Summary

Spatial patterns in species distribution, abundance and community composition are manifestations of the underlying ecological mechanisms operating at a range of spatial scales. These patterns emerge from dynamic interactions between environmental bottom-up, biotic top-down and biotic parallel factors (operating within a trophic level) in combination with stochastic effects. Especially, the role of species interactions both within and across trophic levels, including those involving humans, remain largely unexplored. Large herbivorous mammals are an important part of terrestrial ecosystems influencing their functioning via effects on vegetation or soil at different spatial scales from the local landscape up to the biome level. The spatial distribution of large herbivores often results from their responses to interacting top-down (e.g. humans, large carnivores) and bottom-up (e.g. food availability) ecological gradients that can create landscape-scale variation in the structure of the entire community. Recently there has been much attention on the role of large carnivores in structuring ecosystems via their direct (killing) and indirect (influencing prey behaviour) effects on their herbivorous prey communities. Humans are also increasingly being considered to be a coherent part of complex trophic interaction chains influencing the distribution, space use and behaviour of both predator and prey animal species. As mentioned above, in almost every ecosystem, communities of herbivores are modified by both predators and the availability of the plants they eat. As herbivores use space in response to these different pressures, they shape their impact on plant communities across the landscapes. Yet the role of large plant-eating mammals in structuring ecosystems in the temperate region is often overlooked. Most research on this topic has looked at African ecosystems, like open savannahs, where multi-species large carnivore and herbivore communities have a dominant impact on the landscape. Much fewer researchers have studied these processes in temperate forests like those found across Europe, Asia and North America. In these systems large carnivores and herbivores also co-occur but humans often play a much more pronounced role in shaping natural landscapes. Knowledge on how these factors in combination influence patterns of space use of herbivores, and their impact on the vegetation, is highly relevant for better understanding of the processes structuring terrestrial herbivore communities, especially in the context of ongoing climate change, re-colonization of Europe by large carnivores and the ever-increasing overall anthropogenic pressure on natural ecosystems and wildlife communities.

The core question of this thesis was how the interactive effects of bottom-up and top-down factors (two large carnivore species - *Canis lupus* and *Lynx lynx* - and humans), determine the landscape distribution and community composition of five native ungulate species (*Cervus elaphus, Sus scrofa, Capreolus capreolus, Bison bonasus and Alces alces*) and how these spatial processes affect the regeneration of trees in Białowieża Forest (BF). BF is regarded to be one of the best preserved temperate European lowland forest systems and is inhabited by a natural community of large mammals. In addition, BF is also embedded within an anthropogenic landscape typical for many terrestrial systems across the globe. I studied the complexity of these cascading interactions using high-resolution camera trapping and remote sensing data together with detailed on the ground woody vegetation surveys analysed within a framework of spatially-explicit hierarchical Bayesian models. Moreover, to get better insight into how environmental factors can interact with top-down factors created by wolf and human presence, I investigated in more detail how the red deer (the main prey of wolf in BF) perceives the landscape of fear both at large and fine spatial scales. Recent studies from the Białowieża Forest indicate that the presence of tree logs imposes a fine-scale predation risk factor for red deer. Next to wolves, human activity may pose an additional factor directly or indirectly (via effects on wolves) affecting deer (spatial) behavior. More specifically, I tested how red deer react to tree logs relative to wolf presence and distance to human settlements.

While carrying out a large-scale camera trapping project in BF we experienced difficulties in handling, organizing and processing large amounts of camera trapping data. With more than 1000 camera trap locations, a massive amount of collected data (30 000 pictures and videos, >500 GB of raw data) presented me with the following problems: 1) how to facilitate different people classifying videos in a structured way that prevents mistakes, 2) how to manage these data in a way that allows easy filtering of subsets of data and re-use of already available information, 3) how to process camera trapping data for further analyses. To solve the above issues, I designed and implemented a specialized camera trapping software (‘TRAPPER’): an open source, web-based and database-driven software for data management in camera trapping studies. The source code of the application, developed and maintained by the Open Science Conservation Fund (OSCF) that I co-founded, is available under the GNU GPL license at https://gitlab.com/oscf/trapper-project.

This thesis consists of three published articles, covering the topics briefly described above:

Publication 1:

Bubnicki, J. W., Churski, M., Schmidt, K., Diserens, T. A., & Kuijper, D. P. J. (2019). Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. eLife, 8, e44937, https://doi.org/10.7554/eLife.44937.

Publication 2:

Kuijper, D. P. J., Bubnicki, J. W., Churski, M., Mols, B., & Van Hooft, P. (2015). Context dependence of risk effects: wolves and tree logs create patches of fear in an old-growth forest. Behavioral Ecology, 26(6), 1558-1568, https://doi.org/10.1093/beheco/arv107.

Publication 3:

Bubnicki, J. W., Churski, M., & Kuijper, D. P. J. (2016). Trapper: An open source web based application to manage camera trapping projects. Methods in Ecology and Evolution, 7(10), 1209-1216, https://doi.org/10.1111/2041-210X.12571.

A brief summary of the methodology and the major findings for each article is presented below.

Publication 1

The main ecological process that has been studied in this thesis, the distribution of five ungulate species over the BF landscape, is a spatial process. I recorded and reconstructed the spatial patterns of five large ungulates (European bison, moose, red deer, roe deer, wild boar) by sampling the BF landscape for 2 years (May 2012 - May 2014) with camera traps placed randomly with respect to species and the hypothetical mechanisms driving their distributions (habitat structure, humans, wolf). The sampling scheme was designed to capture the overall landscape scale spatial variation in local abundances of each species. Using detailed data on species distributions (894 camera trap locations), landscape structure (high-resolution GIS and remote sensing data) and detailed woody vegetation surveys (385 study plots monitored by the people from the ForBioSensing project) along with a novel spatially-explicit hierarchical modeling approach, I decomposed the spatial variation in herbivore community structure into ecologically distinct landscape-scale herbivory regimes. To quantify the space use of two large carnivores (wolf and lynx) an additional camera trapping survey was run in September-October 2015. 73 camera traps were deployed on the side of forest roads across the whole landscape for one month. After downloading camera trap data, both ungulate, and wolf datasets were organized and classified using TRAPPER software (see Publication 3). Species, sex, age and group size were determined for every recorded image and video containing an observation of a focal species. I defined the independence interval between successive captures (i.e. event) as five minutes.

To analyse the collected data I developed a hierarchical multi-scale Bayesian spatial model to quantify landscape use by large carnivores and ungulates. The model was fitted to the camera trapping data of wolf and lynx and each of the five ungulate species. To model the intensity of landscape use (or relative densities) by each of the ungulate species, I overlaid a grid of 2303 cells 500 m per side (25 ha each) over the study area. Based on this grid I compiled a set of spatial (raster) covariates, derived from available GIS and remote sensing data. These covariates describe the ecologically relevant environmental and human-induced gradients operating across the BF landscape. Additionally, I generated a high-resolution picture of the spatial structure of the entire community of large herbivores. This spatial structure incorporated both bottom-up and predation- and human-related top-down factors using predicted relative densities of each species (translated into herbivory biomass), functional diversity index (FDis) and hierarchical clustering analysis. Finally, using an independent vegetation dataset from a large-scale inventory of tree regeneration (conducted by the Forest Research Institute), I tested if the predicted variation in the landscape-scale distribution of large herbivores, synthesized into ecologically distinct herbivory regimes, affecting tree browsing intensity and regenerating tree species composition.

We found that spatial interactions between humans, large carnivores and herbivores cascade down in a complex but predictable way to lower trophic levels affecting regeneration of tree species in Białowieża Forest. The results showed that the variation in the spatial distribution of a community of large herbivores in a temperate forest ecosystem can be explained by species-specific associations with major ecological gradients operating at the landscape scale. This creates ecologically distinct landscape-scale herbivory regimes ("herbiscapes"), which are interactively driven both by environmental bottom-up and biotic top-down (large carnivores) factors in combination with human-driven (cascading) effects. In addition, the analyses suggested that these "herbiscapes" differ in browsing intensity and impact on vegetation, indicated by changing proportions of recruitment of browsing-sensitive versus browsing-tolerant tree species. The observed compositional changes in regenerating trees across the "herbiscapes" were in accordance with our earlier experimental studies.

The analysis revealed that humans are the main factor influencing the movements of large carnivores in Białowieża Forest, but not the herbivores directly. Wolves and lynxes avoided areas heavily used by humans whereas large herbivores responded primarily to different environmental factors and not directly to distance to human settlements. Wild boar and bison were mainly influenced by the availability of their preferred habitat for foraging; moose and roe deer by the structure of the landscape (like elevation or openness). The red deer was the only large herbivore species whose distribution was strongly linked to that of its main predator, the wolf.

With our work we aimed at contributing to a general better understanding of the processes structuring terrestrial herbivore communities. While generally a well-researched topic, mainly in African ecosystems, we aimed at providing rare and spatially high-resolution data from a temperate forest system. These findings provide new a understanding of the complex ecological processes shaping Białowieża Forest and serve as a model to help understand other ecosystems around the world. This knowledge is also highly valuable for the ongoing management and conservation of this UNESCO World Heritage Area.

Publication 2

To get better insight into the mechanisms of the indirect effects of predation on prey spatial distribution and behaviour, I investigated how the red deer, the main prey of wolf in BF, perceives the landscape of fear both at large and fine spatial scales. For this, a pseudo-experimental field study was conducted in Białowieża National Park (BNP) to minimize direct human impact. Red deer visitation rates and behavior were estimated using camera traps at 128 camera locations. All locations were further than 100 m from tracks, and 1.5 km from human settlements to minimize direct anthropogenic disturbances. All locations were in deciduous and mixed deciduous forest, which are prime habitat for red deer and the dominant forest types in BNP. Camera traps were placed at locations with and without tree logs (fine-scale risk factor) and at different distances from the core of a wolf territory and human settlements (landscape-scale risk factors). I used a Bayesian approach, for its flexibility in hierarchical modeling and information-rich output, to examine 2 models: 1) red deer visitation rates at the locations and 2) vigilance levels of individuals. I tested how the presence/absence of tree logs and distance to human settlements (as a proxy of risk) and their interaction affected both parameters.

The results of this study showed that red deer avoided coming close to and increased their vigilance levels when in the close vicinity of large tree logs. The strength of these effects depended on the distance to the wolf core area: deer perceived tree logs as more risky when wolves were more often present. Hence, tree logs inside wolf core areas create fine-scale patches of fear with reduced deer browsing pressure, thereby enhancing chances for successful tree recruitment. Human presence shapes this landscape of fear as wolf core areas are located far from human settlements. This "human shadow" on predator–prey interactions is therefore an important component that should be taken into account in human-dominated landscapes to understand potential trophic cascading effects.

Publication 3

According to the so called Fourth Paradigm (Data-Intensive Science) we can observe today in general a massive flow of data ready to get (collect or download) and analyse all across scientific disciplines. A good example comes from the field of ecological studies, which by its nature has very diverse data sources. Camera trapping is increasingly becoming an important tool in ecological research. However, organizing large collections of multimedia files and efficiently searching for subsets of data are challenging tasks. While the development of project-specific software solutions is dominating in the camera trapping community, little attention has been paid to more flexible and open-source solutions supporting diverse camera trapping research projects.

To solve the above issues, I designed and implemented TRAPPER software: a flexible, web-based and database-driven software for data management in camera trapping studies. I exclusively used open source and cross-platform software components. The core programming language of the proposed system is Python, a modern, high-level programming language with a well-developed community. An easy to learn syntax and many available scientific libraries make Python, among other features, a great choice for scientific computing tasks. Although not as popular as R amongst ecologists (which use R mostly for data analysis), Python has the advantage of being a general purpose programming language, thus making possible the implementation of data analysis procedures, new algorithms and web-based database driven applications within one programming environment. The core component of TRAPPER, the web application (database client), was developed using Django. This is a high-level Python web framework maintained by the Django Software Foundation. The Django framework simplifies and significantly speeds up the creation of complex, database-driven websites and emphasizes the reusability and pluggability of their components. The main features of TRAPPER are that (i) it is fully open-source, (ii) it facilitates analysis of videos as well as images, (iii) it provides spatial filtering and web-mapping, (iv) it allows flexible implementation of specific data collection protocols, (v) it is a multi-user and role based system that facilitates collaborative work on camera trapping projects, (vi) it supports data re-use and (re)discovery. TRAPPER can therefore be widely used by ecologists working with a variety of camera trap studies, alone or in collaboration with each other.

Since its original development, TRAPPER has been updated multiple times, including adaptations to its internal data model to support millions of images and videos and integration with an AI classification workflow. To support TRAPPER maintenance and further development I co-founded a dedicated foundation: OPEN SCIENCE CONSERVATION FUND. Currently TRAPPER software supports several camera trapping projects (both research and monitoring-oriented) in Poland, Germany, Sweden and South America.