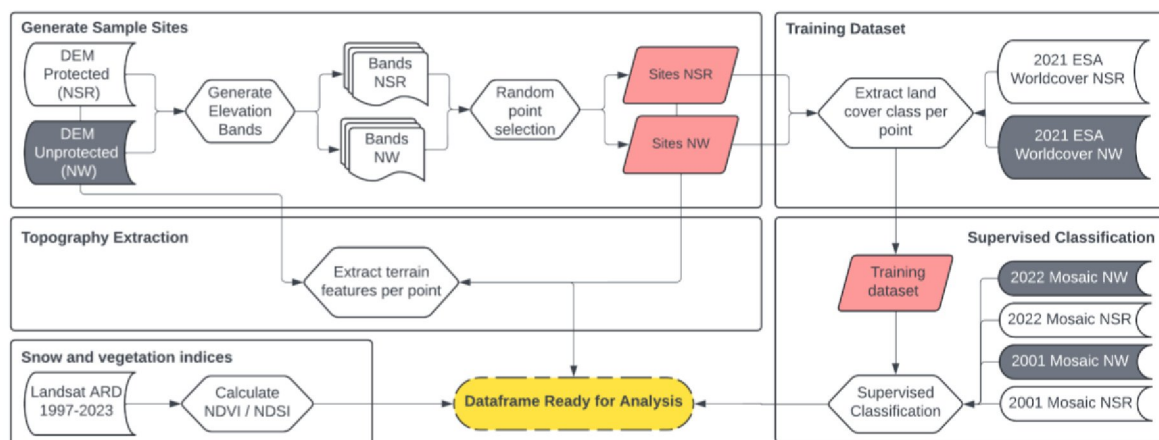


Figure A2. Flowchart describing the data processing steps.

Study areas elevation band and point selection

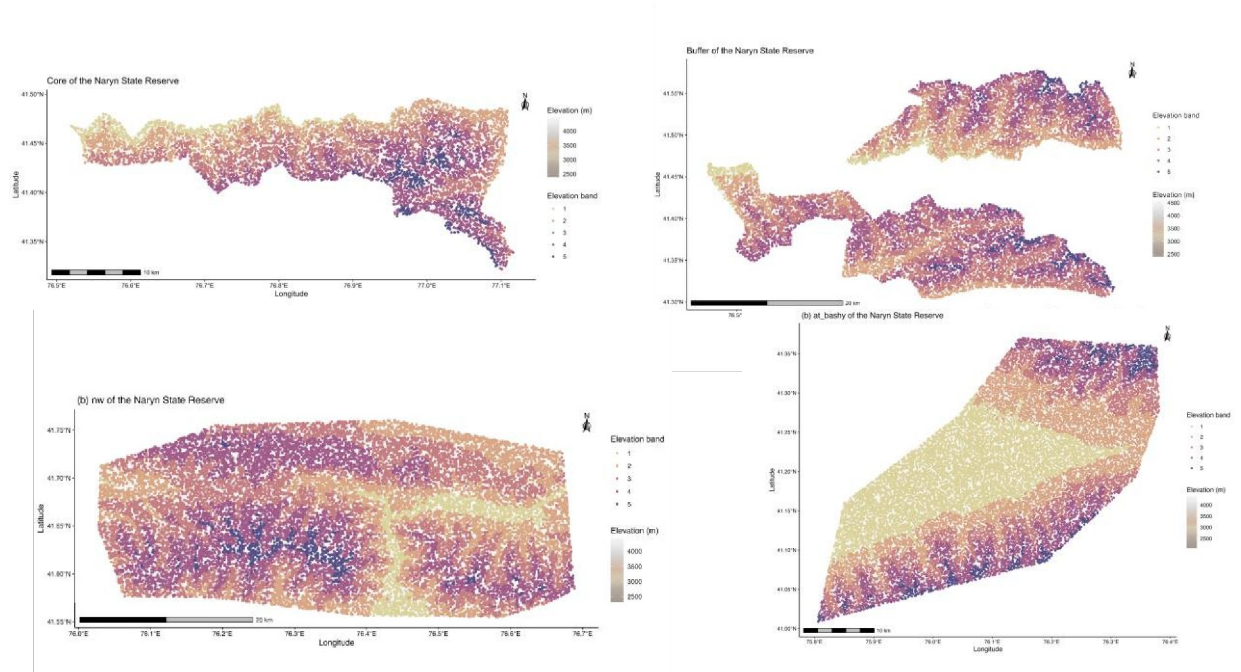


Figure A3. Random selection of points for land cover analysis in the core zone of the Naryn State Reserve (top left) and the buffer zones (top right), the Eki-Naryn region (bottom left) and At-Bashy (bottom right) per elevation band (low = 1, high = 5). The darker colours indicate a higher elevation.

Table A1. Elevation range (m) of each elevation bands for each study area

Area	Elevation bands				
	1	2	3	4	5
Core zone	2396 - 2811	2811 - 3225	3225 - 3640	3640 - 4054	4054 - 4469
Buffer zones	2407 - 2835	2835 - 3264	3264 - 3693	3693 - 4112	4112 - 4551
Eki-Naryn	2313 - 2734	2734 - 3156	3156 - 3577	3577 - 3999	3999 - 4420
At-Bashy	2072 - 2536	2536 - 3001	3002 - 3466	3466 - 3931	3931 - 4396

Table A2. Sample size of randomly selected pixels at elevation band per area using 1% of the total available sample size.

	Elevation bands				
	1	2	3	4	5
Area					
Core zone	638	1889	2605	2418	447
Buffer zones	618	2970	5999	4560	500
Eki-Naryn	1563	5733	8556	6572	694
At-Bashy	8064	5752	4272	4104	954

ESA Land cover classification

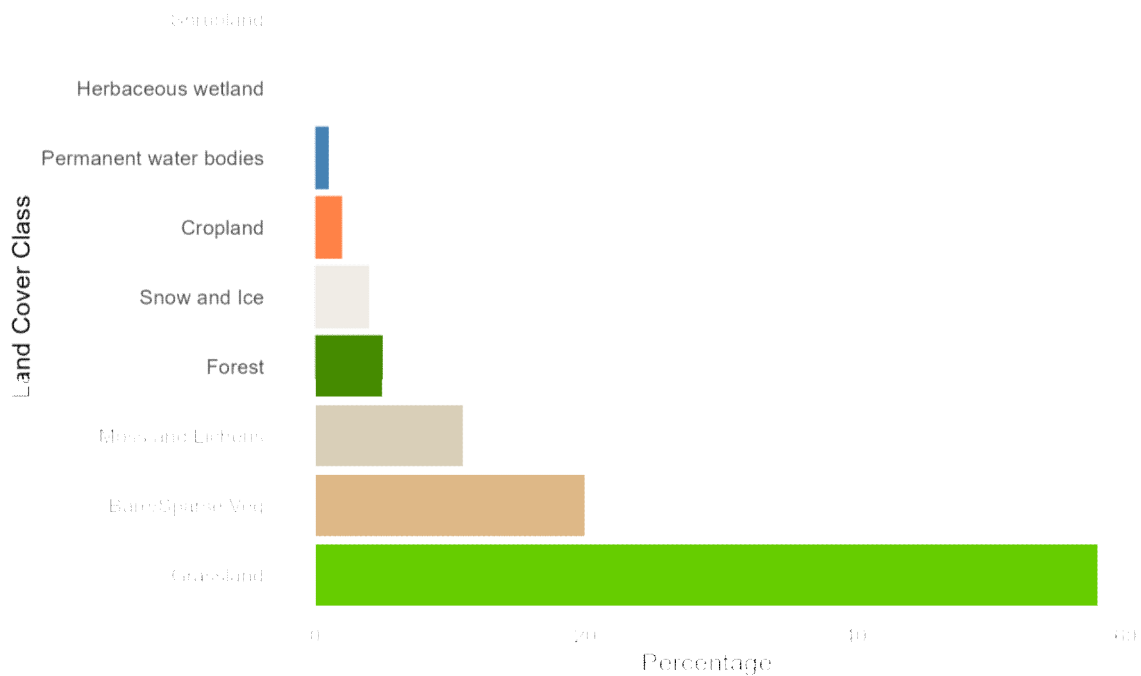


Figure A4. Percentage of land cover class cover in the Naryn region.

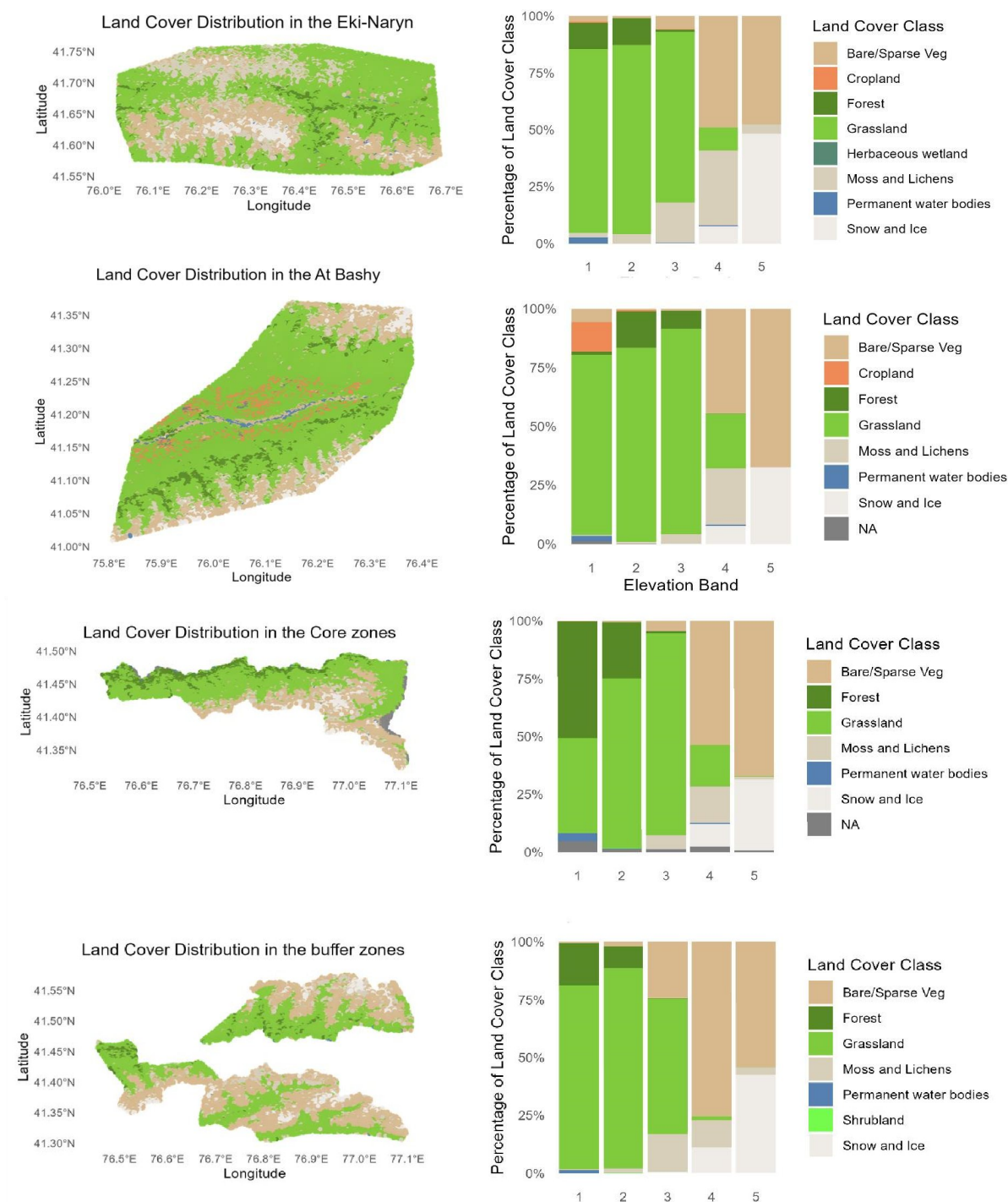


Figure A5. (Left column) Map of the land cover distribution across each study area extracted from the 2021 ESA Worldcover v200. (Right) Distribution of land cover proportion in each study area across elevation bands (See Table A1. in Appendix A for elevation band range).

Supervised Classification

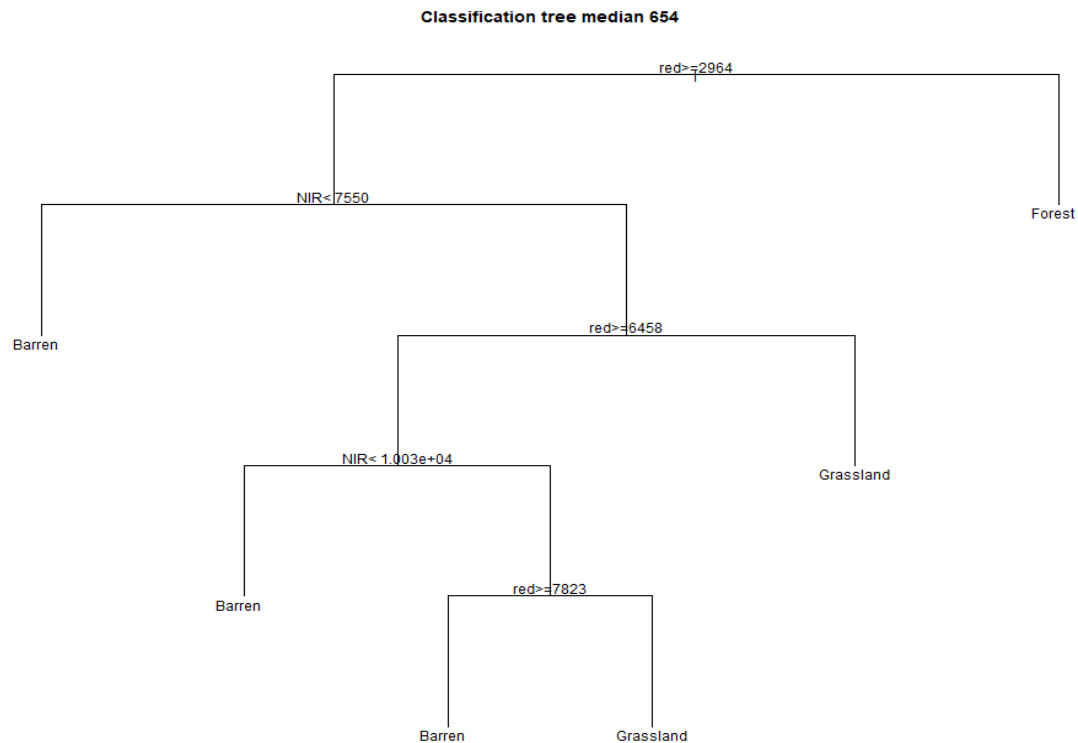


Figure A6. Predicted land cover classes based on the surface reflectance for each pixel using the Classification and Regression Trees (CART) algorithm. The training dataset includes 1035 pixels for each land cover class to be classified. The spectral bands used to classify barren areas, forest and grasslands are the NIR, SWIR1 and red bands (median654 from GLAD Tools) and NIR, SWIR1 and SWIR2 (median567). We set a minimum of 200 observations (minsplit parameter) to constitute a class.

Table A3. Confusion matrix representing the predicted and observed classification values of each given land cover class. The shaded diagonal represents the true positive classifications. The other values indicate the false positive classifications.

2021	predicted		
observed	Bare/Sparse Veg	Forest	Grassland
Barren	978	24	33
Forest	18	896	121
Grassland	173	76	786

Table A4. Classification accuracy of the Landsat multitemporal mosaic for 2017-2021 using 2021 ESA reference data. The user accuracy (UA) and producer accuracy (PA) are calculated per class and indicate the reliability of the classification and the capacity of the classifier to properly classify a pixel, respectively.

2021	Accuracy	
Land cover class	User Accuracy (UA)	Producer Accuracy (PA)
Barren	0.84	0.95
Forest	0.91	0.87
Grassland	0.84	0.76

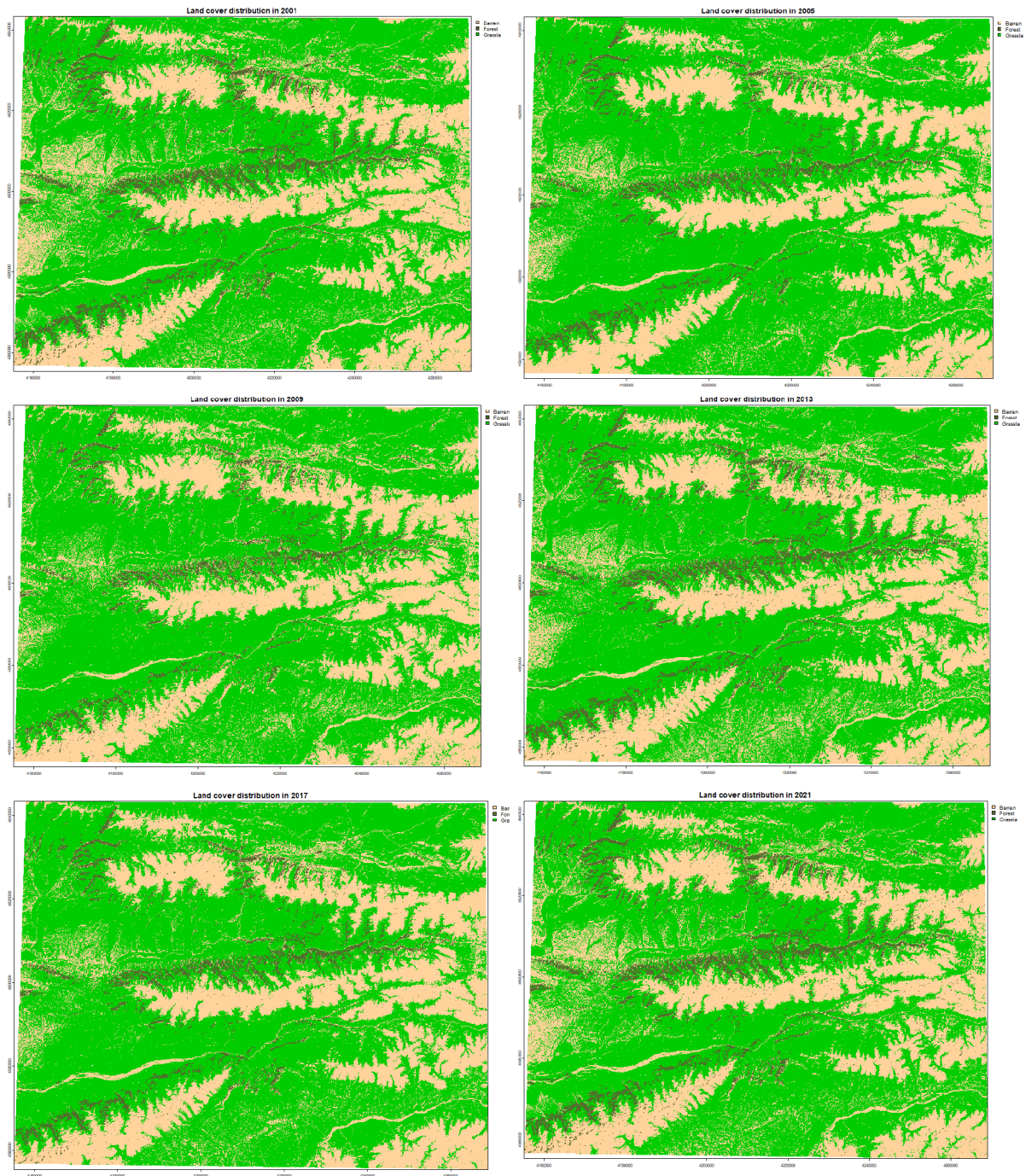


Figure A7. Predicted grassland, barren, forest and snow/ice spatial distributions after the supervised classification of the Landsat multi-year metrics composite for each time period. (a) 1997-2001, (b) 2001-2005, (c) 2005-2009, (d) 2009-2013, (e) 2013-2017, (f) 2017-2021.

Boosted Regression Trees

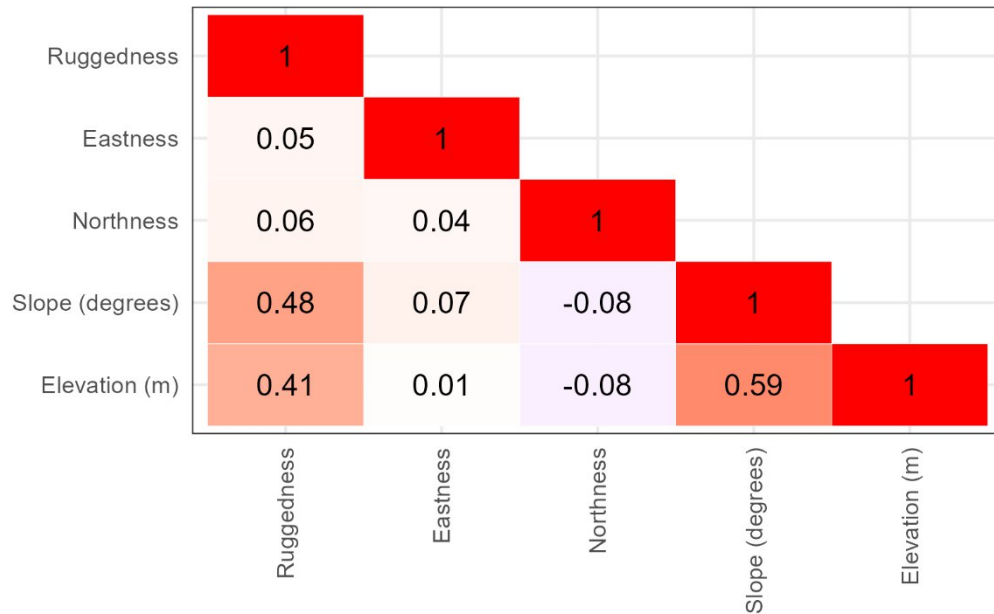


Figure A8. Correlation matrix among explanatory variables from 3105 pixels.

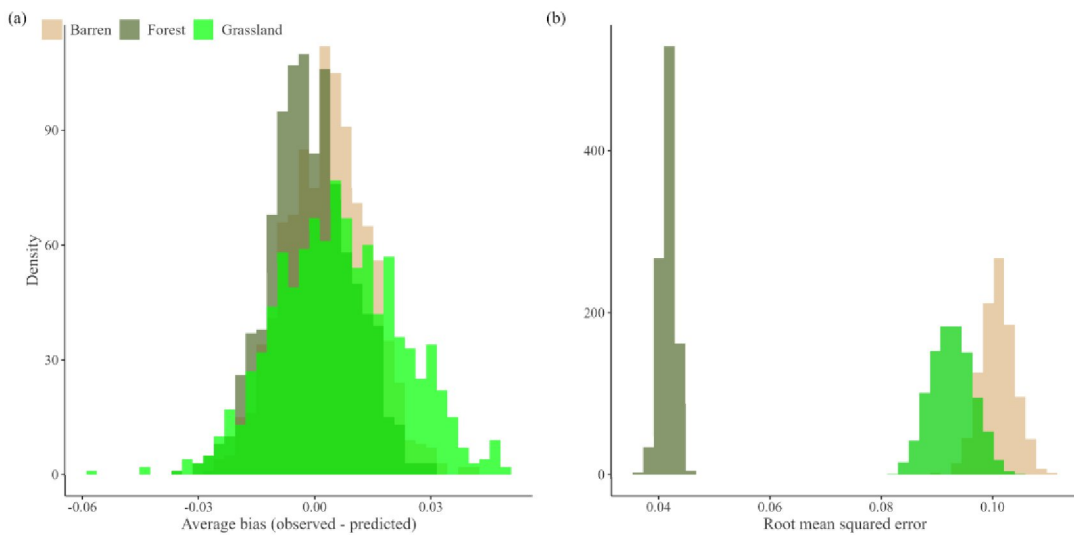


Figure A9. (a) Average bias plot per land cover class. (b) Root mean squared error for each land cover class.

Table A5. Selected hyperparameters for each land cover type. The minimization of the root mean square error selected in each model can be observed by comparing the selected lowest rmse (min_rmse) and the highest rmse (max_rmse) generated during the tuning step.

Land cover	eta	gamma	max_depth	subsample	min_rmse	max_rmse
Grassland	0.5	0.7	10	0.3	0.1943	0.1970
Barren	0.2	0.5	15	0.3	0.0990	0.1024
Forest	0.5	0.5	10	0.9	0.0934	0.0957

Table A6. Mean bias for each land cover class.

Land cover	mean	sd	se	ci	lower	upper
Barren	0.00353	0.227	0.00119	0.00234	0.00119	0.00587
Forest	-0.00096	0.223	0.00118	0.00231	-0.00327	0.00135
Grassland	0.00636	0.337	0.00178	0.00348	0.00288	0.00984

Table A7. Mean root mean square error (rmse) for each land cover class.

Land cover	mean	sd	se	ci	lower	upper
Barren	0.101	0.00300	0.00009	0.000186	0.101	0.101
Forest	0.0417	0.00134	0.00004	0.000083	0.0416	0.0417
Grassland	0.0927	0.000379	0.000120	0.000235	0.0924	0.0929

Table A8. Mean relative importance of each topographic variable on each land cover proportion.

Land cover	Feature	mean	sd	lower	upper
Barren	Elevation	0.561	0.0117	0.561	0.562
Barren	Northness	0.115	0.00749	0.114	0.115
Barren	RRI	0.113	0.00735	0.112	0.113
Barren	Slope	0.109	0.00748	0.109	0.109
Barren	Eastness	0.102	0.00708	0.102	0.102
Forest	Elevation	0.505	0.00844	0.504	0.505
Forest	Northness	0.296	0.00944	0.296	0.297
Forest	Eastness	0.0895	0.00654	0.0891	0.0899
Forest	RRI	0.0553	0.00447	0.0550	0.0556
Forest	Slope	0.0546	0.00655	0.0542	0.0550
Grassland	Elevation	0.265	0.0119	0.265	0.266
Grassland	Northness	0.206	0.0139	0.205	0.206
Grassland	Slope	0.194	0.0158	0.193	0.195
Grassland	RRI	0.173	0.0107	0.173	0.174
Grassland	Eastness	0.161	0.00982	0.161	0.162

Change detection

Table A9. Transition matrix describing the raw number of pixels per land cover class across the three study areas between 2001 and 2021. For each land cover class, the total number of pixels that remained the same throughout the period is presented in the diagonal (shaded). The pixels that permanently transitioned from their initial 2001 classification (row) to another 2021 classification (column) are presented on either side of the diagonal. Each pixel is approximately 30 m x 30 m and our results only include pixels considered accurately classified (i.e. pixels obtained the same classification between the Landsat 2021 and the ESA; n = 54 847). The surface area characterized by each land cover is reported as percentages, as well as the proportion that changed.

2001 detection	2021 detection				Total surface area (%)	Proportion changed (%)
	Barren	Forest	Grassland	Total sites		
Barren	11997	1855	1095	17902	32.6%	5.4%
Forest	298	2142	120	2560	4.7%	0.8%
Grassland	3372	1606	29407	34385	62.7%	9.1%
Surface area with the same land cover remaining (%)				84.8%		

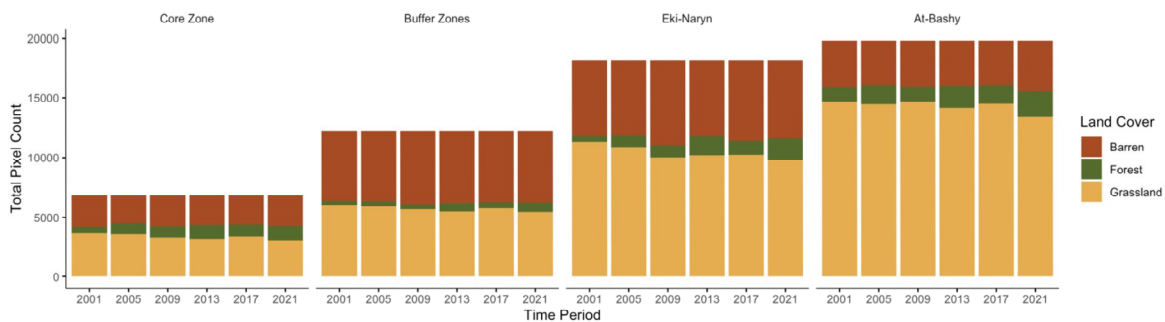


Figure A10. Total numbers of pixels characterized as barren, forest or grassland in each given time period and study area. The study areas are organized from the least disturbed (core zone of Naryn State Reserve) to the most disturbed (At-Bashy). The land cover classification of each pixel was generated through the supervised classification of the 5-year Landsat composites.

Table A10.Percentage of the mean change between the main land cover transitions per (a) area, (b) period, (c) elevation. The direction of transitions between grasslands (G), barren (B) and forest (F) covers is indicated by the arrow.

Mean percentage of change (%)				
(a) Area	G → B	B → G	G → F	B → F
Core	4.20	3.01	1.72	0.02
Buffer	4.35	3.57	0.71	0.01
Eki-Naryn	5.08	4.13	0.48	0.02
At-Bashy	3.56	3.12	0.68	0.01
(b) Time period	G → B	B → G	G → F	B → F
2005	3.67	5.94	0.60	0.02
2009	6.52	4.26	0.71	0.01
2013	6.91	2.94	2.30	0.02
2017	4.09	3.49	0.31	< 0.01
2021	4.59	4.11	1.48	0.02
(c) Elevation band	G → B	B → G	G → F	B → F
1	2.07	1.70	1.85	0.02
2	1.67	1.32	1.80	0.02
3	2.45	2.48	0.409	0.01
4	7.51	6.34	0.180	0.01
5	7.78	5.45	0.259	0.01

Raw data distribution

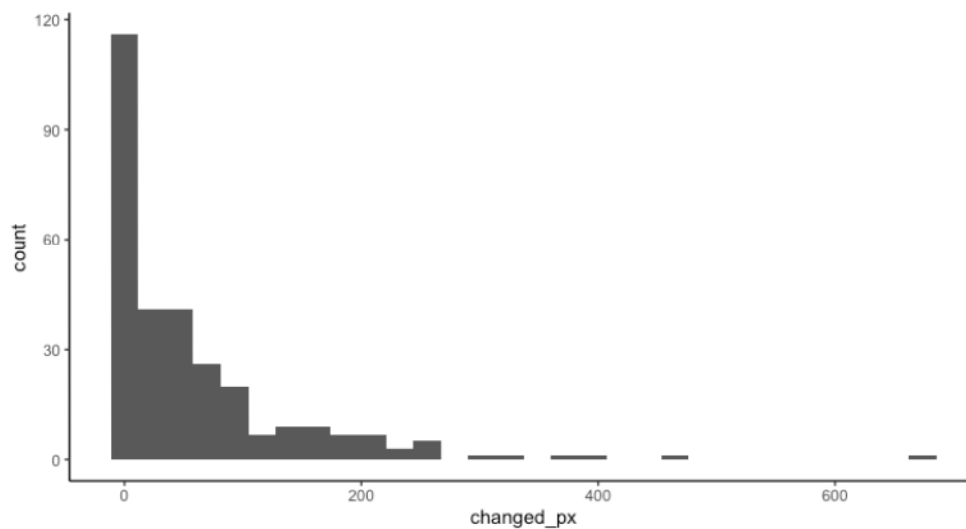


Figure A11. Distribution of the count of pixels that changed between 2001 and 2021, regardless of the direction of change.

Model

Table A11. Output from the generalized linear mixed model with negative binomial distribution showing the role of elevation, time, the degree of disturbance and the interaction between elevation and anthropogenic disturbance on the number of pixels that experienced browning or greening. To obtain proportions, we logged the total number of pixels, including those that did not experience change, and used the log total number of pixels as an offset. Significance codes represent 0 '***', 0.001 '**', 0.01 '*', 0.05 '.' and 1 ''

Predictors	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-3.973	0.25	-15.874	0	***
elevation_band2	0.953	0.27	3.527	0	***
elevation_band3	1.087	0.267	4.064	0	***
elevation_band4	0.701	0.275	2.554	0.011	*
elevation_band5	-0.672	0.371	-1.811	0.07	.
transitionGreening	-0.621	0.275	-2.258	0.024	*
areaBuffer	0.026	0.286	0.091	0.928	
areaEki-Naryn	1.451	0.269	5.387	0	***
areaAt-Bashy	0.584	0.269	2.172	0.03	*
year2009	0.127	0.175	0.726	0.468	
year2013	-0.461	0.174	-2.644	0.008	**
year2017	-0.939	0.176	-5.32	0	***
year2021	-0.043	0.177	-0.243	0.808	
elevation_band2:transitionGreening	0.15	0.231	0.648	0.517	
elevation_band3:transitionGreening	0.245	0.229	1.069	0.285	
elevation_band4:transitionGreening	0.11	0.235	0.467	0.64	
elevation_band5:transitionGreening	-0.117	0.338	-0.345	0.73	
transitionGreening:areaBuffer	-0.023	0.222	-0.103	0.918	
transitionGreening:areaEki-Naryn	-0.084	0.218	-0.386	0.699	
transitionGreening:areaAt-Bashy	0.018	0.219	0.083	0.934	
transitionGreening:year2009	-0.286	0.249	-1.149	0.251	
transitionGreening:year2013	0.314	0.246	1.275	0.202	
transitionGreening:year2017	1.02	0.246	4.148	0	***
transitionGreening:year2021	-0.376	0.251	-1.499	0.134	
elevation_band2:areaBuffer	-0.453	0.348	-1.3	0.193	
elevation_band3:areaBuffer	-0.018	0.346	-0.052	0.959	
elevation_band4:areaBuffer	-1.187	0.353	-3.358	0.001	***
elevation_band5:areaBuffer	0.219	0.476	0.459	0.646	
elevation_band2:areaEki-Naryn	-1.469	0.33	-4.454	0	***
elevation_band3:areaEki-Naryn	-1.434	0.329	-4.36	0	***
elevation_band4:areaEki-Naryn	-1.976	0.334	-5.916	0	***

elevation_band5:areaEki-Naryn	-1.445	0.468	-3.087	0.002	**
elevation_band2:areaAt-Bashy	-1.94	0.332	-5.848	0	***
elevation_band3:areaAt-Bashy	-1.246	0.33	-3.774	0	***
elevation_band4:areaAt-Bashy	-0.857	0.334	-2.57	0.01	*
elevation_band5:areaAt-Bashy	-1.408	0.48	-2.932	0.003	**

Pixel change across elevations and study areas

Table A12. Pairwise contrasts between the model-estimated marginal means in the proportion of pixels changed for different combinations of elevation and area. Estimated marginal means were calculated by marginalizing over levels of year and transition type (i.e., the contrasts represent the differences between elevation bands on average across years and transition types).

contrast	area	estimate	SE	z.ratio	p.value
elevation_band1 - elevation_band2	Core	-1.028	0.248	-4.149	< 0.001
elevation_band1 - elevation_band3	Core	-1.209	0.247	-4.900	< 0.001
elevation_band1 - elevation_band4	Core	-0.756	0.251	-3.008	0.022
elevation_band1 - elevation_band5	Core	0.730	0.346	2.108	0.216
elevation_band2 - elevation_band3	Core	-0.181	0.218	-0.833	0.920
elevation_band2 - elevation_band4	Core	0.272	0.223	1.219	0.740
elevation_band2 - elevation_band5	Core	1.758	0.327	5.384	< 0.001
elevation_band3 - elevation_band4	Core	0.453	0.221	2.047	0.243
elevation_band3 - elevation_band5	Core	1.939	0.325	5.960	< 0.001
elevation_band4 - elevation_band5	Core	1.486	0.328	4.533	< 0.001
elevation_band1 - elevation_band2	Buffer	-0.575	0.245	-2.345	0.131
elevation_band1 - elevation_band3	Buffer	-1.191	0.243	-4.898	< 0.001
elevation_band1 - elevation_band4	Buffer	0.431	0.254	1.698	0.435
elevation_band1 - elevation_band5	Buffer	0.511	0.333	1.533	0.541
elevation_band2 - elevation_band3	Buffer	-0.616	0.217	-2.844	0.036
elevation_band2 - elevation_band4	Buffer	1.006	0.228	4.411	< 0.001
elevation_band2 - elevation_band5	Buffer	1.086	0.315	3.444	0.005
elevation_band3 - elevation_band4	Buffer	1.622	0.224	7.233	< 0.001
elevation_band3 - elevation_band5	Buffer	1.702	0.313	5.436	< 0.001
elevation_band4 - elevation_band5	Buffer	0.080	0.319	0.252	0.999
elevation_band1 - elevation_band2	Eki-Naryn	0.441	0.217	2.031	0.251
elevation_band1 - elevation_band3	Eki-Naryn	0.225	0.217	1.037	0.838
elevation_band1 - elevation_band4	Eki-Naryn	1.220	0.220	5.533	< 0.001
elevation_band1 - elevation_band5	Eki-Naryn	2.175	0.320	6.798	< 0.001

elevation_band2 - elevation_band3	Eki-Naryn	-0.216	0.214	-1.011	0.850
elevation_band2 - elevation_band4	Eki-Naryn	0.779	0.219	3.564	0.003
elevation_band2 - elevation_band5	Eki-Naryn	1.734	0.319	5.445	< 0.001
elevation_band3 - elevation_band4	Eki-Naryn	0.995	0.219	4.553	< 0.001
elevation_band3 - elevation_band5	Eki-Naryn	1.950	0.318	6.129	< 0.001
elevation_band4 - elevation_band5	Eki-Naryn	0.955	0.320	2.988	0.024
elevation_band1 - elevation_band2	At-Bashy	0.912	0.220	4.147	< 0.001
elevation_band1 - elevation_band3	At-Bashy	0.037	0.218	0.170	1.000
elevation_band1 - elevation_band4	At-Bashy	0.101	0.219	0.461	0.991
elevation_band1 - elevation_band5	At-Bashy	2.138	0.334	6.398	< 0.001
elevation_band2 - elevation_band3	At-Bashy	-0.875	0.221	-3.959	0.001
elevation_band2 - elevation_band4	At-Bashy	-0.811	0.224	-3.623	0.003
elevation_band2 - elevation_band5	At-Bashy	1.226	0.337	3.643	0.002
elevation_band3 - elevation_band4	At-Bashy	0.064	0.220	0.290	0.998
elevation_band3 - elevation_band5	At-Bashy	2.101	0.334	6.280	< 0.001
elevation_band4 - elevation_band5	At-Bashy	2.037	0.336	6.068	< 0.001

Appendix B

Supporting Materials for Chapter 3

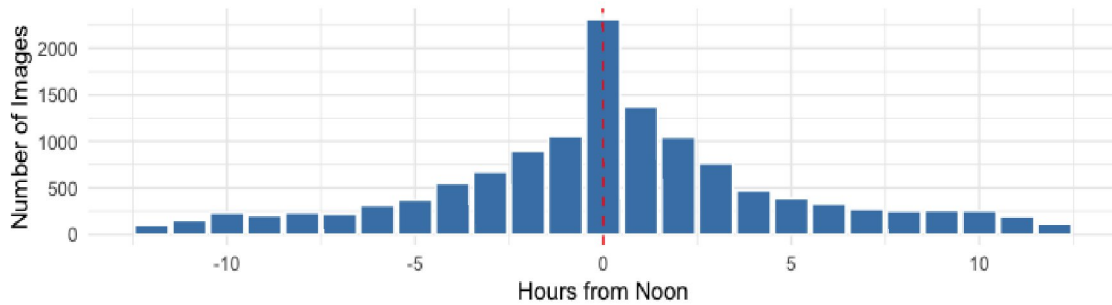


Figure B1 Distribution of the time differences from 12:00 pm for camera trap images selected as the closest to noon. Bars represent the number of images captured within varying hourly offsets from noon to visualize how closely motion-triggered images within the dataset align with commonly used noon-images.

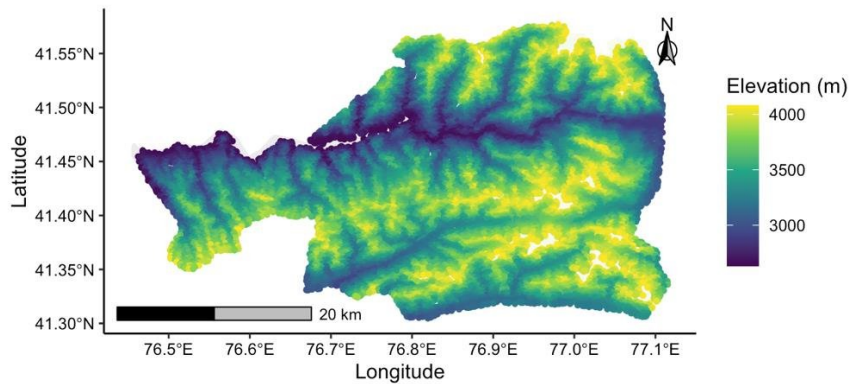


Figure B2 Spatial distribution of the randomly selected pixels (n = 21,352) across the Naryn State Reserve. Pixels located at low elevations are characterized by darker colours, and high elevations by lighter colours. White areas indicate pixels that were not randomly selected.

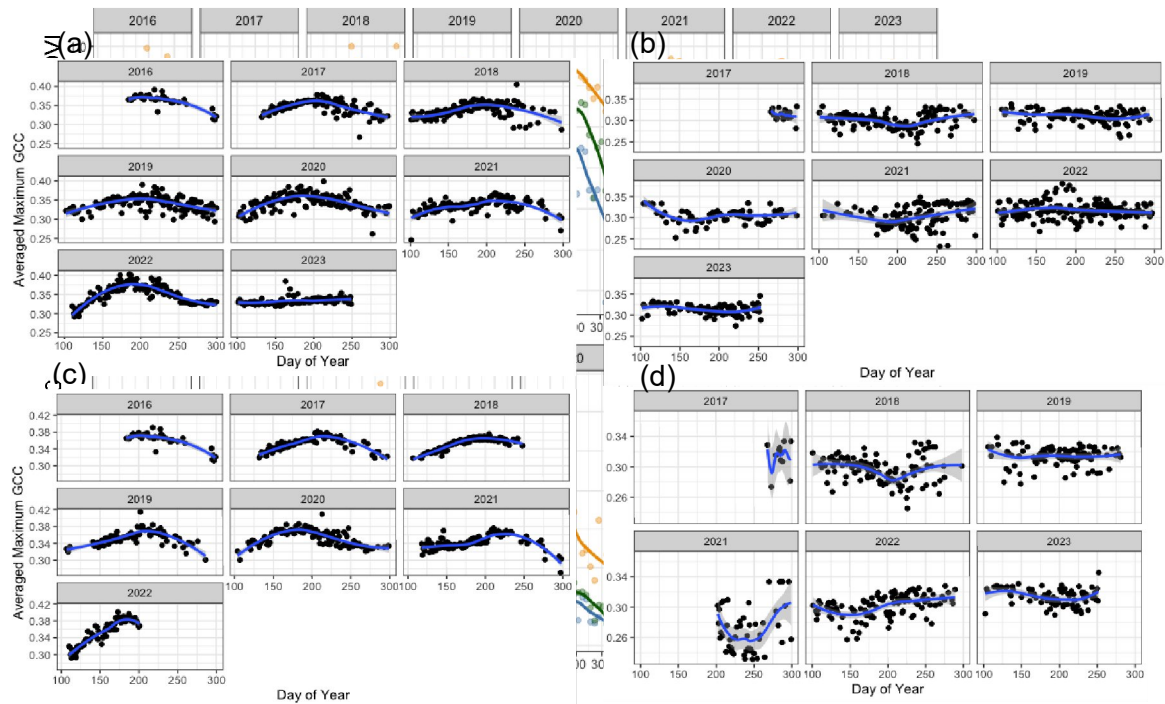


Figure B3 Landsat bi-weekly maximums of (a) NDVI, and (b) GCC values averaged across the four meadow sites (green), Site 9 (blue), and random points (orange) between 2016 and 2023. The annual bi-weekly sample size for each dataset is reported in Table 2.

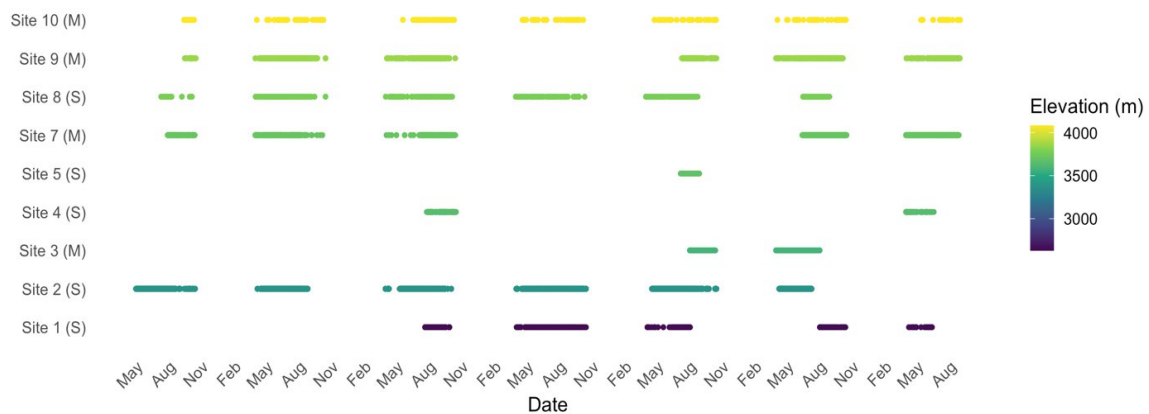


Figure B4 Temporal distribution of daily camera trap sampling effort per site and year across the elevational gradient. Each point represents a day with available camera trap imagery at a given site. Sites are ordered from low to high elevation.

Figure B5 Daily averaged values of maximum camera trap generated GCC across (a) pooled meadow sites between 2016-2023 (n = 4), (b) pooled steppe sites between 2017-2023 (n = 5), (c) single meadow site between 2016-2022, and (d) single steppe site between 2017-2019 and 2021-2023. This plot illustrates annual and inter-annual data availability of GCC values generated by camera traps. The time-series for single and pooled steppe sites were trimmed to exclude 2017 due to the lack of data availability.

Table B1. Daily sampling effort per site and year, based on camera trap data.

	2016	2017	2018	2019	2020	2021	2022	2023
Pooled meadow	44	120	138	155	152	143	175	116
Pooled steppe	-	19	122	119	80	119	158	91
Site 9 – Meadow	44	103	100	97	127	115	83	-
Site 2 - Steppe	-	12	110	99	-	50	105	79

Table B2. Daily sampling effort per site and year, based on bi-weekly Landsat imagery.

	2016	2017	2018	2019	2020	2021	2022	2023
Random Points	20	21	23	22	21	20	22	22
All meadow	21	23	23	23	23	23	22	22
Site 9	21	23	23	23	22	23	22	22

Appendix C

Supporting Materials for Chapter 4

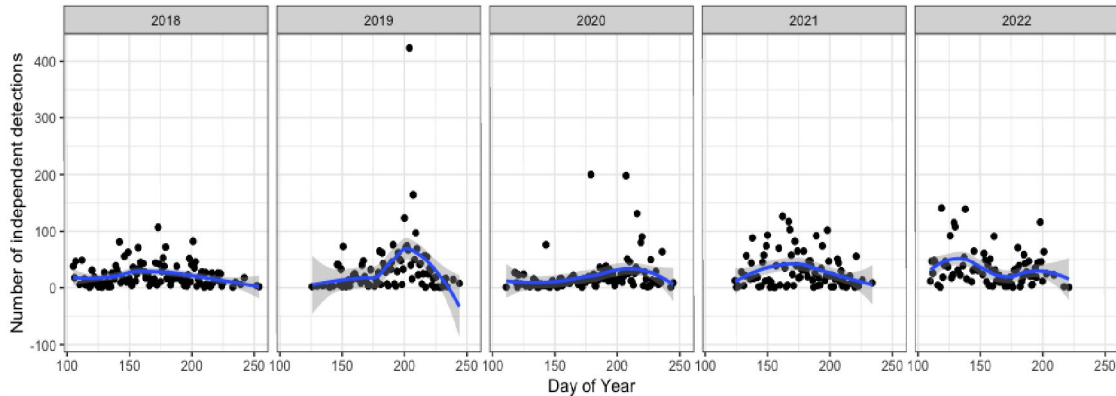


Figure C1. Daily count of independent detections of the presence of gray marmots across all sites ($n = 18$) in the Naryn State Reserve, Kyrgyzstan, between 2018 and 2022. Points represent the daily total number of marmot detections for each year and lines represent the annual detection trend. The x axis begins on day 100 (10 April) and ends on day 254 (11 September), which encompasses the period of above-ground activity of gray marmots.