Leveraging big satellite image and animal tracking data for characterizing large mammal habitats

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Abstract

Habitat models provide critical information for the conservation and management of wildlife, allowing to assess the distribution of species' habitats and help understand their habitat use. The growing availability of satellite remote sensing and animal tracking data opens new opportunities for an improved monitoring of wildlife habitats based on habitat models, yet suitable approaches for making full use of this potential are commonly lacking. The overarching goal of this thesis was to develop and advance approaches for harnessing the potential of big satellite image and animal tracking data in habitat models. Specifically, using three large mammal species in Europe as an example (Eurasian lynx, red deer, and roe deer), I developed approaches for (1) linking habitat models to the largest global and freely available satellite image record, the Landsat image archive, and (2) for integrating animal tracking datasets across wildlife populations in large-area assessments of habitat suitability and use. The results of this thesis demonstrate the enormous potential of Landsat-based variables as predictors in habitat models, allowing to move from static habitat descriptions to a continuous monitoring of habitat dynamics across space and time. The use of Landsat-based variables particularly improved the capacity for capturing temporal habitat dynamics across seasons and related to long-term landscape change, as well as for characterizing fine-scale spatial variation in habitat conditions. In addition, my research underscores the importance of considering context-dependence in species' habitat use in habitat models, particularly also when integrating tracking datasets across wildlife populations. Approaches that incorporated environmentally related variation in habitat use across populations allowed to improve the accuracy of habitat suitability mapping across large spatial extents and were critical for understanding broad-scale variation in habitat use due to gradients in human pressure and landscape composition. The findings of this thesis provide novel ecological insights that help to inform the management and conservation of large mammals and more broadly, demonstrate that a better integration of satellite image and animal tracking data will allow for a new generation of habitat models improving our ability to monitor and understand habitat dynamics, thus supporting efforts to restore and protect wildlife across the globe.

Zusammenfassung

Habitatmodelle liefern wichtige Informationen für den Schutz und das Management von Wildtieren, indem sie es ermöglichen Habitate zu kartieren und die Lebensraumnutzung von Tieren besser zu verstehen. Die zunehmende Verfügbarkeit von Satellitenfernerkundungs- und Wildtier-Telemetriedaten eröffnet neue Möglichkeiten für eine verbesserte Überwachung von Wildtierhabitaten durch Habitatmodelle, doch fehlt es häufig an geeigneten Ansätzen, um dieses Potenzial voll auszuschöpfen. Das übergeordnete Ziel dieser Arbeit bestand in der Konzipierung und Weiterentwicklung von Ansätzen zur Nutzung des Potenzials großer Satellitenbild- und Telemetriedatensätze in Habitatmodellen. Am Beispiel von drei großen Säugetierarten in Europa (Eurasischer Luchs, Rothirsch und Reh) wurden Ansätze entwickelt, um (1) Habitatmodelle mit dem umfangreichsten global und frei verfügbaren Satellitenbildarchiv der Landsat-Satelliten zu verknüpfen und (2) Wildtier-Telemetriedaten über Wildtierpopulationen hinweg in großflächigen Analysen der Habitateignung und -nutzung zu integrieren. Die Ergebnisse dieser Arbeit belegen das enorme Potenzial von Landsat-basierten Variablen als Prädiktoren in Habitatmodellen, die es ermöglichen von statischen Habitatbeschreibungen zu einem kontinuierlichen Monitoring von Habitatdynamiken über Raum und Zeit überzugehen. Die Verwendung von Landsat-basierten Variablen verbessert vor allem die Erfassung von zeitlichen Lebensraumdynamiken, sowohl saisonal bedingt als auch im Zusammenhang mit langfristigen Landschaftsveränderungen, und ermöglicht ferner die Charakterisierung feinräumiger Lebensraumstrukturen. Die Ergebnisse meiner Forschung zeigen darüber hinaus, wie wichtig es ist, die Kontextabhängigkeit der Lebensraumnutzung von Wildtieren in Habitatmodellen zu berücksichtigen, insbesondere auch bei der Integration von Telemetriedatensätzen über Wildtierpopulationen hinweg. Ansätze, die umweltbedingte Variation in der Habitatnutzung berücksichtigen, ermöglichten es, die Genauigkeit von großräumigen Habitatanalysen zu verbessern, und waren entscheidend, um Unterschiede in der Lebensraumnutzung über Gradienten menschlicher Einflüsse und verschiedener Landschaftsstrukturen hinweg zu verstehen. Die Ergebnisse dieser Dissertation liefern neue ökologische Erkenntnisse, welche zum Management und Schutz großer Säugetiere beitragen können. Darüber hinaus zeigt meine Forschung, dass eine bessere Integration von Satellitenbild- und Telemetriedaten eine neue Generation von Habitatmodellen möglich macht, welche genauere Analysen und ein besseres Verständnis von Lebensraumdynamiken erlaubt und so Bemühungen zum Schutz von Wildtieren unterstützen kann.

Contents

Chapter III: Satellite-based habitat monitoring reveals long-term dynamics of deer habitat in response to forest disturbances   **45**

Chapter IV: Integrating large animal tracking datasets across multiple populations for mapping wildlife habitat at a continental scale   **71**

Chapter V: Prerequisites for coexistence: human pressure and refuge habitat availability shape continental-scale habitat use patterns of a large carnivore   **107**

List of Figures

List of Tables

List of Supplementary Information

Supplementary Figures

Supplementary Tables

Supplementary Text

Chapter I:
Introduction

1   Habitat modeling for wildlife conservation and management

Conserving and restoring biodiversity in the face of a rapid expansion of the human footprint on our planet is one of humankind's central challenges of our time (Steffen et al., 2015). As up to one million species are currently facing extinction (IPBES, 2019), human activities have caused the onset of Earth's sixth mass extinction event (Ceballos et al., 2015). This rapid decline and irreversible loss of biodiversity poses serious threats to human societies, as it puts at risk the integrity of ecosystem functions critical to human wellbeing (Díaz et al., 2019). Even where wildlife populations are recovering regionally, the coexistence of humans and wild animals in shared landscapes often is challenging (Nyhus, 2016). As the loss, modification and overexploitation of species' habitats remain the most important drivers of biodiversity loss (Hanski, 2011; Newbold et al., 2016), information on where wildlife habitats are available, how they are changing and how species are using them are critically needed for steering the management and conservation of wildlife populations (Guisan et al., 2013; Tulloch et al., 2015).

Generating such habitat information is often done through various modeling approaches (Elith and Leathwick, 2009; Guisan and Thuiller, 2005). Most widely used among these approaches are correlative models, which describe relationships between species' occurrence and environmental conditions through statistical modeling (Dormann et al., 2012). While several closely related types of methodological concepts have been developed in this context (e.g., species distribution models, environmental niche models, resource selection functions, habitat suitability models), all are based on the same fundamental principle: By overlaying data on where species occur with information on environmental habitat conditions in geographical space, the niches of species are derived in environmental space (Figure I-1; Hirzel & Le Lay, 2008). The resulting models provide insights into how species respond to environmental factors and, by translating them back into geographical space, allow mapping where potentially suitable habitats for species are available. Together, this provides critical information for wildlife management and conservation, allowing to identify key areas for species protection, assess potential habitats for range expansions and reintroductions, and analyze the connectivity of habitats (Guisan et al., 2013).
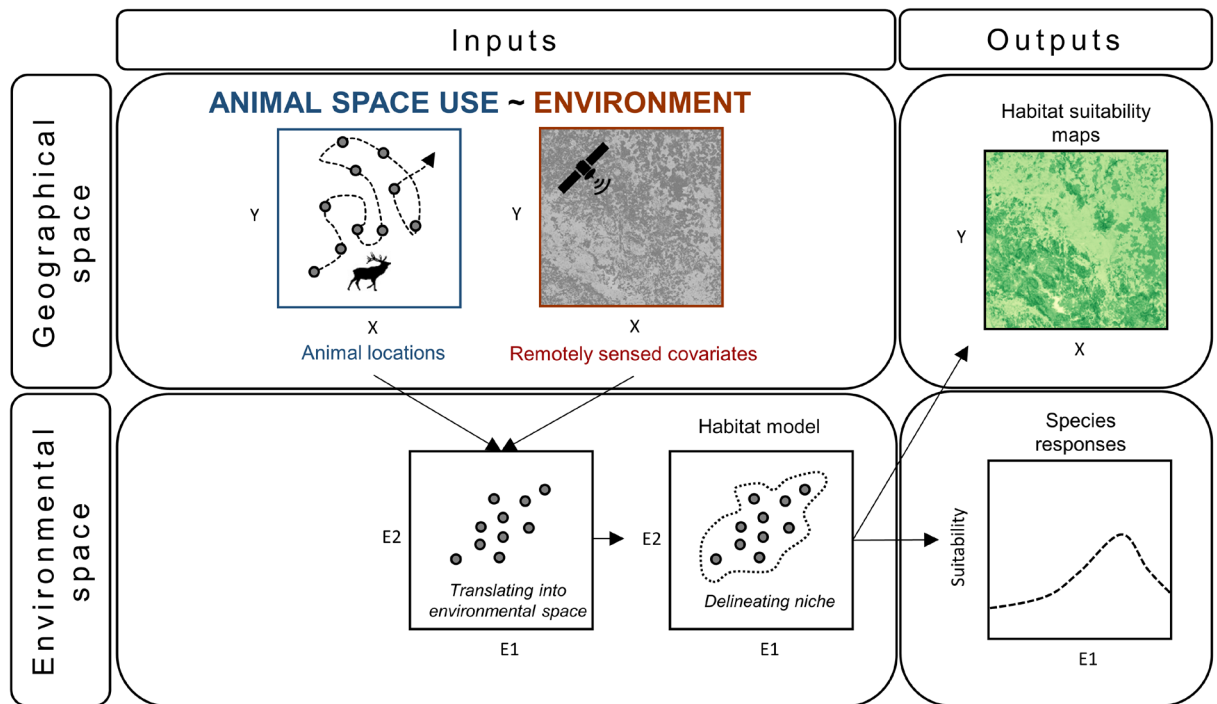
Figure I-1: Schematic overview of habitat modeling. Using spatial data on animal locations and remotely sensed covariates as inputs, animal space use is modeled as a function of environmental conditions, thereby delineating species' niches in environmental space. The model can then be applied to create different outputs, allowing to infer species responses to environmental factors as well as to create maps of potential habitat suitability by applying the model in geographical space.

Although correlative habitat models are offering a powerful approach for characterizing wildlife responses and habitats, many applications of these models also come with limitations. Most importantly, correlative habitat models are often *static*, not reflecting spatiotemporal variation in either habitat conditions or in wildlife habitat use (Franklin, 2010). Due to a lack of temporally varying or change-sensitive environmental datasets, habitat suitability maps typically provide only single-time snapshots of habitat conditions and further are often not able to resolve fine-scale variations in habitat suitability (Coops and Wulder, 2019). Moreover, by broadly summarizing species-environment relationships over space or time, habitat models commonly do not reflect the complex and context-dependent nature of wildlife habitat use (Paton and Matthiopoulos, 2016). More generally, correlative habitat models frequently suffer from a lack of transferability over space or time (Sequeira et al., 2018; Yates et al., 2018). Together, these limitations can stifle the usefulness of habitat models for informing wildlife conservation and management.

2 Entering big-data eras in satellite remote sensing and animal tracking

A key development having the potential to help overcome these limitations are the growth of two remote sensing technologies providing potentially powerful sources of information for habitat modeling: Satellite remote sensing and animal tracking. Both technologies have now entered what has been conceptualized as *big-data eras* (Gorelick et al., 2017; Kays et al., 2015), in which larger, yet also more complex datasets open new possibilities for monitoring land surface dynamics and wildlife behavior, respectively. Specifically, recent technological advancements in satellite remote sensing and animal tracking can be summarized in terms of three key aspects: (1) data quantity, (2) data quality, and (3) data accessibility & processing capacities (Table 1).

Table I-1: Key advancements in satellite remote sensing and animal tracking technologies opening new possibilities for habitat modeling. Advancements are grouped into three categories: (1) data quantity, (2) data quality, and (3) data accessibility & processing capacities.

Technology	Data quantity	Data quality	Data accessibility & processing capacities
Satellite remote sensing	*Continuation of earth observation programs and addition of new sensors*	*Higher spatial and spectral resolutions provided by new satellite sensors*	*Open data policies, analysis-ready data, cloud computing platforms*
Animal tracking	*Cheaper and less invasive sensors allowing for larger samples of tracked individuals and populations, development of high-throughput GPS sensors*	*Improved locational accuracy through GPS technology*	*Building of animal tracking research networks and databases*

In satellite remote sensing, the launch of new sensors has improved data quantity and quality (Masek et al., 2020). Moreover, the implementation of open data policies has radically improved data accessibility, also making old image records available (Turner et al., 2015). As probably the most striking example, the opening of the Landsat satellite archive in 2008 has made the longest-standing earth observation record providing global, continuous and consistent image records since 1972 available to the public (Wulder et al., 2012; Zhu et al., 2019). Finally, the increasing provision of imagery in pre-processed and analysis-ready formats (Dwyer et al., 2018) as well as improved processing capacities through new types of processing infrastructures, particularly cloud-computing platforms (Gorelick et al., 2017), have made it much easier to make use of the growing wealth of image data. These trends

have spurred the development and use of time-series based approaches in satellite remote sensing, particularly also for medium resolution imagery (i.e., around 10-30m spatial resolution; Banskota et al., 2014; Zhu, 2017). Together, these developments have strongly enhanced the potential for characterizing earth surface dynamics from satellite imagery.

In animal tracking, reduced costs associated with tagging animals, as well as more efficient and less invasive sensor technologies have led to increasing numbers of individual animals being tracked by monitoring programs (Kays et al., 2015), thus increasing the representativity of tracking datasets for wildlife populations or species as a whole (Hebblewhite and Haydon, 2010). In terms of data quality, particularly the proliferation of GPS-tracking technology is notable. Compared to older tracking technologies, such as very high frequency (VHF) radio telemetry, GPS tracking allows for higher locational accuracy, higher sampling frequencies as well as longer and uninterrupted monitoring periods (Kays et al., 2015; Wilmers et al., 2015). As a key development improving data accessibility, tracking datasets collected across different populations of the same species are increasingly consolidated, shared and harmonized through research networks and openly accessible databases (Kranstauber et al., 2011; Urbano et al., 2021), which facilitates new research on broad-scale variation in animal habitat use and suitability (Thompson et al., 2021). In sum, these advancements have dramatically improved the potential of tracking data for characterizing how animals use their habitats (Cagnacci et al., 2010).

3   Opportunities and challenges for harnessing big data in habitat modeling

The concurrent advancement of technologies for characterizing both habitat conditions through satellite remote sensing (i.e., predictor variables in habitat models) as well as wildlife habitat use through animal tracking (i.e., the response variable in habitat models) creates synergies that may help to dramatically extend the capacity of habitats models. An important aspect in this context is the enhanced potential to assess wildlife habitat use and suitability *across spatial and temporal scales* (i.e., spatial and temporal extents and resolutions). For example, combining freely available satellite imagery offering a global, multi-decadal coverage with the wealth of data provided by emerging animal tracking databases allows to widen the spatial and temporal extent of habitat assessments, enabling to characterize habitat use and suitability across large areas and long time periods. Moreover, dense time series of medium-resolution satellite imagery and GPS tracking data allow to analyze wildlife habitat use and suitability at finer spatial and temporal resolutions: While

medium-resolution imagery allows to capture fine-scale spatial variation in habitat conditions (e.g., related to variations in forest structure) and can reflect seasonal variability in habitat conditions (He et al., 2015; Leitão and Santos, 2019), GPS tracking data offers detailed characterizations of fine-scale animal movements and of the variability of habitat use at diurnal (i.e., day-night differences) or seasonal scales (Kays et al., 2015). In combination, these developments have the potential to overcome scale-related trade-offs traditionally associated with habitat assessments, making it possible to create habitat suitability maps covering large spatial extents while still offering high levels of spatial detail.

The flexibility to assess habitat use and suitability across scales is particularly important as it allows to *match the spatiotemporal scales* of analysis (i.e., response and predictor variables in habitat models) with ecological processes of interest acting at different spatial and temporal scales. For example, generating annual time series of satellite-based metrics allows to fully capture habitat changes associated with landscape dynamics, such as forest disturbance and recovery (Kearney et al., 2019). Similarly, matching satellite-based variables capturing intra-annual variability in habitat conditions (e.g., due to vegetation phenology or snow cover) with GPS-tracking datasets allows to better predict and understand why and how animals are varying their habitat use patterns throughout the year, for example related to seasonal migration events (Aikens et al., 2020). Thus, integrating big satellite image and tracking data for habitat modeling also opens new possibilities for enhancing our understanding of the ecology of wildlife species.

While satellite remote sensing and animal tracking harbor enormous potential for advancing habitat modeling, their use also brings challenges with regards to how the new wealth of data can best be utilized, as growing data amounts collected at higher resolutions also results in more complex, high-dimensional datasets. A key challenge when working with satellite imagery in habitat models lies in generating variables that effectively capture spatiotemporal habitat dynamics at fine scales, while offering interpretability and ensuring consistency across space and time. The latter is challenging, as satellite time series may contain large variability due to the mixing of different signals, for example seasonal phenological variation, long-term vegetation changes (e.g., disturbance and recovery dynamics), as well as noise (Verbesselt et al., 2010). Regarding the use of dense animal tracking data, on the other hand, a main challenge lies in developing approaches allowing to account for or reveal the complex and highly context-dependent habitat use patterns that are reflected in these datasets, as wildlife habitat use frequently varies across space or time depending on behavioral states or the environmental context animals are experiencing (Aarts et al., 2013;

Bouyer et al., 2015b; Suraci et al., 2019). Finally, an overarching and more general challenge when working with correlative habitat models lies in ensuring the transferability of models across space or time (Sequeira et al., 2018; Yates et al., 2018). As high-dimensional datasets are particularly prone to problems of overfitting, it is critical to evaluate approaches for their transferability when working with satellite image and animal tracking data in habitat models. In sum, the goal of modeling approaches should be to reflect the underlying complexity of the data (e.g., capture spatial and temporal variation in habitat conditions and use), while ensuring robust and generalizable inferences. However, much of the potential of big satellite image and animal tracking data for habitat modeling remains untapped because suitable approaches are lacking.

Yet, there exist promising approaches for utilizing both satellite image and animal tracking data in habitat models that can help overcome the abovementioned challenges. While most applications of habitat models are relying on satellite imagery only indirectly, for example in the form of categorical land-cover map products, the direct use of continuous satellite-based variables offers a potentially powerful alternative approach (Coops and Wulder, 2019; Leitão and Santos, 2019). Satellite-based variables allow to directly link habitat models to the enormous monitoring potential of global, free and multi-decadal satellite image archives (Randin et al., 2020). As a method for generating such variables, pixel-based image compositing is particularly powerful. In such approaches, all available images recorded over a period of interest are combined and after removing invalid observations (e.g., due to cloud cover), variation at the pixel-level is summarized by either selecting best available observations (Griffiths et al., 2013) or by calculating summary statistics (e.g., mean or standard deviation), also referred to as *spectral-temporal metrics* (Frantz, 2019; Pflugmacher et al., 2019). While spectral-temporal metrics have recently become a new paradigm for deriving predictors in the field of land-cover mapping based on medium-resolution satellite imagery (Azzari and Lobell, 2017), their usefulness for habitat modeling so far has remained largely unexplored. Yet, spectral-temporal metrics derived from medium-resolution imagery offer several important advantages for characterizing wildlife habitats, allowing to create temporally consistent, change-sensitive variables allowing to capture both intra- and inter-annual variation in habitat conditions as well as to describe fine-scale spatial variation. A unique source of image data in this context is the Landsat satellite archive, providing the most comprehensive source of information for characterizing land surface dynamics with a freely available, global image record reaching back to 1972 (to 1984 at a resolution of 30m; Wulder et al., 2016). Developing approaches that utilize Landsat-based spectral-temporal

metrics thus has a large potential to improve the capacity of habitat models for characterizing wildlife habitat dynamics.

Similarly, approaches to account for or reveal the context-dependency of wildlife habitat use based on dense animal tracking data have increasingly been developed, particularly also to assess or account for regional variation across wildlife populations (Holbrook et al., 2019; Matthiopoulos et al., 2011). A key analytical concept in this context are *functional responses in habitat use*. Functional responses describe the dependence of a habitat use on the environmental context an animal is experiencing (i.e., which habitats are available to it; Mysterud and Ims, 1998). For example, how strongly an animal selects for a resource (e.g., forest cover) might be strongly influenced by how much of this resource is available in the wider landscape, or else by other habitat factors (e.g., the level of human disturbance; Aarts et al., 2013; Beyer et al., 2010). Incorporating functional responses in habitat models helps to achieve more transferable models that better capture regional variation in habitat use (Matthiopoulos et al., 2011) and analyses of functional responses may help to understand the adaptive capacity of wildlife species across gradients of landscape composition or anthropogenic influences (Thompson et al., 2021). While the concept of functional responses has recently gained increasing attention, its application for large-area habitat mapping has been limited (Muhly et al., 2019; Paton and Matthiopoulos, 2016). Similarly, analyses of functional responses have commonly been limited to assessing how the use of a single habitat factor varies with its availability in the landscape (Northrup et al., 2022), thus neglecting the potential interactive effect multiple habitat factors may have on the use of a given resource (e.g., forest cover use depending on forest availability and human disturbance). Incorporating functional responses in large-area habitat assessments and extending approaches for characterizing functional responses therefore can help to improve our understanding of wildlife habitat suitability and use across large spatial extents.

4   European large mammals as a model system

Large mammals provide an interesting case for developing novel approaches in habitat modeling based on satellite remote sensing and animal tracking data. Due to their body size, large mammals can easily be tagged with tracking sensors, allowing to generate large datasets covering many individuals and several populations (Heurich et al., 2021; Kays et al., 2015; Urbano et al., 2021). At the same time, large mammals are globally threatened (Dirzo et al., 2014; Ripple et al., 2015; Wolf and Ripple, 2017) and are disproportionally

affected by negative anthropogenic impacts such as habitat loss and fragmentation, as well as human-induced mortality (Cardillo et al., 2005). Large mammals also play critical roles in structuring ecosystems (Ripple et al., 2014) and often are important focal species for conservation due to their roles as flagship and umbrella species (Sergio et al., 2008). Despite this importance, the conservation of large mammals is particularly challenging as they require extensive habitats and often persist only in small and fragmented populations, necessitating coordinated, transboundary conservation efforts (Mason et al., 2020). Moreover, the coexistence of humans and large mammals in shared landscapes poses challenges, as both large carnivores and herbivores frequently come into conflict with human activities (e.g., conflicts over livestock depredation with large carnivores or over browsing damages in forests with large herbivores; Beguin et al., 2016; van Eeden et al., 2018). Because of these factors, consistent, up-to-date, and large-area habitat information is needed for informing large mammal conservation and management.

In Europe, large mammals have historically suffered from long-lasting human impacts, including habitat loss and persecution, leading to widespread extirpations of most large mammal species (Chapron et al., 2014; Crees et al., 2016). Over the last decades, however, a strong reduction in persecution due to changing perceptions and legislative protections as well as better habitat conditions brought about by rural outmigration, land abandonment, forest expansion, and the recovery of prey populations have led to a remarkable comeback of several large mammal species, driven by both natural recolonizations and reintroductions (Chapron et al., 2014; Cimatti et al., 2021; Linnell et al., 2020). This creates unique possibilities for protecting threatened large carnivores and herbivores such as wolves (*Canis lupus*), brown bears (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), European bison (*Bison bonasus*) and moose (*Alces alces*) and restoring their missing ecological functions. In contrast, some large herbivores such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*) are regionally overabundant, leading to conflicts with agriculture and forestry (Carpio et al., 2021; Côté et al., 2004). Together, this creates a strong need for information on potentially available habitats, how habitats vary in space and time, and how animals use these habitats to allow developing conservation and management strategies that support the coexistence of large mammals and people in the landscapes they share in Europe.

5 Objectives and research questions

The overarching goal of this thesis was to develop and advance approaches exploiting the potential of (1) Landsat time series and (2) cross-population animal tracking data for characterizing large mammal habitat suitability and use across space and time based on habitat modeling. Applying these approaches to three study species, a threatened but recovering large carnivore, the Eurasian lynx, as well as two widespread large herbivores, red deer and roe deer, my research also provides novel insights into the ecology of European large mammals. The research was guided by two overarching research questions, focusing on either side of the modeling equation of habitat models: (1) the use of satellite-based predictor variables for characterizing spatiotemporal dynamics in habitat conditions and (2) the use of cross-population animal tracking data for characterizing wildlife habitat use across large spatial and ecological gradients. Both research questions are targeted by two chapters, each of which follows an own, more specific research objective. The chapters focus on habitat modeling at different spatial and temporal scales, ranging from fine spatial and temporal scales to large-area and long-term assessments (Figure I-2).
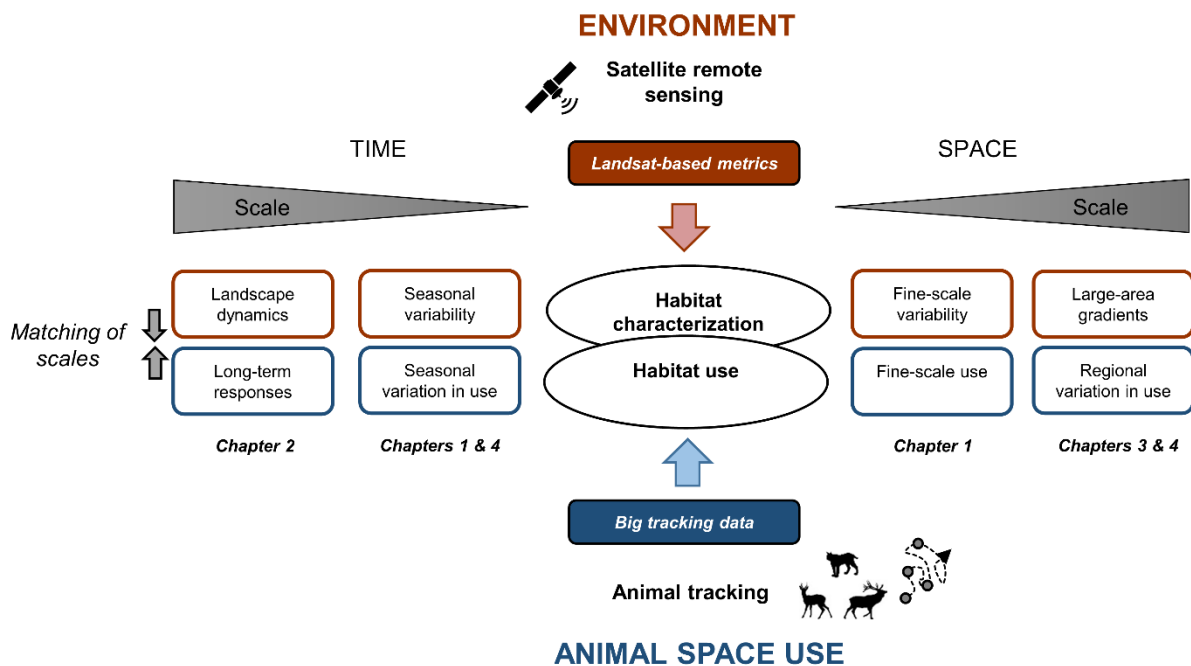
Figure I-2: Combining satellite remote sensing and animal tracking for assessing large mammal habitats across spatiotemporal scales. Throughout the research chapters of this thesis satellite image and animal tracking data are used to characterize habitat use and suitability at different spatial and temporal scales by matching the datasets at the respective scales.

Research question 1: *What is the potential of using Landsat imagery in habitat models for characterizing wildlife habitat across space and time?*

Although the Landsat archive offers an unparalleled source of information for monitoring land surface dynamics, its use for habitat modeling has been limited so far. Commonly, habitat models rely on categorical land cover map products for characterizing wildlife habitats, which limits their ability for capturing spatial and temporal variation in habitat conditions. Approaches generating variables for habitat modeling directly from Landsat data and are making full use of all available imagery have been lacking. Such approaches potentially allow generating consistent yet change-sensitive variables (i.e., capturing intra- and inter-annual habitat variation), which could be highly useful for describing spatiotemporal habitat dynamics.

Objective 1.1: Develop habitat metrics (Chapter II):

In chapter II, I developed *habitat metrics*, which are spectral-temporal metrics derived from Landsat time series that characterize different aspects of wildlife habitat. Specifically, I selected and derived spectral-temporal metrics allowing to capture five different habitat aspects (productivity, phenology, moisture, openness, snow cover) and tested their usefulness for habitat modeling. To this end, I compared habitat models for the three study species red deer, roe deer and Eurasian lynx built with either habitat metrics or, as traditionally done, using different land-cover maps. Moreover, I tested the potential of Landsat-based habitat metrics for capturing fine-scale variation in habitat conditions related to forest structure.

Objective 1.2: Develop an approach for reconstructing habitat suitability changes continuously over long time periods (Chapter III)

In chapter III, I developed an approach for continuously reconstructing long-term habitat dynamics based on annual time series of Landsat-based spectral-temporal metrics. To ensure the consistency and transferability of the habitat mapping across time, I harmonized the metric time series by applying a time series segmentation algorithm, and further used a multi-temporal modeling approach, in which multi-year tracking data is temporally matched with the time series of Landsat-based metrics. Applying this approach for red deer and roe deer in a highly dynamic forest landscape shaped by large-scale forest disturbance events allowed to gain novel insights into long-term responses by deer to forest disturbances, an increasingly important driver of habitat dynamics for large mammals in Europe and elsewhere.

Research question 2: *How can animal tracking data be integrated across wildlife populations for large-area assessments of habitat suitability and use?*

The availability of animal tracking datasets across several populations of the same species increasingly opens possibilities for assessing wildlife habitat suitability and use across large spatial extents. This, however, also means having to consider geographical variation in habitat use, caused for example by animals experiencing different environmental conditions across regions. Approaches that can capture environmentally related variation in habitat use are needed both when mapping habitat suitability in large-area habitat assessments as well as when trying to understand the adaptive capacity of wildlife across ecological gradients. Yet, different approaches for integrating tracking datasets across populations have rarely been compared and analyses describing broad-scale variation in habitat use by large mammal species are lacking.

Objective 2.1: Compare approaches for integrating tracking datasets across populations for large-area habitat mapping (Chapter IV)

In Chapter IV, I compared approaches for integrating animal tracking datasets across populations for large-area habitat mapping. Specifically, I tested both global approaches in which tracking datasets are pooled across study sites, as well as local approaches in which the predictions of separate site-specific models are combined. Among local approaches, I also tested a novel approach based on characterizing model transferability in space. Applying these mapping approaches, I created continental-scale, yet high-resolution habitat suitability maps for the Eurasian lynx, providing detailed information on available potential habitats for this recolonizing large carnivore.

Objective 2.2: Assess variation in habitat use by Eurasian lynx across gradients of human pressures and landscape composition (Chapter V)

In Chapter V, I assessed the variation of habitat use by lynx across its distribution in Europe. Building on the analytical framework of functional responses, in which variation in habitat use is described as a function of which habitats are available to animals, I tested how lynx' use of refuge habitats (i.e., habitats helping lynx to avoid anthropogenic impacts) and their association with human landscape modification varies across landscape contexts in Europe. Importantly, I extended a commonly used approach for modeling functional responses to allow considering the interactive effect of multiple habitat factors (i.e., refuge habitat availability and human pressure gradients) on variation in habitat use. This first continental-

scale assessment of functional responses for any large carnivore provided novel insights into the adaptive capacity of this species and carnivores more generally.

6   Structure of this thesis

This thesis consists of six chapters: the introduction (chapter I), four research papers (chapters II-V), representing individual studies that contribute to the overarching research questions and objectives described above, and a synthesis chapter (chapter VI) that summarizes the main results of the research papers, synthesizes overarching findings, and provides an outlook on potential further applications and future research directions. All four research chapters were written as stand-alone articles and have either been published in or submitted to international, peer-reviewed journals. The chapters were published or submitted as follows:

Chapter II: Habitat metrics based on multi-temporal Landsat imagery for mapping large mammal habitat. *Remote Sensing in Ecology and Conservation* (2020).

Julian Oeser, Marco Heurich, Cornelius Senf, Dirk Pflugmacher, Elisa Belotti, and Tobias Kuemmerle.

Chapter III: Satellite-based habitat monitoring reveals long-term dynamics of deer habitat in response to forest disturbances. *Ecological Applications* (2021).

Julian Oeser, Marco Heurich, Cornelius Senf, Dirk Pflugmacher, and Tobias Kuemmerle.

Chapter IV: Integrating large animal tracking datasets across multiple populations for mapping wildlife habitat at a continental scale. *Ecography* (Submitted).

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Chapter V: Prerequisites for coexistence: human pressure and refuge habitat availability interactively shape continental-scale variation in habitat use by a large carnivore. *Proceedings of the Royal Society B* (Submitted).

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Chapter II:
Habitat metrics based on multi-temporal Landsat imagery for mapping large mammal habitat

Julian Oeser, Marco Heurich, Cornelius Senf, Dirk Pflugmacher, Elisa Belotti, and Tobias Kuemmerle

Abstract

Up-to-date and fine-scale habitat information is essential for managing and conserving wildlife. Studies assessing wildlife habitat commonly rely on categorical land-cover maps as predictors in habitat models. However, broad land-cover categories often do not adequately capture key habitat features and generating robust land-cover maps is challenging and laborious. Continuous variables derived directly from satellite imagery provide an alternative for capturing land-cover characteristics in habitat models. Improved data availability and processing capacities now allow integrating all available images from medium-resolution sensors in compositing approaches that derive spectral-temporal metrics at the pixel level, summarizing spectral responses over time. In this study, we assessed the usefulness of such metrics derived from Landsat imagery for mapping wildlife habitat. We categorize spectral-temporal metrics into habitat metrics characterizing different aspects of wildlife habitat. Comparing the performance of these metrics against categorical land-cover maps in habitat models for lynx, red deer, and roe deer, we found that models using habitat metrics consistently outperformed models based on categorical land-cover maps, with average improvements of 13.7% in model AUC and 9.7% in the Continuous Boyce Index. Performance increases were larger for seasonal habitat models, indicating that the habitat metrics capture intra-annual variability in habitat conditions better than land-cover maps. Comparing suitability maps to ancillary data further revealed that our habitat metrics were sensitive to fine-scale heterogeneity in habitat associated with forest structure. Overall, our study highlights the considerable potential of Landsat-based spectral temporal metrics for assessing wildlife habitat. Given these metrics can be derived directly and in an automatized fashion from globally and freely available Landsat imagery, they open up new possibilities for monitoring habitat dynamics in space and time.

1   Introduction

Habitat maps can provide critical information for wildlife management and conservation planning (Margules and Pressey, 2000; Sutherland et al., 2004). Such maps are typically derived using correlative habitat models (i.e., species distribution models, environmental niche models or resource selection functions; Boyce and McDonald, 1999; Elith et al., 2006; Guisan and Zimmermann, 2000). Habitat models can improve the understanding of a species' ecology while providing data on their actual or potential distribution (Elith and Leathwick, 2009; Guisan and Thuiller, 2005), which, in turn, are important indicators for assessing biodiversity change (Jetz et al., 2019; Pereira et al., 2013). Moreover, habitat suitability maps often are the basis for downstream-analyses, such as modeling population dynamics or assessing landscape fragmentation and connectivity (Larson et al., 2004; Zeller et al., 2012). Thus, habitat models are particularly valuable if they can be applied across large areas (McDermid et al., 2005) and with regular repeat intervals (Pressey et al., 2007).

Most studies mapping wildlife habitat use categorical land-cover maps derived from satellite imagery as spatial predictor variables (Pearson et al., 2004; Thuiller et al., 2004; Zuckerberg et al., 2016). The frequent use of land-cover maps can likely be attributed to the wide availability of freely available map products (Wulder et al., 2018), as well as their easy interpretability. However, using land-cover maps for habitat assessments also comes with several limitations. First, available broad-scale land-cover maps have predefined, typically coarse thematic legends that do not necessarily reflect a species' habitat requirements (Bradley and Fleishman, 2008; Coops and Wulder, 2019). Otherwise, land-cover maps can be created for a specific purpose, but doing so is laborious, requires considerable technical expertise and adequate reference datasets. Second, a classification of the spectral information contained in satellite images implies a loss of information (Krishnaswamy et al., 2009). Thus, fine-scale gradients of habitat suitability associated with variation within land-cover classes (e.g., forest composition and structure) might be missed by categorical maps. Finally, satellite-based land-cover maps always contain errors (Pflugmacher et al., 2011; Powell et al., 2004), which are typically not accounted for in habitat models (Cord et al., 2014).

Alternatively, continuous variables derived directly from satellite images, such as vegetation indices (Pettorelli et al., 2011, 2005), can be used as predictors in habitat models (Coops and Wulder, 2019; Leitão and Santos, 2019). Several studies have demonstrated the usefulness of Landsat imagery in this context (Lahoz-Monfort et al., 2010; Shirley et al., 2013; West et al., 2017). In contrast to coarser resolution sensors, Landsat imagery allows resolving fine-scale habitat features (Remelgado et al., 2018; Shirley et al., 2013). Moreover, the Landsat

archive provides freely available, global imagery back to the 1970s (Wulder et al., 2019, 2016), which should represent major opportunities for assessing wildlife habitat in space and time (He et al., 2015; Nagendra et al., 2013). However, using Landsat imagery also comes with distinct challenges, which likely explains its relatively limited use in habitat assessments so far. On one hand, the comparably low temporal resolution of Landsat (16-day revisit time for a single satellite) can make the selection of suitable individual images difficult or even impossible due to cloud cover. On the other hand, the combination of many Landsat images in space or time can imply considerable technical challenges and computational costs (Young et al., 2017). While time-series based approaches have been widely adopted for characterizing habitat with coarse resolution sensors such as MODIS (Bischof et al., 2012; Coops et al., 2009; Cord and Rödder, 2011), Landsat-based habitat studies instead have frequently relied on images-based analysis of only a single or few selected images (Lahoz-Monfort et al., 2010; but see Jantz et al., 2016; Remelgado et al., 2018).

Recently, the provision of Landsat data in analysis-ready formats (Dwyer et al., 2018; Wulder et al., 2019) and rapidly improving computational capacities (e.g., through cloud computing platforms; Gorelick et al., 2017), have dramatically improved the possibilities for analyzing large sets of Landsat images. One development underpinning these advances is the shift from image-based analyses to the increasing use of pixel-based compositing approaches (Bleyhl et al., 2017; Hansen et al., 2014; Potapov et al., 2011). In one such compositing approach, all available images in a time frame are combined by calculating pixel-wise, spectral-temporal metrics to create cloud-free composite images summarizing spectral responses over time (Gómez et al., 2016; Griffiths et al., 2013; Pflugmacher et al., 2019). While Landsat metric-based composites have allowed for substantial progress in land-cover mapping (Azzari and Lobell, 2017), their usefulness for assessing wildlife habitat via habitat models remains largely unexplored.

In this study, we investigate the potential of Landsat-based spectral-temporal metrics for mapping large mammal habitat and compare them against land-cover maps. Large mammals play crucial roles in structuring ecosystems (Ripple et al., 2015, 2014), and often are important focal species for conservation (Branton and Richardson, 2011; Clucas et al., 2008; Sergio et al., 2006). However, their conservation is particularly challenging, as they require extensive habitats (Cardillo et al., 2005) and often come into conflict with humans (Treves and Karanth, 2003; Young et al., 2005). Thus, pro-active management and monitoring of

their populations is important, which requires timely and detailed spatial information on habitat across large areas.

We mapped habitat suitability for a large carnivore (Eurasian lynx; *Lynx lynx*) and two large herbivores (red deer, *Cervus elaphus*; and roe deer, *Capreolus capreolus*) in the Bohemian Forest Ecosystem in Germany and Czechia, using spectral-temporal metrics derived from Landsat imagery together with large GPS tracking datasets in habitat models. To improve the usefulness of spectral-temporal metrics for habitat mapping, we categorize spectral-temporal metrics into groups of *habitat metrics* specifically targeting key aspects of large mammal habitat. We test these habitat metrics as predictors in habitat models and compare their performance against models based on categorical land-cover maps. Specifically, we ask the following research questions:

1.   Do habitat metrics improve the predictive performance of habitat models compared to land-cover maps?

2.   Can habitat suitability maps based on habitat metrics capture fine-scale variation in habitat related to forest structure?

3.   Do habitat models based on habitat metrics capture differences in habitat use between lynx, red deer, and roe deer and across seasons?

2   Methods

2.1   Study area

The Bohemian Forest Ecosystem is a low-elevation, forested mountain chain approximately 130 km long and 60 km wide, situated along the border of Austria, Czechia, and Germany. Two protected areas form the center of the study area: The Bavarian Forest National Park (240 km²) and the Šumava National Park (690 km²; Figure II-1). These protected areas are mostly forested, while their surroundings consist of mosaics of smaller forest patches, meadows, cropland, and villages. Roe deer and red deer are widely distributed in the area (Heurich et al., 2015) and Eurasian lynx has been reintroduced in the 1970s (Wölfl et al., 2001). Lynx mainly prey on roe deer and to a much lesser extent on red deer (Belotti et al., 2015).
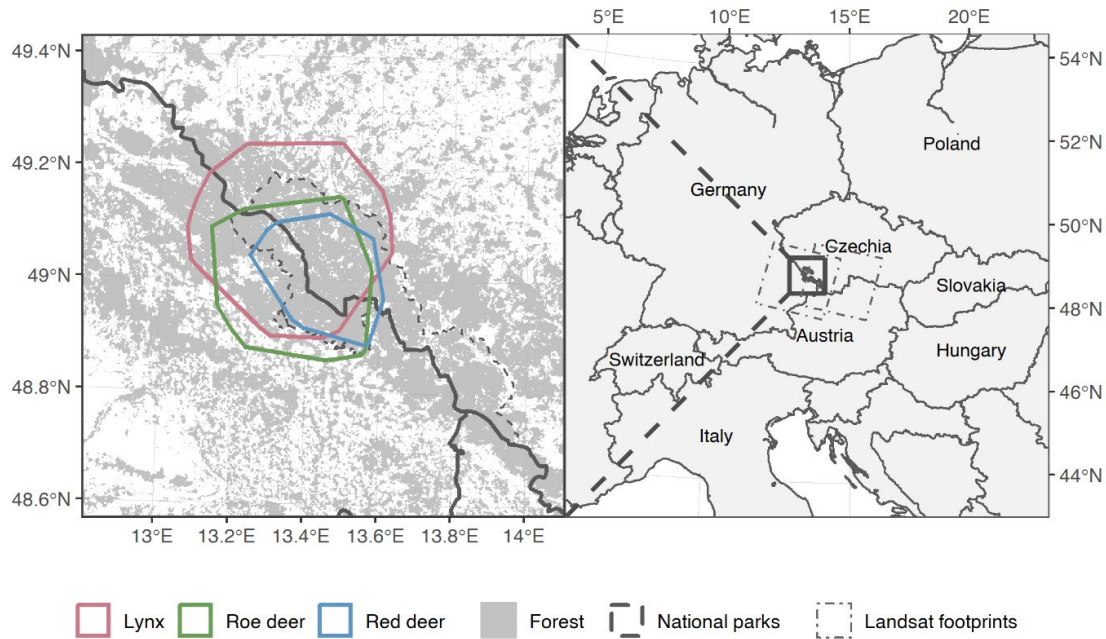
Figure II-1: Map of the study area (left) including Minimum Convex Polygons derived from all lynx, red deer, and roe deer locations (see 2.2), with forested areas highlighted in grey. Overview map (right) showing the location of the study region, national parks, and the used Landsat footprints.

2.2   Wildlife data

As information on species presence, we used a large GPS tracking dataset from radio-collared lynx (seven individuals), red deer (41 individuals), and roe deer (82 individuals), collected between 2011 and 2013. To account for seasonal changes in habitat selection (Dupke et al., 2017; Filla et al., 2017; Godvik et al., 2009), we fitted separate models using presence data from the entire year (hereafter: year-round models) as well as seasonal models using presence data only from winter or summer (Table II-1; hereafter: summer and winter models). Summer observations included all GPS recordings collected between April 1st and October 31st, winter observations all recordings between November 1st and March 31st (Filla et al., 2017; Godvik et al., 2009). Since some of the radio-collared red deer are kept in enclosures during winter (Rivrud et al., 2016), we removed red deer locations inside winter enclosures. To reduce spatial auto-correlation, we randomly selected one location per day and individual for each dataset (Holloway and Miller, 2017; Magg et al., 2016). The size of our final presence datasets used for building habitat models ranged from ca. 1,000 locations for the lynx winter model to ca. 18,000 locations for the roe deer year-round model (Table II-1).

Table II-1: Summary of the wildlife data (GPS telemetry observations) used as presence information in our habitat models.

Species	No. of Individuals	No. of year-round observations	No. of summer observations	No. of winter observations
Lynx	7	2,671	1,629	1,042
Red deer	41	10,329	7,648	2,681
Roe deer	82	18,151	10,215	7,936

2.3 Landsat habitat metrics

To characterize large mammal habitat directly from multi-temporal Landsat imagery, we derived a set of spectral-temporal metrics (Azzari and Lobell, 2017; Hansen et al., 2014; Pflugmacher et al., 2019) describing different aspects of wildlife habitat. These composite images are generated from time series of spectral indices by calculating pixel-level statistical indicators summarizing the spectral properties of all imagery in a given time window (Figure II-2). Based on available studies linking satellite-derived variables to wildlife habitat characteristics (Table II-2), we then categorize these spectral-temporal metrics into groups of *habitat metrics* relating to different aspects of wildlife habitat. For calculating metrics, we used all available Collection 1 Tier 1 surface reflectance images from the Landsat sensors 5 TM, 7 ETM+ and 8 OLI recorded between 2011-2013 (165 images across two Landsat footprints). The Tier 1 surface reflectance product contains atmospherically-corrected data (Masek et al., 2006; Vermote et al., 2016) with the lowest georegistration errors (Young et al., 2017). To account for different Landsat sensor specifications, we used the coefficients provided by Roy et al. (2016) to cross-calibrate Landsat 8 surface reflectance data to Landsat 7 reflectance values. We performed all processing of Landsat imagery, including metric calculation, in the Google Earth Engine (Gorelick et al., 2017; see Supplementary Information for Google Earth Engine code).
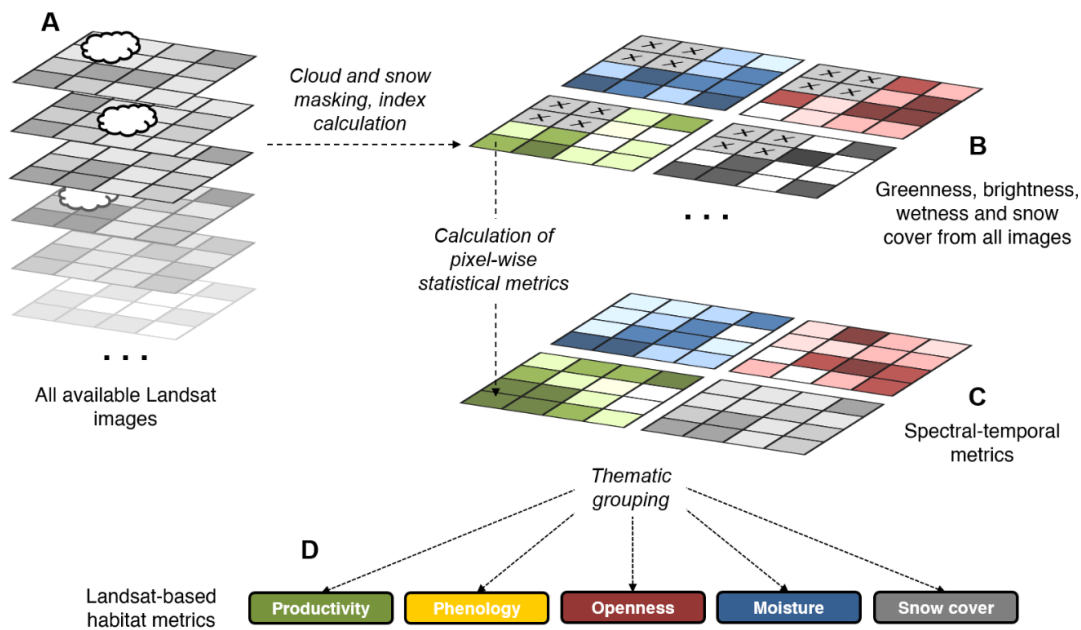
Figure II-2: Illustration of habitat metrics calculation. A: All available, pre-processed (e.g., atmospherically corrected) images are acquired. B: Invalid observations (e.g., clouds, snow) are masked and spectral indices (in our case Tasseled Cap greenness, brightness, and wetness, as well as snow masks) are derived. C: These indices are summarized at the pixel level using different statistical metrics (e.g., median, interquartile range). D: The resulting spectral-temporal metrics are then categorized into habitat metrics characterizing different aspects of wildlife habitat (productivity, phenology, openness, moisture, and snow cover).

For every Landsat image, we calculated (1) the Tasseled Cap (TC) components greenness, brightness and wetness (Crist and Cicone, 1984), and (2) binary snow masks created from quality flags in the Pixel-Quality Assessment (QA) band derived from the CFMask algorithm (Foga et al., 2017). For calculating the TC components, we masked out all observations containing clouds, cloud shadows or snow using the respective flags in the QA-band and used the coefficients for surface reflectance data provided in Crist (1985). The TC components capture different spectral characteristics describing land-cover features (Crist and Cicone, 1984; Pasquarella et al., 2016). For example, greenness relates to the amount of photosynthetically active vegetation, similar to vegetation indices such as NDVI (De Jong, 1994). Brightness has been linked to albedo (e.g., open habitats including bare soil, certain agricultural crops and built-up areas; Yang and Liu, 2005). Wetness has been associated with vegetation and soil moisture (Crist and Cicone, 1984), but is also widely used to capture forest characteristics and disturbances (Cohen et al., 1995; Hansen et al., 2001; Jin and Sader, 2005).

We summarized Tasseled Cap greenness, brightness and wetness over time by calculating a set of robust statistical metrics (median, interquartile and interdecile range, and Theil-Sen slope; Table II-2; Flood, 2013). To capture spectral variations throughout the year, we calculated metrics using all available images, on the one hand, and images from specific temporal windows within the year, on the other. We set the temporal windows to represent key phenological stages in our study region (Senf et al., 2017), which should help capturing important habitat characteristics, such as vegetation types or food availability (Hamel et al., 2009; Remelgado et al., 2018). For defining the temporal windows, we used the day of year (DOY) of image recording to categorize Landsat images into start-of-season (DOY 60-151, 42 images), peak-of-season (DOY 152-243, 53 images), and end-of-season observations (DOY 244-334, 54 images). We also tested metrics based on DOY 335 - 59 observations but omitted them from further analysis due to persistent cloud and snow cover leading to low observation numbers during winter in our study area. To describe the rate of vegetation green-up, we used the Theil-Sen approach (Fernandes and G. Leblanc, 2005; Theil, 1992) for estimating the rate of change in greenness values during spring. Previous studies have linked vegetation productivity increase during spring to forage quality for large herbivores (Hamel et al., 2009; Pettorelli et al., 2007). As a measure of snow-cover frequency, we divided the number of observations flagged as snow by the number of clear observations for each pixel. A comparison of the Landsat-derived snow-cover frequency against the MODIS snow-cover product (Hall et al., 2010) showed overall good agreement between both datasets (see Supplementary Information).

In total, our set of metrics included 14 variables (Table II-2), which we categorized into five groups of habitat metrics: (1) productivity (based on TC greenness), (2) phenology (based on variability in greenness), (3) openness (based on TC brightness), (4) moisture (based on TC wetness), and (5) snow cover.

Table II-2: Overview of habitat metrics derived from Landsat imagery.

Habitat metric group	Specific metrics (number of metrics)	Related habitat features
Productivity	Median TC greenness for start-of-season, peak-of-season, and end-of-season (3)	Food availability (Coops et al., 2008; Pettorelli et al., 2005)
Phenology	Interquartile and interdecile range of TC greenness based on all observations; Theil-Sen estimator for regression of TC greenness against day of year for start-of-season (3)	Food availability, forage quality (Hamel et al., 2009; Pettorelli et al., 2007)
Openness	Median TC brightness for start-of-season, peak-of-season, and end-of-season (3)	Absence of protective cover, food availability (Carroll et al., 2001; Holbrook et al., 2017b)
Moisture	Median TC wetness for start-of-season, peak-of-season, and end-of-season (3)	Forest type and structure, protective cover, vegetation and soil moisture (Cohen et al., 1995; Hansen et al., 2001; Roy and Ravan, 1996)
Snow cover	Frequency of snow cover (relative to number of clear observations) based on all observations, frequency of snow cover during start-of-season (2)	Resource accessibility, movement, predation risk (Macander et al., 2015; Michaud et al., 2014)
TOTAL	14 metrics	

2.4 Land cover mapping

To compare the usefulness of our habitat metrics for assessing large mammal habitat against categorical land-cover maps, we derived two land-cover maps for our study region. First, we mapped land cover for the target year 2012 by applying a random forest classifier (Breiman, 2001) to the set of habitat metrics. This map thus represents a site-specific land-cover map, which are sometimes produced for habitat assessments (Bleyhl et al., 2017; Kuemmerle et al., 2010). We sampled training pixels within reference polygons that were digitized based on (1) aerial surveys (Gonzalez et al., 2018) and (2) high-resolution imagery in Google Earth. We mapped 13 land-cover classes: broadleaf forest, built-up, clear-cut, coniferous forest, cropland, deadwood, forest regrowth, grassland, mixed forest, natural grassland, rock, shrub and water. The resulting land-cover map was validated using a set of independent test pixels not used for training and had an overall accuracy of 91.5% (see Supplementary Information for a more detailed description of the classification and validation procedure).

As a second land-cover map, we downloaded the CORINE land-cover dataset (Büttner et al., 2004) for the year 2012, representing a broad-scale, general land-cover product. This European-wide land-cover map is available at a spatial resolution of 100m and is frequently

used to map habitat suitability for large mammals in Europe (Kuemmerle et al., 2018; Magg et al., 2016; Schadt et al., 2002). The CORINE data for our study area included a total of 27 classes on five major land-cover types (artificial surfaces, agricultural areas, forest and semi-natural areas, wetlands, and water bodies; see Table SI II-2 in Supplementary Information).

2.5 Parametrization of habitat models

We fitted habitat models for lynx, red deer and roe deer using maximum entropy (Maxent) modeling (Phillips et al., 2006). Maxent contrasts the values of environmental predictors at presence observations with their overall distribution obtained from a sample of background points (or pseudo-absences; Merow et al., 2013). To generate background points, we randomly sampled 30,000 points inside the Minimum Convex Polygons of presence datasets (Northrup et al., 2013; Phillips and Dudík, 2008). We used the R-package *dismo* (Hijmans et al., 2020) for building Maxent models, using all feature classes and a regularization multiplier of $\beta = 1$ (Merow et al., 2013).

For each species, we fitted year-round, summer, and winter habitat models using (1) the set of habitat metrics, (2) site-specific land-cover map created from Landsat imagery, and (3) the CORINE land-cover map. This resulted in a total of nine habitat models per species. To evaluate the predictive performance of our models, we used ten-fold cross-validation. We calculated two performance measures capturing two different aspects of predictive performance: The area under the Receiver Operator Characteristic curve (AUC) as an indicator of discrimination capacity (i.e., how well a model separates presence from background points; Jiménez-Valverde et al., 2013), and the Continuous Boyce Index (CBI; Hirzel et al., 2006) as an indicator of model calibration (i.e., how well predicted suitability values correspond with observed proportions of occupied sites; Phillips and Elith, 2010). For assessing changes in predictive performance associated with using the habitat metrics instead of the land-cover maps, we calculated the percent changes in AUC and CBI compared to the best-performing land-cover map for each model. Finally, we derived habitat suitability maps from each Maxent model by creating spatial predictions, using the bounding box of all GPS telemetry locations as a reference extent.

2.6 Assessing habitat metrics

To assess whether the habitat metrics allow capturing fine-scale habitat characteristics associated with forest structure, we compared (1) the metric values, and (2) the derived suitability maps from year-round models against information on fine-scale forest attributes

(i.e., stand age, lying and standing deadwood, type of forest regrowth). For this comparison, we used a high-resolution vegetation type map available for the Bavarian Forest National Park that was created by manual interpretation of aerial imagery (Gonzalez et al., 2018).

To assess whether the habitat metrics allowed capturing differences in habitat use between species and across seasons, we compared the contribution of the different habitat metrics across models. Since the groups of metrics (productivity, phenology, openness, moisture, snow-cover) were selected to characterize different aspects of habitat, their importance in habitat models can be expected to be consistent with known patterns of habitat selection for lynx, red deer, and roe deer. We computed permutation importance scores indicating relative variable importance (Searcy and Shaffer, 2016). Then, we summed the importance scores of all variables belonging to a metric group and used this group-wise sum as an indicator for the contribution of the habitat metrics to a model. Lastly, we compared the importance of metrics based on the temporal windows used for their computation (i.e., all observations, start of season, peak of season, end of season), by calculating the mean importance of metrics from each temporal window across all habitat models.

3   Results

3.1   Comparison of predictive performance and habitat suitability maps

Models based on our habitat metrics showed higher AUC and CBI values (mean AUC = 0.76, standard error ±0.02; mean CBI = 0.97 ± 0.01) than models based on categorical land-cover maps (mean AUC = 0.60 ±0.03, mean CBI = 0.84 ± 0.03; Figure II-3a). Comparing habitat models based on the two land-cover maps, models using the site-specific map had higher AUC values than CORINE-based models (mean AUC = 0.66 ± 0.02 vs. 0.54 ± 0.06), but slightly lower CBI values (mean CBI 0.82 ± 0.05 vs. 0.85 ± 0.03). Using the habitat metrics improved the predictive performance, both in terms of discrimination capacity (AUC) and model calibration (CBI), of all habitat models relative to the best-performing land-cover based model (Figure II-3c-d). Relative improvements in ranged from 9-23% for AUC values (mean = 13.7), and 3-21% for CBI values (mean = 9.2), showing variations across species and time periods covered. On average, performance increases were larger for seasonal habitat models compared to year-round models (relative improvement in AUC: 14.5% vs. 12.3%; improvement in CBI: 11.3% vs. 5.1%). Performance improvements were also larger for winter models than for summer models (improvement in AUC 16.0% vs.

13.0%; improvement in CBI 12.1% vs. 10.4%). Average improvements in AUC were largest for roe deer (19.0%), improvements in CBI largest for red deer (11.7%).
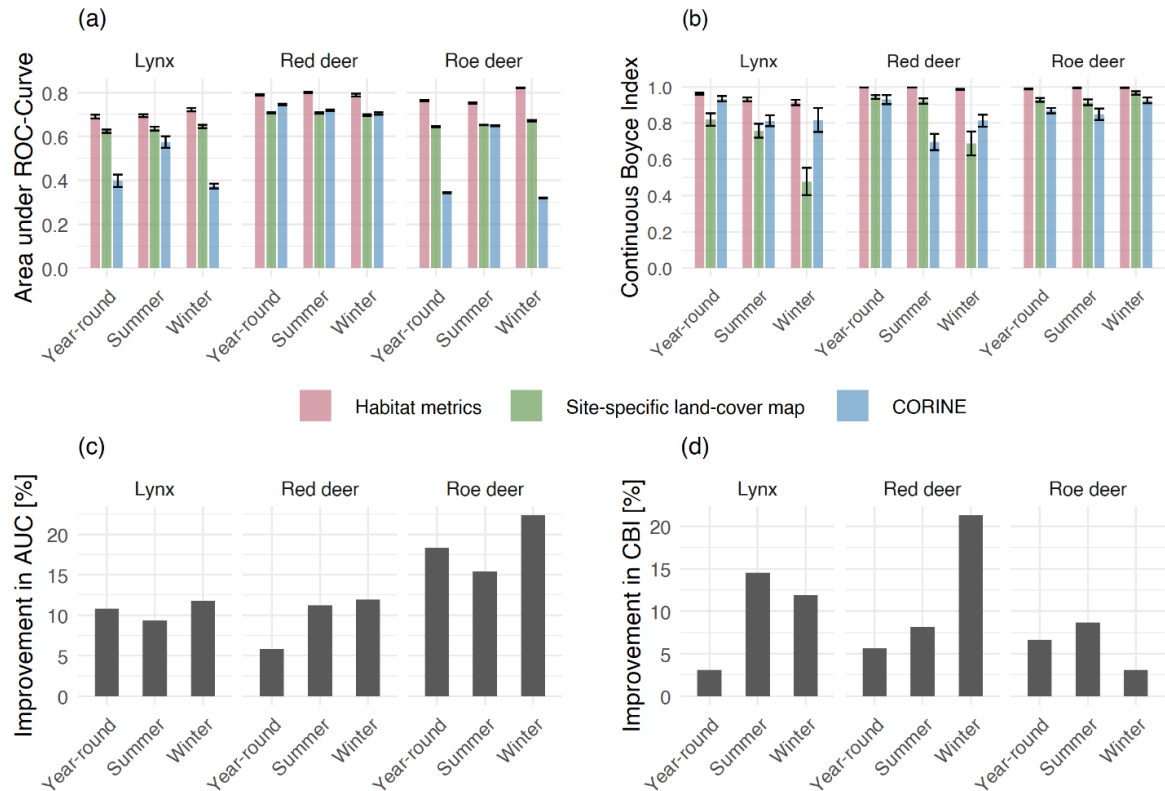
Figure II-3: Performance of habitat models based on habitat metrics vs. models based on land-cover maps. (a) Mean AUC across ten cross-validation runs, (b) Mean CBI across ten cross-validation runs, (c) average percent improvement in AUC when comparing the habitat metrics model vs. the best-performing land-cover map model, (d) average percent improvement in CBI. Error bars in (a) and (b) indicate standard errors of the mean.

Overall, spatial patterns of habitat suitability were similar between maps derived from models using the habitat metrics and those based on the land-cover maps (Figure II-4; see Figure SI II-5 and Figure SI II-6 in Supplementary Information). However, some differences were discernible, such as the lower spatial resolution of the CORINE map, as well as variation in habitat suitability within land-cover classes in the map based on the habitat metrics. In addition, suitability maps based on the habitat metrics exhibited striping artefacts corresponding to scan line errors of Landsat 7. These artefacts were most pronounced in areas with persistent cloud cover (i.e., high elevations). We found these striping artefacts mainly to occur in metrics calculated from start-of-season observations (Figure SI II-7 in Supplementary Information for an example).
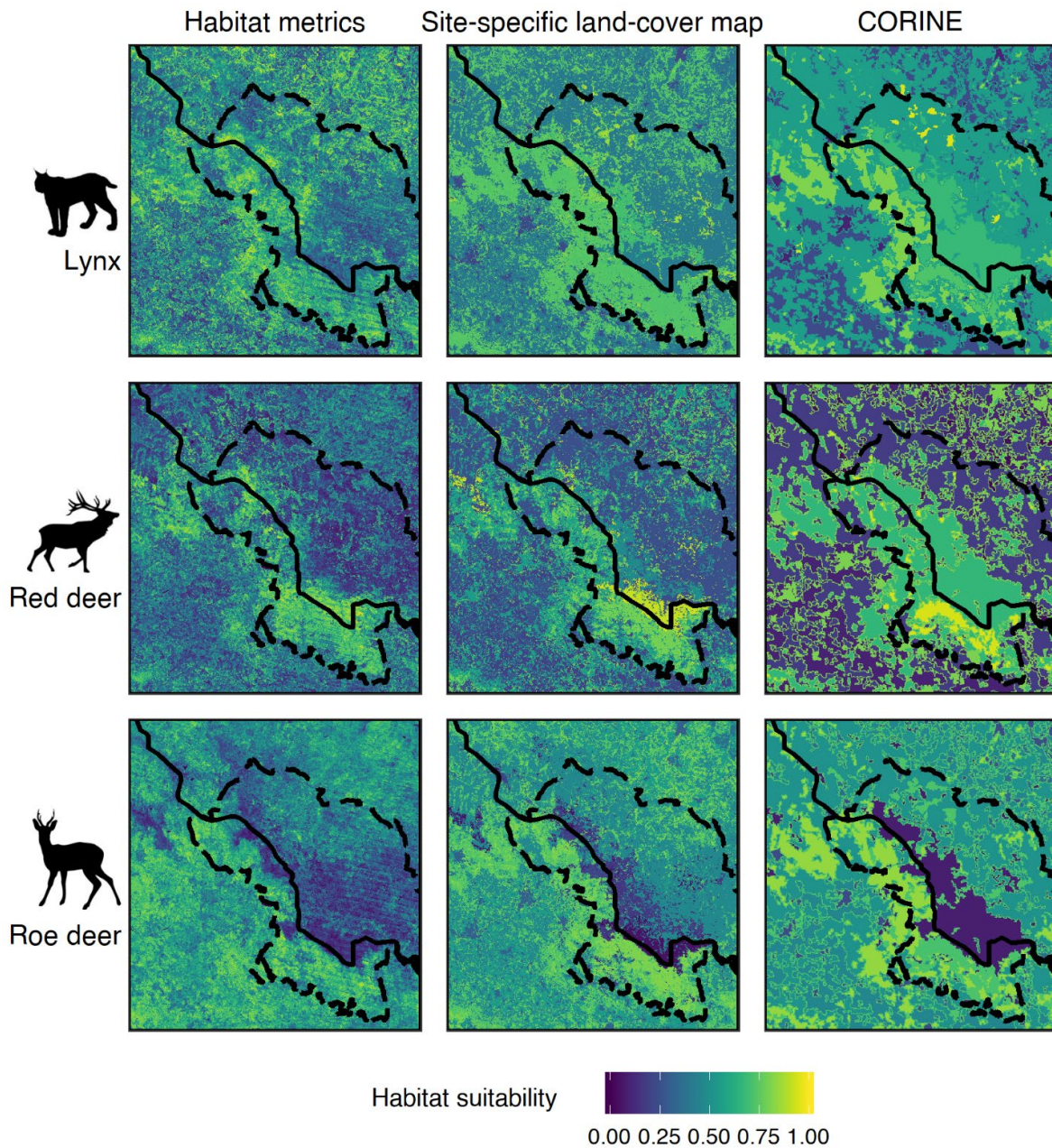
Figure II-4: Habitat suitability maps based on year-round habitat models using the habitat metrics (left column), the site-specific land-cover map (middle column) and the CORINE land-cover map (right column) for lynx, roe deer and red deer. Continuous line indicates country border, dashed lines show the extents of the national parks.

3.2 Variation of habitat suitability with forest structure

The values of habitat metrics varied considerably for classes of forest type and age and showed patterns consistent with forest type and age characteristics (Figure II-5; see Figure SI II-8 in Supplementary Information for comparison with deadwood and forest regrowth classes). For example, openness metrics tended to decrease with stand age. Productivity and

phenology metrics tended to be higher for broadleaf forest than for coniferous forest, with differences increasing with stand age, while mixed forests showed intermediate productivity and phenology values.
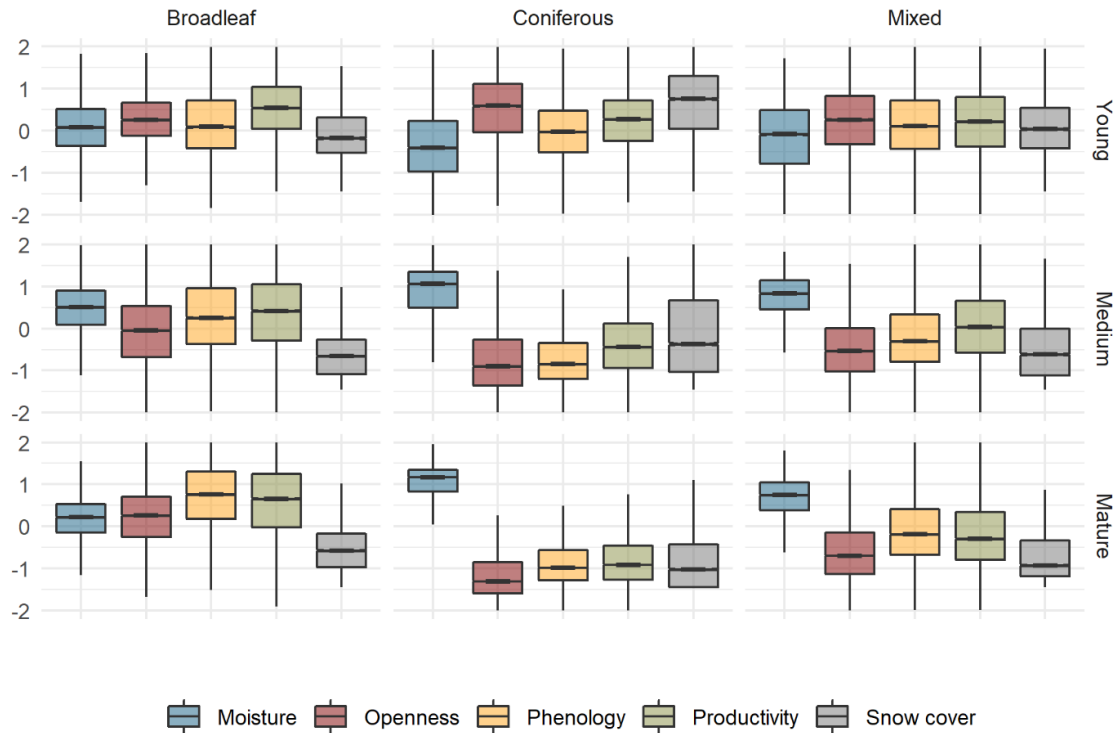
Figure II-5: Variation of habitat metric values with forest type and age. All individual metrics were standardized via a z-transformation to ensure comparability between spectral indices.

Next to the metric values themselves, the predicted suitability values also varied with forest structure classes (Figure II-6). For example, lying deadwood had lower suitability for roe deer and lynx than standing deadwood, but a higher suitability for red deer. Habitat suitability for lynx and roe deer varied with the type of regrowth, with higher suitability for broadleaf than for coniferous or mixed regrowth. Finally, habitat suitability for red and roe deer showed relationships with forest age. While suitability generally declined with stand age for red deer, it increased for roe deer.
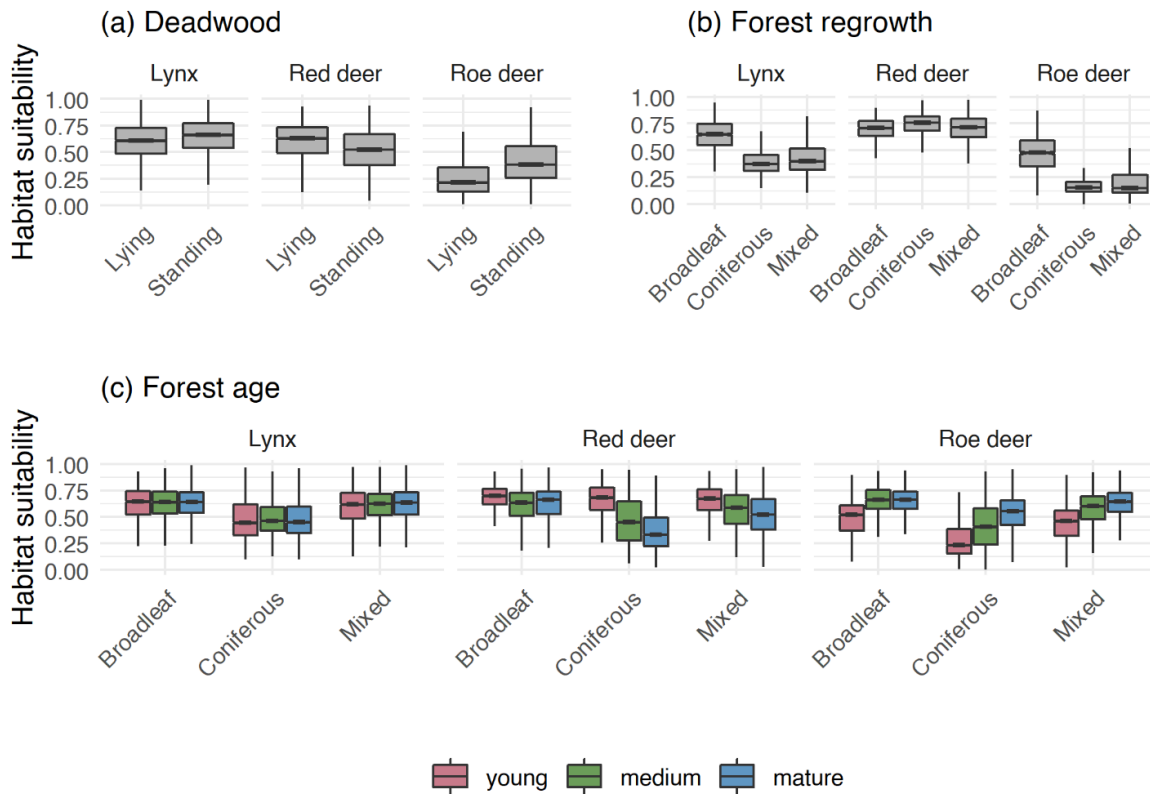
Figure II-6: Variation in habitat suitability in models based on habitat metrics for classes capturing forest structure. (a) Different types of deadwood, (b) different types of forest regeneration, and (c) different forest age classes.

3.3 Importance of different habitat metrics across models

The importance of the different habitat metrics varied markedly between species, and also between models fitted for different time periods (Figure II-7a). For instance, in our lynx models, the openness metrics were consistently among the most important, while being generally less important in the red and roe deer models. In contrast, the contribution of phenology metrics, relating to forage availability and quality, was much larger in red deer and roe deer models than in lynx models. The contributions of habitat metrics in seasonal models for the three species were consistent with differences in habitat use between summer and winter. For example, snow-cover metrics were more important in winter models than in summer models for all species. Similarly, the phenology metrics were less important in winter models than in summer models for the two deer species. Comparing the importance of metrics calculated from the different temporal windows of Landsat observations, metrics calculated from start-of-season observations were most important in habitat models for all

three species, showing particularly high importance scores in models for red and roe deer (Figure II-7b).

Figure II-7: Importance of habitat metrics in lynx, red deer, and roe deer habitat models. (a) Sums of permutation importance scores for habitat metrics in year-round, winter and summer habitat models. (b) Mean variable importance score of metrics calculated from different temporal windows of the Landsat images across all habitat models (i.e., year-round, summer and winter models).

4   Discussion

Our assessment of Landsat-based spectral-temporal metrics in habitat models for lynx, red deer and roe deer yielded four major insights. First, models using the habitat metrics consistently outperformed models based on land-cover maps. Both performance measures (AUC and CBI), indicating discrimination capacity and model calibration, showed considerable increases when compared to models using land-cover maps. This is in line with previous research highlighting the advantages of continuous satellite-derived variables over categorical maps for characterizing species' habitat (Coops and Wulder, 2019; Cord et al., 2014). Calculating spectral-temporal metrics from time series of medium-resolution satellite

imagery provides for an effective way to generate continuous variables that allow assessing habitat with high levels of spatial detail. Remelgado et al. (2018) previously used seasonal Landsat surface reflectance composites for modeling resource availability for white storks (*Ciconia ciconia*). Our study showcases how spectral-temporal metrics from multiple spectral indices can be linked to different habitat aspects, allowing for a comprehensive and meaningful characterization of wildlife habitat from medium resolution imagery.

Second, the habitat metrics allowed capturing variation in habitat between seasons, which categorical land-cover maps typically do not reflect. Performance improvements from using habitat metrics instead of land-cover maps were larger for our seasonal models than for year-round models (Figure II-3b). At the same time, metrics relating to intra-annual variability of habitat conditions (e.g., snow cover, phenology) were highly important in our habitat models (Figure II-7a). These results demonstrate that spectral-temporal metrics can be useful to move away from static depictions of habitat. This is important, as many animals adapt their habitat use in reaction to changing habitat conditions throughout the year (Dupke et al., 2017; Filla et al., 2017; Godvik et al., 2009). Accounting for such variation in habitat models can provide useful information for wildlife management and conservation (Brambilla and Saporetti, 2014; Frans et al., 2018). Combining high-resolution wildlife tracking data (Kays et al., 2015; Pimm et al., 2015) with satellite time series holds great potential in this regard, since it allows simultaneously describing how habitat conditions vary within a year, and how animals respond to these changes (Bischof et al., 2012; Gschweng et al., 2012).

Third, habitat metrics allowed describing fine-scale heterogeneity in habitat associated with forest structure. The suitability maps based on the habitat metrics were consistent with prior studies on habitat selection of our study species. For instance, roe deer in our study area have been shown to preferentially select older forest stands (Dupke et al., 2017). Likewise, the higher suitability of broadleaf regrowth compared to coniferous regrowth likely is related to the observation that roe deer, as selective browsers, prefer young broadleaved trees for browsing (Götmark et al., 2005; Heinze et al., 2011; Kullberg and Bergström, 2001). Conversely, for red deer, being a mixed feeder (Krojerová-Prokešová et al., 2010), the type of regrowth is less influential. Together, this suggests that our habitat metrics were able to characterize fine-scale habitat variation that is extremely difficult to classify in satellite-based land-cover maps (e.g., forest age classes, different types of forest regrowth).

Finally, models using the habitat metrics were able to represent differences in habitat selection between species and seasons, as indicated by the differences in relative variable

importance scores among our models. For example, the importance of the openness metrics in our lynx models, with habitat suitability decreasing with increasing brightness, likely reflects the known avoidance of open habitats (e.g., croplands or built-up areas) by lynx (Bouyer et al., 2015b; Filla et al., 2017; Magg et al., 2016). Likewise, phenology metrics characterizing forage availability and quality were important predictors in our habitat models for red and roe deer. This is in line with previous studies demonstrating the effectiveness of satellite-derived phenology-information for characterizing ungulate habitat (Merkle et al., 2016; Pettorelli et al., 2007), and the finding that habitat selection by roe deer in our study area is largely driven by forage availability (Dupke et al., 2017). Moreover, metrics calculated from start-of-season observations showed the largest relative importance in our models. This corroborates findings on the effectiveness of characterizing spring conditions for capturing habitat features for large herbivores (Hamel et al., 2009; Pettorelli et al., 2007, 2006), particularly in temperate forests (Borowik et al., 2013).

Snow-cover metrics were important predictors in many of our habitat models. While the importance of snow-cover variables was particularly high in our winter models, they also showed considerably high importance scores in some of our summer models. This is likely since snow-cover distribution in winter is correlated with other factors influencing habitat quality in our study area. For example, areas with high snow cover tend to be located at higher elevations where higher levels of natural forest disturbance are found (Oeser et al., 2017), and disturbed forest stands are important habitat features for lynx, red deer and roe deer (Filla et al., 2017; Heurich et al., 2015). While numerous habitat studies have used snow-cover variables from coarse-resolution sensors such as MODIS (Hebblewhite et al., 2011; Kuemmerle et al., 2014; Michaud et al., 2014), our study highlights the underused potential of Landsat imagery in this context (Macander et al., 2015; Niittynen et al., 2018; Niittynen and Luoto, 2018).

Despite these potential benefits of habitat metrics, some limitations need to be mentioned. First, while our habitat metrics allow characterizing different habitat aspects that manifest in spectral properties, there are several factors typically influencing habitat quality that our metrics cannot easily capture (e.g., human disturbance or competition with other species). Whereas including such additional predictors will improve models, we did not do so since this would have hindered the direct comparison of the habitat metrics with land-cover maps for the purpose of habitat modeling. Second, interpreting the relationships between habitat metrics and habitat use can be difficult without reference information, since these relationships are often indirect (Bradley and Fleishman, 2008). Other continuous satellite-

based variables that are directly related to vegetation structure, such as fractional tree or shrub cover (Baumann et al., 2018), or biophysical variables, such as the leaf area index or the fraction of absorbed photosynthetically-active radiation (Viña et al., 2008), can provide more ecologically meaningful habitat information. However, the creation of such datasets is typically based on statistical models and thus, like land-cover mapping, requires reference information for training and validation. Fourth, we selected the temporal windows used for calculating metrics to capture phenological stages at our study site. Adapting the temporal windows to local phenology (Remelgado et al., 2018) or using metric definitions that allow comparing values across different phenological curves (e.g., highest/lowest quarterly median; Coops et al., 2008; Hijmans et al., 2005) might be necessary when transferring our approach to other regions. Finally, for areas and temporal windows with very high levels of cloud cover, some of our spectral-temporal metrics exhibited striping artefacts relating to scan line errors of Landsat 7. Integrating Landsat imagery with data from other sensors, such as Sentinel 2 (Claverie et al., 2018; Wulder et al., 2015) has the potential to reduce impacts of data gaps and further improve the ability to capture seasonal habitat dynamics.

Overall, our study highlights the considerable potential of spectral-temporal metrics from medium-resolution satellite imagery for monitoring, managing and conserving wildlife. A key advantage of Landsat in this regard lies in the global availability of 30m-resolution imagery since the 1980s (at lower spatial resolutions even since the 1970s; Wulder et al., 2019). This offers great flexibility in terms of generating consistent predictors for habitat modeling across space and time and matching predictor data with available species records. This extraordinary potential for assessing habitat across large areas (Hansen and Loveland, 2012) and long time periods (Kennedy et al., 2014; Kerr and Ostrovsky, 2003; Vogelmann et al., 2012) has so far not been fully exploited (but see Jantz et al., 2016). The approach introduced in this study can help bridging this gap, opening up new possibilities to monitor spatiotemporal habitat dynamics based on Landsat imagery. Finally, further integrating the rich information of satellite image archives with habitat models has great potential to advance global biodiversity monitoring, as targeted by the Essential Biodiversity Variables framework (Jetz et al., 2019; Pereira et al., 2013; Pettorelli et al., 2016).

Acknowledgements

Supplementary Information

Figure SI II-1: Strength of correlation between Landsat habitat metrics of different metric groups, expressed as absolute Pearson correlation coefficients. Within-group correlation refers to correlation coefficients of all metrics belonging to a given group, out-of-group correlation refers to correlation coefficients of metrics of a given group with metrics not belonging to that group.

Text SI II-1: Comparison of Landsat-derived snow cover frequency with MODIS snow-cover product.

To check the consistency our snow-cover frequency metrics derived from the Pixel Quality-Assessment bands of Landsat images, we compared them with the daily MODIS snow-cover product (MOD10A1; Hall et al., 2010). While the Landsat snow masks are binary, the MODIS product gives a continuous estimate of snow cover, taking values between 0-100, with all values above 0 indicating the presence of snow in a pixel. Thus, the two datasets are not fully comparable, but spatial patterns should be similar given good agreement between both sources. As reference images to compare our snow-cover metrics to, we calculated the average snow-cover per pixel from images in the MODIS product collection for the entire year (1095 images) and for the start of season window (279 images; see 2.3 in main text). We divided the MODIS snow-cover images by 100 to align them with the Landsat-based snow-cover metrics.

The spatial patterns between the Landsat-based snow-cover frequency metrics and the average snow cover derived from MODIS were generally similar (Figure SI II-2), showing moderate to high correlations (r = 0.70 for snow-cover frequency for the entire year, and r = 0.85 for snow-cover frequency for the start of season period; Figure SI II-3). Compared to the MODIS snow-cover values, Landsat snow-cover metrics showed higher values in areas with high levels of snow cover. This bias could be related to the fact that the Landsat snow masks only allow a binary classification of snow cover. Landsat-pixels partially covered by snow (e.g., 40%) might be flagged as snow (i.e., with a value of 1), while the MODIS product allows for a continuous description of snow cover percentages.
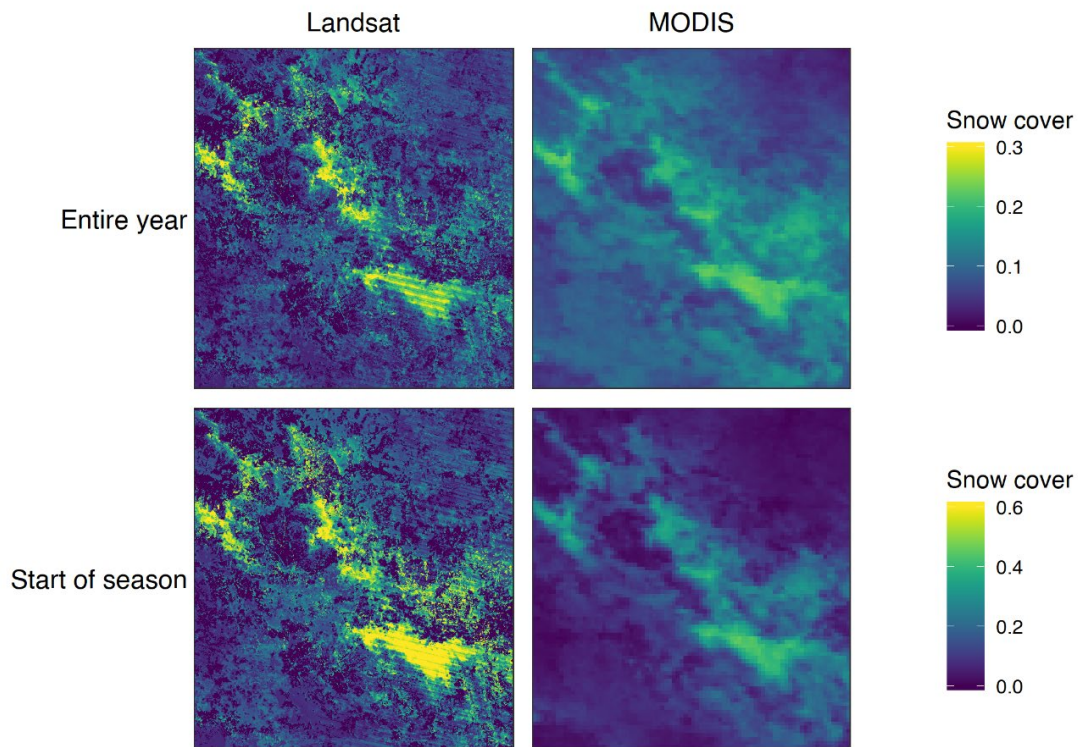
Figure SI II-2: Comparison of Landsat-based snow-cover frequency metrics with average snow cover derived from MODIS daily snow cover. While both datasets show similar spatial patterns, values of the Landsat metrics were higher in areas with high snow cover. Moreover, striping artefacts relating to Landsat 7 scan line errors are visible in the Landsat-based metrics.
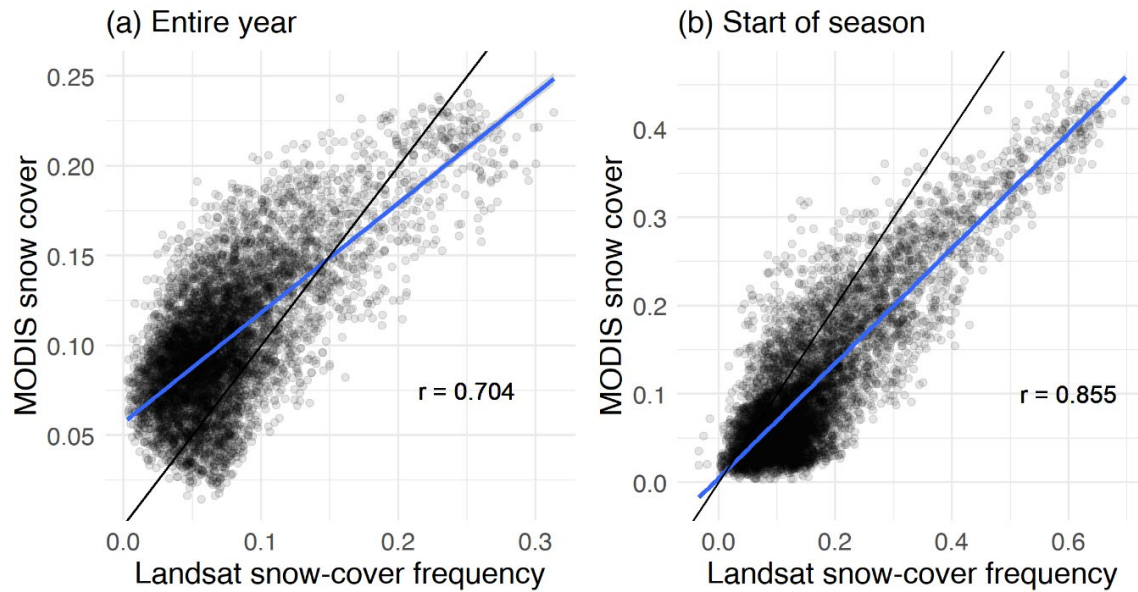
Figure SI II-3: Scatterplots between the Landsat snow-cover frequency metrics and average snow-cover values from MODIS 10A1 snow-cover product, based on observations from (a) the entire year, and (b) only start of season observations. Landsat metrics were resampled to 500m resolution of the MODIS data to allow comparison. Blue line indicates slope of linear regression between both datasets, black line indicates perfect agreement between values.

Text SI II-2: Land cover mapping approach and results

For classifying land cover in our study region, we used a Random Forest classification model with default parameters of the *randomForest*-package in R (Liaw and Wiener, 2002). We produced the land-cover map for a region around the two national parks (i.e., a larger extent than the one we used for creating habitat suitability maps; Figure SI II-4). As classification features, we used all spectral-temporal habitat metrics (see 2.3 in main text). For collecting reference data for model training and validation, we combined two sources of information. First, we used an existing vegetation type map (polygon data) from the year 2012 covering the Bavarian Forest National Park (BFNP) and derived based on interpretation of high-resolution aerial imagery by local experts (Gonzalez et al., 2018). Second, to sufficiently cover land-cover classes less widespread inside the park, we manually digitized additional reference polygons outside the national park based on high-resolution imagery available in Google Earth.

For each of the 13 land-cover classes, we took a random sample of Landsat pixels covered by our reference polygons, dividing the class-wise samples into separate datasets for model training and testing. For all classes except two small classes (rock, shrub), we used a sample of 2,000 pixels for training models, and a sample of 1,000 pixels to evaluate model accuracy

(Table SI II-1). To remove salt-and-pepper structures that likely represent misclassifications, we applied a minimum-mapping-unit of 0.36 ha (i.e., four Landsat pixels) to our final land-cover

map. For the calculation of map accuracies, we adjusted error estimates for possible sampling bias based on the class distribution of the land-cover classes (Olofsson et al., 2014).

Our final land cover map had an overall accuracy of 91.5%. Class-wise accuracies were generally high, particularly for the larger classes (Table SI II-1). However, some of the smaller classes, namely rock, forest regrowth, shrub, clearcut and deadwood, were associated with higher uncertainty (Table SI II-1).

Table SI II-1: Map accuracies and area estimates for our Landsat-based land-cover map. All numbers are sampling-bias-adjusted and are given with 95% confidence intervals.

Overall accuracy [%]	Class name	Training samples	Testing samples	User's accuracy [%]	Producer's accuracy [%]	Adjusted area estimates [ha]
91.5 ± 7.2	Broadleaf forest	2000	1000	86.2 ± 2.1	86.9 ± 2.8	97443 +- 3700
	Built-up	2000	1000	97.4 ± 1	98.9 ± 1.2	61054 +- 956
	Clear-cut	2000	1000	84.9 ± 2.1	60.1 ± 14.1	5001 +- 1174
	Coniferous forest	2000	1000	89.8 ± 2	88.5 ± 1.9	168634 +- 4914
	Cropland	2000	1000	99.7 ± 0.3	97.8 ± 1.1	148116 +- 1740
	Deadwood	2000	1000	91.4 ± 1.7	65.1 ± 10.2	9200 +- 1446
	Forest regrowth	2000	1000	84.7 ± 2.2	42.0 ± 7.4	11357 +- 1999
	Grassland	2000	1000	97.7 ± 0.9	99.4 ± 0.3	218424 +- 2174
	Mixed forest	2000	1000	80.5 ± 2.6	87.4 ± 1.7	177554 +- 5934
	Natural grassland	2000	1000	93.8 ± 1.6	66.2 ± 7.5	16294 +- 1853
	Rock	50	31	100 ± 0	5.7 ± 5.2	264 +- 238
	Shrub	300	159	96.2 ± 3	57.8 ± 27	1340 +- 627
	Water	2000	1000	100 ± 0	100 ± 0	7287 +- 0
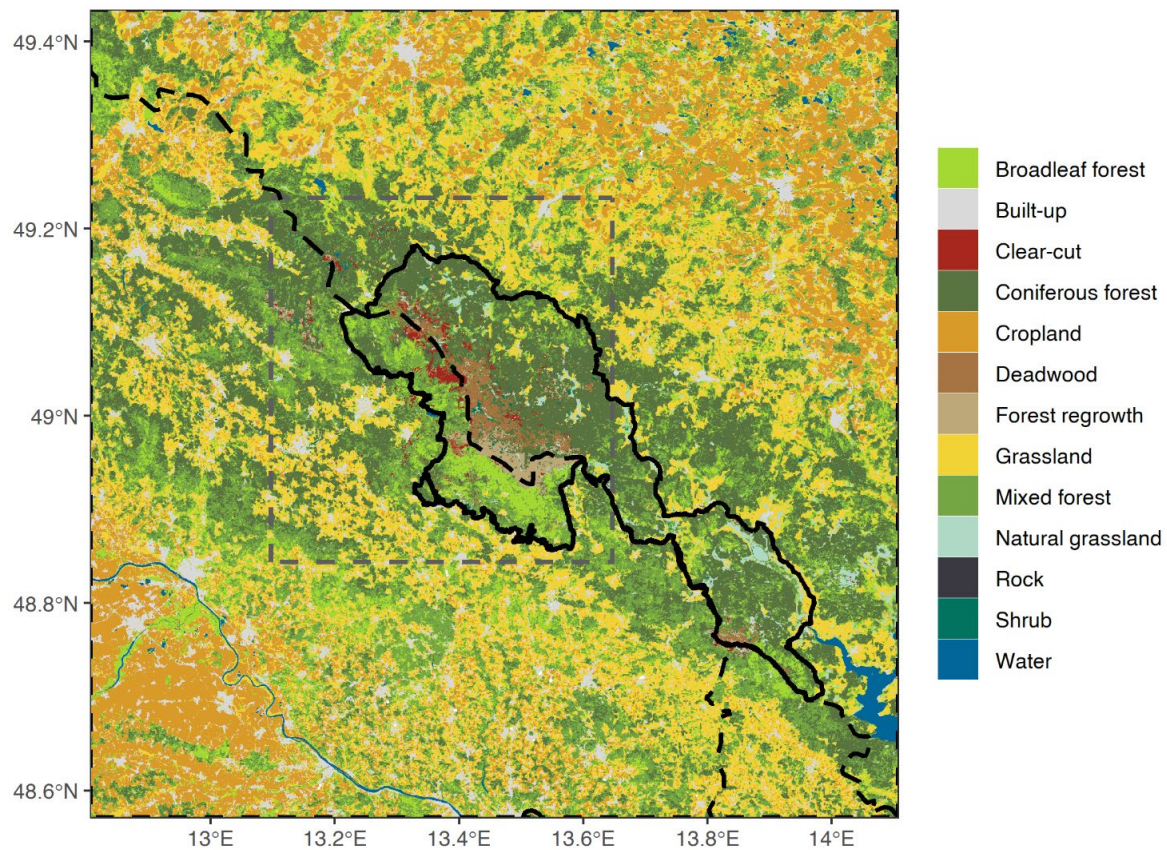
Figure SI II-4: Land-cover map produced for the area around the study region. Black lines show national park borders; black dashed lines indicate country borders. Grey dashed line show the extent of the study region for which habitat suitability maps were created.

Table SI II-2: Pooling of CORINE land-cover classes for CORINE-based habitat suitability models. Not all CORINE codes are included, since not all classes are present in the study area.

Pooled class name	Definition	CORINE class code*
Human	Settlements, industry, artificial surfaces	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11
Acre	Non-irrigated arable land	12
Natural Agriculture	Agricultural areas with significant natural vegetation or complex cultivation patterns	15, 16, 20, 21
Pastures	Pastures	18
Broadleaved forest	Broadleaved forest	23
Coniferous forest	Coniferous forest	24
Mixed forest	Mixed forest	25
Natural grassland	Natural grassland	26

| Wood- and shrubland | Transitional woodland, shrubland and wetlands | 27, 29, 35, 36 |
| Water | Inland water bodies | 40, 41 |

*Definitions of grid codes are available from CORINE land cover data.
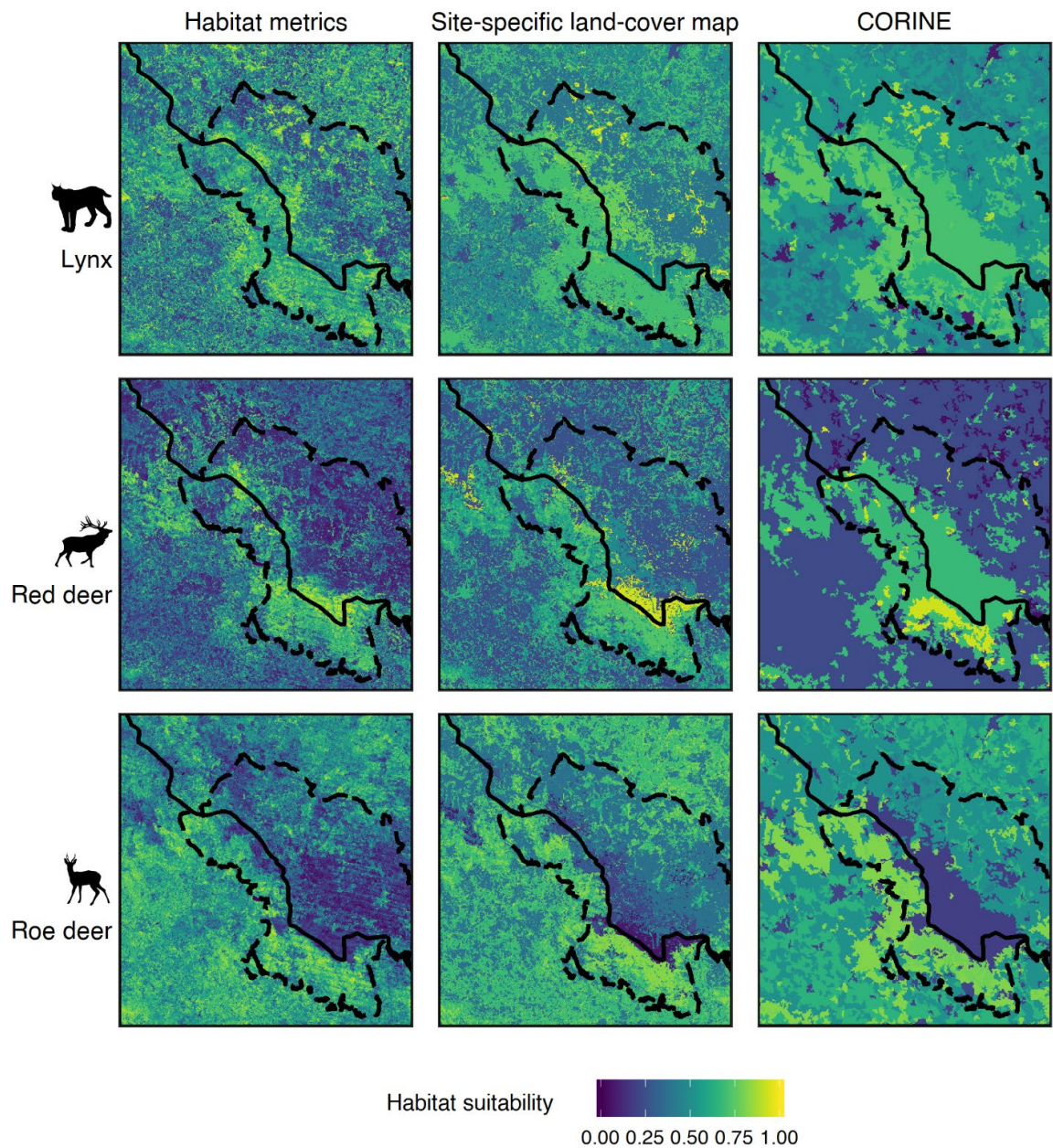
Figure SI II-5: Habitat suitability maps of summer habitat models using the habitat metrics (left column), the site-specific land-cover map (middle column) and the CORINE land-cover map (right column) for lynx, red deer, and roe deer. Continuous line indicates country border, dashed lines show the extents of the national parks.
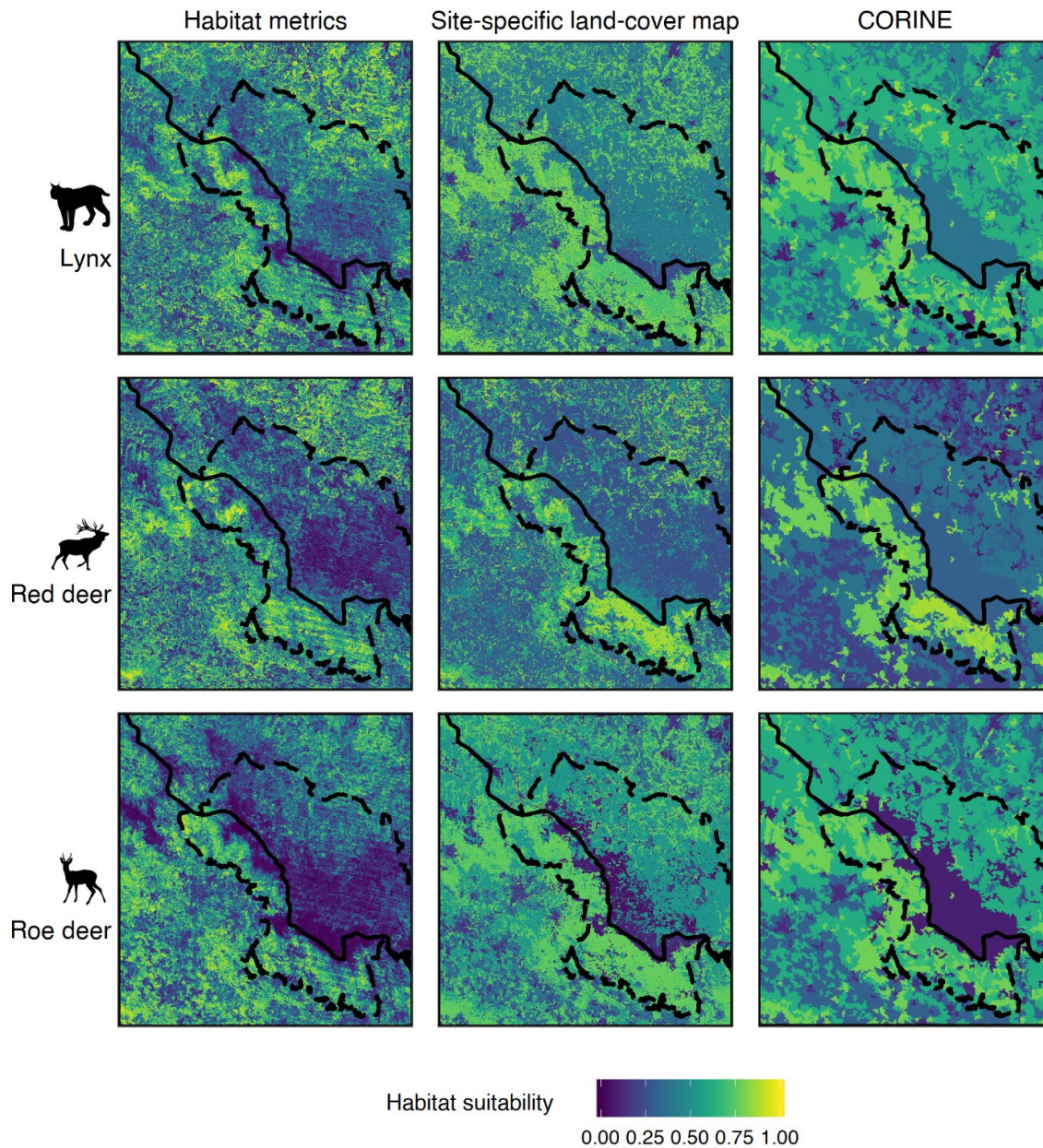
Figure SI II-6: Habitat suitability maps of winter habitat models using the habitat metrics (left column), the site-specific land-cover map (middle column) and the CORINE land-cover map (right column) for lynx, red deer, and roe deer. Continuous line indicates country border, dashed lines show the extents of the national parks.
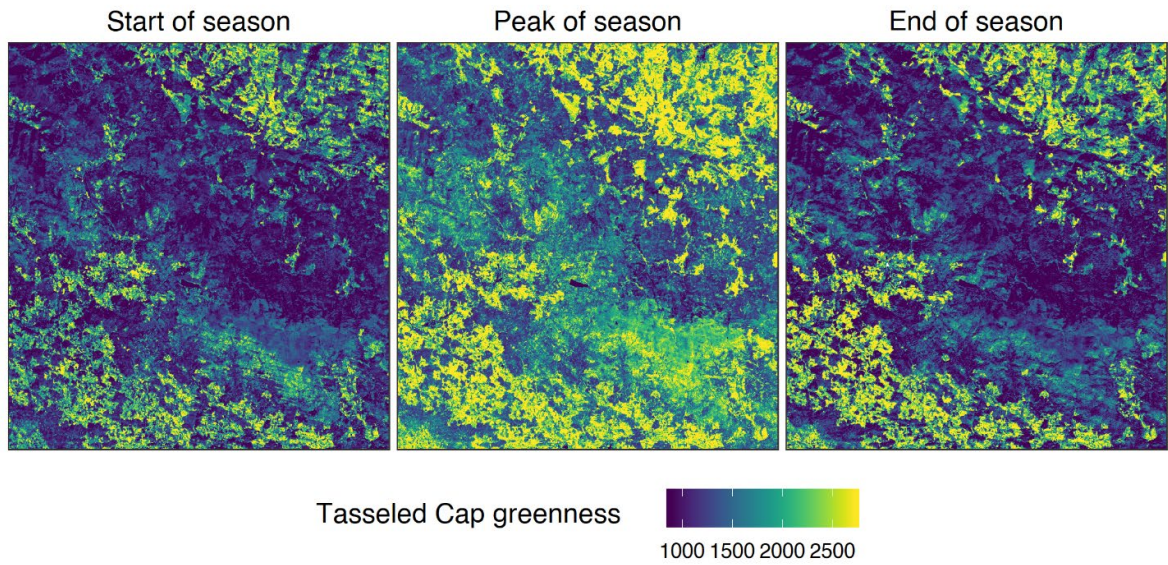
Figure SI II-7: Productivity metrics (median of Tasseled Cap greenness) calculated based on start-of-season, peak-of-season, and end-of-season observations (see 2.3 in main text). Striping artefacts mainly occurred in metrics calculated from start-of-season observations, which was the temporal window with the fewest number of available images, and the strongest influence of cloud cover.
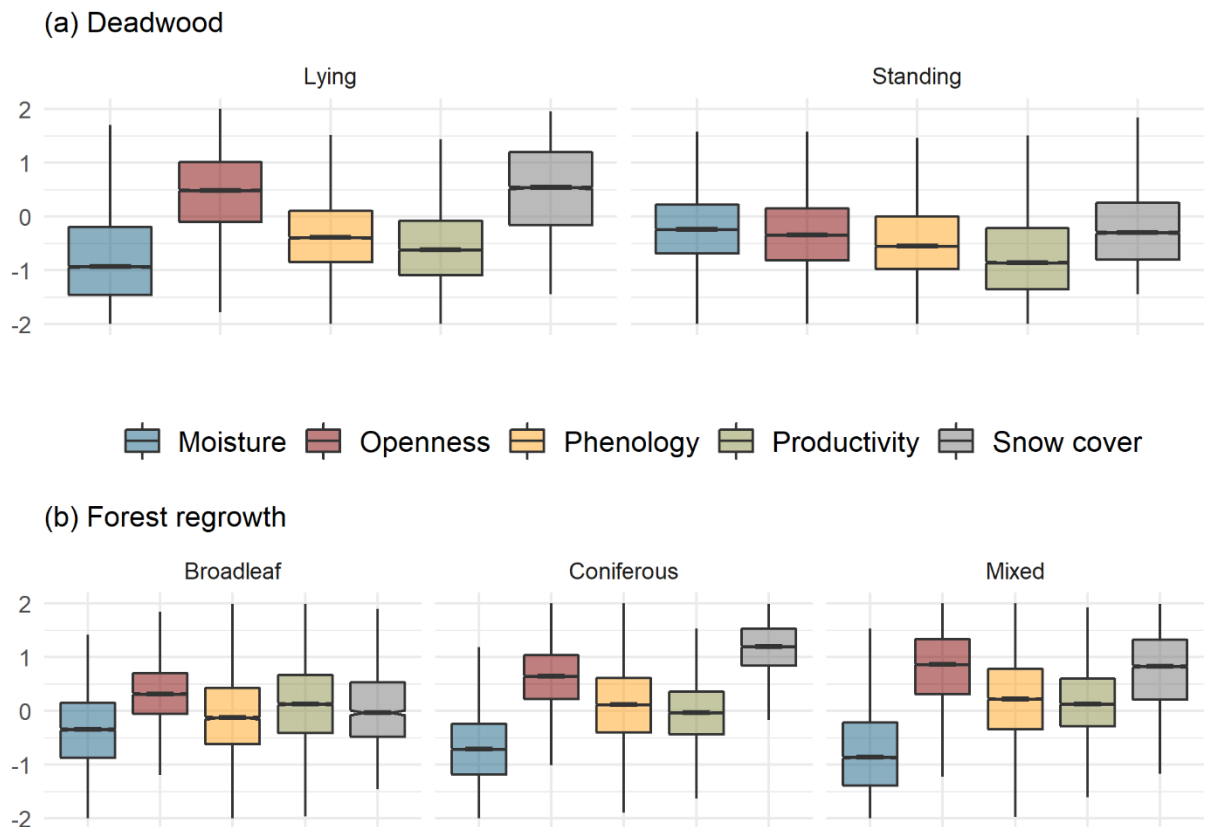
Figure SI II-8: Variation of metric values (by metric groups) with vegetation classes relating to forest structure. (a) Deadwood and (b) Forest regrowth. All metrics were standardized via a z-Transformation to allow comparability between different spectral indices.

Chapter III:

Satellite-based habitat monitoring reveals long-term dynamics of deer habitat in response to forest disturbances

Julian Oeser, Marco Heurich, Cornelius Senf, Dirk Pflugmacher, Elisa Belotti, and Tobias Kuemmerle

Abstract

Disturbances play a key role in driving forest ecosystem dynamics, but how disturbances shape wildlife habitat across space and time often remains unclear. A major reason for this is a lack of information about changes in habitat suitability across large areas and longer time periods. Here, we use a novel approach based on Landsat satellite image time series to map seasonal habitat suitability annually from 1986 to 2017. Our approach involves characterizing forest disturbance dynamics using Landsat-based metrics, harmonizing these metrics through a temporal segmentation algorithm, and then using them together with GPS telemetry data in habitat models. We apply this framework to assess how natural forest disturbances and post-disturbance salvage logging affect habitat suitability for two ungulates, roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), over 32 years in a Central European forest landscape. We found that red and roe deer differed in their response to forest disturbances. Habitat suitability for red deer consistently improved after disturbances, whereas the suitability of disturbed sites was more variable for roe deer depending on season (lower during winter than summer) and disturbance agent (lower in windthrow versus bark-beetle-affected stands). Salvage logging altered the suitability of bark beetle-affected stands for deer, having negative effects on red deer and mixed effects on roe deer, but generally did not have clear effects on habitat suitability in windthrows. Our results highlight long-lasting legacy effects of forest disturbances on deer habitat. For example, bark beetle disturbances improved red deer habitat suitability for at least 25 years. The duration of disturbance impacts generally increased with elevation. Methodologically, our approach proved effective for improving the robustness of habitat reconstructions from Landsat time series: integrating multi-year telemetry data into single, multi-temporal habitat models improved model transferability in time. Likewise, temporally segmenting the Landsat-based metrics increased the temporal consistency of our habitat suitability maps. As the frequency of natural forest disturbances is increasing across the globe, their impacts on wildlife habitat should be considered in wildlife and forest management. Our approach offers a widely applicable method for monitoring habitat suitability changes caused by landscape dynamics such as forest disturbance.

1   Introduction

Forest disturbances significantly alter the amount and quality of habitat available to wildlife (Thom and Seidl, 2016) and, through their long-lasting effects on forest structure, shape habitat conditions over long time periods (Schieck and Song, 2006). Yet, information on how forest disturbances modify habitat suitability for wildlife, particularly across large areas and long time periods, is not commonly available to wildlife management and conservation (Clare et al., 2019). At the same time, generalized predictions about wildlife responses to forest disturbances are difficult, as different disturbance types vary in their impacts on forests. For example, natural forest disturbances (e.g., insect outbreaks and windthrows) create biological legacies promoting structural complexity (Johnstone et al., 2016), while forest management interventions such as clear-cutting or salvage logging homogenize forest structure (Thorn et al., 2017). As natural forest disturbances are becoming more frequent across large parts of globe (Seidl et al., 2017; Senf et al., 2018), a better understanding of forest disturbance impacts on wildlife habitat is important to develop adequate management and conservation strategies.

Habitat suitability models allow the assessment of wildlife responses to forest disturbances (Berland et al., 2008) and provide spatially explicit habitat suitability maps which are critical for informing wildlife management and conservation (Guisan and Thuiller, 2005). Typically, however, habitat models only provide a snapshot of habitat for single points in time (Franklin, 2010), limiting the usefulness of such models for monitoring the effects of landscape dynamics on species' habitat. Integrating satellite time series into habitat models has great potential for overcoming this limitation (Randin et al., 2020). Satellite images offer detailed characterizations of wildlife habitat (Bellis et al., 2008; Lahoz-Monfort et al., 2010; Oeser et al., 2020), and long-term satellite records, such as the Landsat archive, provide consistent information on landscape change, including forest disturbances (Wulder et al., 2019). Linking habitat models to Landsat time series thus could allow a wall-to-wall mapping of habitat suitability several decades back in time. Yet, whereas Landsat time series have been widely and successfully used for monitoring forest disturbances (Banskota et al., 2014), their application for monitoring disturbance-related dynamics in wildlife habitats has been scarce (but see Kearney et al., 2019 for a recent example).

Reconstructing habitat dynamics based on Landsat time series, however, entails challenges particularly with regards to ensuring the consistency of habitat maps over time. As available wildlife records often only cover parts of multi-decadal Landsat time series, model transfers in time are typically necessary, which pose challenges for habitat models (Tuanmu et al.,

2011; Yates et al., 2018). At the same time, sampling schemes for collecting wildlife data often vary over time. To tackle these issues, species records collected over time can be integrated into single habitat models, where species records are matched with time-varying predictors (Nogués-Bravo, 2009). Such a multi-temporal calibration approach of habitat modeling (hereafter: multi-temporal habitat models) makes model predictions independent of year-to-year variations in sampling bias and can improve model transferability (Maiorano et al., 2013). While satellite time series generally facilitate building multi-temporal habitat models (Randin et al., 2020), time series of satellite-based metric also often exhibit year-to-year fluctuations unrelated to actual changes in habitat, caused for example by variations in satellite image availability or cloud cover. Thus, to avoid mapping spurious habitat change, satellite time series must be harmonized across time. In this context, satellite time series algorithms have been developed to separate change signals from noise (Zhu, 2017), but their applicability for monitoring habitat dynamics remains untested.

Multi-decadal time series of habitat suitability maps also have considerable potential to provide new insights into how forest disturbance affect wildlife habitat, particularly regarding long-term effects (Kearney et al., 2019). Understanding such impacts of forest disturbances on large herbivore species, such as ungulates, is an important concern for forest and wildlife management (Vospernik and Reimoser, 2008). Forest disturbances are a key driver of ungulate habitat dynamics (Fisher and Wilkinson, 2005) and, in turn, ungulate herbivory has important effects on forest ecosystem dynamics and functions by altering forest structure and successional trajectories (Côté et al., 2004). Forest openings created by disturbance typically provide good foraging conditions to ungulates due to a high abundance of plant biomass on the ground (Kuijper et al., 2009). On the other hand, forest openings offer low levels of cover, which increases the exposure to thermal extremes and predation risk (Mysterud and Østbye, 1999). The studies available indicate variation of ungulate responses to forest disturbance across species and study systems (see e.g., Kuijper et al., 2009; Lamont et al., 2019; Moser et al., 2008). However, these studies are overwhelmingly limited to single types of disturbance, as well as initiation stages immediately after disturbance events. How ungulate habitat changes as disturbed areas recover, and whether habitat suitability varies between different natural disturbances and post-disturbance management interventions remain, therefore, largely unresolved questions.

Here, we use a novel approach linking habitat models with Landsat satellite time series for monitoring wildlife habitat dynamics consistently and continuously over multiple decades. Specifically, we assess how habitat suitability for red deer (*Cervus elaphus*) and roe deer

(*Capreolus capreolus*) changed in response to forest disturbance in the Bohemian Forest Ecosystem, a Central European montane forest landscape. We characterized forest disturbance and recovery dynamics using time series of Landsat-based spectral-temporal metrics, which we harmonized across time using a temporal segmentation algorithm (Kennedy et al., 2010). Then, we integrated these Landsat-based metrics with GPS telemetry data collected over 13 years (2002-2014) in multi-temporal habitat models. By projecting habitat models across the full length of our satellite time series, we mapped changes in summer and winter habitat suitability annually for all years between 1986-2017. Finally, we used this time series of habitat suitability maps to investigate how deer respond to forest disturbance caused by bark beetle outbreaks, windthrow and salvage logging. Specifically, we sought to answer the following research questions:

1.   Does our approach of multi-temporal data integration and harmonization improve the transferability and consistency of habitat models across time?

2.   Do red and roe deer respond differently to forest disturbances by bark beetle, windthrow and salvage logging?

3.   How does habitat suitability evolve as disturbed sites recover?

2   Methods

2.1   Study area

We conducted our study in the Bohemian Forest Ecosystem situated along the border of Austria, Czechia, and Germany (Figure III-1). Two protected areas form the center of the study site: the Bavarian Forest National Park (240 km²) and the Šumava National Park (680 km²). Elevations range from ca. 400 to 1450 m. The area's forests are typical for Central European mountainous forests, dominated by Norway spruce (*Picea abies*) and accompanied by mountain ash (*Sorbus aucuparia*) at higher elevations (>1100 m). Lower elevations are characterized by mixed montane forests composed mainly of European beech (*Fagus sylvatica*), Norway spruce and silver fir (*Abies alba*). Since the 1990s, large-scale forest disturbances caused by bark beetle outbreaks and windthrow have restructured large parts of the Bohemian Forest (Oeser et al., 2017). Inside the core zones of the national parks, disturbed sites were left to recover naturally, but salvage logging was applied in the management zones to prevent an uncontrolled spread of bark beetle (Thorn et al., 2017).
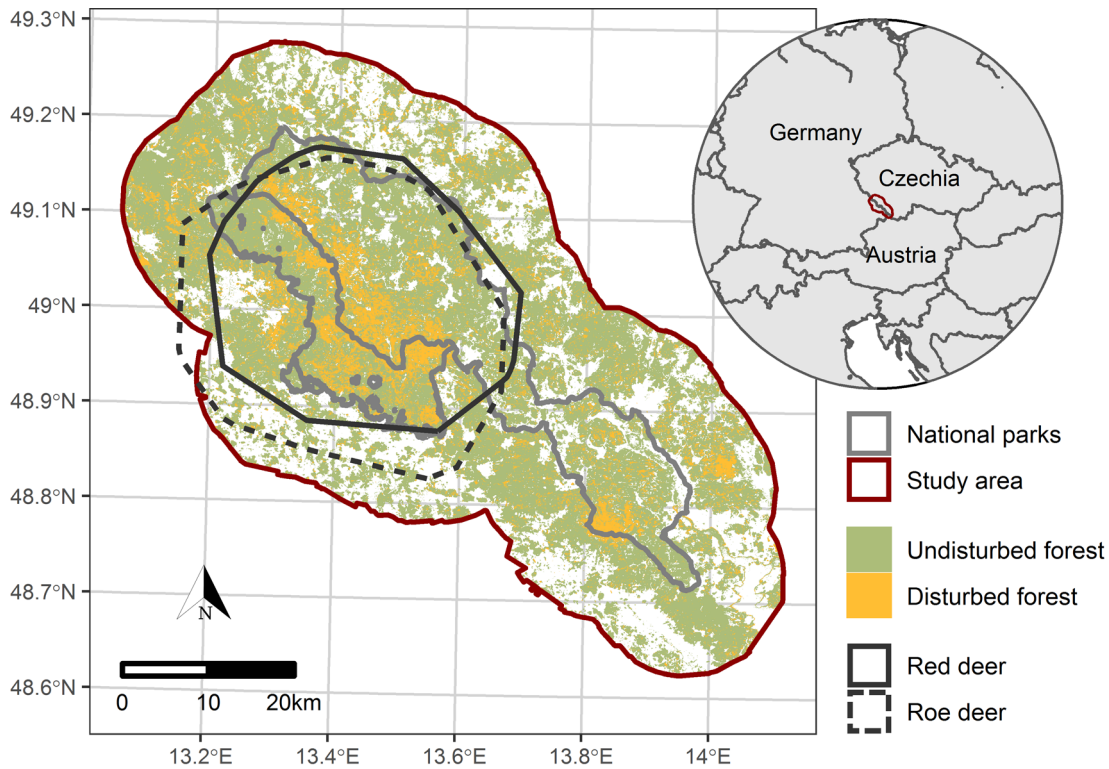
Figure III-1: Map of the study area. Forest disturbances between 1986-2014 were mapped based on Landsat time series (Oeser et al., 2017). Polygons for red and roe deer show minimum convex polygons around GPS telemetry observations.

2.2   GPS telemetry data for roe deer and red deer

We used GPS telemetry records containing a total of 111 red deer and 164 roe deer individuals. Red deer data were collected between 2002 and 2014, and roe deer data between 2004 and 2013. As some of the GPS-collared red deer were kept in winter enclosures (Heurich et al., 2015), we removed all red deer locations falling into these enclosures and only used locations from red deer outside the enclosures for further analysis. We standardized the sampling frequency among individuals to four observations per day, retaining one observation each from four temporal windows: nighttime (22:00-04:00), dawn (04:00-10:00), daytime (10:00-16:00) and dusk (16:00-22:00). We further split observations into summer (April 1st - October 31st) and winter (November 1st - March 31st) locations and created a random subset of 100 observations per individual and season. This allowed using data from most deer individuals, while ensuring that individuals monitored over longer time periods than others were not overrepresented in our habitat models. We excluded individuals with fewer than 100 observations per season (after standardizing the sampling frequency). The final datasets used for building habitat models consisted of 10,999 summer

and 7,997 winter observations from 110 and 80 red deer individuals, respectively, and 14,723 summer and 14,925 winter observations from 148 and 150 roe deer individuals, respectively.

2.3 Characterizing habitat change with time series of Landsat-based metrics

We used Landsat satellite image time series to characterize changes in deer habitat caused by forest disturbance and post-disturbance recovery. Our approach consisted of three main steps (Figure III-2).
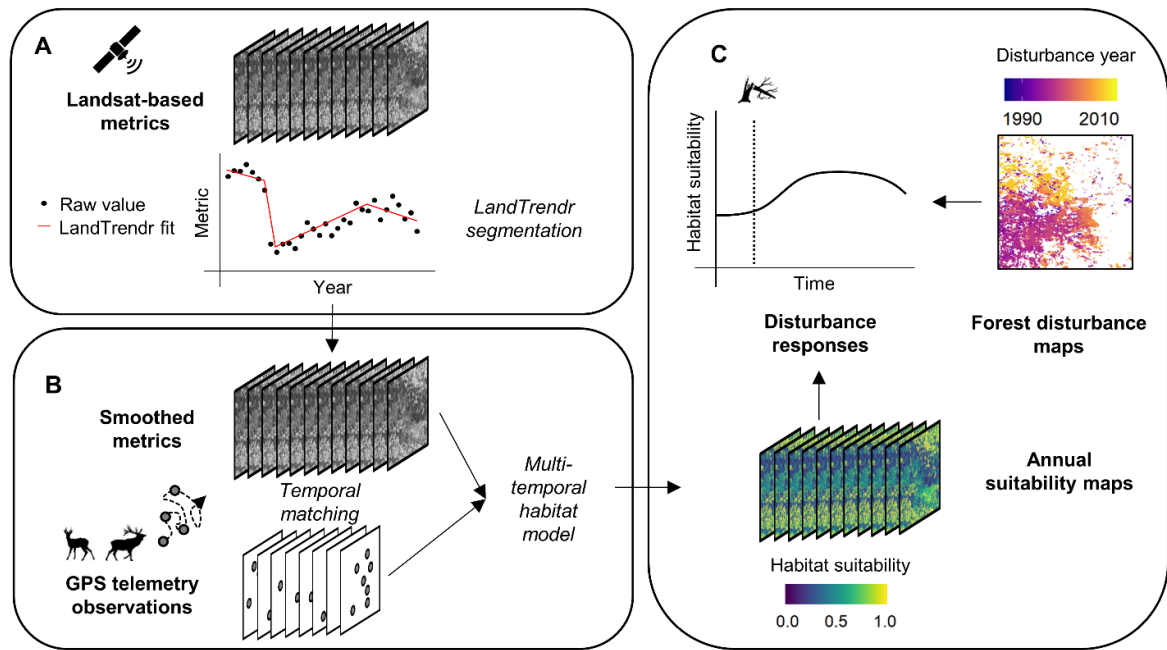
Figure III-2: Schematic overview of our workflow. (A) We derived Landsat-based metrics that we harmonized across time using time series segmentation. (B) GPS telemetry records collected over 13 years were temporally matched with the smoothed metrics to train multi-temporal habitat models. These models were then used to predict habitat suitability across all years (1986-2017). (C) We subsequently linked the annual habitat suitability maps to independent forest disturbance maps to assess habitat suitability changes in response to forest disturbances.

In our first main step, we derived spectral-temporal metrics from Landsat satellite images. For each Landsat image, we derived the Tasseled Cap indices brightness, greenness, and wetness (Crist and Cicone, 1984), which are sensitive to forest types, structure and disturbance (Dymond et al., 2002; Hansen et al., 2001; Healey et al., 2005). Calculating the tasseled cap indices for all available images from a given year results in distributions of index values for each image pixel, since spectral indices vary along characteristic seasonal profiles, which are indicative of land-cover and vegetation characteristics (Pasquarella et al., 2016). To summarize the intra-annual phenological variation of the three tasseled cap

indices, we then calculated the 10th, 50th (i.e., the median) and 90th percentiles at the pixel level, resulting in a total of nine spectral-temporal metrics. In an earlier study, we found that spectral-temporal metrics based on the tasseled cap indices allow for detailed characterizations of wildlife habitat, including deer habitat (Oeser et al., 2020). Here, we extend our approach of linking habitat models with Landsat imagery to map long-term habitat dynamics. Therefore, we created annual time series of the Landsat-based metrics using all images recorded by the sensors 4 TM, 5 TM, 7 ETM+ and 8 OLI between 1985 to 2018 covering our study area (1,455 images with 30m spatial resolution; see Text SI III-1 for a detailed description of the image processing). Due to high levels of cloud cover in our study area, we did not calculate metrics for each year separately, but instead used three-year moving windows, including all images from the year before and after for calculating metrics for a given year. This resulted in annual time series for all nine metrics from 1986-2017 (hereafter: raw metrics). While the use of three-year windows effectively reduced the temporal resolution of our time series, it ensured the robust calculation of metrics, as year-to-year variations in the number and seasonal timing of observations otherwise would have strongly affected the calculation of metrics and hence the consistency of our habitat monitoring.

To further improve the consistency of the Landsat-based metrics, we removed ephemeral year-to-year variations in the raw metric time series. To this end, we applied the satellite time series segmentation algorithm LandTrendr, which has been developed for detecting and characterizing land surface changes with Landsat time series (Kennedy et al., 2010). LandTrendr partitions time series of spectral indices by first identifying breakpoints and subsequently fitting straight-line segments between these breakpoints (see Kennedy et al., 2010 for details). This results in linear trajectories of stable, decreasing or increasing values, which strongly reduces noise while capturing both abrupt and gradual changes (Vogeler et al., 2018). We derived trajectories from LandTrendr for all nine metric time series (hereafter: smoothed metrics). We performed all satellite image processing in the Google Earth Engine (Gorelick et al., 2017; Kennedy et al., 2018) and provide the code via a link in Text SI III-1.

2.4 Multi-temporal habitat modelling

In our second main step, we built multi-temporal habitat models for red and roe deer. For calibrating models, we used the subsampled telemetry datasets containing observations from 2002-2014 for red deer and 2003-2012 for roe deer. We temporally matched the telemetry observations with the Landsat-based metrics (Figure III-2) and built four habitat models for

each deer species, generating separate models using the raw metrics (without temporal segmentation) and smoothed metrics (with temporal segmentation), as well as for summer (April 1st - October 31st) and winter (November 1st - March 31st). The latter was important since habitat use of red and roe deer differs between seasons in our study area (Heurich et al., 2015). We built all habitat models using the MaxEnt algorithm (Phillips et al., 2017). As background points (pseudoabsences), we sampled five random points in our study area for every presence observation and assigned the observation's year to these background points. To limit model complexity and to improve transferability, we fitted MaxEnt models using only hinge features (Elith et al., 2010). Finally, we projected each habitat model across the entire time series of Landsat-based metrics to create habitat suitability maps for each year between 1986 and 2017. For predicting models, we used the 'cloglog' output of MaxEnt (Phillips et al., 2017), which we use as an index of relative habitat suitability.

To compare the temporal consistency of habitat suitability maps based on the smoothed and raw metrics, we analyzed the year-to-year variability of habitat suitability in undisturbed forests. In undisturbed forests, habitat suitability should vary little between consecutive years, thus serving as a benchmark for the temporal stability of our habitat models. As a measure of year-to-year variability, we calculated the mean absolute difference in habitat suitability between consecutive years at the pixel level. To evaluate whether variability in the habitat suitability maps was influenced by satellite image availability, we correlated the variability in habitat suitability with the average number of clear Landsat observations at a given location.

To test whether the integration of deer observations from multiple years improved the temporal transferability of habitat models, we built seasonal habitat models using deer observations from each individual year, as well as all possible windows of three and five consecutive years. Then, to validate these models, we created habitat suitability predictions for each of the remaining annual datasets (i.e., presence and background points from deer individuals not used for model training). As our dataset only allowed transferring models built from five years of deer data up to eight and five years in time for red and roe deer, respectively, we limited model transfers of all models to this time range to ensure comparability. We assessed model transferability by calculating two performance metrics from the model predictions: (1) the area under the Receiver Operating Characteristic curve (AUC) and (2) the Continuous Boyce Index (CBI; Hirzel et al., 2006). These metrics provide complementary measures for two different aspects of habitat model performance. While the AUC measures the discriminatory ability of models (i.e., their ability to discriminate

presence from background points), the CBI can be used as an indicator of model calibration (i.e., how well the predicted habitat suitability values match with the frequency of presence locations; see Phillips and Elith, 2010 for more details on both validation metrics).

2.5   Assessing habitat suitability changes in response to forest disturbance

We linked our time series of habitat suitability maps to Landsat-based forest disturbance maps from our study area (Oeser et al., 2017). These disturbance maps capture forest disturbances occurring between 1986 and 2014 at the level of Landsat pixels (30m resolution), and further differentiate four disturbance types: bark beetle infestations, windthrows, salvage-logged windthrows and other logging, which includes salvage logging of bark beetle-infested stands inside the national parks. Based on our time series of habitat suitability maps, we built chronosequences of habitat suitability for salvaged and unmanaged bark beetle and windthrow disturbances by grouping values based on the number of years since a pixel had been disturbed. Because bark beetle outbreaks overwhelmingly occurred after 1992 and windthrow disturbances after 2006 at our study site, we capped chronosequences at 25 years for bark beetle disturbances, and at 11 years for windthrows.

The disturbance types tend to occur at different elevations in our study area (e.g., windthrows predominantly occurring at higher elevations; Figure SI III-1). As elevation has strong effects on the distribution of deer in our study area (Heurich et al., 2015) and further affects post-disturbance forest recovery (Senf et al., 2019), we thus separately compared salvaged and non-intervention sites at low (600-900m), medium (900-1100m) and high elevations (1200-1400m) and further summarized habitat suitability changes for all bark beetle and windthrow disturbances across elevation-bins of 50m.

3   Results

3.1   Consistency and transferability of habitat models

Using the smoothed metrics obtained from LandTrendr improved the temporal consistency of habitat suitability maps, as the year-to-year variability of habitat suitability in undisturbed forests (i.e., stable habitat) was lower compared to habitat suitability maps based on the raw metrics (average reduction of 52% across all habitat models; Figure III-3a). The temporal consistency of habitat suitability time series generally decreased with fewer available Landsat observations at a given location, but this negative effect was dampened when using

the smoothed metrics (Figure III-3a; correlation coefficient for smoothed and raw metrics: -0.72 and -0.47, respectively).

The transferability of habitat models in time improved on average through the integration of deer data from multiple years for model calibration (Figure III-3b; mean AUC and CBI for five-year vs. single-year models: 0.74 and 0.91 vs 0.69 and 0.81). In addition, models based on the smoothed metrics showed better average performance during model transfers than those based on the raw metrics (Figure III-3b; mean AUC and CBI for five-year models based on the smoothed vs. raw metrics: 0.73 and 0.91 vs. 0.70 and 0.84).
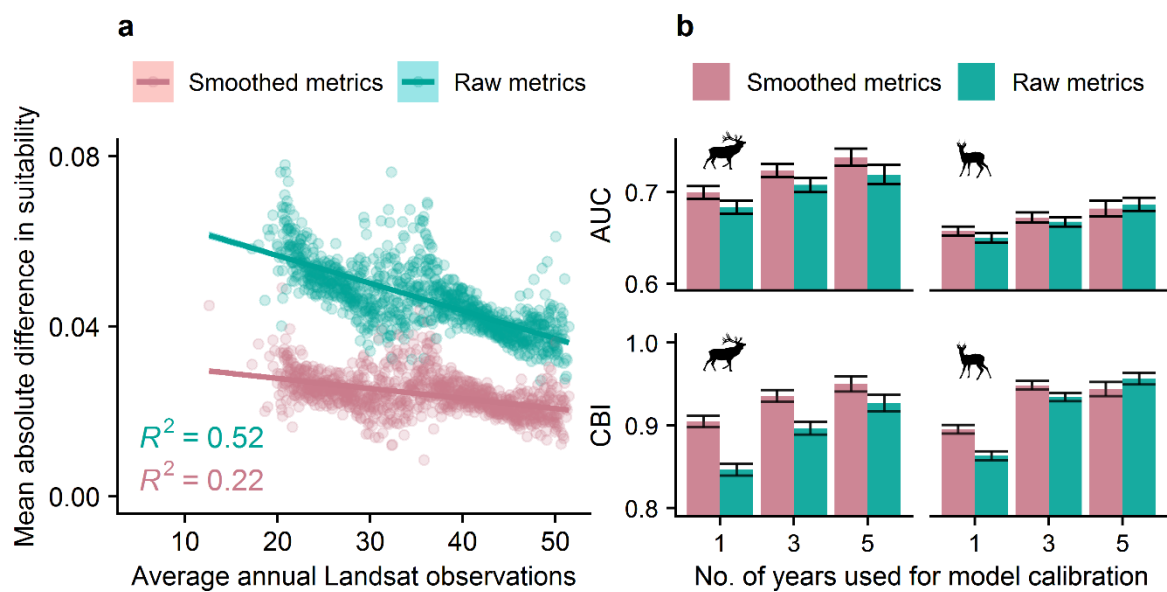
Figure III-3: Temporal consistency and transferability of Landsat-based habitat models. (A) Relationship between Landsat observation density and temporal consistency of habitat suitability maps. (B) Transferability of habitat models calibrated with deer data from one-, three- and five-year windows. Bars indicate average performance across cross-validation folds, error bars indicate standard error of the mean.

3.2 Habitat suitability changes after forest disturbances

Our habitat suitability maps revealed pronounced changes in deer habitat following forest disturbances (Figure III-4). Overall, the widespread forest disturbances in our study area led to improved habitat conditions for both deer species over our monitoring period (see Figure SI III-3 for a summary of habitat suitability changes across all forest areas). However, deer responses to forest disturbances varied between deer species, seasons, and disturbance types (Figure III-5). While red deer benefitted from forest disturbances throughout the year, roe deer showed a seasonally changing response to disturbances. Habitat suitability for red deer

initially increased steeply after disturbances but started to gradually decrease after a few years (peak of median winter and summer habitat suitability across all disturbance types after 4 years). For roe deer, disturbances also led to increases in summer habitat suitability (peaking after 5 years) but caused decreases in winter habitat suitability before recovering again after a few years (reaching a minimum after 3 years).
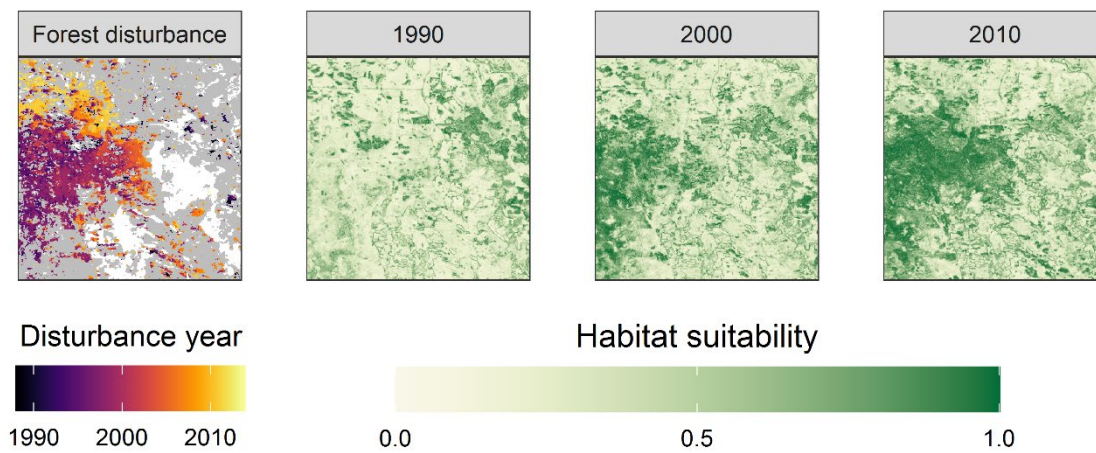
Figure III-4: Example of habitat time series obtained from Landsat-based habitat models. Plots show timing of forest disturbances (left) and changes in red deer summer habitat between 1990-2010 (three right plots) within a subset of our study region (100 km²). Grey indicates undisturbed forest, white non-forest areas.
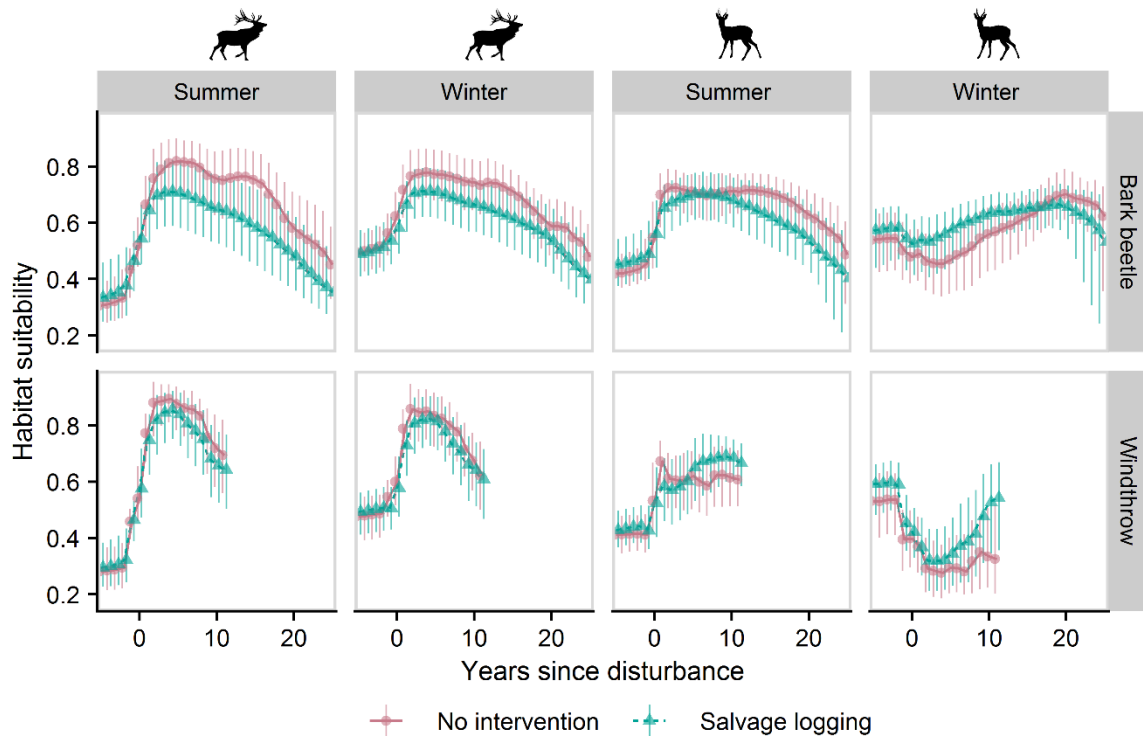
Figure III-5: Changes in habitat suitability following disturbances with no intervention and salvage logging at medium elevation in our study area (900-1100m; for low and high elevations see Figure SI III-4 and Figure SI III-5). Points indicate median; vertical lines show inter-quartile range.

Red and roe deer responded differently to bark beetle and windthrow disturbances. For the first few years after disturbance, habitat suitability for red deer was similar at bark beetle and windthrow disturbances (Figure III-5). Conversely, for roe deer, habitat suitability was higher after bark beetle than after windthrow disturbances, which caused substantial decreases in suitability for this species during winter (Figure III-5). The habitat suitability of disturbed sites also varied with the post-disturbance management strategy (i.e., salvage logging versus no intervention). Salvage logging, however, had much clearer effects on deer habitat suitability in bark beetle-affected areas than in windthrows. Salvage-logged bark beetle disturbances were generally less suitable for red deer and less suitable for roe deer during summer when they were recently disturbed (i.e., <10 years). Yet, seasonal habitat suitability for roe deer also improved due to salvage logging: During winter, recently disturbed sites were more suitable for roe deer after salvage logging than after no intervention.
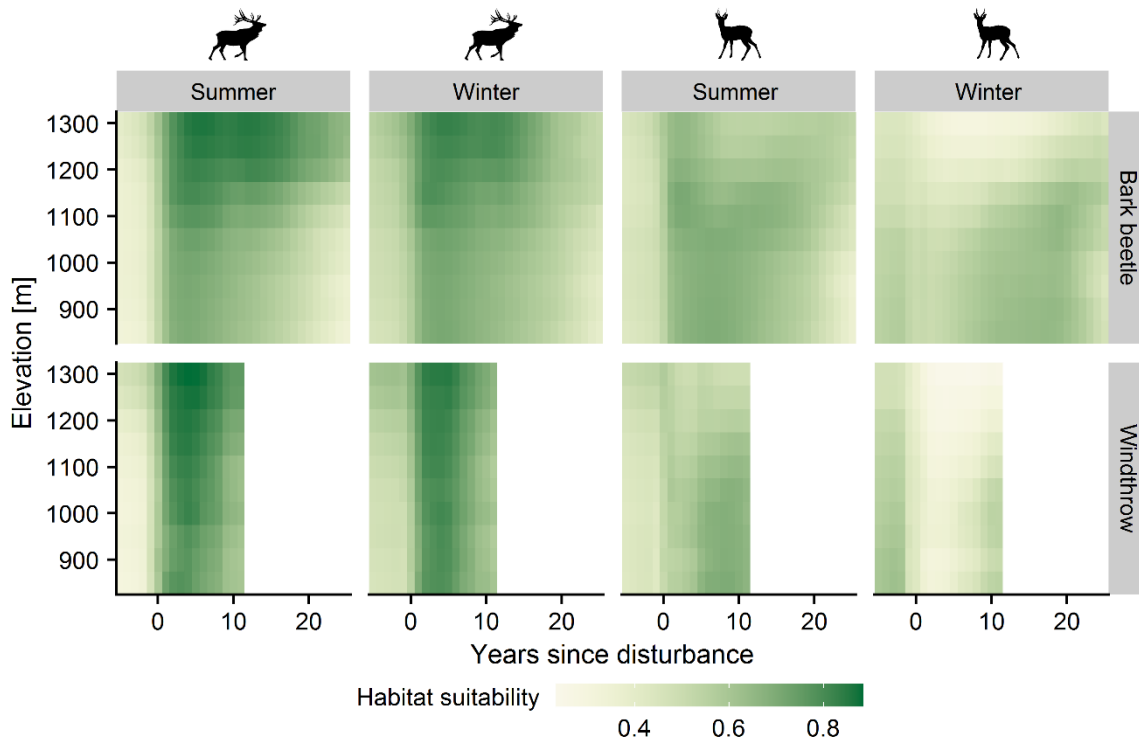
Figure III-6: Variation of habitat suitability changes along the elevation gradient in our study area, combining salvage-logged and non-intervention sites. Habitat suitability changes are summarized by calculating the average habitat suitability across elevation bins of 50m for each year on the x- axis.

With advancing regeneration over time, habitat suitability tended to return to pre-disturbance conditions. Changes in habitat suitability, however, were generally long-lasting. For instance, bark beetle disturbances altered red deer habitat suitability for a minimum of around 25 years (Figure III-5). While we could assess habitat suitability changes after windthrows for only 11 years post-disturbance (due to windthrows occurring only after 2006 in our study area), our habitat suitability time series indicate that the duration of disturbance impacts on deer habitat differ between windthrow and bark beetle disturbances. For example, after its initial increase, red deer habitat suitability declined faster at windthrows than at bark beetle disturbances (Figure III-5). Regarding differences in post-disturbance management, salvage-logged and non-intervention sites showed overall similar temporal patterns, but habitat suitability generally returned more quickly to pre-disturbance conditions at salvage-logged sites. Finally, we also observed clear effects of the elevation gradient in our study area on disturbance-related habitat suitability changes (Figure III-6). Habitat suitability for both deer species remained changed for longer periods with increasing elevation. Disturbed

sites were most suitable for red deer in the spruce-dominated forest zone (>1100m), but at lower elevations for roe deer.

4   Discussion

Wildlife responses to forest disturbance often remain poorly understood and spatially explicit information on disturbance-related habitat suitability dynamics is rarely available to wildlife management and conservation. Here we provide new insights into how natural disturbances and salvage logging affect habitat suitability for two of the most widespread European ungulates, and highlight the great, but currently underused potential of Landsat time series for monitoring forest disturbance impacts on wildlife habitat across long time periods. Specifically, our study yielded three main findings: First, red and roe deer showed distinct, and partly diverging, responses to forest disturbances, indicating that disturbance impacts on ungulate habitat vary between species with different foraging strategies. Second, disturbance impacts on deer habitat were generally long-lasting, but legacy effects varied along the elevation gradient in our study area. This highlights that variation in site conditions, and hence in forest recovery, can cause considerable heterogeneity in ungulate habitat quality after disturbances. Finally, the integration of species records in multi-temporal habitat models, as well as the temporal segmentation of the Landsat-based metrics, improved the transferability and stability of habitat models across time. This underlines the potential of our approach for consistent monitoring of habitat dynamics directly from satellite imagery.

4.1   Different responses by red and roe deer to forest disturbances

The seasonally changing response to forest disturbances by roe deer, with lower habitat suitability of forest openings during winter, can likely be explained by two factors: First, during spring and summer roe deer in the Bohemian Forest feed heavily on forbs and grasses, which are widespread at disturbed sites during the vegetation season, but increase forage intake through browsing during winter (Barančeková et al., 2010). Second, disturbed sites provide low levels of cover for roe deer during winter. Roe deer are sensitive to thermal exposure and snow accumulation, which inhibits forage accessibility and movement (Mysterud and Østbye, 1999). To escape harsh winter conditions, roe deer in the Bohemian Forest migrate to lower elevations and use more densely-vegetated habitats (Cagnacci et al., 2011; M. Ewald et al., 2014). Our results therefore underscore the importance of cover as a

habitat element for roe deer during winter, and corroborate findings that red deer use forest openings more intensively than roe deer (Kuijper et al., 2009).

Roe deer also showed more variable responses with regards to the disturbance type. Whereas habitat suitability for red deer increased similarly after windthrow and bark-beetle disturbances, windthrows were less suitable for roe deer, even decreasing habitat suitability during winter. A likely contributing factor are differences in deadwood structure, as windthrow gaps are dominated by lying deadwood, while bark beetle-affected stands initially remain as standing deadwood. Fallen logs impede both the movement and habitat visibility for deer, which can increase predation risk (Kuijper et al., 2013). Thus, roe deer might avoid windthrows to reduce predation risk by lynx, an ambush predator and the main predator of roe deer in the Bohemian Forest (Heurich et al., 2015). In addition, differences in foraging conditions are likely important: Windthrows tend to have lower tree regeneration densities than bark beetle-disturbed sites (Jonášová et al., 2010), and full-light conditions in windthrow gaps can lead to a reduction of forage quality (Moser et al., 2008). Our results therefore indicate that concentrate selectors, such as roe deer, show temporally and spatially variable responses to forest disturbances depending on the availability of high-quality forage, while less selective feeders, such as red deer, consistently benefit from the increase in forage quantities following disturbance.

Even though salvage logging of naturally disturbed forests is widely applied, our understanding of how it affects ungulate habitat quality remains largely incomplete (Hebblewhite et al., 2009). We found that salvage logging of bark beetle-affected stands reduced habitat suitability for red deer. This could be due to salvage logging removing ground vegetation that has survived under dead canopy, and thus reducing forage quantities (Jonášová and Prach, 2008). On the other hand, recently disturbed sites that were salvage-logged were more suitable as winter habitat for roe deer, potentially because the removal of deadwood allows for easier movements and lowers predation risk by lynx (Kuijper et al., 2013). In contrast to this finding, Hebblewhite et al., (2009) found that elk (*Cervus canadensis*) avoid postfire salvage-logged sites because of an increased predation risk by wolves. The use of clear-cut areas by ungulates could therefore also depend on the hunting strategy of their main predators (i.e., stalking vs. cursorial predators; Schmidt and Kuijper, 2015).

4.2 Evolution of deer habitat with forest recovery

Our approach using satellite time series allowed tracking disturbance impacts on deer habitat for up to 25 years, thus offering new insights into long-term effects of disturbances on ungulate habitat. Our results show that variations in site conditions, in our case along the elevation gradient of our study site, play an important role in modifying disturbance impacts on ungulate habitat. Disturbed sites in high-elevation, spruce-dominated forests in our study area regenerate more slowly, offer higher forage quantities (e.g., grasses and ferns), but lower forage quality (J. Ewald et al., 2014). Forest disturbances thereby amplified the variation of habitat quality along the elevation gradient for both species, thus likely contributing to higher concentrations of red and roe deer at high and low elevations, respectively (Heurich et al., 2015).

The length of disturbance impacts on deer habitat was also affected by salvage logging, which caused habitat suitability to return more quickly to pre-disturbance conditions. Forest recovery progresses faster and more homogeneously at salvage-logged than at non-intervention sites in our study area (Senf et al., 2019). This demonstrates that the removal of biological legacies through salvage logging can negatively affect ungulates by shortening the access to highly attractive foraging habitat. Overall, the temporal patterns of habitat suitability we observed here match well with expected changes in forage availability with stand development (Smolko et al., 2018). This indicates that forage availability likely remains the most important factor determining habitat quality for deer in forest openings even as disturbed sites are recovering (Dupke et al., 2017).

4.3 Potential and limitations of our approach

Methodologically, we demonstrated that linking habitat suitability models to time series of Landsat-based metrics offers an effective approach for monitoring wildlife habitat dynamics continuously across multiple decades. Despite the potential of Landsat imagery for characterizing wildlife habitat (Bellis et al., 2008; Lahoz-Monfort et al., 2010; Oeser et al., 2020), very few studies have leveraged the unique temporal depth of the Landsat archive for mapping long-term habitat dynamics (Clare et al., 2019; Kearney et al., 2019; Romero-Muñoz et al., 2019). Information on habitat dynamics is key for informing wildlife management and conservation, but creating consistent time series of habitat suitability maps from satellite-based variables poses challenges due to high noise levels in satellite time series (Tuanmu et al., 2011). Here, we showed that combining all available Landsat imagery to produce time series of spectral-temporal metrics and temporally segmenting these time series

with the LandTrendr algorithm allows for robust characterizations of habitat dynamics directly from Landsat imagery. Habitat suitability maps based on smoothed Landsat metrics were more consistent in time, showing less year-to-year variation in undisturbed forests, and were less affected by low levels of satellite data availability. Similarly, habitat models based on the smoothed metrics were more transferable in time. Because our approach relies solely on freely and globally available Landsat imagery, it is potentially widely applicable for informing wildlife management and conservation (Lahoz-Monfort et al., 2010).

We also found that integrating deer observations from multiple years in multi-temporal habitat models improved model transferability in time. In a recent review, Randin et al. (2020) emphasized the potential of multi-temporal habitat models calibrated using satellite time series. Yet, thus far, only few studies (e.g., Sieber et al., 2015) have made use of this potential. Multi-temporal calibration allows using more observations for model training, and further captures species' responses to changing habitat conditions over time (e.g., by characterizing deer habitat use at different stages of forest regeneration in our case; (Nogués-Bravo, 2009). Our model validation shows that this improves the transferability of Landsat-based habitat models, as previously shown for species distribution models calibrated with species data from different climate periods (Maiorano et al., 2013). As Landsat imagery is available retrospectively up until the 1970s, it offers unique possibilities to integrate species records for reconstructing habitat dynamics.

While our approach provides a cost-effective and transferable method for monitoring wildlife habitat dynamics, some limitations need to be mentioned. First, although integrating species records in multi-temporal habitat models offers important advantages, it also leads to species responses being averaged over time. Animals, however, can adjust habitat selection when the availability of resources is varying across space or time (through so-called functional responses; Mysterud and Ims, 1998). In our case, deer might change their selection for forest openings as more forest area was disturbed in our study area over time. Methods that allow incorporating functional responses in habitat models are an active field of research (Paton and Matthiopoulos, 2016), and could help improve the reliability of long-term habitat monitoring in the future. Second, by only using spectral information at the pixel level, our approach cannot capture effects related to the spatial configuration or size of disturbed patches, which can affect habitat suitability for deer (Massé and Côté, 2012). Finally, when relying on spectral-temporal metrics alone, additional sources of information are often needed to better understand the drivers of mapped habitat changes (such as the forest disturbance maps from a previous study we used here). Patterns in our time series of

habitat suitability maps generally matched very well with the independent forest disturbance maps, but sometimes indicated habitat suitability changes earlier than the disturbance date assigned in the disturbance maps. These temporal mismatches between both datasets are likely caused by the three year-moving windows we had to use for producing the Landsat-based metrics in order to deal with low satellite observation densities, as well as errors and inconsistencies in the satellite-based disturbance maps (Oeser et al., 2017). In areas with better Landsat data availability, metric time series with annual temporal resolutions can be produced without using moving window averages to improve to temporal accuracy of the habitat monitoring. In addition, information from independent forest disturbance maps can also be incorporated directly into habitat models to ensure the temporal consistency between disturbance maps and habitat time series (e.g., by using the number of years since disturbance as a model predictor; Kearney et al., 2019).

4.4   Implications for wildlife and forest management

Overall, widespread disturbances in our study area have substantially improved habitat conditions for red and roe deer (Figure SI III-3), also implying increases in the carrying capacity of the landscape for deer. The frequency of natural disturbances in European Forests has been increasing over the last decades (Senf et al., 2018), and likely will continue to increase as a consequence of global warming (Seidl et al., 2017). Thus, considering disturbance impacts on deer habitat will be increasingly important in the management of ungulate populations (e.g., when setting hunting quotas). Deer overabundance in many parts of Europe and North America already has considerable negative economic and ecological effects on forests (Côté et al., 2004). As disturbed sites provide attractive foraging habitat, they lead to a concentration of deer, as well as higher levels of browsing pressure in forest openings (Kuijper et al., 2009). More frequent disturbances thus have the potential to trigger an exacerbating feedback on forest structure: Deer densities could increase because of improved resource availability (Gaillard et al., 2003), which in turn increases browsing damages that impede forest regeneration (Tremblay et al., 2007). The relationship between more frequent forest disturbances and ungulate populations dynamics, however, remains poorly understood. Linking observed trends in ungulate populations to satellite-derived time series of habitat dynamics opens new possibilities to explore possible links across space and time.

Acknowledgements

Supplementary Information

Text SI III-1: Detailed description of satellite image processing.

We used all available Collection 1 Tier 1 surface reflectance images from the Landsat sensors 4 TM, 5 TM, 7 ETM+ and 8 OLI covering our study area and recorded between 1985 and 2018 available in the Google Earth Engine (Gorelick et al., 2017). The Tier 1 surface reflectance product contains atmospherically corrected data with the lowest geo-registration errors (Young et al., 2017). To account for different Landsat sensor specifications, we used the coefficients from Roy et al. (2016) to cross-calibrate Landsat 8 surface reflectance data to previous sensor specifications (i.e., Landsat 4, 5 and 7). We masked out all observations containing clouds, cloud shadows or snow using the respective flags in the quality assessment-band of the Landsat images. Then, for every image, we calculated the Tasseled Cap components brightness, greenness and wetness using the transformation coefficients for Landsat surface reflectance data provided in (Crist, 1985).

We calculated spectral-temporal metrics (i.e., statistical metrics calculated at the pixel level summarizing the intra-annual variability of spectral indices; Pflugmacher et al., 2019) for all three-year intervals in our monitoring period (i.e., for all years between 1986-2017). We used three-year moving windows to ensure a robust calculation of metrics despite relatively low levels of available cloud and snow-free Landsat observations at our study site, particularly during the 1980s and 1990s (Figure SI III-1). We derived a total of nine metrics by calculating three percentiles (the 10th, 50th, 90th percentile) for each tasseled cap index (brightness, greenness, and wetness). Then, we applied the LandTrendr segmentation algorithm (Kennedy et al., 2010) available in the Google Earth Engine (Kennedy et al., 2018) using the parameter settings in Table SI III-1. We provide a Google Earth Engine repository including all code used for processing the Landsat imagery under the following link (free-to-use upon registration):

https://code.earthengine.google.com/?accept_repo=users/julianoeser/Oeser_et_al_2020_Landsat_habitat_dynamics
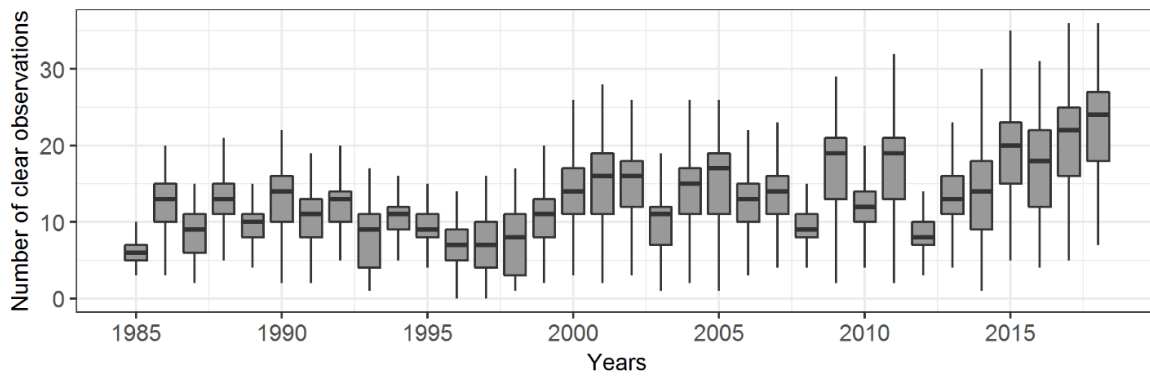
Figure SI III-1: Number of available cloud and snow-free Landsat observations for pixels covering our study area, for all years between 1985-2018.

Table SI III-1: Parameter settings used for LandTrendr algorithm. See Kennedy et al. (2010) for a full description of the parameter's functions.

Parameter	Used value
maxSegments	6
spikeThreshold (β)	0.9
vertexCountOvershoot	3
preventOneYearRecovery	False
recoveryThreshold	1
pvalThreshold	0.1
bestModelProportion	0.75
minObservationsNeeded	6
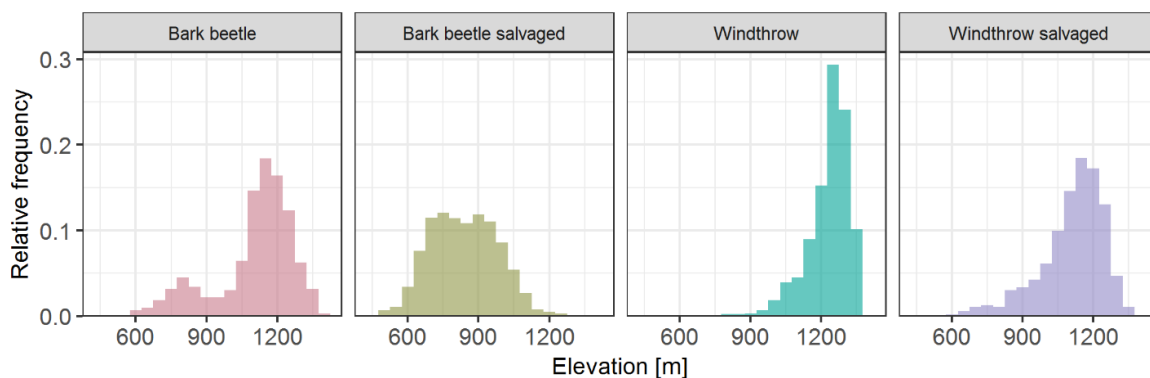
Figure SI III-2: Relative frequency of disturbance types at different elevations in our study area. Frequencies are calculated separately for each disturbance agent (i.e., summing to one in each plot panel).
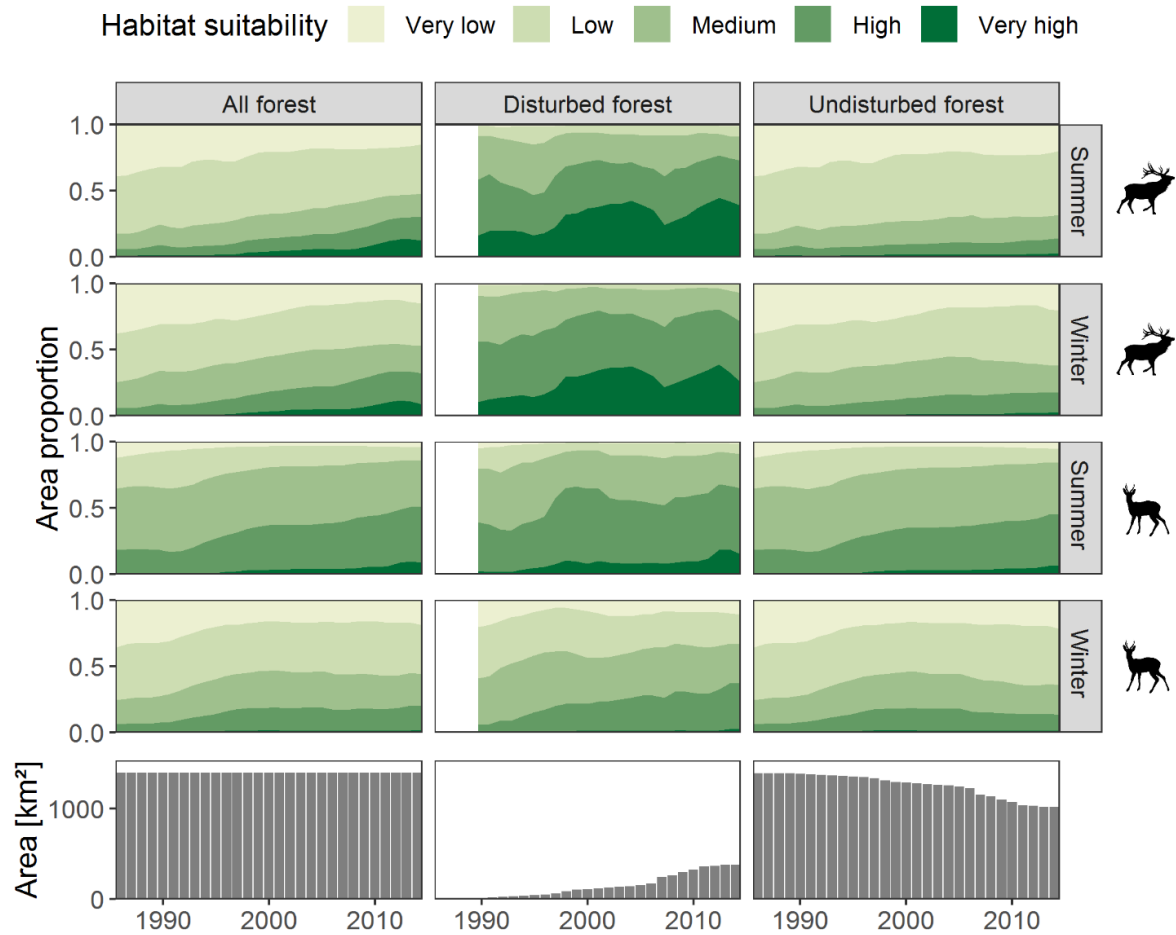
Figure SI III-3: Habitat suitability changes for red and roe deer between 1986-2014 (period covered by the disturbance maps) in forest areas. Habitat suitability classes represent binned habitat suitability from MaxEnt models (range: 0-1, bin width: 0.2). Top three rows show relative area proportion of habitat suitability bins in all forests (left column) and split up in disturbed and undisturbed forests (middle and right column). Suitability of disturbed forest before 1990 are not shown since very few pixels were identified as disturbed in this time period. Bottom row shows absolute area of each forest class across time.
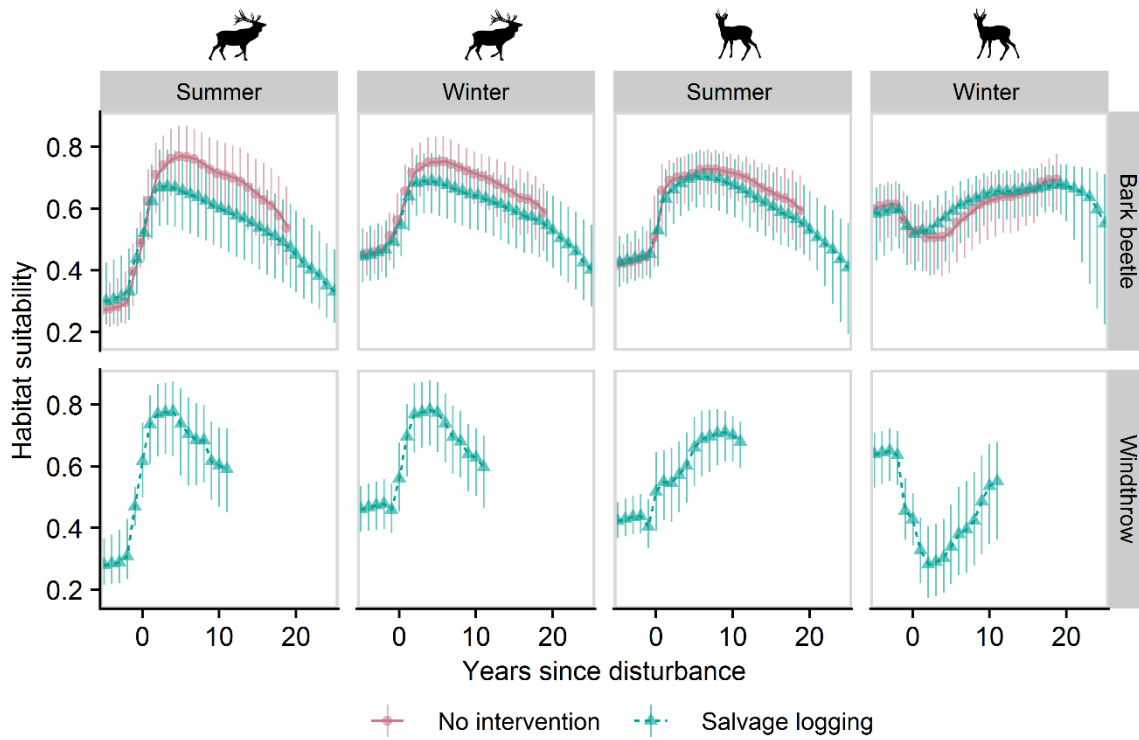
Figure SI III-4: Changes in habitat suitability after no intervention and salvage logging at low elevations (600-900m). Points indicate median; vertical lines show inter-quartile ranges. Unmanaged windthrows do not appear because they were limited to higher elevations in our study area.
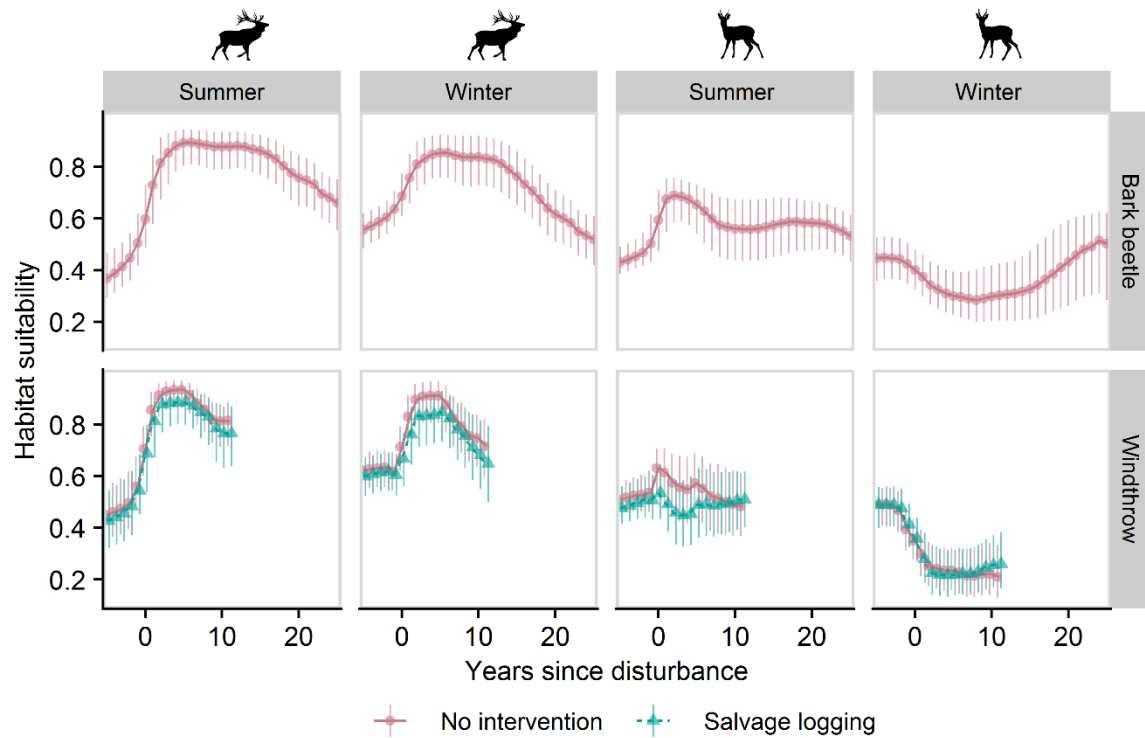
Figure SI III-5: Changes in habitat suitability after no intervention and salvage logging at high elevations (1200-1400m). Points indicate median; vertical lines show inter-quartile ranges. Salvage-logged bark beetle disturbances do not appear because they were limited to lower elevations in our study area.

Chapter IV:
Integrating large animal tracking datasets across multiple populations for mapping wildlife habitat at a continental scale

Submitted to Ecography

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Abstract

The increasing availability of animal tracking datasets collected across multiple wildlife populations provides novel opportunities to move beyond local habitat assessments and enable detailed habitat mapping at biogeographic scales. However, integrating wildlife datasets across multiple populations remains a major challenge, as species' varying responses to different environmental settings must be reconciled. Here, we assess approaches for continental-scale mapping of wildlife habitat using a large tracking dataset of Eurasian lynx (*Lynx lynx*; 450 individuals from 14 study sites). Specifically, we compared different approaches for incorporating non-stationarity in habitat models (i.e., regional variation in habitat selection), testing both global modeling approaches that combine datasets from all study sites into a single model as well as ensemble approaches combining multiple local, site-specific models, including a novel approach based on characterizing local model transferability in a meta-model. We found both global and local modeling approaches to perform best when non-stationarity in habitat selection due to environmental gradients was accounted for. Among non-stationary approaches, a global model including environmental variables at multiple spatial scales yielded the most transferable habitat predictions. Local habitat model transferability was well explained by environmental dissimilarity and the amount of tracking data. Although habitat suitability maps derived from different modeling approaches were overall similar (mean r = 0.90), spatial patterns of habitat patch maps differed considerably between local and global approaches, highlighting that the choice of modeling approach can impact conservation recommendations. Overall, our study demonstrates the considerable promise of integrating tracking datasets across multiple wildlife populations for creating more robust and spatially detailed habitat maps across large areas. Moreover, our analysis is the first fine-resolution, continental-wide assessment of lynx habitat across Europe, highlighting large areas of unoccupied but suitable habitat and providing an important basis for informing continental-scale conservation planning for this recovering large carnivore.

1   Introduction

Habitat suitability maps are important for informing ecological and biogeographical research, wildlife management and conservation planning (Guisan et al., 2013). Today, an increasing wealth of wildlife and environmental data provide new opportunities for assessing habitat suitability at higher detail and across larger extents than ever before (He et al., 2015; Oeser et al., 2020). Animal tracking technology provides a growing and powerful data source in this context (Kays et al., 2015). As tracking datasets collected across an increasing number of individuals and animal populations are integrated and harmonized, they become more robust sources of information for characterizing habitat suitability across large areas (Fraser et al., 2018). Yet, combining wildlife datasets sampled across wildlife populations and potentially large environmental gradients for mapping habitat is far from trivial. As wildlife datasets are often geographically restricted and unrepresentative of species' current or potential ranges, large-area habitat assessments typically require extensive model transfers, constituting a key challenge for habitat modeling (Sequeira et al., 2018; Yates et al., 2018). Moreover, differences in population density, species interactions or environmental conditions often cause habitat selection to vary across wildlife populations (Aarts et al., 2013; Avgar et al., 2020), such that varying local responses have to be reconciled when combining wildlife datasets for large-area habitat mapping.

Non-stationarity in habitat selection (i.e., the variation of a species' response to an environmental factor across space) forces a trade-off between specificity and generality when developing habitat models. Local, site-specific models typically capture local responses well, but often show limited transferability. Conversely, global models that pool datasets from several sites provide more general characterizations of habitat selection, but may fail to capture non-stationary responses, thus missing the nuance needed to make habitat predictions relevant locally (Bamford et al., 2009; Paton and Matthiopoulos, 2016). Both global and local modeling strategies, have been used for assessing wildlife habitat across large areas (DeCesare et al., 2012; Muhly et al., 2019; Scharf and Fernández, 2018), but have rarely been compared (Olson et al., 2021; Reisinger et al., 2021). How to best integrate wildlife datasets covering many populations and large environmental gradients for large-area habitat mapping therefore remains a largely unresolved question.

Non-stationary habitat selection is commonly ignored in habitat assessments (Paton and Matthiopoulos, 2016), yet some potential solutions for accounting for non-stationarity have been proposed. For example, in global modeling approaches non-stationary responses can be included via interaction effects, treating variation in habitat selection either as a function

of space (Hothorn et al., 2011) or of regional-scale environmental conditions (i.e. *habitat availability*; Matthiopoulos et al., 2011; Paton and Matthiopoulos, 2016). Habitat assessments based on combining the predictions of local models have sought to consider non-stationarity using model weights that reflect the potential applicability of models, for example based on the geographic distance or environmental dissimilarity between training and prediction regions (DeCesare et al., 2012). However, which factors determine model transferability is typically unknown *a priori*. A potentially powerful alternative therefore might be to directly model the transferability of local models and using the resulting meta-model to inform the weighting of model predictions across space (Gavish et al., 2018). Yet, such a meta-model approach has never been used for habitat assessments.

Large carnivores have long been focal taxa for conservation, due to their charisma, their declining populations in many parts of the world (Ceballos et al., 2005), their role as umbrella species (Sergio et al., 2006), and their key roles in ecosystems (Ripple et al., 2014). At the same time, large carnivore conservation is often particularly challenging since they are prone to interact and come into conflict with humans due to their large spatial needs and food requirements (Treves and Karanth, 2003), and as a result of historical persecution and habitat loss, often remain only in small and fragmented and populations (Cardillo et al., 2005). Together, this translates into a need for coordinated efforts in the conservation and management of large carnivore metapopulations at broad scales, often across national borders and jurisdictions (Trouwborst, 2015). Such efforts, in turn, require consistent habitat information across large areas, yet at sufficiently detailed spatial resolution to support conservation decision-making (Guisan et al., 2013).

Europe's large carnivores provide an interesting case for comparing different habitat modeling strategies. Many European large carnivores have historically been extirpated from much of their former ranges and today only occur in fragmented populations scattered across the continent. Recently, several species have re-expanded their range, mainly thanks to a better legal protection leading to reductions in wildlife persecution, reintroductions, recovering prey populations, as well as rural outmigration, farmland abandonment, and forest-cover increase (Chapron et al., 2014; Cimatti et al., 2021). This potentially allows for large-scale recoveries of these species but making use of these opportunities requires knowledge on the spatial distribution, size, and connectivity of suitable habitat patches in both unoccupied and occupied areas. Yet, while local habitat assessments for Europe's large carnivores are commonly done, consistent and detailed habitat information at a continental scale is lacking (Scharf and Fernández, 2018).

We here compare approaches for large-area habitat mapping based on cross-population animal tracking data using the Eurasian lynx (*Lynx lynx*; hereafter: lynx) as an example. Lynx have recently expanded their range, mainly through reintroductions as well as some recolonizations of nearby habitat patches (Linnell et al., 2009; Molinari-Jobin et al., 2010). This resulted in highly fragmented populations across Europe, making them susceptible to loss of genetic diversity and jeopardizing their long-term survival (Schmidt et al., 2011). Particularly due to the genetic isolation of many European lynx populations and limited success of natural recolonization through dispersal so far, better data on lynx habitat suitability across Europe is key to inform conservation actions aiming to create viable metapopulations (Hemmingmoore et al., 2020). For mapping lynx habitat across Europe, we use a large collection of telemetry data encompassing 450 lynx individuals tracked at 14 study sites in Europe, representing eight out of eleven extant European lynx populations (Kaczensky et al., 2021). Specifically, we compared global and local modeling strategies and tested different approaches for incorporating non-stationary habitat selection, including a novel approach for combining local habitat models through a meta-model. We addressed the following research questions:

1. How do global and local habitat modeling approaches compare in terms of predictive performance and resulting habitat maps?

2. Does considering non-stationarity in habitat selection improve the predictive performance of large-area habitat models?

3. Which factors determine the transferability of local habitat models?

2 Material and Methods

2.1 Study area and tracking data

We used GPS and VHF tracking datasets collected at 14 sites located in 13 different countries (Figure IV-1). Our dataset (450 animals, 448,038 locations before subsampling) was collected through the research network *EUROLYNX*, which provides a collaborative, bottom-up platform for bringing together datasets and expertise of lynx researchers across Europe (Heurich et al., 2021). Prior to all analyses, tracking datasets were harmonized through a standardized procedure of quality checks (Urbano et al., 2021; see Table SI IV-1 for a detailed overview).

We filtered the tracking datasets by first removing dispersing individuals, which often differ strongly in their habitat selection compared to resident animals (Hemmingmoore et al., 2020). Second, we standardized the sampling frequency of our tracking data to one observation per day and one per night, deriving sunrise and sunset times using the R-package *suncalc* (Thieurmel and Elmarhraoui, 2019). Finally, we balanced the sample sizes across individuals and study sites to avoid bias towards animals or study sites with more available data. Specifically, we removed individuals with fewer than 50 locations to ensure robust calculations of home ranges (Seaman et al., 1999) and limited the maximum number of locations to 500 per individual. Then, we randomly sampled up to 7,104 locations for each study site, corresponding to twice the number of locations of the study site with the fewest available observations. The resulting dataset used for training habitat models contained 92,077 unique locations from 450 lynx individuals. Our study area comprised entire Europe but excluded the Iberian Peninsula to avoid extrapolating habitat models into the potential range of the endangered Iberian lynx (*Lynx pardinus*).
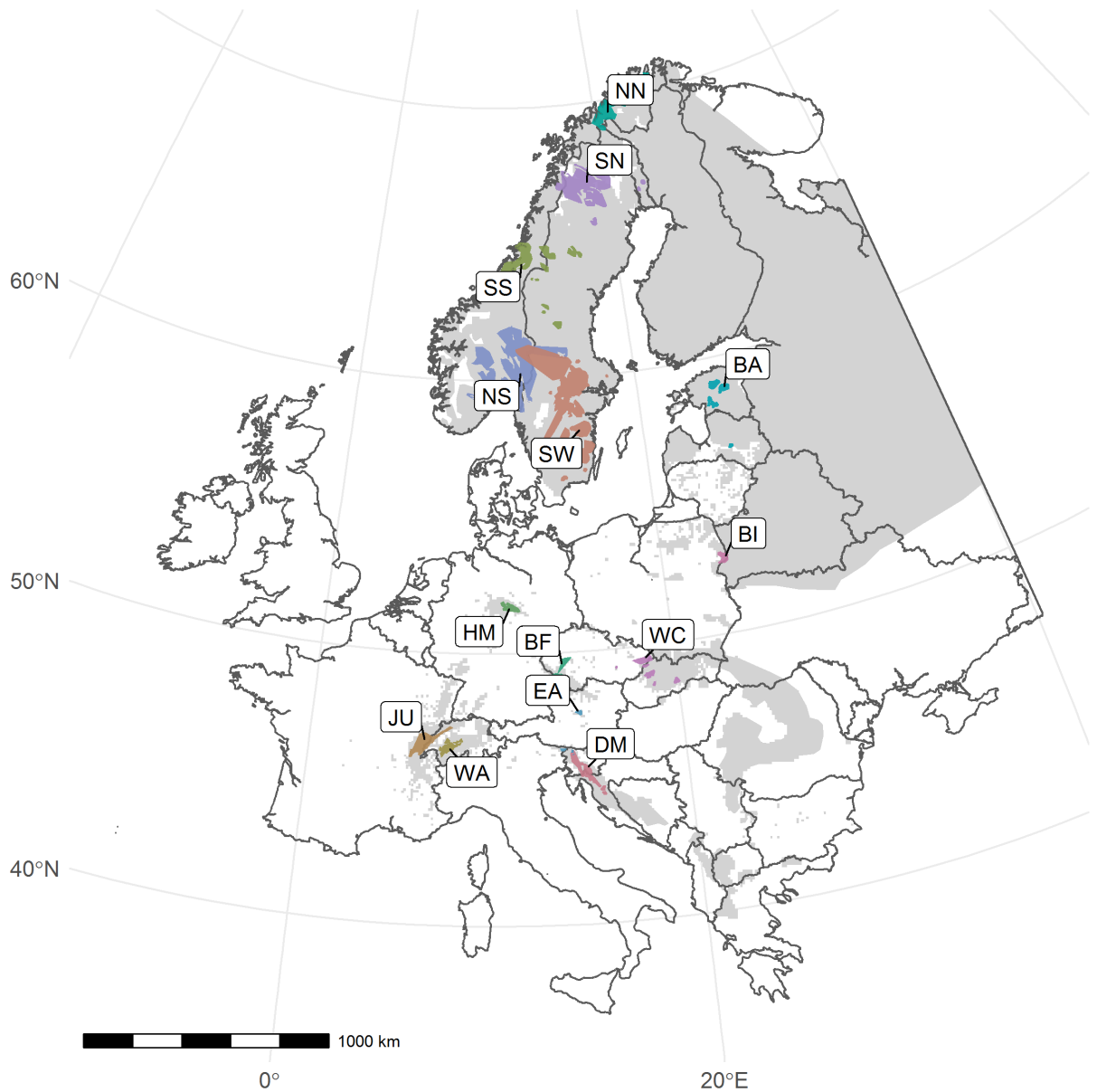
Figure IV-1: Overview of the study area and extent of the lynx tracking data used in this study. Colored polygons show areas covered by lynx home ranges. Abbreviations of the study site names: BA – Baltic, BF – Bohemian Forest, BI – Białowieża Forest, DM – Dinaric Mountains, EA – Eastern Alps, HM – Harz Mountains, JU – Jura Mountains, NN – Norway North, NS – Norway South, SN – Scandinavia North-Central, SS – Scandinavia South-Central, SW – Sweden South, WA – Western Alps, WC – Western Carpathians. Light grey areas indicate the current distribution of Eurasian lynx (Breitenmoser et al., 2015; Kaczensky et al., 2021).

2.2 Habitat suitability modeling

We collected 13 predictor variables for modeling lynx habitat suitability, which we selected based on previous studies on lynx habitat selection (Basille et al., 2009; Filla et al., 2017; Hemmingmoore et al., 2020). Variables included information on land-cover, topography,

human presence and modification of the landscape, as well as satellite-based metrics characterizing fine-scale habitat variability (Oeser et al., 2020; see Text SI IV-1 for a full overview of variables and details on their selection, data sources and processing). As a modeling algorithm, we used maximum entropy modeling (Maxent; Phillips et al., 2006), which is commonly regarded as one of the best-performing presence-only species distribution modeling algorithms (Valavi et al., 2021). We fitted Maxent models using linear, quadratic and hinge features, as well as product features in models requiring interaction effects (see below for details; Merow et al., 2013). For all fitted models, we tuned model regularization for all models based on cross-validation (Radosavljevic and Anderson, 2014; see Text SI IV-4).

We analyzed habitat selection of lynx at two hierarchical levels: selection of home ranges within the landscape (hereafter *landscape level*, also referred to as second-order selection; Johnson, 1980; Mayor et al., 2009), and within-home range selection (hereafter *home range level*, also referred to as third-order selection). We used a nested use/availability sample for training habitat models, which allows combining the outputs of models fitted at different levels of selection into a single, level-integrated prediction of habitat suitability (see Text SI IV-2 for details on our use/availability sampling design; DeCesare et al., 2012).

For landscape-level models, we used predictor variables at a scale corresponding to the median home range size of lynx across study sites (392 km²) in order to better reflect the scale of the habitat selection process (McGarigal et al., 2016; Remm et al., 2017). We applied a circular moving average (22km diameter) to rescale predictor variables. For home-range level models, we used variables at a fine scale of 100 m, the target resolution of our habitat suitability maps.

2.3   Comparison of modeling approaches

We compared a total of six modeling approaches: two strategies for model training (global and local) and, within each of them, two approaches for incorporating non-stationary habitat selection plus one stationary approach (Figure IV-2). First, we established baseline models assuming stationary habitat selection by using a simple global model (*global stationary*) and a simple average of local model predictions (*local stationary*). We contrasted these with approaches explicitly allowing for non-stationary responses. In global models, we let responses vary as a function of space (*global spatial*) or environmental settings (*global environment*). For combining local model predictions, we used weights based on the distance to training sites (i.e., inverse distance weighting, *local spatial*) and based on expected

performance scores derived from a meta-model (*local meta-model*; see below for details). An overview of all modeling approaches is given in Figure IV-2 and Table IV-1.
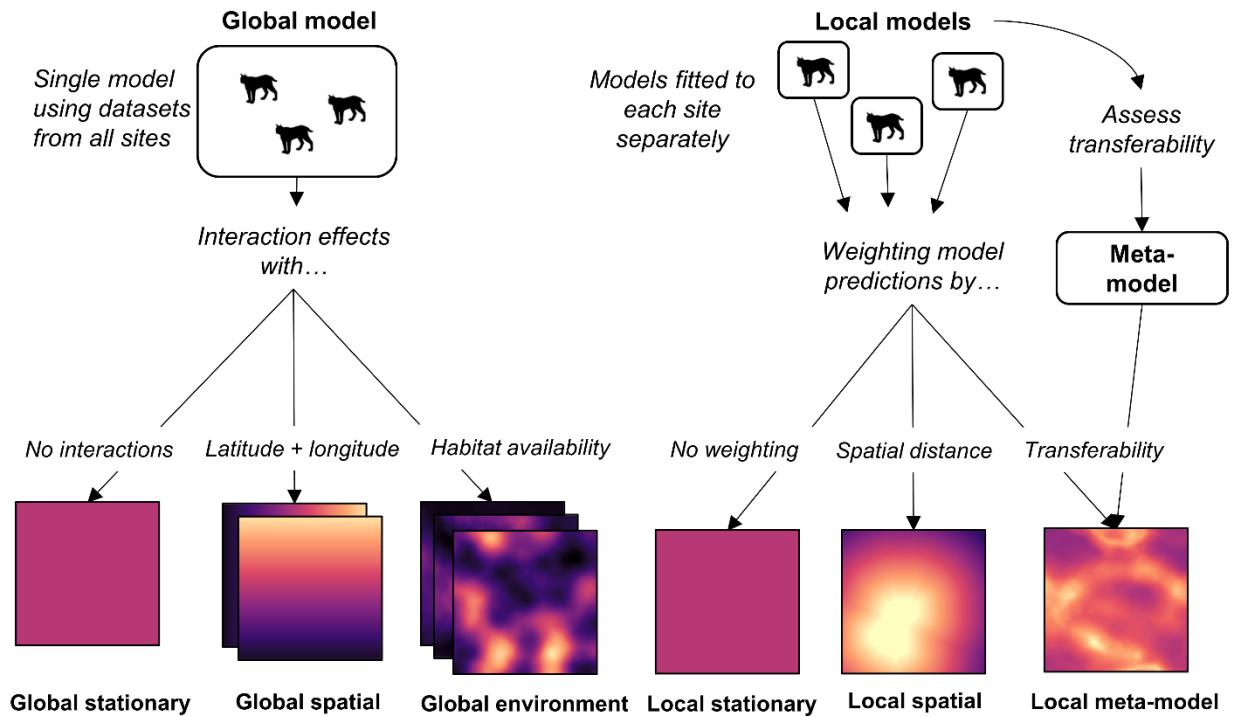
Figure IV-2: Schematic overview of the different modeling approaches. In the global modeling strategy, a single model is fitted using all data. In the local modeling strategy, site-specific models are fitted and then combined using an ensemble approach. In each strategy, we tested two different ways to incorporate non-stationarity and contrasted these with a stationary model (for more explanation see Table IV-1).

Table IV-1: Overview of the six modeling approaches.

Modeling approach	Training data	Non-stationary responses
Global stationary	Single model pooling all tracking datasets	None (no interaction effects)
Global spatial	Single model pooling all tracking datasets	Interaction effects with latitude and longitude
Global environment	Single model pooling all tracking datasets	Interaction effects with regional-scale variable means (i.e., habitat availability; Matthiopoulos et al., 2011)
Local stationary	Separate models for each study site	None (simple average of all site-specific models)
Local spatial	Separate models for each study site	Site-specific models weighted by distance to training sites (inverse distance-weighting)
Local meta-model	Separate models for each study site	Site-specific models weighted by their expected performance - Expected performance is estimated from a meta-model regressing model transferability against indicators of spatial and environmental distance

In global models, we implemented spatially-varying responses by including latitude and longitude as model predictions and enabling interaction effects (*global spatial*; Osborne et al., 2007). To let responses vary between different environmental settings and capture so-called functional responses in habitat selection (Mysterud and Ims, 1998; *global environment*), we added predictor variables at scales reflecting habitat availability and enabled interaction effects (an approach previously referred to as *generalized functional responses*; Paton and Matthiopoulos, 2016). In addition to the regular scales of predictor variables (22 km and 100 m at the landscape- and home range level, respectively), we added variables at scales reflecting the median extent of pseudo home ranges (80 km scale) and median home range sizes (22 km scale) at the landscape and home range level, respectively. We derived rescaled variables by applying circular moving averages.

In local modeling strategies, we weighted individual local models based on the distance from training sites (i.e., inverse distance weighting - *local spatial*). As a second approach to incorporate non-stationarity, we built a meta-model characterizing the transferability of local habitat models (*local meta-model*). We built this meta-model by regressing the performance of local models (1) when transferred to other study sites and (2) when predicted onto the training datasets against several variables potentially affecting model transferability. We assessed the predictive performance of individual local models using two performance metrics: the Area under the Curve (AUC) and the Continuous Boyce Index (CBI; Hirzel et al., 2006). We combined both metrics into a relative performance score by normalizing AUC

and CBI values on a $\in [0, 1]$ scale and calculating their mean (hereafter: *model performance*). As predictors of model performance, we used four types of variables (see Text SI IV-3 for an overview of all variables and details on model specification): (1) environmental dissimilarity (as indicated by differences in the mean values of habitat predictor variables at the training *vs.* testing site), (2) the spatial distance between sites, (3) the number of lynx individuals in our training datasets, indicating how representative a dataset is for population-level selection (Hebblewhite and Haydon, 2010), and (4) the extent of extrapolation in environmental space as measured by the ExDet tool (Mesgaran et al., 2014).

Based on the meta-models, we created maps of the estimated model performance of each local model across our study area, using predictor variables at scale sizes corresponding to the median extent of training datasets. Finally, we combined local model predictions as a weighted average based on their estimated performance at a given location. For both the *local spatial* and the *local meta-model* approach, we tested different transformations of model weights, using weights transformed to powers ranging between 1 to 20. Higher powers result in giving more weight to more similar or nearby sites and down-weighting more dissimilar or distant sites.

2.4 Comparison of habitat model outputs

We compared the six habitat modeling approaches (Figure IV-2, Table IV-1) in terms of their predictive performance as well as the resulting habitat suitability maps. We assessed the performance of all models using two types of cross-validation: (1) testing our models' ability to predict lynx occurrence within sites used for model training (internal validation), as well as (2) transferring models to sites not used for model training (external validation). For external validation, we left out one study site at a time, resulting in 14 cross-validation folds. For internal validation, we created five cross-validation folds based on lynx individuals (Roberts et al., 2017), using random samples of 70% of lynx individuals at all sites to train models, and testing models on the held-out 30% of individuals, one site at a time.

For each of our six modeling approaches, we predicted landscape-level and home-range-level habitat maps using the most recent layers of environmental predictors and multiplied both to create level-integrated habitat suitability maps (DeCesare et al., 2012). To compare among the maps from our six approaches, we calculated pairwise correlation scores between habitat suitability maps. Furthermore, we derived habitat patches by thresholding maps, using the 90%, 95% and 97.5% suitability value at lynx locations used for training habitat

models as low, medium, and high thresholds. To compare among habitat patch maps, we derived the percent overlap between patches for all pairs of modeling approaches.

3   Results

3.1   Performance of habitat modeling approaches

Global and local modeling approaches performed similarly overall (overall mean AUC/CBI scores of 0.67/0.73 and 0.68/0.77 for global and local approaches, respectively). Approaches accounting for non-stationarity in habitat selection improved model performance compared to stationary approaches, although overall variance in performance scores was low (mean improvement of AUC/CBI: 0.014/0.034; Figure IV-3). The *global environment* approach was the only approach that improved model transferability (i.e., external validation performance) compared to a stationary prediction at both levels of habitat selection (Figure IV-3). Local non-stationary approaches yielded considerable gains in internal model performance, particularly at the landscape level, but did not improve model transferability compared to a simple average of local models.

Tuning model regularization considerably improved the transferability of landscape-level models in both local and global approaches (mean external performance of tuned vs. untuned global/local models: 0.75/0.74 vs 0.61/0.61; Figure IV-3). For example, while the *global environment* approach was less transferable than a stationary model with default regularization settings, tuned models with stronger regularization (i.e., lower model complexity) were more transferable than a stationary prediction. Conversely, tuning had only a small effect on the performance of home-range-level models (see Text SI IV-4). Among local non-stationary approaches, the up-weighting of models from more similar study sites had a positive impact on the performance of the *local-meta-model* approach, while it did not improve performance in the *local spatial* approach (see Figure SI IV-4).

Among non-stationary approaches, those in which variation in habitat selection was captured as a function of environmental variation between sites (i.e., *global environment* and *local meta-model*) outperformed approaches that used only the spatial location of sites to consider non-stationarity (i.e., *global spatial* and *local spatial*), though differences in performance were relatively small (4% and 3% over stationary approaches, respectively). At the landscape level, the *local meta-model* had the highest average performance score across both validation

types (mean AUC/CBI: 0.75/0.83), while at the home range level the *global environment* approach performed best (mean AUC / CBI: 0.64/0.93).
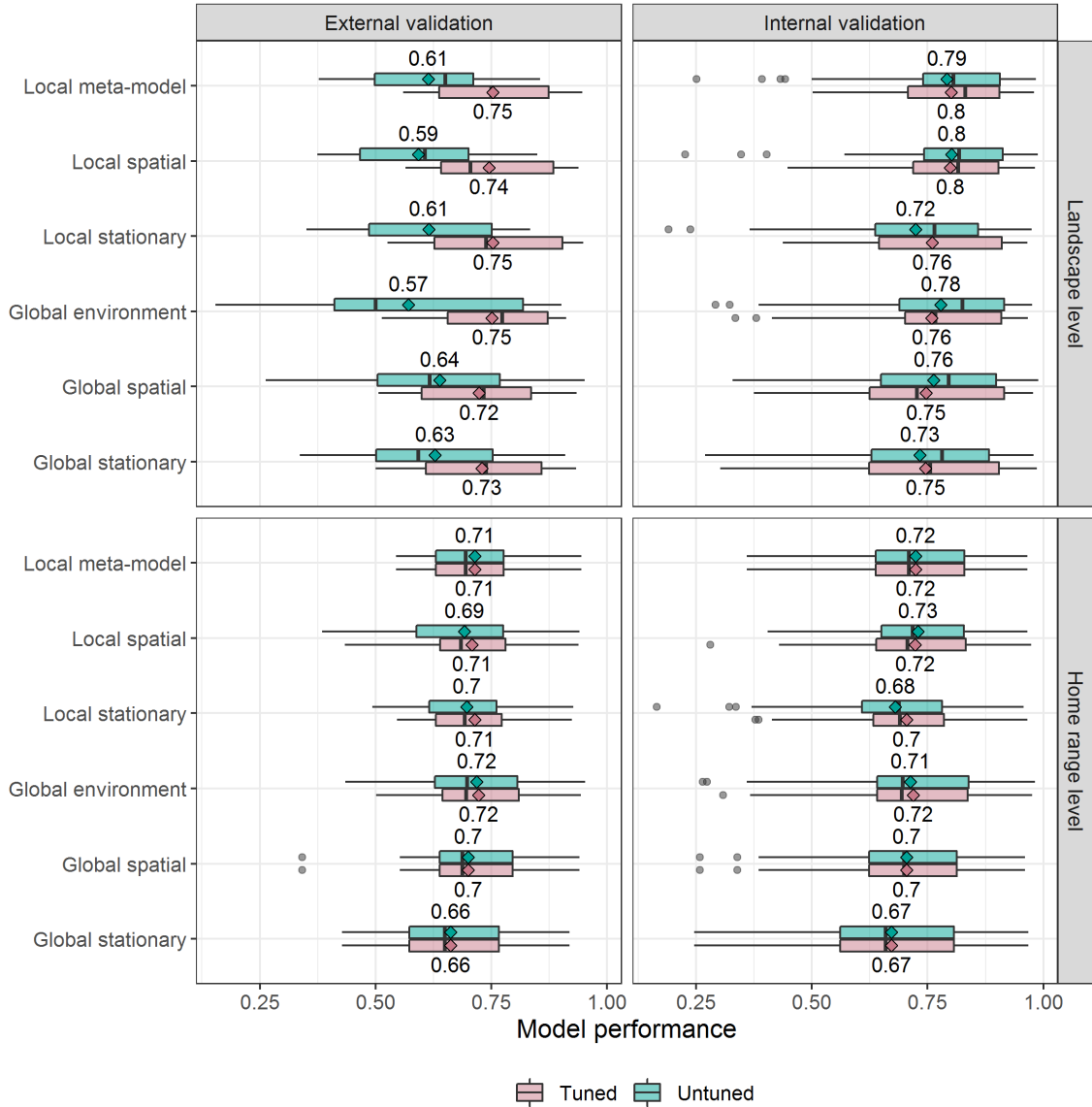
Figure IV-3: Model performance of the different habitat modeling approaches. We tested six modeling approaches (rows) at two levels of habitat selection (home range level and landscape level). For each modeling approach, we also compared tuned and untuned parameter settings (red vs. green boxplots). Model performance was calculated by combining two performance metrics (AUC and CBI) into a relative performance score (see Figure SI IV-5 and Figure SI IV-6 for plots of AUC / CBI values). Diamonds indicate mean model performance.

3.2   Comparison of habitat suitability maps

The correlation between suitability maps generated by the different modeling approaches was generally high (mean r= 0.90; Figure SI IV-7). Similarly, habitat patch maps derived by

classifying suitability maps showed fairly high levels of overlap (mean overlap of habitat patches: 0.82; Figure SI IV-8). Global and local approaches tended to result in more similar habitat predictions among another than when comparing local vs. global approaches (correlation within and between local / global approaches: 0.93 and 0.88; overlap: 0.87 and 0.82). Although suitability maps of the best-performing global and local approaches (i.e., *global environment* and *local meta-model*) showed similar spatial patterns, the local approach resulted in more contrasted predictions, with a clearer distinction of hot- and coldspots of suitability (Figure IV-4) The integration of habitat models fitted at different levels of habitat selection (i.e., landscape level and home range level) effectively filtered out habitat patches too small for the establishment of lynx home ranges (see Figure SI IV-9). Using different thresholds for deriving habitat patches from suitability maps had a large impact on the total habitat area identified, with habitat area varying on average by 36% between the low and high thresholds. Moreover, mapped suitable habitat areas varied between modeling approaches by 9-15% within thresholds.

Suitable habitat areas identified by the best-performing approaches aligned well with the current distribution of lynx in Europe (Figure IV-5). Both approaches predicted large areas of currently unoccupied lynx habitat across our study area (486,000 - 815,000 km² and 664,000 - 1,125,000 km² for the global and local approaches, respectively, depending on the threshold used). Our maps identified Scandinavia, northeastern Europe, the Carpathians, the Alps, and the Balkan Peninsula as important regions of lynx habitat in Europe and highlighted the lack of habitat connectivity between the Northern European and the Carpathian / Central-European lynx populations. The *local meta-model* approach identified considerably more suitable lynx habitat in Southern and Western Europe, whereas the *global environment* approach resulted in more suitable habitat area in northeastern Europe (Figure IV-5). Despite these differences, most identified habitat areas overlapped between approaches (78% for the medium threshold).
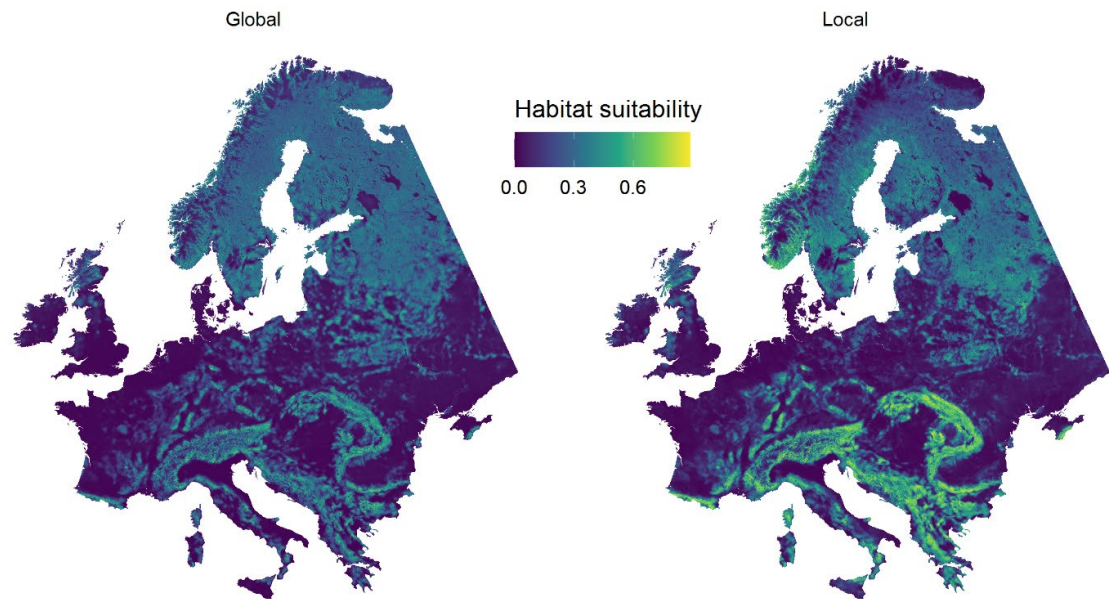
Figure IV-4: Habitat suitability maps of the best-performing global and local modeling approaches. Left: Global environment approach. Right: Local meta-model approach.
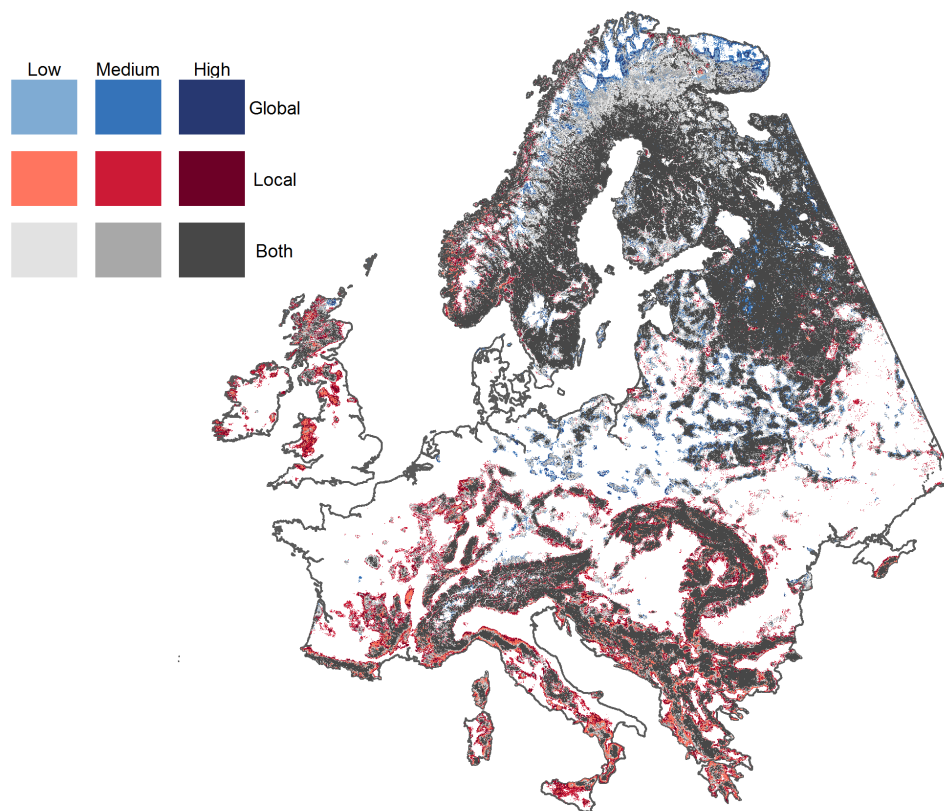
Figure IV-5: Suitable habitat areas derived by thresholding habitat suitability maps of the best-performing global and local approaches. Color tints correspond to different thresholds used for classifying habitat (low, medium, high).

3.3 Transferability of local habitat models

On average, local habitat models trained on lynx tracking data from single sites showed low transferability (mean AUC/CBI of 0.68/0.49 and 0.60/0.84 at the landscape and home range level, respectively). In contrast to global models, projecting local models across our study area required extensive extrapolation in environmental space (see Figure SI IV-10, Figure SI IV-11, and Figure SI IV-12). Model transferability was predicted relatively well by our meta-models, with models explaining 50% and 61% of the observed variance in performance scores at the landscape and home range levels, respectively. At the landscape level, the difference in the accessibility of study sites (i.e., travel time to cities) as well as two indicators of environmental dissimilarity (i.e., the average difference in mean standardized predictor variable values and the frequency of univariate extrapolation) were most important for predicting transferability, while at the home range level, the number of lynx individuals and the difference in ruggedness were the most important determinants of transferability (Figure SI IV-13).

4 Discussion

As animal tracking is entering the big data era (Kays et al., 2015), the growing availability of tracking datasets provides new opportunities to assess habitat consistently and at high resolution across large geographic extents. A key challenge in this context is how to best integrate tracking datasets across wildlife populations and environmental gradients, while appropriately accounting for local variation in habitat selection (Paton and Matthiopoulos, 2016). Here, we systematically assessed different approaches potentially suitable for addressing this challenge, yielding four key insights, which we discuss further in the below: First, predictive performance was best for approaches that capture response variation across environmental gradients, highlighting the importance of considering non-stationary habitat selection in large-area habitat mapping. Second, while both global approaches that pool datasets and local approaches that combine site-specific models map habitat suitability robustly, we found considerable differences in the extent and spatial patterns of identified habitat patches, indicating that the choice of modeling approach can impact potential conservation recommendations. Third, measures of environmental dissimilarity and tracking data quantity allowed predicting the transferability of local habitat models to other sites and our meta-model approach for weighting site-specific habitat models had the highest average performance of all local approaches. Yet, weighting local models did not improve model

transferability compared to a stationary prediction, highlighting limitations of using local modeling approaches for predicting habitat in unobserved regions. Finally, we here provide the first fine-resolution habitat assessment of European lynx habitat across Europe, highlighting vast areas of currently unoccupied habitat and therefore considerable potential for continued range expansions.

Incorporating non-stationary habitat selection in habitat models outperformed stationary approaches in our comparison. Among non-stationary approaches, those that characterized variation as a function of environmental gradients (i.e., *global environment* and *local meta-model*) performed better than approaches in which selection varied only as a function of space. Variation in environmental conditions more closely reflects the ecological mechanisms causing animals to adjust their habitat selection (Aarts et al., 2013), whereas spatial proximity alone is often a poor proxy of model transferability (Yates et al., 2018). Among non-stationary approaches, the *global environment* approach was the only one that consistently improved model performance (i.e., both in training regions and when transferring models to unobserved regions). Thus, our results corroborate that considering interactions among environmental predictors across spatial scales can effectively capture variation in habitat selection (previously referred to as *generalized functional responses*; Matthiopoulos et al., 2011). We also found that tuning model regularization was critical for ensuring good model transferability at the landscape level, in line with findings highlighting the importance of regularization for avoiding overfitting in complex model setups (Radosavljevic and Anderson, 2014).

Our study is the first to use a spatial meta-model characterizing model transferability to combine local habitat models for large-area habitat mapping. Previously, Gavish et al. (2018) highlighted the potential of such a meta-model approach in the context of land-cover classification. While our meta-models were able to predict model transferability well (explaining around 50-60% of the observed variance in performance), the weighting of local habitat models based on the meta-model did not improve model transferability. Translating estimated model weights into performance gains can be difficult in ensemble approaches, for example due to uncertainty in estimated weights (Dormann et al., 2018). Despite increasing awareness of the importance of regional variation in habitat selection, few studies have so far considered this variation when combining local habitat models (but see Reisinger et al., 2021). Nevertheless, the meta-model approach performed best among local approaches and offers a widely applicable, yet largely unexplored framework for integrating local habitat

models, providing a promising avenue for future research into approaches trying to overcome the trade-off between regional specificity and model transferability.

Overall, the best-performing local and global approaches achieved similar predictive performance. We therefore suggest that deciding between global or local modeling approaches should depend on the goal of the habitat assessment. Local approaches typically provide better calibrated predictions in regions close to or environmentally similar to training regions, whereas global approaches are more robust when the goal is to extrapolate in geographic or environmental space (Paton and Matthiopoulos, 2016). In fact, extrapolation in the environmental space (i.e., prediction outside of variable ranges covered by the training dataset or to novel variable combinations) is a main limitation when applying local habitat models across large areas (Mesgaran et al., 2014). This was also apparent in our models, with considerable extrapolation in our local, but not global models. Thus, the *global environment* approach likely offers the most robust prediction of lynx habitat for the entire European continent.

The habitat suitability maps from different modeling approaches were overall similar, as indicated by high map correlations, yet differences in the extent and spatial patterns of habitat patches became apparent when applying thresholds to the suitability maps. Discrete habitat maps are often needed for conservation planning and wildlife management (e.g., to identify corridors between core patches, to identify potential reintroduction sites, or to assess potential carrying capacities). In line with prior work, we observed a large impact of the selection of thresholds on mapped habitat extent (Norris, 2014). Additionally, we here show that the choice of modeling approach used for integrating wildlife data across populations can significantly affect mapping results. In our case, mapped potential habitat areas differed by ~15% between the best-performing local and global approaches, with marked differences in some regions. Together, this highlights the need to critically evaluate the impact of modeling choices on habitat mapping results and potential conservation recommendations (Muscatello et al., 2021). Similar to ensembles of modeling algorithms (Araújo and New, 2007), combining the results of multiple modeling approaches into consensus maps, as we did here, allows delineating areas most robustly identified as suitable habitats, thus helping to reduce mapping uncertainty.

While we used tracking data from a single species, a growing body of research suggests functional responses in habitat selection (i.e., variation of selection with environmental conditions) to be practically ubiquitous among large mammals (Godvik et al., 2009;

Herfindal et al., 2009; Holbrook et al., 2019). Thus, accounting for non-stationary habitat selection in large-area habitat assessments is likely important in the case of many other species as well. However, it should be mentioned that other factors we did not explicitly address in our approaches can also cause variation in habitat selection between wildlife populations. For example, differences in density, interactions with other species or genetic variation have all been linked to variation in habitat selection (Avgar et al., 2020; Fletcher, 2007). How to account for such sources of variation is an active field of research (Elith et al., 2006; Smith et al., 2019), but could be integrated with approaches capturing environmentally-related variation (Tikhonov et al., 2017). Furthermore, in addition to variation at the population level, there is often considerable variation in habitat selection among individuals (Fieberg et al., 2010). In our analyses, the number of individuals available for training local models was an important factor influencing model transferability at the home range level, highlighting the importance of tracking many animals for describing population-level habitat selection (Hebblewhite and Haydon, 2010). While we balanced sample sizes between individuals and study sites to avoid biasing models, mixed-effects models offer an alternative powerful statistical approach to account for individual-level variation inherent in tracking datasets (Muff et al., 2020). However, their considerable computational cost for large sample sizes and numerous random effects (i.e., including random slopes) currently still limit their application for very large datasets like the one we used here.

Our maps provide the most comprehensive and detailed assessment of potential Eurasian lynx habitat in Europe so far, highlighting large areas of suitable, but currently unoccupied habitat (corresponding to areas the size of 18-42% of the current lynx range in the study region). Despite the availability of suitable habitat surrounding extant lynx populations, the success of recolonization through natural dispersal has been limited in Europe (Linnell et al., 2009). Several studies have shown the importance of movement barriers, traffic mortality, and poaching in limiting the expansion of the lynx populations (Arlettaz et al., 2021; Heurich et al., 2018; Port et al., 2021). To improve connectivity and to counteract the decrease of genetic diversity, particularly for the small and fragmented Central-European lynx populations (Bull et al., 2016; Mueller et al., 2020) the establishment and protection of transboundary migration corridors, as well as the creation of stepping-stone populations through reintroductions can play important roles (Bonn Lynx Expert Group, 2021). Evaluating the human acceptance of lynx in regions providing suitable habitat would be an additional important requirement for implementing such conservation strategies (Behr et al.,

2017; Drouilly and O'Riain, 2021). Bearing these constraints in mind, our habitat suitability maps can provide an important basis for identifying candidate sites for potential reintroductions and migration corridors, thus supporting lynx conservation and management at a continental level.

More generally, our study highlights the considerable potential of integrating animal tracking data across populations for habitat assessments. Large-area habitat maps are crucial for informing the transboundary conservation of wide-ranging species, such as large carnivores, yet consistent large-area habitat maps providing levels of spatial detail required for guiding conservation and management decisions are typically lacking. Animal tracking has become a key instrument for investigating animal space use and behavior (Cagnacci et al., 2010; Kays et al., 2015), yet the considerable potential of tracking data for habitat assessments often remains untapped. Our results highlight that the integration of tracking data across many animal populations through curated and openly accessible databases can provide for a step change in our ability to map wildlife habitat consistently, robustly, at high resolution, and across large geographic extents (Kranstauber et al., 2011; Urbano et al., 2021). Importantly, as we show here, large-area mapping does not have to come at the cost of losing regional context, when local variations in habitat selection across gradients of human modification, climate, or landscape composition are taken into account. A new generation of habitat models harnessing the enormous potential of the emerging big data in animal tracking and remote sensing will increasingly allow us to overcome the traditional trade-offs between local, fine-scale habitat assessments and broad-scale, biogeographical analyses.

Supplementary Information

Table SI IV-1: Overview of tracking datasets. Number of tracking locations correspond to the full datasets before subsampling.

Study site (countries)	Number of used individuals (GPS / VHF)	Share of male / female observations	Monitoring period	Number of tracking locations
Baltic	14 (13/1)	0.78/0.22	2004 - 2016	22,182
Białowieża Forest	30 (4/27)	0.58/0.42	1991 - 2012	13,509
Bohemian Forest	19 (10/12)	0.58/0.42	1997 - 2013	17,519
Dinaric Mountains	21 (21/0)	0.64/0.36	2007 - 2021	16,610
Eastern Alps	10 (10/0)	0.42/0.58	2011 - 2021	7,122
Harz Mountains	9 (7/2)	0.58/0.42	2009 - 2019	6,484
Jura Mountains	30 (0/30)	0.37/0.63	1988 - 1999	13,365
Norway North	22 (22/0)	0.32/0.68	2007 - 2014	67,466
Norway South	85 (33/53)	0.53/0.47	1995 - 2015	47,621
Scandinavia North-Central	45 (29/32)	0.28/0.72	1993 - 2017	106,176
Scandinavia South-Central	17 (17/0)	0.35/0.65	2003 - 2016	22,499
Sweden South	83 (36/49)	0.46/0.54	1996 - 2017	39,091
Western Alps	48 (18/31)	0.49/0.51	1997 - 2018	51,857
Western Carpathians	17 (17/0)	0.88/0.12	2011 - 2021	26,537
TOTAL	450	0.5/0.5	1988 - 2021	458,038

Text SI IV-1: Selection and processing of predictor variables

We used previous studies characterizing lynx habitat selection to identify potential predictor variables for our habitat models (Basille et al., 2009; Filla et al., 2017; Hemmingmoore et al., 2020) ; Table IV-1 in main text), collecting a total of 13 different environmental predictors (Table SI IV-2).Throughout most of their range, lynx depend heavily on forests (Schadt et al., 2002), and we therefore included forest-cover fraction derived from a recent high-resolution land-cover product (Buchhorn et al., 2020). Like forest cover, mountain ridges, terrain ruggedness and steepness have frequently been identified as a key habitat features for lynx, as more rugged terrain offers resting habitats during the day and possibilities to avoid human disturbance (Bouyer et al., 2015b; Filla et al., 2017; Hočevar et al., 2021). We used the terrain ruggedness index available through Geomorpho90, a suite of global high-resolution geomorphometry variables (Amatulli et al., 2018). To snow cover,

which affects habitat use of lynx and their main prey species (Nilsen et al., 2009), we used snow-cover data from the MODIS snow cover product (Hall et al., 2002) available in the Google Earth Engine (Gorelick et al., 2017). We generated a map of snow-cover frequency across our study area, calculating the long-term average snow-cover fraction from all available images between 2000-2020.

In addition to these environmental factors, human presence and disturbance are important determinants of habitat suitability for lynx (Basille et al., 2009; Krofel et al., 2017; Ripari et al., 2022). To characterize the presence of human pressures in the landscape, we included four predictors: road density (Meijer et al., 2018), the travel time to cities ('accessibility'; Weiss et al., 2018), the human modification index (Kennedy et al., 2019), combining 13 anthropogenic stressors to quantify the degree of land modification, and the forest landscape integrity index (Grantham et al., 2020), providing a measure of the modification and connectivity of forest areas.

In addition, we used Landsat-based spectral-temporal metrics as indicators of fine-scale habitat variability. In a previous study, these satellite-based metrics showed considerable potential for characterizing wildlife species' habitat, including lynx (Oeser et al., 2020). We used the Google Earth Engine (Gorelick et al., 2017) to calculate spectral-temporal metrics based on all cloud-free observations recorded by the satellite sensors 4 TM, 5 TM, 7 ETM+, and 8 OLI between 1988 and 2020. For each Landsat image, we derived Tasseled Cap indices brightness, greenness, and wetness (Crist, 1985), resulting in seasonal profiles of index values per pixel and year (Pasquarella et al., 2016). We then summarized intra-annual variation of all indices by calculating the median as an indicator of average conditions, as well as the difference between the 80th and 20th percentile as an indicator of seasonality (resulting in a total of six metrics). To ensure the robustness of the spectral-temporal metrics even in areas with low densities of Landsat observations (Oeser et al., 2021), we calculated them using five-year windows centered on the years 1990, 1995, 2000, 2005, 2010 and 2015 (e.g., using all images from 1998-2002 for calculating metrics for the year 2000).

Table SI IV-2: Overview of predictor variables used for modeling lynx habitat suitability.

Variable category	Variables	Native spatial resolution	Available time steps	Data source	Reference
Forest	Forest cover fraction	100m	2015	Copernicus Land cover	(Buchhorn et al., 2020)
Topography	Ruggedness	90m	-	Geomorpho 90	(Amatulli et al., 2018)
Human presence and modification	Travel time to cities	~1km	2015	Multiple	(Weiss et al., 2018)
	Road density	~8km	2018	GRIP global roads database	(Meijer et al., 2018)
	Forest landscape integrity index	300m	2019	Multiple	(Grantham et al., 2020)
	Human modification index	1km	2016	Multiple	(Kennedy et al., 2019)
Climate	Snow cover	500m	2000-2020 (long-term average)	MODIS satellite imagery	(Hall et al., 2002)
Fine-scale vegetation and habitat structure	Six spectral temporal metrics (Greenness average, Brightness average, Wetness average, Greenness variability, Brightness variability, Wetness variability)	30m	1990, 1995, 2000, 2005, 2010, 2015	Landsat satellite imagery	(Oeser et al., 2020)

Text SI IV-2: Use/availability sampling design

To sample habitat use/availability, we derived home ranges for each lynx individual by calculating 95% minimum convex polygons (MCPs). We chose 95% MCPs since our goal was to define approximate home ranges at the landscape level while creating a comprehensive sample of available habitats at the home range level (Fattebert et al., 2018; Holbrook et al., 2017a). To characterize home range use at the landscape level, we sampled as many random points within the home ranges of each lynx individual as available tracking locations. To sample habitat availability, we created pseudo home ranges by shifting the centroid of lynx home ranges (Holbrook et al., 2017a). We created 100 pseudo home ranges per individual and shifted home ranges in random XY-directions 1-80 km away from the original centroid, representing likely dispersal distances (Samelius et al., 2012; Zimmermann

et al., 2005). At the home range level, we used the tracking locations as used points and sampled available locations inside home ranges of lynx individuals.

To determine the background sample size for Maxent coefficients to be stable (Northrup et al., 2013; Warton and Shepherd, 2010), we built models using lynx tracking observations from all study sites, gradually increasing background sample size from ratios of 1:1 to 1:15. We observed fairly stable coefficient estimates (lambda values; Elith et al., 2011) beyond 11 background samples per presence observation (Figure SI IV-1), indicating that this sampling ratio was sufficient for building habitat models.
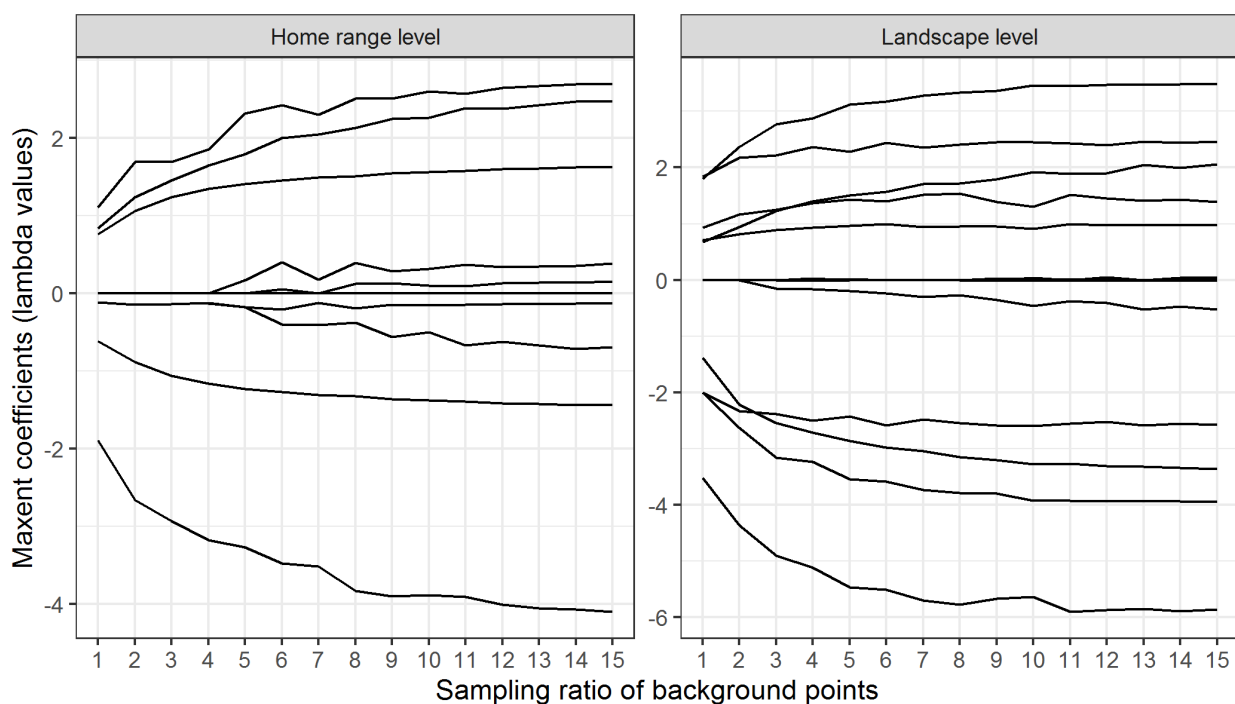
Figure SI IV-1: Change of Maxent coefficients (lambda values) for linear and quadratic features with increasing size of the background sample. Each line represents one variable used in the model.

Text SI IV-3: Meta-models for characterizing local habitat model transferability

We used boosted beta regression for modeling performance scores (R packages *mboost* and *betaboost*; Schmid et al., 2013), choosing the number of boosting iterations based on cross-validation. To ensure realistic response curves, we used monotonic splines (Hofner et al., 2016), meaning that modeled performance scores could only decrease with greater spatial or environmental distance. In addition, we added random intercepts for each testing site, as in presence-only models, absolute AUC values may vary between study sites due to different levels of species prevalence (Yackulic et al., 2013).

Table SI IV-3: Overview of predictor variables used in the meta-models.

Variable category	Variables
Environmental dissimilarity	Difference between mean values for each habitat predictor variable (N = 13) at training vs. testing site
	Average difference between mean predictor values after standardizing variables
Spatial distance	Spatial distance (km) between training and testing sites
Data quantity	Number of lynx individuals available for model training
Extrapolation frequency	Frequency of univariate extrapolation (type I novelty; Mesgaran et al., 2014)
	Frequency of combinatorial extrapolation (type II novelty; Mesgaran et al., 2014)

Text SI IV-4: Tuning of model regularization

We evaluated Maxent models fitted with different levels of model regularization (β multiplier values of 1, 4, 8, 16, 32, and 64) using cross-validation (see 2.4 in main text). We selected regularization values that best balanced internal and external performance (i.e., performance when predicting on known sites used for model training and performance when predicting on held-out sites not used during model training). To calculate performance scores, we combined the AUC and CBI metrics into an integrated relative performance score by scaling them on a [0,1] scale and taking the mean of both scores. Finally, we averaged the resulting performance scores from internal and external validations to create a balanced model performance score that we used to select the best-performing model parametrizations.

Performance of global models improved with higher than default (β=1) regularization multipliers at the landscape level, with an optimal β value of 16 for all approaches (average performance gain compared to default regularization: 7.0%; Figure SI IV-2). Performance gains of tuning the regularization strength were lower at the home range level, where only the performance of the *global environment* approach improved at higher-than-default β values (best performance at β=4). Similarly, performance gains for tuning local models were highest at the landscape level (average performance gain of 12.3% vs. 5.3% at the home range level), where optimal β values tended to be much higher than at the home range level (median selected β value of 4 and 48 at the landscape and home range level, respectively; Figure SI IV-3).
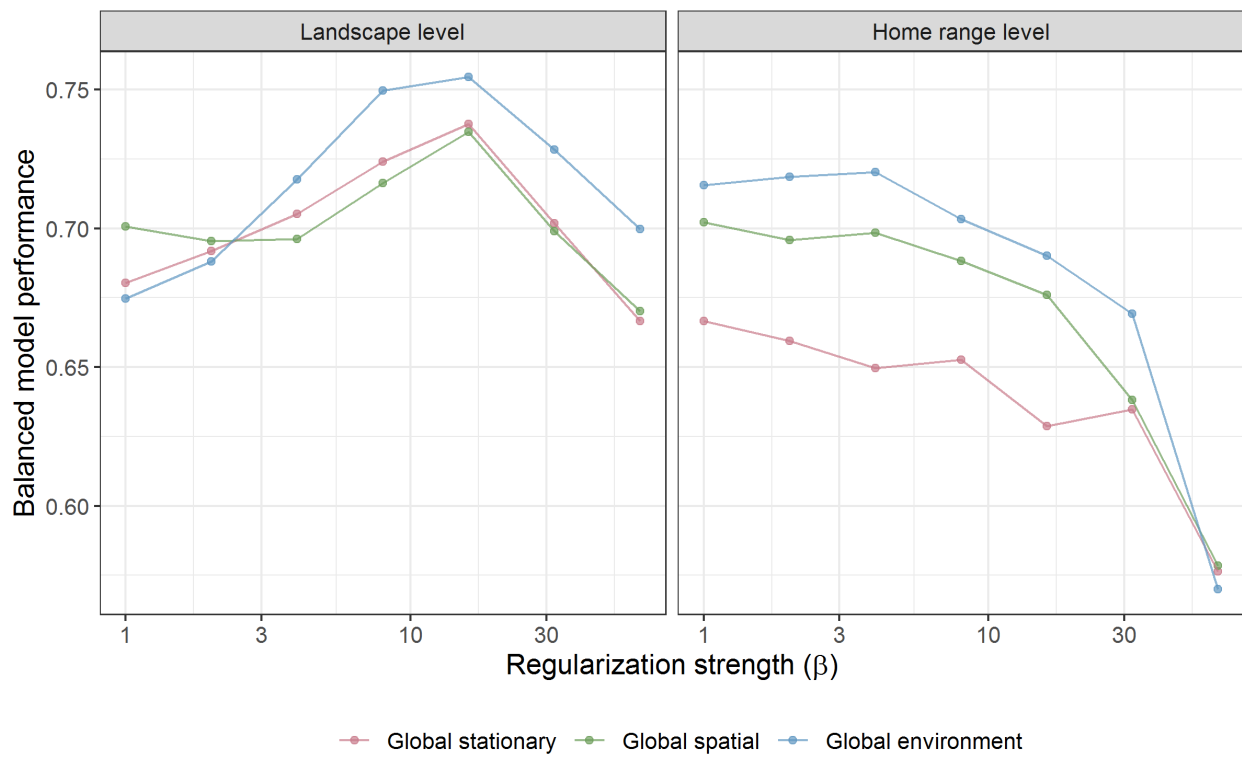
Figure SI IV-2: Model performance for global models for different levels of model regularization (regularization parameter β). Regularization values are shown on a logarithmic scale.
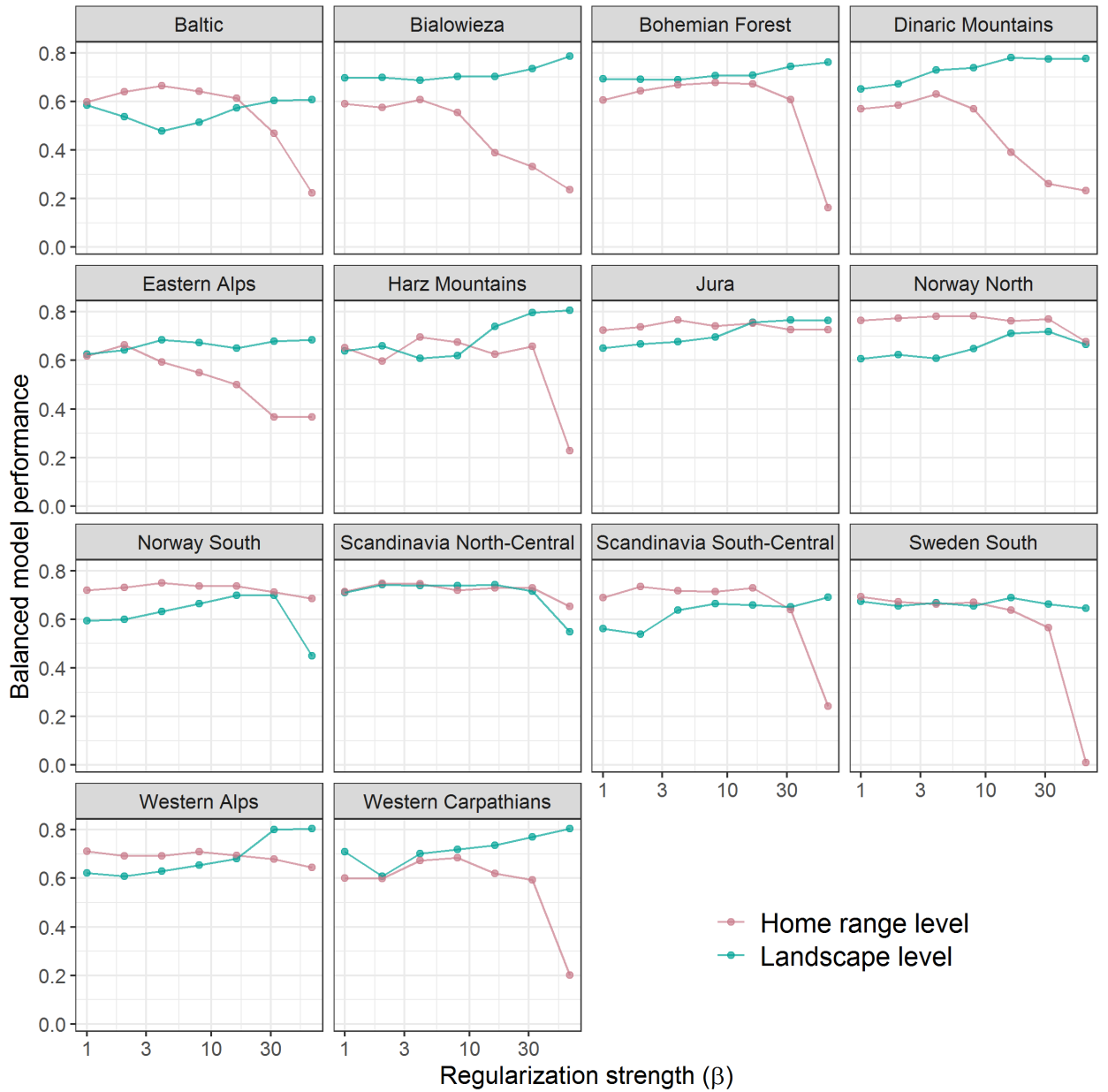
Figure SI IV-3: Change of model performance for individual local models with increasing regularization strength (regularization parameter β). Regularization values are shown on a logarithmic scale.
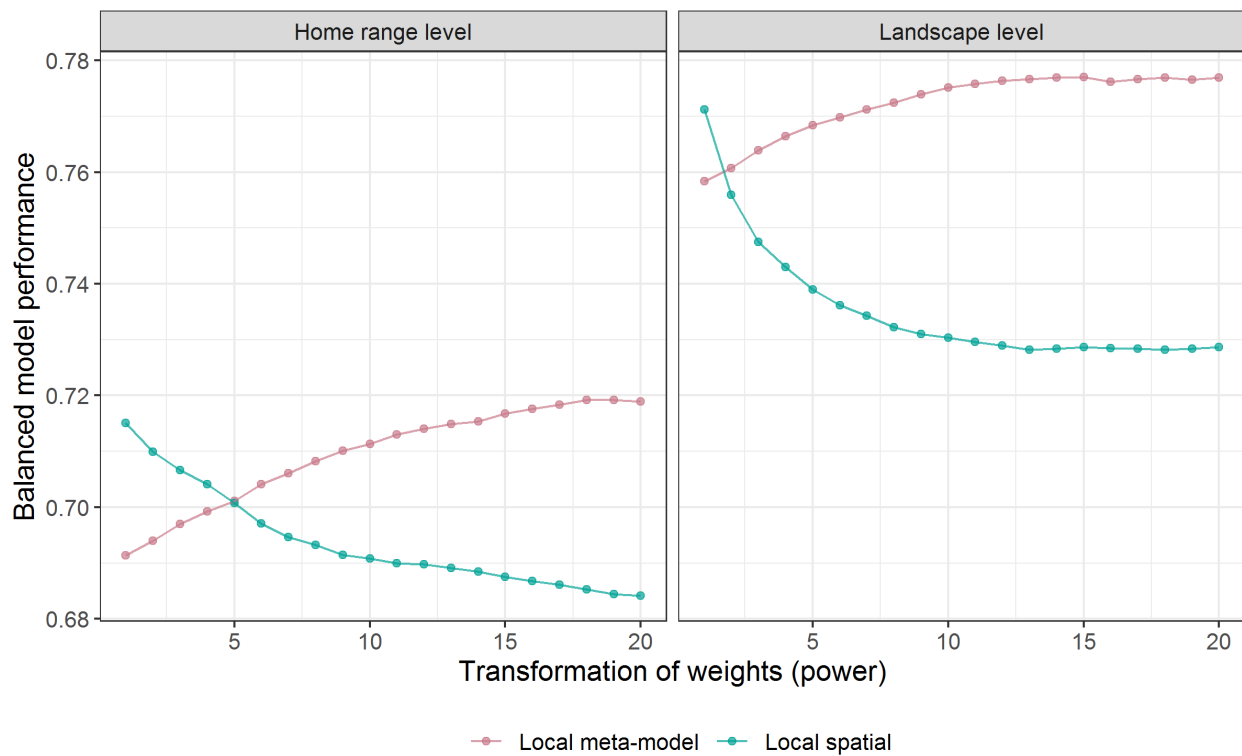
Figure SI IV-4: Change of model performance for non-stationary local approaches with transformation of model weights to higher powers (i.e., up-weighting of more similar study sites). Whereas performance of the local spatial approach decreased with higher weights for nearby sites, performance of the local meta-model approach improved when most weight was given to the site with the highest expected performance.
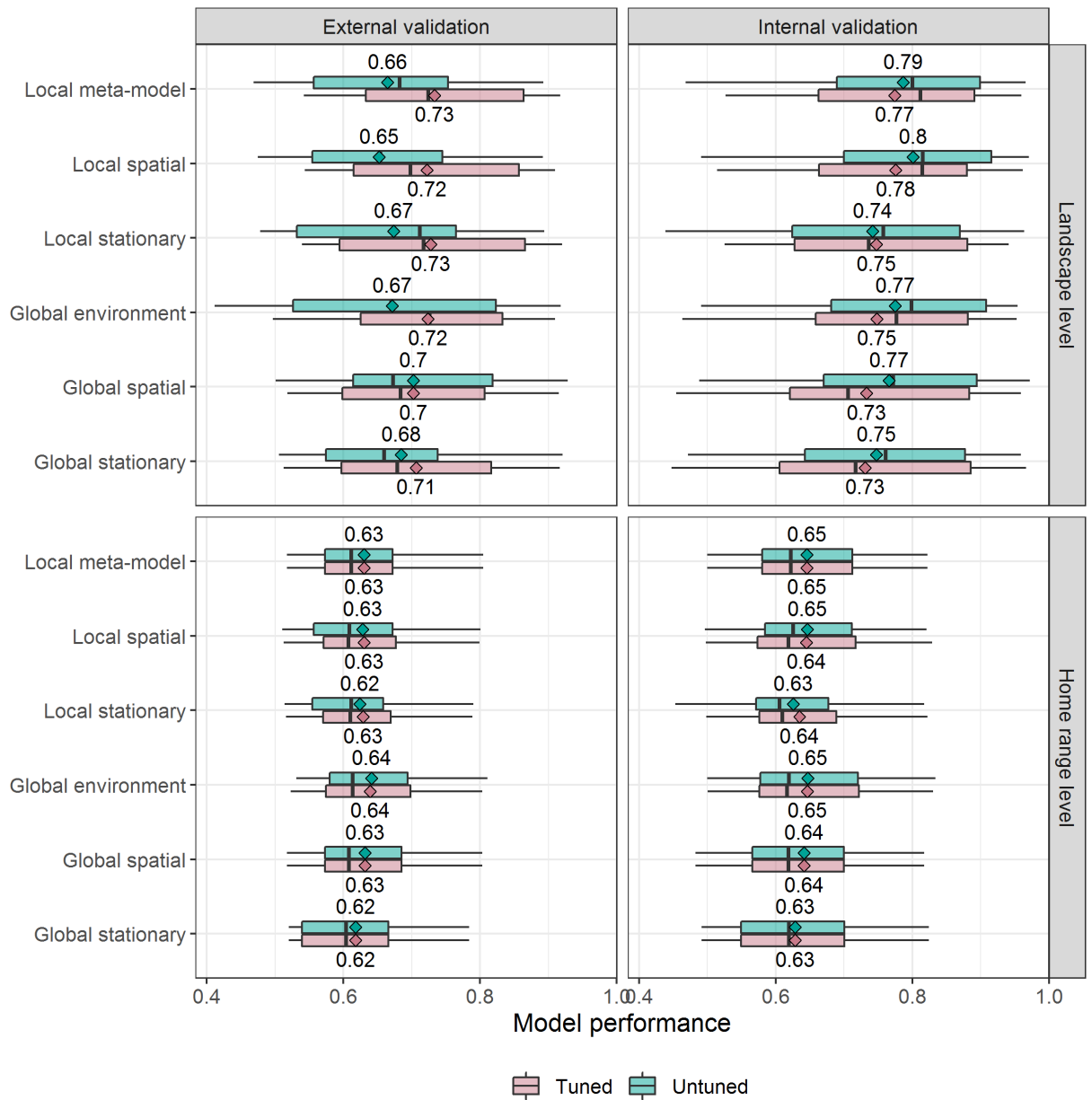
Figure SI IV-5: Model performance of habitat models fitted with different modeling approaches at two levels of habitat selection, as measured by AUC. Colors distinguish models fitted with default ('untuned') and optimized ('tuned') model regularization. Mean performance scores are printed above or below boxplots and indicated by the diamond-shaped points.
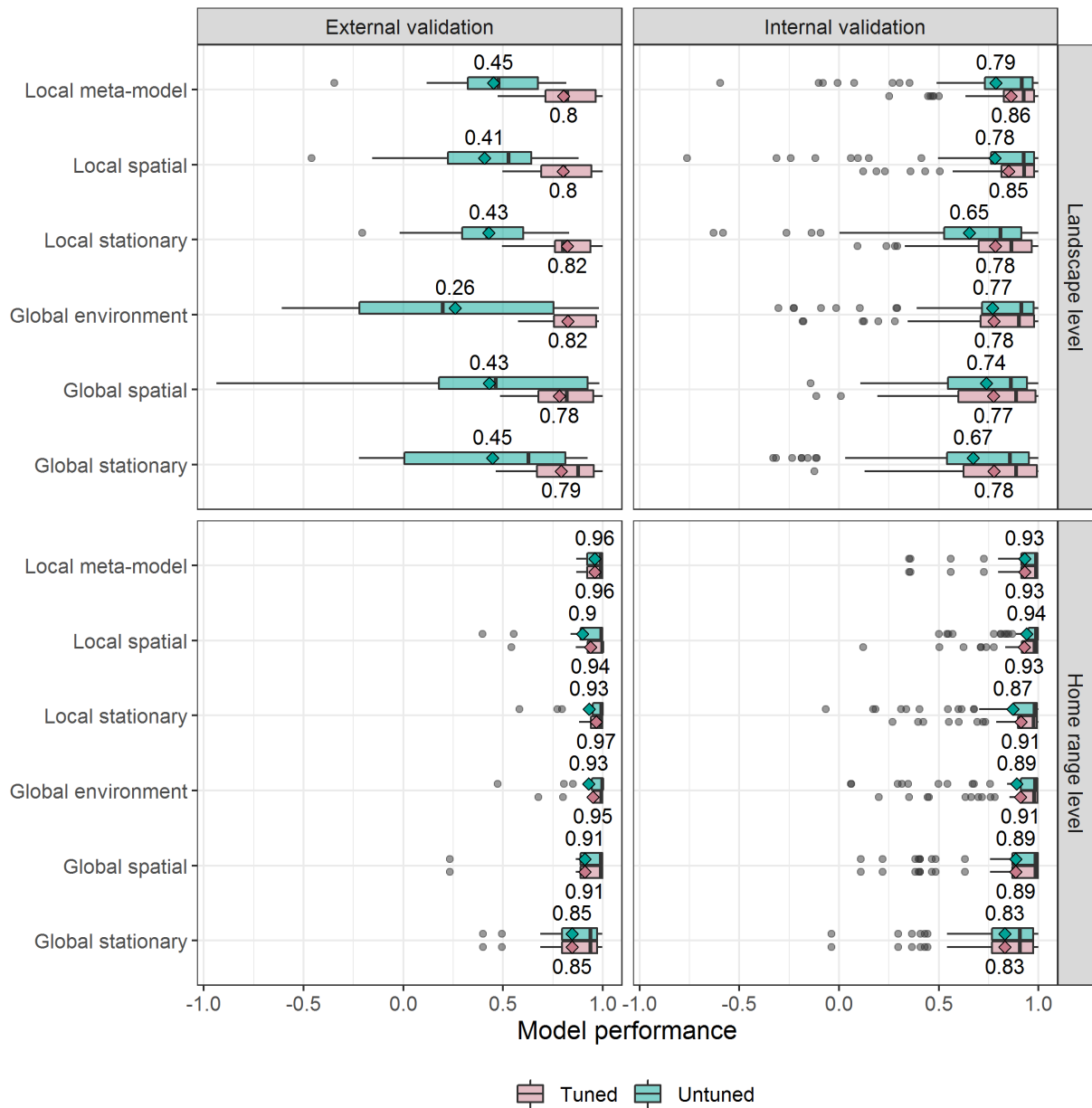
Figure SI IV-6: Model performance of habitat models fitted with different modeling approaches at two levels of habitat selection, as measured by the CBI. Colors distinguish models fitted with default ('untuned') and optimized ('tuned') model regularization. Mean performance scores are printed above or below boxplots and indicated by the diamond-shaped points.
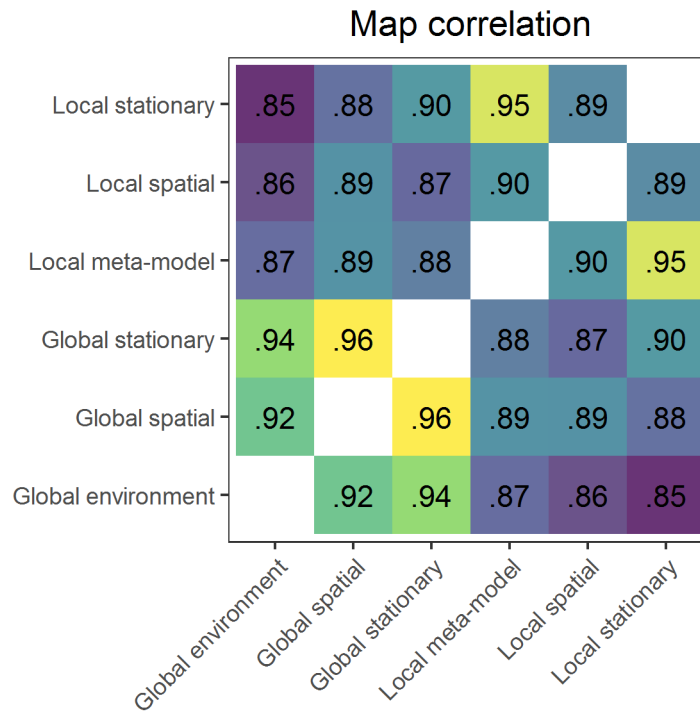
Map correlation

Figure SI IV-7: Pairwise correlation between habitat suitability maps created with different mapping
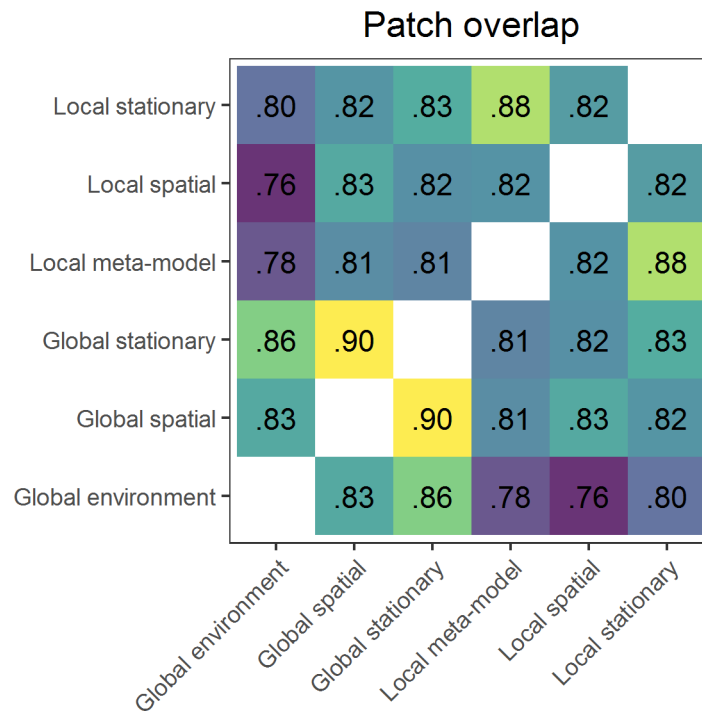
Patch overlap

approaches.

Figure SI IV-8: Pairwise percent overlap of suitable habitat patches for maps created with different mapping approaches. Colors distinguish models fitted with default ('untuned') and optimized ('tuned') model regularization. Mean performance scores are printed above or below boxplots and indicated by the diamond-shaped points.
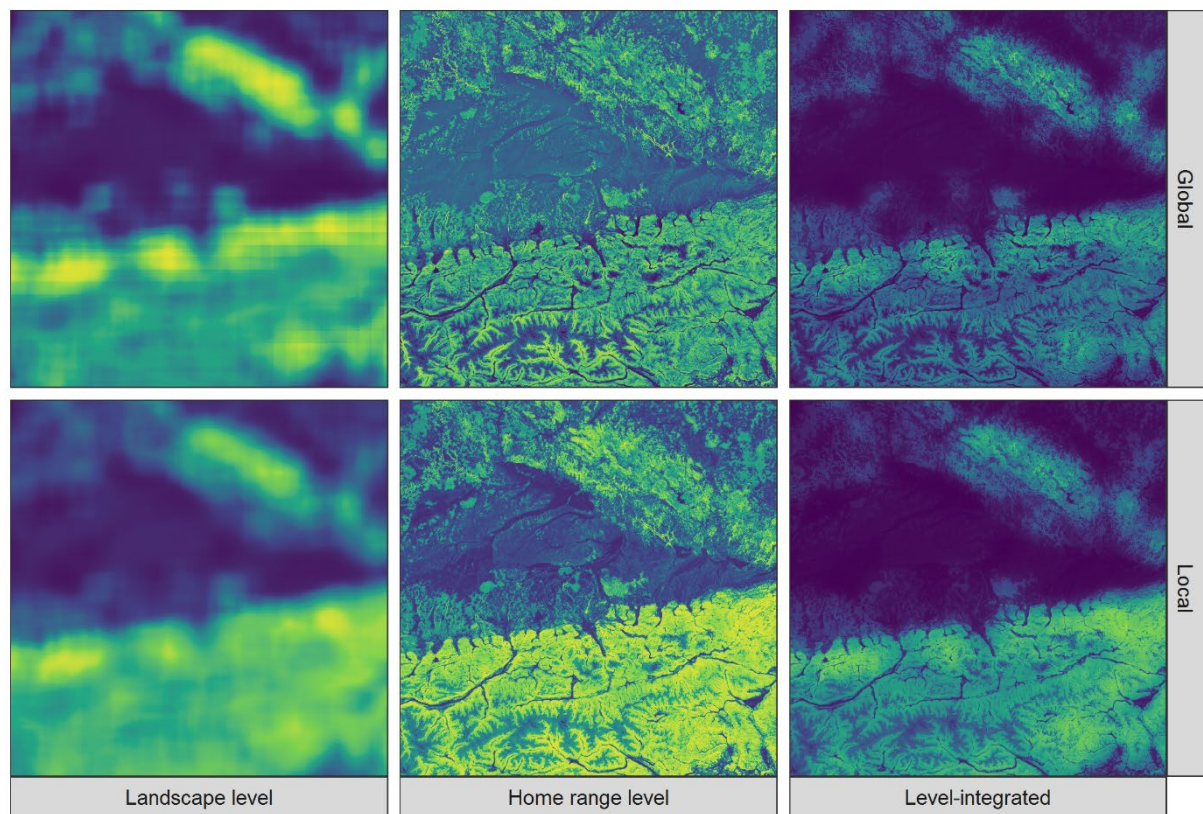
Figure SI IV-9: Example illustrating the integration of habitat suitability predictions at different levels of selection. Map window shows habitat suitability predictions (low suitability in blue, high suitability in yellow) of the best-performing local and global approaches in a part of the study area (border region of Germany and Austria).
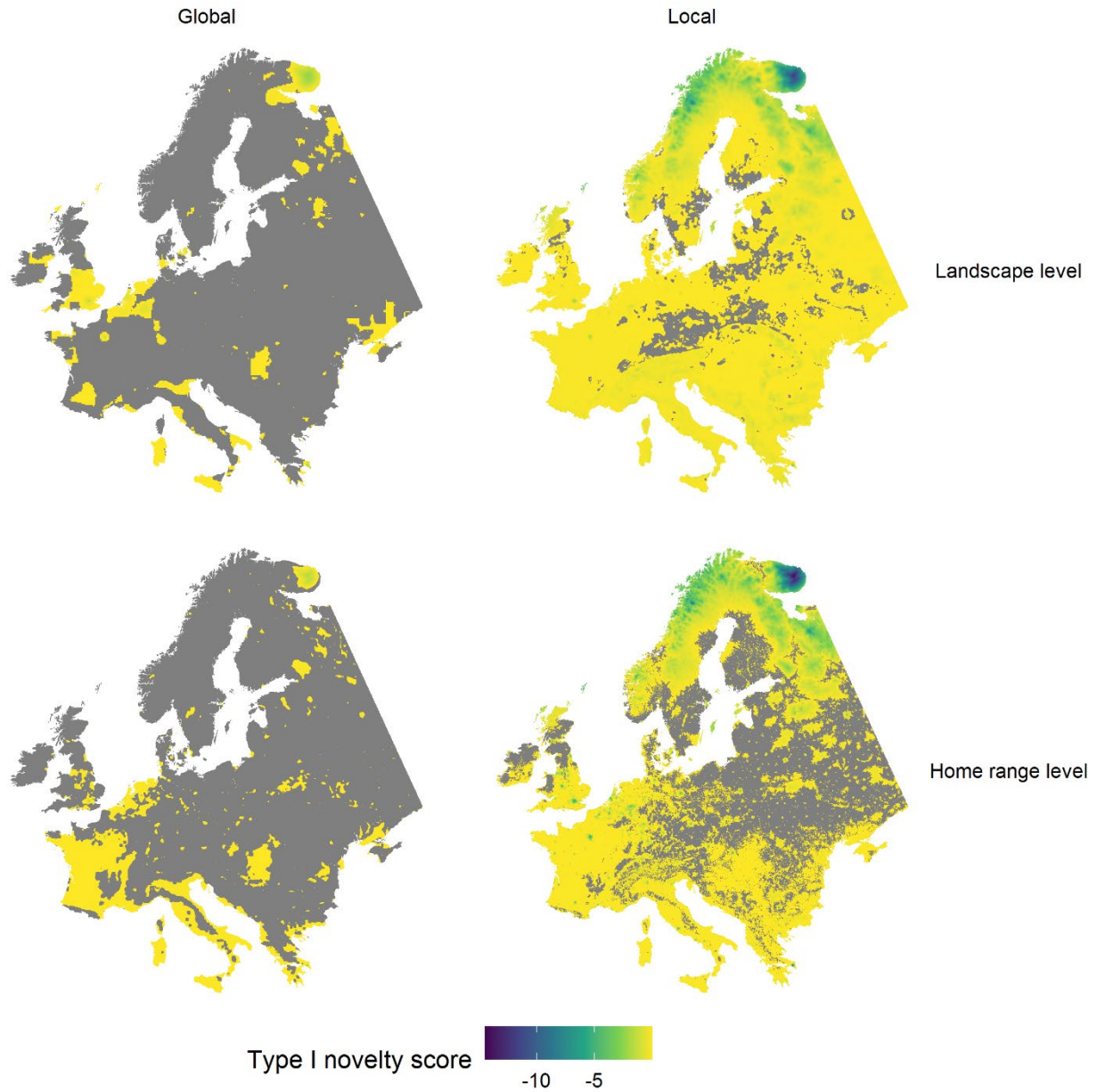
Figure SI IV-10: Extent of extrapolation (Type I novelty) in global and local modeling approaches as calculated by the ExDet tool (Mesgaran et al., 2014). Type I novelty corresponds to univariate extrapolation (i.e., values outside of the training ranges of variables). For local models, median novelty scores of all site-specific models are shown. Type I scores below 0 indicate univariate extrapolation, with extrapolation strength increasing with decreasing values. Grey areas represent regions with no univariate extrapolation.
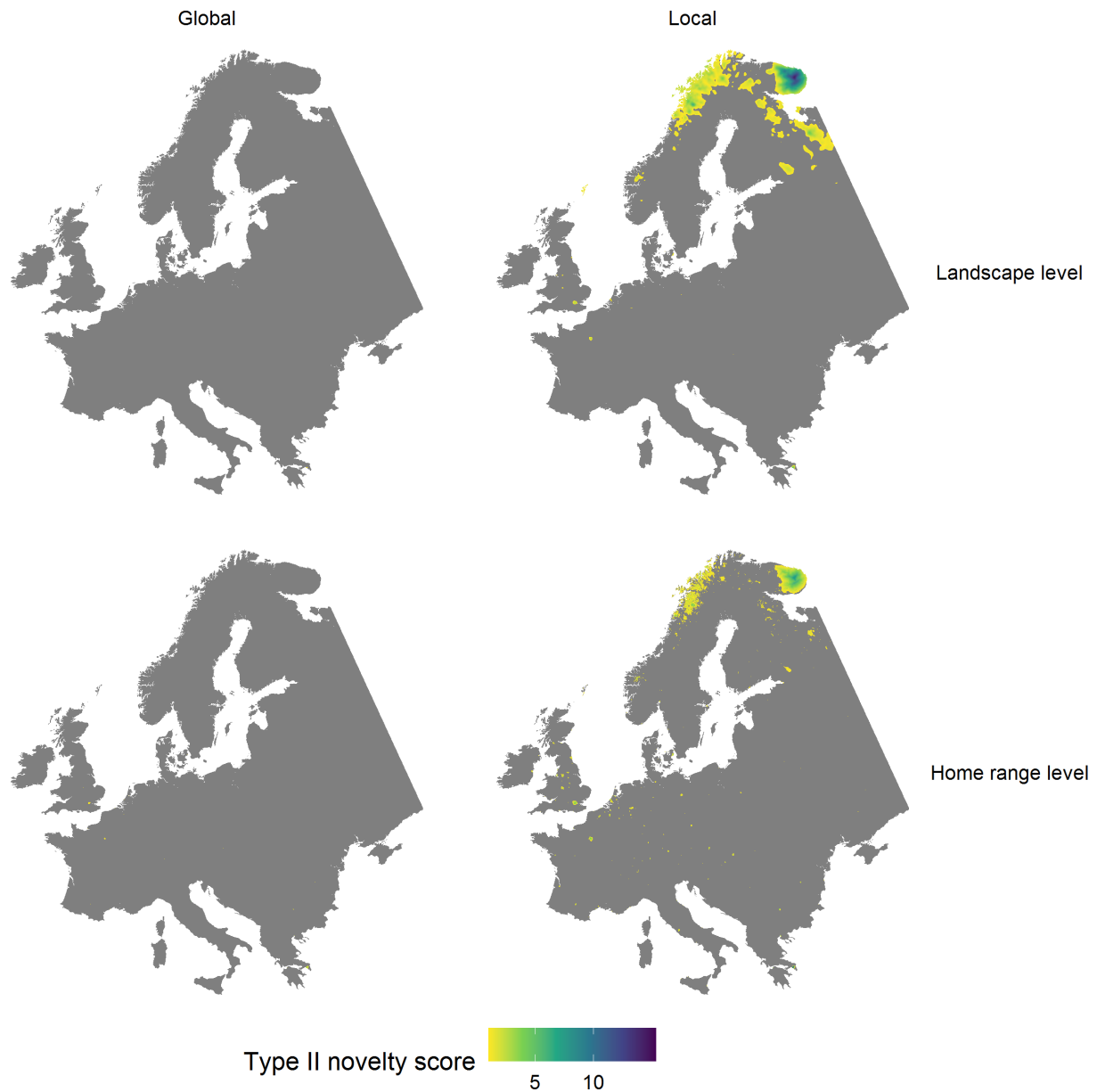
Figure SI IV-11: Extent of extrapolation (Type II novelty) in global and local modeling approaches as calculated by the ExDet tool (Mesgaran et al., 2014). Type II novelty corresponds to combinatorial extrapolation (i.e., new combinations of variable values). For local models, median novelty scores of all site-specific models are shown. Type II scores above 1 indicate combinatorial extrapolation, with higher values corresponding to stronger extrapolation. Grey areas represent regions with no combinatorial extrapolation.
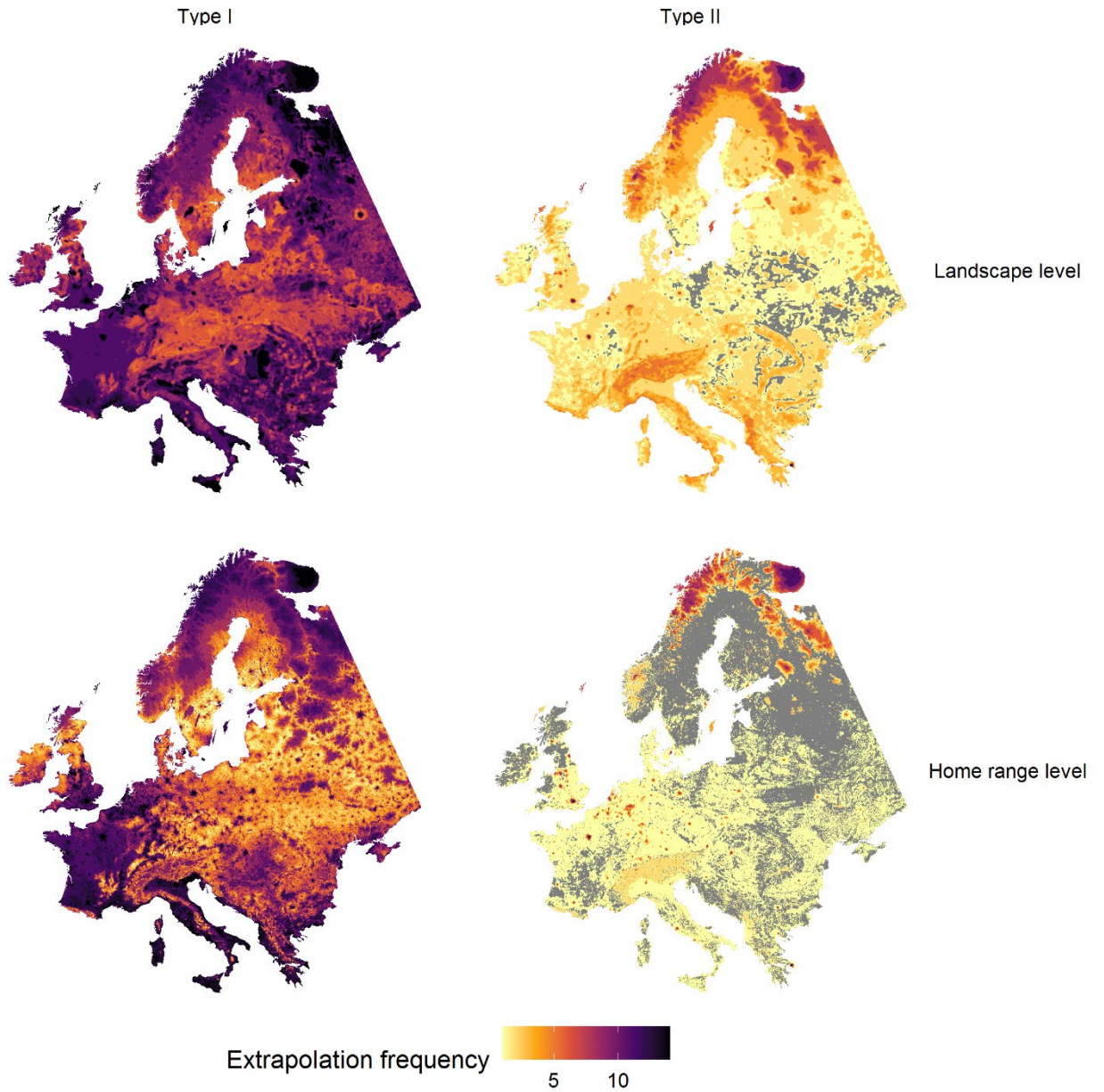
Figure SI IV-12: Frequency of extrapolation (Type I and II novelty) in local habitat models as calculated by the ExDet tool (Mesgaran et al., 2014). Colors relate to the number site-specific habitat models having to extrapolate in a given area. Grey areas correspond to regions where no local model extrapolated.
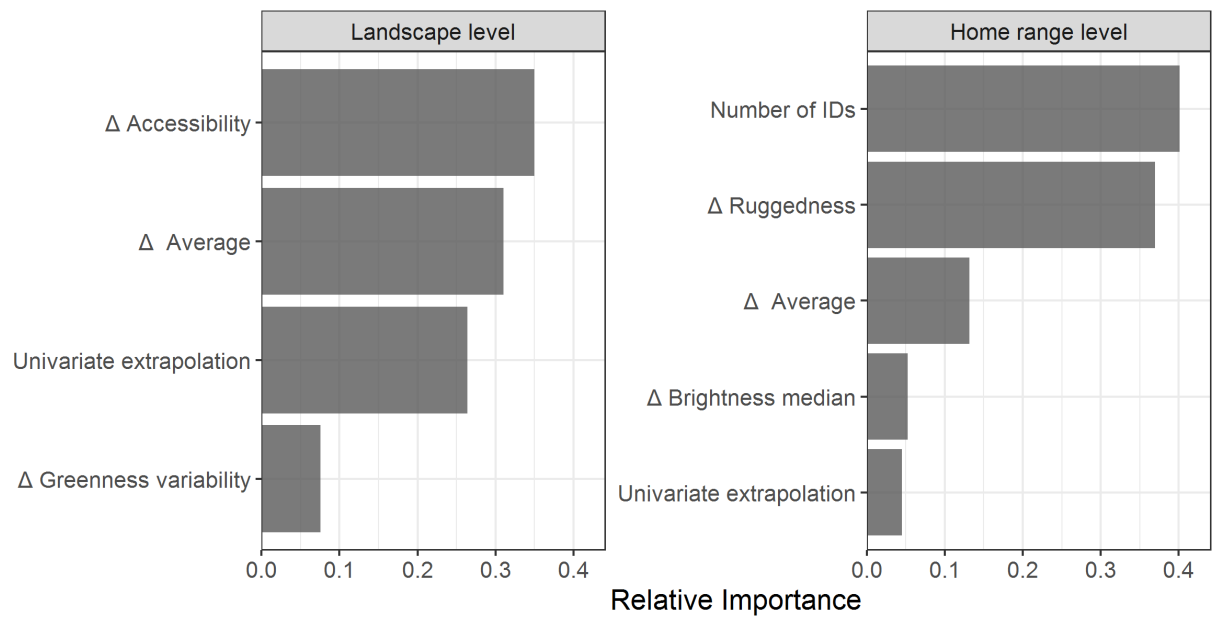
Figure SI IV-13: Determinants of model transferability. Bars show relative variable importance of predictors used in the meta-model.

Chapter V:
Prerequisites for coexistence: human pressure and refuge habitat availability shape continental-scale habitat use patterns of a large carnivore

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Abstract

Behavioral adjustments by large carnivores can be a key factor facilitating their coexistence with people. Here, we investigate how Eurasian lynx (*Lynx lynx*) adjust their habitat use at a continental scale, analyzing functional responses (i.e., variation in habitat use with habitat availability) in lynx' use of refuge habitats and human landscape modification based on a large tracking dataset (434 individuals from seven populations). We found that lynx increased their use of refuge habitats as human modification increases, with higher forest use in otherwise open landscapes and higher use of rugged terrain in mountainous regions. At the same time, a higher availability of forest cover enabled lynx to place their home ranges in more human-modified landscapes. Finally, landscape context also shaped temporal patterns of lynx habitat use, affecting daytime-nighttime differences in refuge habitat use, as well as female lynx' association with human-modified habitats during the first months after kittens are born. Our findings suggest a remarkable adaptive capacity of lynx towards human pressure and underline the importance of refuge habitats for enabling coexistence between large carnivores and people. More broadly, we uncover how human pressure and refuge habitat availability interact to shape large carnivore distributions and habitat use at broad scales.

1   Introduction

Human activities pose manifold threats to wildlife, including habitat loss and modification, as well as anthropogenic mortality, making human pressure a key factor shaping wildlife behavior (Gaynor et al., 2018; Tucker et al., 2018). Large carnivores are particularly susceptible to human pressure, because of their large home ranges, naturally small population sizes, frequent conflicts with humans, as well as a lack of evolutionary adaptation to predation pressure (Ripple et al., 2014). Given an increasing awareness of the important roles that large carnivores play in ecosystems (Atkins et al., 2019), as well as an ongoing expansion of the global human footprint into large carnivore habitats (Wolf and Ripple, 2017), how to foster coexistence of large carnivores and humans has emerged as a key conservation challenge of our time (Carter and Linnell, 2016).

An important mechanism allowing large carnivores to co-occur and potentially to co-exist with humans are behavioral adjustments. For example, pumas (*Puma concolor*) in California select smaller prey when living close to human settlements (Smith et al., 2016), African lions (*Panthera leo*) exploit human-modified areas during times of low human activity to access prey (Suraci et al., 2019), and numerous carnivore species shift their temporal activity patterns in response to human pressures, typically becoming more nocturnal (Gaynor et al., 2018; Lamb et al., 2020). Available studies have mostly highlighted specific behavioral adaptations within single populations, yet broad-scale patterns of large carnivore habitat use might also be shaped in major ways by varying human pressure (Muhly et al., 2019; Thompson et al., 2021). However, studies analyzing variation in large carnivore habitat use across multiple populations and gradients of human pressure are lacking. A better understanding of how human pressure shapes large carnivore habitat use could provide important insights into their adaptive capacity and reveal opportunities and limitations for *landscapes of coexistence* where large carnivores and people co-occur sustainably (Oriol-Cotterill et al., 2015).

Next to human pressure, a second factor likely influencing broad-scale patterns of habitat use are variations in the environmental context that large carnivores experience, that is, different landscape compositions in terms of land covers, topography, or climate (hereafter: landscape composition). Which landscape features are available to an animal defines their option space for behavioral adjustments and thus should determine how large carnivores can adapt to human pressures (Bouyer et al., 2015b; Muhly et al., 2019). A growing body of research has highlighted the strong dependence of wildlife habitat use on habitat availability (Aarts et al., 2013). A key concept in this context are so-called *functional responses* in habitat

use (Mysterud and Ims, 1998; Northrup et al., 2022). Functional responses describe how an animal adjusts the use of a habitat feature with changes in its availability (e.g., changes in forest use with changing forest cover in the landscape), thereby providing insights into the plasticity of habitat use across environmental gradients.

Refuge habitats are likely particularly important to allow large carnivores to adapt to human pressures. Refuge habitats refer to landscape features that are characterized by overall low human presence and provide cover for large carnivores to avoid human encounters, such as forests or rugged terrain. Although such landscape features are also important to large carnivores for other reasons, such as hosting prey species as well as providing cover for resting, denning, and hunting (May et al., 2008; Podgórski et al., 2008), large carnivores could additionally depend on these features to reduce human-induced mortality (Oriol-Cotterill et al., 2015). Several studies have documented fine-scale behavioral adjustments resulting in an increased use of cover by large carnivores near humans (Gehr et al., 2017; Schuette et al., 2013). Yet, although it has been suggested that broad-scale distribution patterns of large carnivores, showing a strong association with forests and rugged terrain, are, at least partly, a result of human influence (Martínez-Abraín et al., 2020; May et al., 2008), broad-scale studies investigating the connection between large carnivores' dependence on refuge habitats and gradients of human pressures are missing.

Understanding how large carnivore habitat use varies across gradients of human pressures and different landscape compositions requires datasets spanning multiple populations. While such datasets have traditionally been missing, the ongoing proliferation of animal tracking data, along with efforts to share and integrate datasets in harmonized databases through the establishment of collaborative networks opens new opportunities in this regard (Thompson et al., 2021; Urbano et al., 2021). Methodologically, such analyses require disentangling how habitat use varies in response to changes in multiple variables simultaneously (e.g., human pressure *and* refuge habitat availability). However, functional responses so far have commonly been studied by regressing the use of a single habitat feature against its availability (Holbrook et al., 2019), thus neglecting the potential synergistic effects of multiple habitat factors (Northrup et al., 2022).

Europe represents an interesting case for studying how large carnivore habitat use varies along gradients of human pressure and landscape composition. After the widespread extirpation of large carnivores in Europe during the last centuries, several species have recently expanded their ranges through reintroductions and natural recolonizations (Chapron

et al., 2014). Yet, the high degree of human pressure in many parts of Europe makes coexistence between large carnivores and humans challenging. Despite a recent population recovery and range expansion, partly driven by several reintroductions, the European populations of Eurasian lynx (*Lynx lynx*; hereafter lynx) remain highly fragmented, endangering their long-term survival (Schmidt et al., 2011). In addition to lynx' dispersal ability (Zimmermann et al., 2007), their capacity to adjust to human pressure is therefore likely key for determining whether lynx can persist in Europe's human-dominated areas and therefore, to what extent currently isolated populations can be connected into viable metapopulations (Bonn Lynx Expert Group, 2021). Several recent studies have highlighted that human pressure is a central driver of lynx habitat selection in Europe (Ripari et al., 2022; Thorsen et al., 2022), but how lynx adapt their habitat use in relation to human pressure and landscape composition across its distribution in Europe remains unclear.

Here, we make use of a large collection of telemetry data encompassing seven lynx populations across Europe to investigate functional responses by lynx across gradients of refuge habitat availability and human landscape modification, also analyzing variation of habitat use relating to sex, daytime, and season. Specifically, we test the following research hypotheses:

H1: Lynx use refuge habitats (forests and rugged terrain) more intensively at higher levels of human pressure.

H2: Lynx' daytime use of refuge habitats increases with increasing human pressure.

H3: Female lynx show a stronger avoidance of human-modified habitats during the postnatal period (i.e., the first months after kittens are born).

2 Methods

2.1 Animal tracking data

We used GPS and VHF telemetry datasets collected in 13 countries, covering seven lynx populations from across Europe (Kaczensky et al., 2021; Figure V-1). Prior to all analyses, tracking datasets were harmonized through a standardized procedure of quality checks (Urbano et al., 2021).
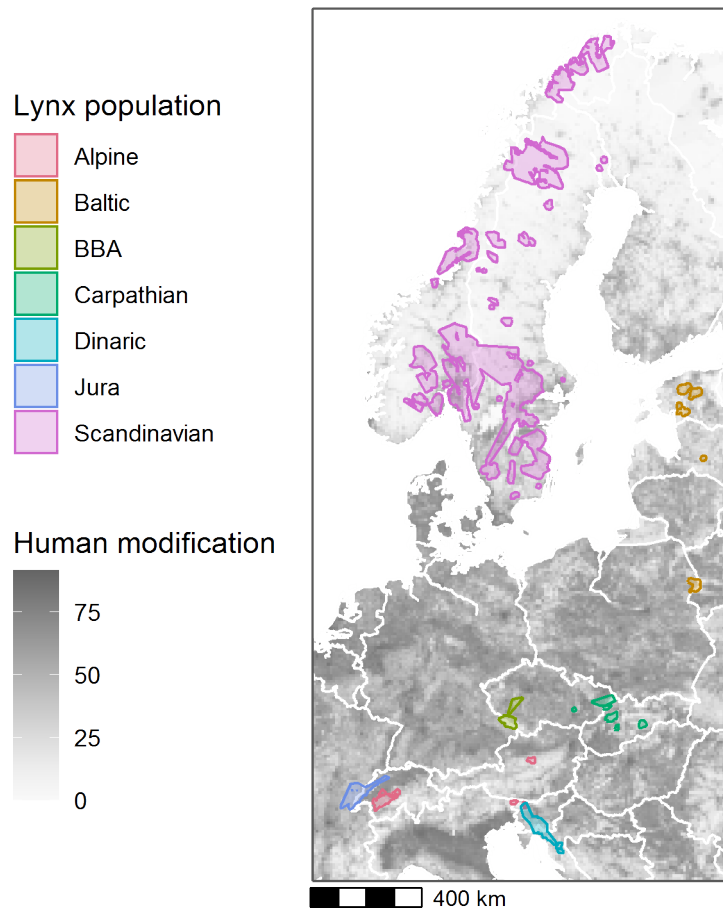
Figure V-1: Extent of lynx telemetry data. Polygons correspond to the extent of lynx home ranges per lynx population in our dataset (BBA = Bohemian-Bavarian-Austrian). Background raster shows the degree of landscape modification (human modification index; Kennedy et al., 2019) in grey colors at a 10km resolution.

We filtered lynx individuals, discarding animals with fewer than 50 telemetry locations to ensure a robust estimation of lynx home ranges (Seaman et al., 1999). Moreover, we removed dispersing individuals, which often differ in their habitat use compared to resident animals (Hemmingmoore et al., 2020). To reduce potential issues of spatiotemporal autocorrelation, we standardized the sampling frequency of our tracking data to one location per two hours. Our final dataset contained ca. 417,000 unique telemetry locations from 434 lynx individuals (230 females / 204 males; see Table SI V-1 for a full overview).

In addition to filtering data, we classified locations into day- and nighttime locations (daytime: 07:01 – 21:00; nighttime 21:01 – 07:00). We used fixed day and nighttime windows since our goal was to capture effects of human activity on lynx habitat use. We further assigned locations to two seasons within the year (postnatal period vs. the rest of the year) to allow testing whether females adapted their habitat use during the first months of

kitten rearing. Due to the lack of consistent information on the breeding status of females, we defined the postnatal period as the first 100 days of the reproductive year for all individuals, irrespective of their breeding status (most female lynx are reproducing each year (López-Bao et al., 2019). Based on data on the distribution of parturition dates of lynx across Europe, we defined the beginning of the reproductive year as 145th day of the year for datasets north of 65° latitude (May 25th in non-leap years), and as the 130th day of the year for all other locations (May 10th).

2.2   Environmental variables

To characterize gradients of human pressure and landscape composition, we compiled environmental rasters from several sources. As a proxy for human pressure, we used the human modification index (Kennedy et al., 2019). The human modification index is derived by integrating information on the extent and intensity of 13 anthropogenic stressors, such as human population density, road density, built-up areas, and agriculture and thus provides an aggregate indicator of the overall degree of human pressure potentially affecting wildlife habitat use (Kennedy et al., 2019). Similar aggregate measures of human modification have previously shown promise in explaining patterns of habitat use and population dynamics for large carnivores (Lamb et al., 2020).

As variables characterizing the availability of habitat features offering protection for lynx from human pressures, we used data on the distribution of two refuge habitats: forest cover and terrain ruggedness. Both variables have been identified as key habitat features for lynx, particularly in the context of providing cover for resting and for escaping from human disturbance (Filla et al., 2017; Hočevar et al., 2021; Podgórski et al., 2008). We derived the distribution of forest cover from a recent global high-resolution land cover map (Buchhorn et al., 2020) and the terrain ruggedness index from a suite of topographic variables (Amatulli et al., 2018).

2.3   Characterizing habitat use and availability

To reflect the hierarchical, multi-scale nature of habitat selection (Mayor et al., 2009), we assessed functional responses of lynx at two spatial scales: the placement of home ranges in the wider landscape (hereafter *landscape scale*, also referred to as second-order habitat selection; Johnson, 1980), and the use of locations within home ranges (hereafter *home range scale*; also referred to as third-order habitat selection). We derived home ranges for each lynx individual using 95% minimum convex polygons (MCPs). We chose 95% MCPs since our

goal was to define approximate home ranges while creating a comprehensive sample of available habitats at the home range scale (Fattebert et al., 2018; Holbrook et al., 2017a). We derived summaries of habitat use and availability for each lynx individual, randomly sampling 10 potentially available locations for each used location at both scales, also transferring other attributes such as sex and observation time to available locations. At the landscape scale, we defined used locations by sampling random points within lynx home ranges equal to the number of tracking locations available for an animal and characterized availability by sampling random points within 100 pseudo-home ranges that we created by shifting individuals' home ranges in random XY-directions at distances of 1-80 km, corresponding to likely dispersal distances by lynx (Samelius et al., 2012; Zimmermann et al., 2007). At the home range scale, we used the telemetry locations as used points and sampled available locations randomly within lynx home ranges.

2.4 Assessing functional responses

Functional responses can be analyzed either at the level of *habitat use* or *habitat selection* (Holbrook et al., 2019). A functional response in habitat use describes how the values of an environmental variable vary at locations used by an animal dependent on habitat availability (i.e., average values of environmental variables across the wider landscape). A functional response in habitat selection, describes how the ratio of habitat use to availability varies along a gradient of availability (Holbrook et al., 2019). We here focus on the former, since our goal was to understand general patterns of lynx' association with different habitat factors throughout its European range. Most commonly, functional responses are assessed in two-stage approaches (Northrup et al., 2022) (although see e.g., (Matthiopoulos et al., 2011) for a single-stage approach using interaction effects in resource selection functions). First, habitat selection or use are characterized by either deriving selection coefficients for each individual animal through resource selection functions or by calculating average variable values at used tracking locations (Holbrook et al., 2019). Then, in a second step, selection coefficients or average values are regressed against habitat availability to assess how use/selection changes with availability (hereafter referred to as functional response models), with a regression slope of $\beta=1$ indicating proportional increases with availability (Mysterud and Ims, 1998).

We calculated mean values at used and available locations for each individual, calculating multiple means based on the date and time of locations. At the landscape scale, we grouped locations by season (postnatal period vs. rest of year). At the home range scale, we grouped

locations by season as well as daytime (day vs. night; see Table SI V-2 for a summary of variable distributions). While functional response models have typically been univariate, that is, regressing the use/selection of a single habitat feature against the availability of that feature (Northrup et al., 2022), we here use a multivariate approach allowing to assess the influence of multiple variables concurrently. To that end, we fitted multiple linear regression models including the availability (i.e., mean values) of all environmental variables (i.e., forest cover, rugged terrain, and human modification) as well as their two-way interactions as predictors (correlations between all variables were below 0.45; Figure SI V-1). We built separate functional response models for each variable at the two spatial scales (landscape and home range scale), resulting in a total of six models.

We additionally tested for variation in habitat use by season (postnatal period vs. rest of year), sex (male vs. female), and, at the level of home range use, variation by daytime (day vs. night). To that end, we tested adding binary factor variables for season, sex and daytime (for models of home range use), as well as their interaction effects with all other terms to our models. We tested models with increasing levels of complexity, including one (daytime/sex/season), two (daytime and sex / season and sex) or all three factor variables and their interactions at a time and then compared the support for model setups using the Akaike Information Criterion (AIC). To visualize functional responses, we derived marginal model effects using the *ggeffects* package (Lüdecke, 2018). To assess variation in habitat use by sex, season and daytime, we calculated contrasts between regression coefficients using the *contrast* package (O'Callaghan et al., 2021).

3 Results

Lynx increased their use of refuge habitats with increasing human pressure. Specifically, lynx increased their use of forests at both scales of habitat use (landscape and home-range - scale use) as an adjustment to increasing human modification. This adjustment was particularly strong in open landscapes with low forest cover (Figure V-2A+C), whereas this pattern was not observable when forest availability was high. Lynx also increased their use of rugged terrain in response to increasing human modification at both scales, but only in landscapes offering relatively high levels of available rugged terrain (Figure V-2C+D). The effect of human modification on altering lynx' use of rugged terrain, however, was considerably smaller than the effect of human modification on forest use. Based on AIC values, there was support for sex differences in lynx' use of forest cover at the landscape

scale (see Figure SI V-2 for an overview of AIC values for all model setups and Table SI V-3 for an overview of model coefficients of all selected models). Specifically, female lynx tended to place their home ranges so that they include more forest cover particularly at low levels of human modification and high forest availability in the landscape (Figure SI V-3).
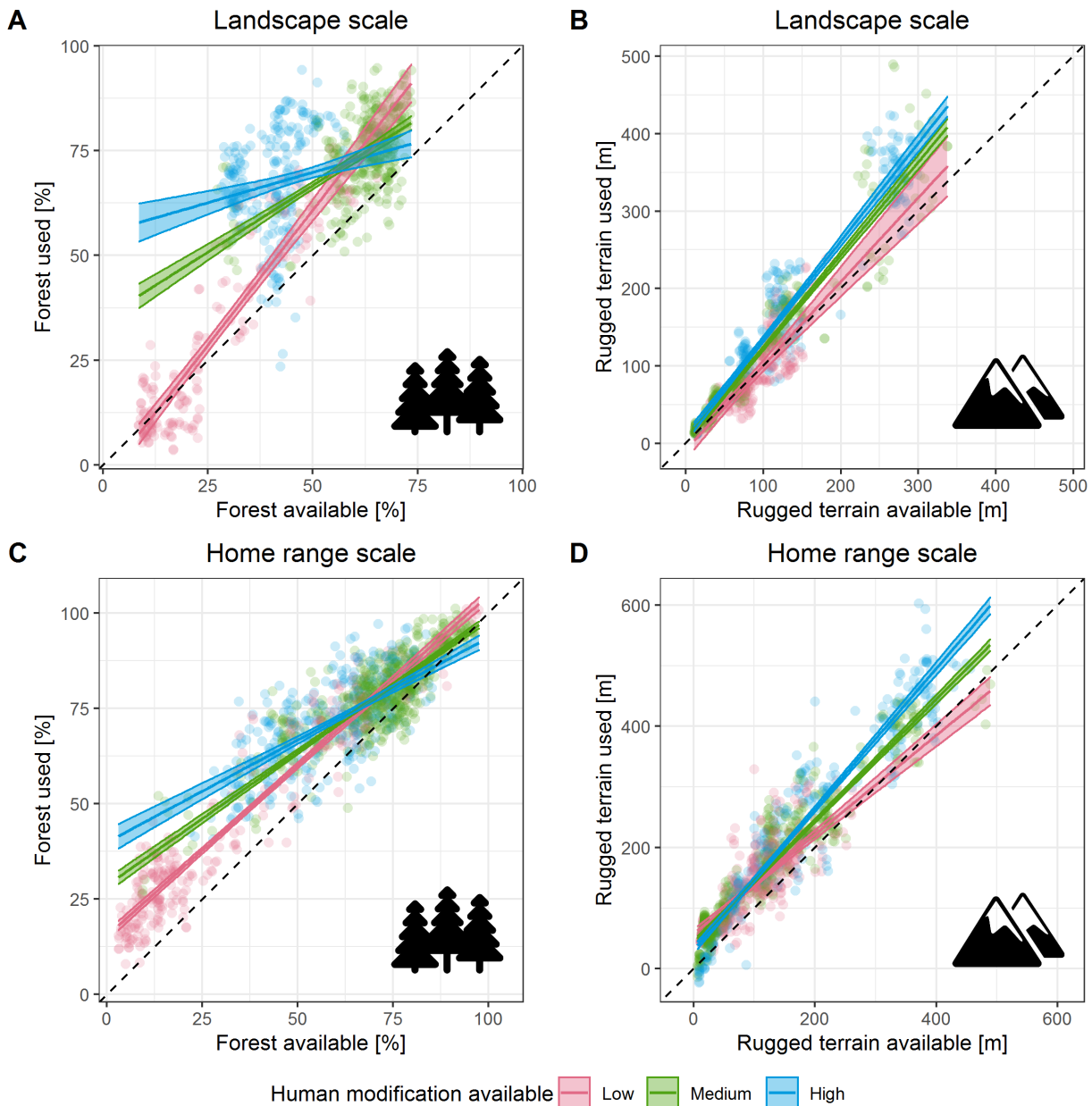
Figure V-2: Lynx' use of refuge habitats (forest cover and rugged terrain) with varying human modification at two scales of habitat use. Plots show functional responses in habitat use (i.e., use in dependence on availability), with dashed diagonal lines indicating proportional use. Marginal model effects with 95% confidence intervals and partial residuals for low, medium, and high levels of human modification (10th, 50th and 90th percentile in our dataset) are highlighted in different colors. Other variables are kept at their mean values for computing marginal effects.

At the home range scale, lynx tended to use both types of refuge habitat (forest and rugged terrain) more during daytime than nighttime (models including interaction effects with daytime were supported based on AIC). Day-night differences were stronger in open landscapes (low forest availability; Figure V-3A) and rugged landscapes (high availability of rugged terrain; Figure V-3B). Moreover, in open landscapes, lynx increased their daytime use of forests as human modification of the landscape increased (Figure V-3A). While a similar trend was discernible for the use of rugged terrain, differences between different levels of human modification were less clear than for forest cover (overlapping confidence intervals; Figure V-3B).
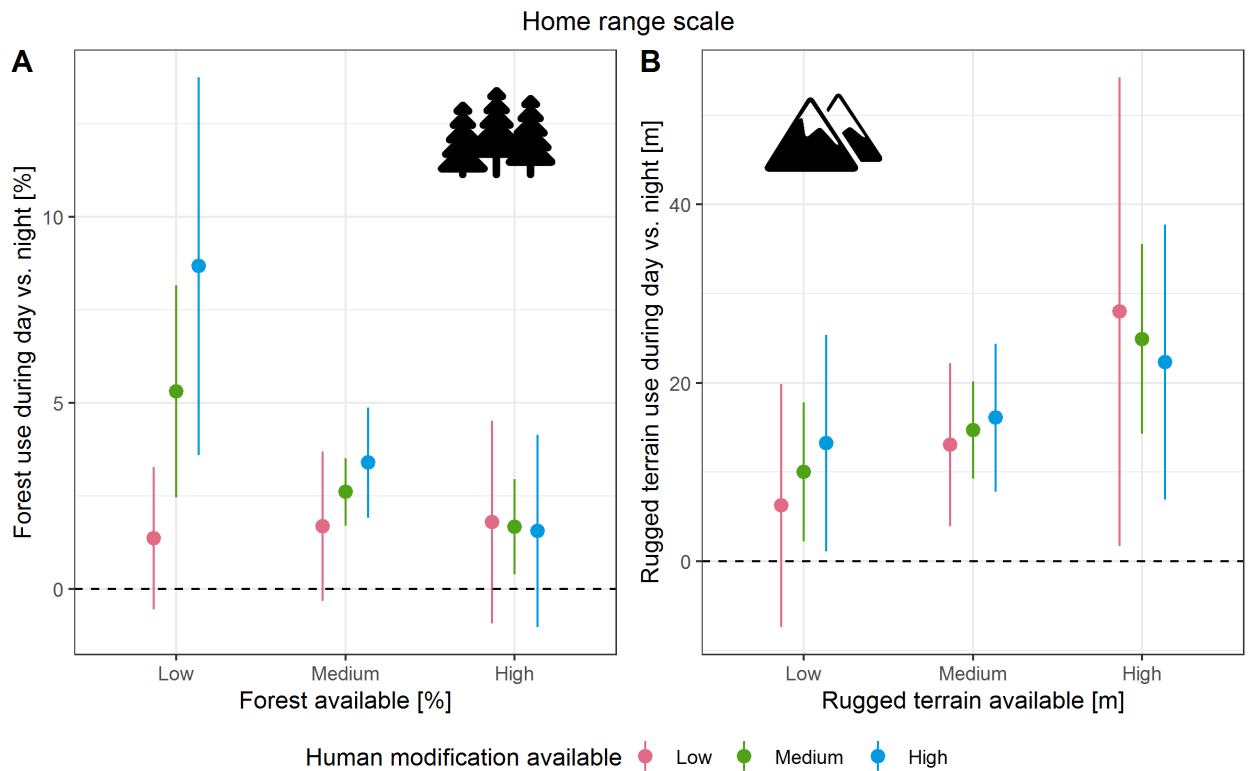
Figure V-3: Difference between daytime and nighttime use of refuge habitats (forest cover and rugged terrain) at the home range scale, depending on the level of human modification within home ranges. Values above zero indicate higher use of the respective refuge habitat type during daytime than nighttime. Low, medium, and high values of human modification correspond to 10th, 50th and 90th percentile in our dataset.

In addition to human modification affecting the use of refuge habitats, the availability of refuge habitats also affected lynx' association with human modification. Lynx established home ranges in more human-modified landscapes when more forest cover was available (Figure V-4A). Conversely, at the home range scale, lynx occurring in highly modified

landscapes (i.e., high levels of human modification within their home ranges) used locations with lower human modification when forest availability was at intermediate to high levels (Figure V-4B). In contrast to forest availability, availability of rugged terrain did not have clear effects on lynx' association with human modification (Figure SI V-4).
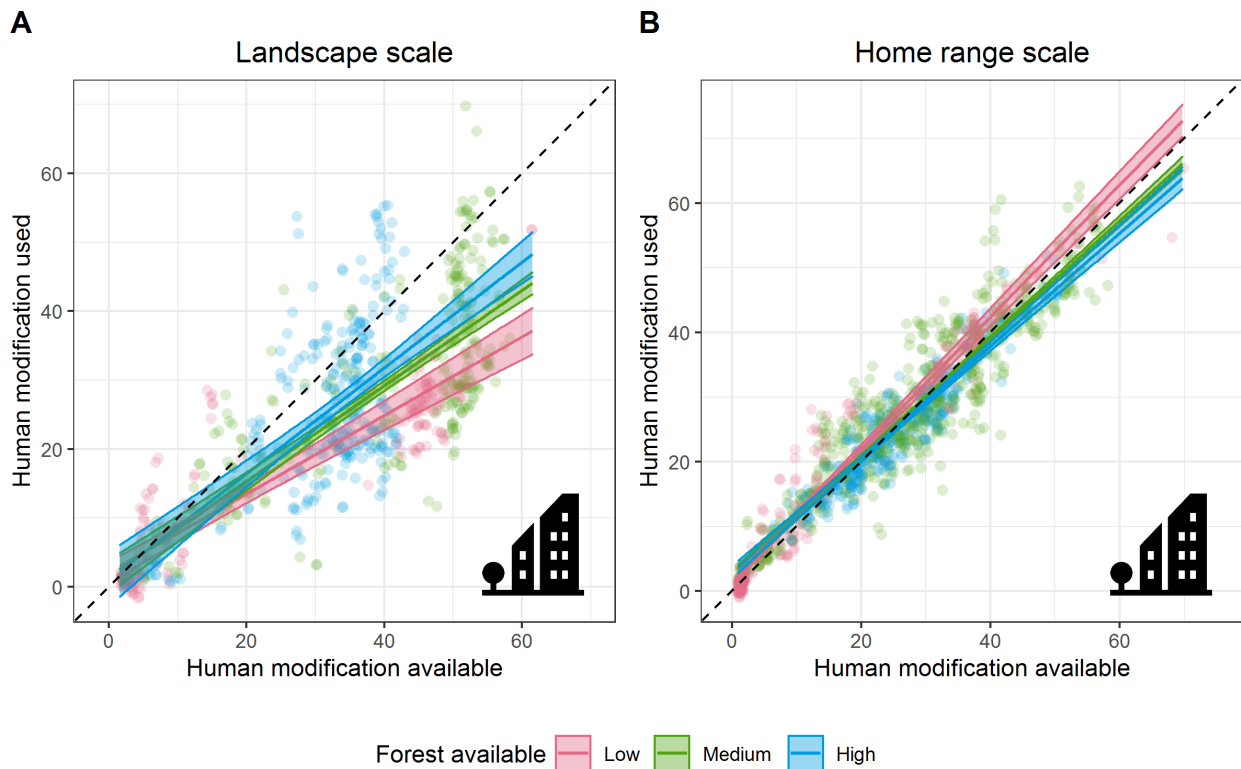
Figure V-4: Association of lynx with human modification for varying levels of available forest cover at two scales of habitat use. Plots show functional responses in habitat use (i.e., use in dependence on availability), with dashed diagonal lines indicating proportional use. Marginal model effects with 95% confidence intervals and partial residuals for low, medium, and high levels of forest cover (10th, 50th and 90th percentile in our dataset) are highlighted in different colors. Other variables are kept at their mean values for computing marginal effects.

We also found an indication for seasonal variation in habitat use (postnatal period vs. rest of year), as models of lynx' use of human modification including interaction effects with the season variable were favored based on AIC. Specifically, the use of human-modified areas by lynx tended to be lower during the postnatal period, especially for female lynx and at intermediate to high levels of forest availability (Figure V-5). A lower use of human modified areas during the postnatal period, although much less clear, was also detectable for male lynx.

Home range scale
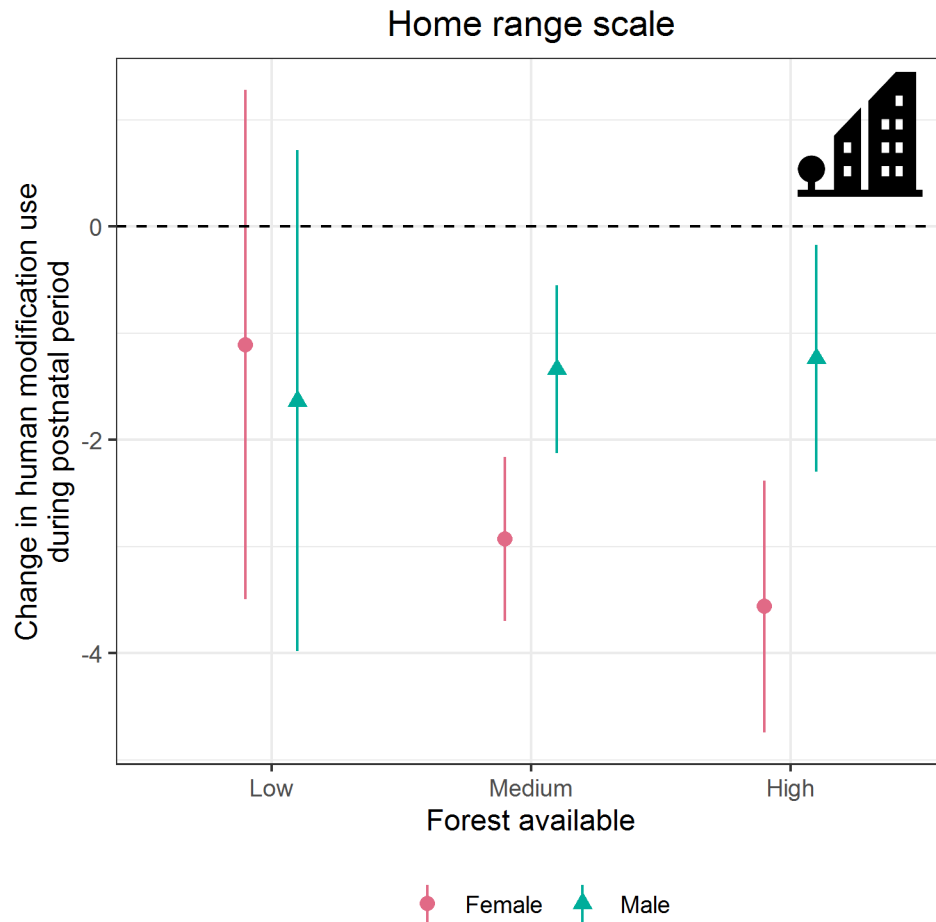
Figure V-5: Changes in lynx' association with human modification during the postnatal period, grouped by sex and different levels of forest availability. Values below zero indicate lower use during the postnatal period compared to the rest of the year.

4   Discussion

Large carnivore's capacity to adapt to humans is a key factor determining whether or not they can coexist with people in shared landscapes (Carter and Linnell, 2016). We here assessed, for the first time, functional responses in habitat use for a large carnivore at a continental scale. Our study yielded three main findings: First, lynx' use of refuge habitats (i.e., forests and rugged terrain) was influenced by human pressure gradients across the continent, with lynx increasing their use of refuge habitats in landscapes with a higher level of human modification. Second, landscapes with a higher availability of forest cover allowed lynx to occur (i.e., place home ranges) in more human-modified landscapes despite higher human pressure, further underscoring the importance of refuge habitat availability for human-carnivore coexistence. Finally, we found that human pressure and landscape

composition shaped differences in temporal habitat use of lynx, influencing both the diurnal use of refuge habitats as well as lynx' seasonal association with human landscape modification. More generally, our study highlights that it is the interaction of human pressure and refuge habitat availability, not human pressure alone, that determines whether large carnivores can recover and persist in human-dominated landscapes, having implications for efforts to conserve and restore large carnivore populations.

We found that lynx used refuge habitats more intensively with increasing human modification at two scales of habitat use: the placement of home ranges in the landscape and use of locations within home ranges. This supports our first hypothesis and is in line with previously published results. Several studies have shown similar adjustments by large carnivores at local scales, with carnivores increasing their use of cover habitats when being close to humans, for example lynx in Switzerland and lions in southern Kenya (Gehr et al., 2017; Schuette et al., 2013). Here, we provide the first continental-scale perspective showing that broad-scale patterns of refuge habitat use are strongly shaped by gradients of human pressure. Adjustments of refuge habitat use by lynx were particularly strong in open landscapes with low levels of forest availability as well as in landscapes with high levels of rugged terrain. Both are plausible results: large carnivores are most vulnerable to anthropogenic impacts in open landscapes (Suraci et al., 2019) and more rugged topography allows carnivores to avoid people more effectively (Grilo et al., 2019). Collectively, this highlights the outstanding importance of refuge habitats in human-dominated landscapes for enabling human-carnivore coexistence.

On the other hand, our results also imply that lynx are indeed able to persist in relatively open landscapes if levels of human pressure are low. For example, lynx in northern Norway occur at very low levels of forest cover (ca. 25% forest cover within home ranges; Linnell et al., 2021), likely also enabled by the low anthropogenic influences in these regions. Similarly, other large carnivores commonly associated with forest habitats can persist in savannas and steppes provided sufficient protection and low levels of human disturbance, such as wolves in Central Asian steppes or North American prairies (Riley et al., 2004; Tiralla et al., 2021), but these habitats have often been the first to lose large carnivores once human pressure increased (Laliberte and Ripple, 2004). More broadly, our findings thus support the hypothesis that the strong association of carnivore distributions with refuge habitats that today is observable in many large carnivores is largely driven by human pressure (Martínez-Abraín et al., 2020; May et al., 2008).

Our analyses suggest that the availability of refuge habitat influences whether large carnivores can occur in human-dominated landscapes. In landscapes characterized by high levels of human modification, lynx could establish home ranges despite higher human pressure if these landscapes had intermediate or high forest availability. In such situations, lynx compensated for the increasing human pressure by avoiding more strongly human modified areas within their home range than in situations of lower human pressure. This finding is in line with regional-scale studies on lynx habitat use in Norway (Basille et al., 2013; Thorsen et al., 2022), underlining the importance of assessing habitat use across scales for understanding wildlife responses to human pressure. Lynx commonly face a trade-off between accessing prey and avoiding negative anthropogenic impacts, since important prey species, particularly roe deer (*Capreolus capreolus*), occur at higher densities in mixed-use landscapes characterized by higher levels of human modification (Basille et al., 2009; Gehr et al., 2017). Human pressure has commonly been identified as a key variable determining lynx habitat suitability, in line with our results. For example, (Ripari et al., 2022) recently found human disturbance to be the most important factor driving general patterns of home range selection by lynx across Europe. However, we here highlight that it is the interaction between human-pressure and refuge habitat availability (forest availability in our case) that enables lynx, and likely other large carnivores, to navigate the trade-off outlined above and to establish themselves and ultimately persist in human-dominated landscapes.

Several previous studies have highlighted temporal variation in large carnivore habitat use as an adaptation to human pressure, particularly increased nocturnality (Gaynor et al., 2018; Lamb et al., 2020). While the generally higher use of refuge habitats by lynx during daytime also reflects natural circadian activity patterns of a crepuscular and nocturnal hunter (Heurich et al., 2014; Hočevar et al., 2021), we also found a clear influence of human pressure on diurnal patterns of refuge habitat use (Thorsen et al., 2022). In both open landscapes providing little cover for avoiding humans, as well as in rugged landscapes offering effective cover for co-occurring near humans, lynx depended more strongly on refuge habitats during daytime (i.e., phases of high levels of human activity). Moreover, we also observed a direct effect of human modification on diurnal refuge habitat use under some conditions, as in open landscapes, lynx increased their use of forest cover with increasing human modification, thus partly confirming our second hypothesis. A strong dependence on refuge habitats for resting during daytime has been documented for other large carnivores occurring in open or human-dominated landscapes, such as lions in the African savannah (Suraci et al., 2019) or wolves in northwestern Iberia (Llaneza et al., 2016). In sum, we thus

highlight that not only large carnivores' overall activity patterns, but also diurnal patterns of refuge habitat use are shaped by human pressure at a broad scale.

Our findings confirmed our third hypothesis, showing that female lynx avoid human modified habitats more strongly during the first months after kittens are born when their movements are strongly constrained by proximity to the natal den (Breitenmoser et al., 1993; Jędrzejewski et al., 2002). This corroborates previous findings by (Bunnefeld et al., 2006), who observed female lynx selecting for locations further from human activity when having newborn kittens. The somewhat surprising pattern of lower use of human-modified habitats during the postnatal period by males in our dataset might be an artefact caused by generally higher risks associated with human-modified habitats during summer due to increased recreational activity by humans (Ordiz et al., 2011). As the postnatal period likely reflects the time of the highest sensitivity of lynx towards human pressure, the availability of suitable natal den sites for females might be an important limiting factor for the persistence of lynx in human-dominated landscapes (White et al., 2015).

Combining tracking datasets collected across several Eurasian lynx populations at a continental scale allowed us to provide new insights into how lynx adjust their habitat use in response to human pressure and refuge habitat availability. Such 'big' tracking datasets, enabled by large-scale collaborations and initiatives for harmonizing and sharing tracking datasets (Kranstauber et al., 2011; Urbano et al., 2021) are particularly valuable for large carnivore research as they allow understanding the adaptive capacity of species under different environment contexts and overcome the often small sample sizes of local studies, thereby providing important information to transboundary conservation efforts needed to safeguard many large carnivores (Thompson et al., 2021). Methodologically, our analysis demonstrates that using functional response models offers a simple, yet effective approach for understanding how the availability of multiple factors interactively shape patterns of wildlife habitat use. While functional response models have highlighted the context-dependence of habitat use in relation to habitat availability, they typically have been limited to univariate analyses (Northrup et al., 2022). We here show that functional responses themselves can be context dependent. The interactive effects of human pressure and refuge habitat availability on lynx habitat use we found, as well as the considerable temporal and sex-specific variation we observed underline the importance of considering complexity when assessing functional responses. We here demonstrate that such context-dependence can be analyzed in functional response models through multiple regressions including interaction effects. Thus, in sum, our study exemplifies how better data availability and improved

methodologies enable a more nuanced understanding of complex patterns of wildlife habitat use at broad scales (Cagnacci et al., 2010).

Although our findings suggest considerable flexibility of lynx in adapting to human pressure through adjusting their habitat use, it remains unclear which fitness costs are associated with these behavioral adjustments. Studies on large carnivore demography have commonly shown higher mortality in human-dominated landscapes (Lamb et al., 2020). Thus, while lynx seem able to behaviorally adjust to living in landscapes characterized by high levels of human pressure, the long-term viability of populations occurring in human-dominated landscapes remains unclear. Directly linking data on variation in habitat use to demographic data can help determining under which conditions actual coexistence between large carnivores and people is taking place or where carnivores' behavioral adjustments might create population sinks or ecological traps (Nisi et al., 2022). While studies from Scandinavia have found no clear effect of habitat characteristics on lynx survival (Andrén et al., 2022; López-Bao et al., 2019), it is unclear whether these findings also hold for more human-dominated landscapes such as Central Europe.

The ongoing comeback of large carnivores in Europe and other parts of the world provides unique possibilities for protecting these species and for restoring the ecological functions they provide. However, carnivore comebacks pose considerable challenges given increasing human-wildlife conflicts where carnivores and people co-occur (Carter and Linnell, 2016). Landscapes of coexistence require areas large carnivores perceive as 'safe enough' (i.e., that are not avoided due to fear of human-caused mortality) and where actual mortality levels remain low enough not to create population sinks (Oriol-Cotterill et al., 2015). Given the striking adaptive capacity of large carnivores highlighted in this study and elsewhere (Kautz et al., 2021; Suraci et al., 2019), human-caused mortality (e.g., from poaching, legal hunting and vehicle collisions) typically will remain the most limiting factor determining where coexistence between carnivores and people can take place (Lamb et al., 2020). Yet, our work highlights the critical role of refuge habitats as prerequisites for coexistence, allowing large carnivores to persist even at high levels of human pressure. Maintaining such refuges in human-dominated landscapes, particularly also beyond protected areas (e.g., military training grounds; Reinhardt et al., 2019) thus should be a key goal for large carnivore conservation and restoration efforts.

Acknowledgements

Supplementary Information

Table SI V-1: Overview of tracking datasets from different lynx populations.

Population	Number of individuals (GPS / VHF)	Share of male / female locations	Monitoring period	Number of locations
Alpine	58 (28/31)	0.52/0.48	1997 - 2021	56,620
Baltic	44 (17/28)	0.67/0.33	1991 - 2016	28,287
Bohemian-Bavarian-Austrian	19 (10/12)	0.53/0.47	1997 - 2013	17,472
Carpathian	17 (17/0)	0.9/0.1	2011 - 2021	26,537
Dinaric	21 (21/0)	0.63/0.37	2006 - 2021	15,864
Jura	23 (0/23)	0.36/0.64	1988 - 1998	9,595
Scandinavian	252 (137/137)	0.38/0.62	1993 - 2017	250,159
TOTAL	**434 (230/231)**	**0.47/0.53**	**1988 - 2021**	**417,648**

Table SI V-2: Summary of model variable distributions.

Variable	Scale	Min	10th Quantile	Mean	Median	90th Quantile	Max
Forest	Landscape	8.61	20.06	47.95	50.03	68.03	73.47
Human modification	Landscape	1.62	4.79	32.22	35.47	51.73	61.52
Rugged terrain	Landscape	10.59	20.67	103.03	82.3	254.78	337.46
Forest	Home range	3.04	16.24	59.32	66.67	84.21	97.5
Human modification	Home range	0.97	3.92	24.77	24.74	42.55	69.74
Rugged terrain	Home range	6.62	18.26	126.52	110.5	312.48	489.19
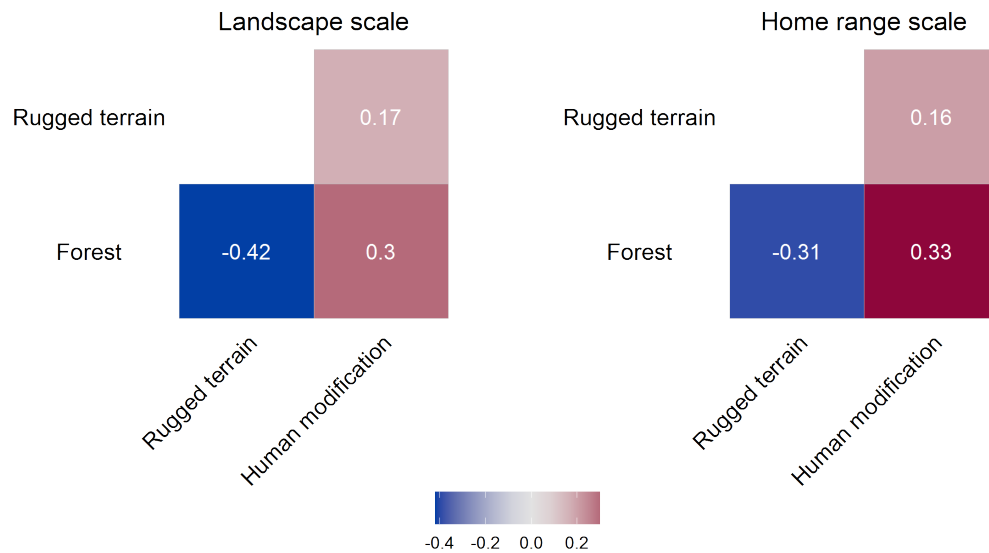
Figure SI V-1: Correlation matrix of model variables used at the landscape and home range scale.
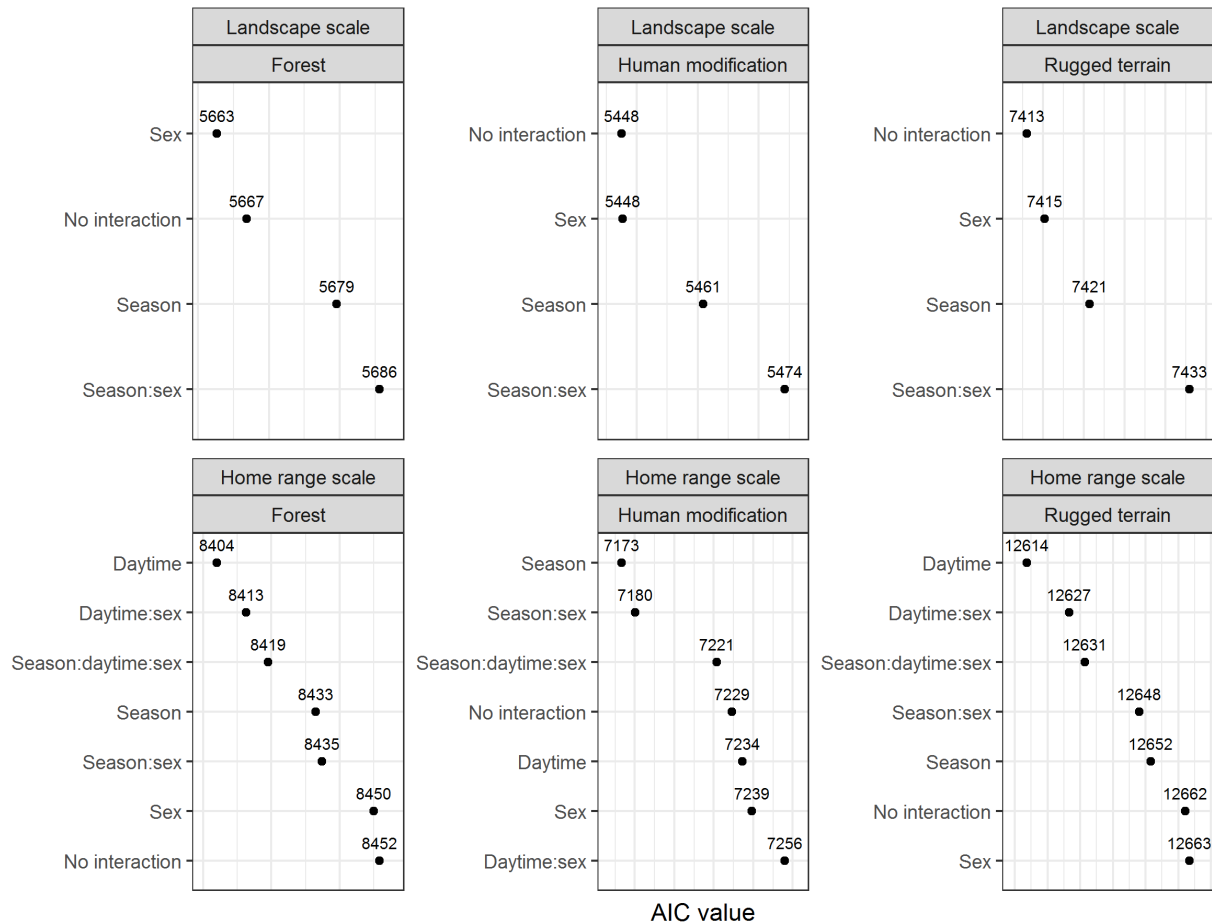
Figure SI V-2: Comparison of model support (AIC values) for different model setups of functional response models at the landscape scale (top panels) and home range scale (bottom panels). Model setups differ in terms of interacting variables (daytime, season, sex) used to account for temporal and sex-specific variation in lynx habitat use.

Table SI V-3: Overview of model coefficients for model setups selected based on AIC.

Forest: Landscape scale

Term	Estimate	SE	T-statistic	p value
Intercept	-9.69	5.79	-1.67	0.0944
forest	1.01	0.0825	12.3	1.04E-31
rugged_terrain	-0.0321	0.0426	-0.754	0.451
human_modification	1.97	0.167	11.8	1.64E-29
male	20.1	9.14	2.2	0.0285
forest:rugged_terrain	0.0053	5.11E-04	10.4	1.28E-23
forest:human_modification	-0.0262	0.00273	-9.58	1.31E-20
rugged_terrain:human_modification	-0.00574	8.78E-04	-6.54	1.12E-10
forest:male	-0.249	0.123	-2.02	0.0433
rugged_terrain:male	-0.131	0.0735	-1.79	0.0744
human_modification:male	-0.589	0.225	-2.61	0.00914
forest:rugged_terrain:male	-8.14E-04	7.84E-04	-1.04	0.299
forest:human_modification:male	0.00964	0.0039	2.47	0.0136
rugged_terrain:human_modification:male	0.00344	0.00133	2.58	0.0102

Forest: Home range scale

Term	Estimate	SE	T-statistic	p value
Intercept	18.1	2.14	8.47	6.78E-17
forest	0.922	0.029	31.8	4.65E-163
rugged_terrain	-0.0404	0.0136	-2.96	0.00312
human_modification	0.646	0.0731	8.83	3.44E-18
night	-0.906	3.23	-0.281	0.779
forest:rugged_terrain	1.28E-04	1.54E-04	0.83	0.407
forest:human_modification	-0.0107	0.00105	-10.2	1.57E-23
rugged_terrain:human_modification	8.42E-04	2.61E-04	3.23	0.00127
forest:night	-0.0331	0.0431	-0.768	0.442
rugged_terrain:night	0.0046	0.021	0.219	0.827
human_modification:night	-0.194	0.122	-1.59	0.112
forest:rugged_terrain:night	1.22E-04	2.37E-04	0.514	0.607
forest:human_modification:night	0.00288	0.00171	1.68	0.0928
rugged_terrain:human_modification:night	-3.35E-04	4.11E-04	-0.815	0.415

Human modification: Landscape scale

Term	Estimate	SE	T-statistic	p value
Intercept	-9	3.81	-2.36	0.0184
forest	0.266	0.0532	5	6.95E-07
rugged_terrain	0.112	0.0294	3.8	1.56E-04

human_modification	0.415	0.0962	4.32	1.79E-05
forest:rugged_terrain	-0.00279	3.23E-04	-8.62	3.74E-17
forest:human_modification	0.00413	0.00163	2.53	0.0116
rugged_terrain:human_modification	6.85E-04	5.47E-04	1.25	0.211

Human modification: Home range scale

Term	Estimate	SE	T-statistic	p value
Intercept	-1.8	1.46	-1.23	0.217
forest	0.017	0.0195	0.869	0.385
rugged_terrain	0.0215	0.00938	2.29	0.0221
human_modification	1.11	0.0522	21.2	3.99E-85
rest_of_year	0.401	1.97	0.204	0.838
forest:rugged_terrain	-6.14E-05	1.06E-04	-0.579	0.563
forest:human_modification	-0.00195	7.37E-04	-2.64	0.00834
rugged_terrain:human_modification	-5.05E-04	1.81E-04	-2.79	0.00537
forest:rest_of_year	0.0258	0.0264	0.979	0.328
rugged_terrain:rest_of_year	0.00168	0.0127	0.132	0.895
human_modification:rest_of_year	0.0329	0.0712	0.462	0.644
forest:rugged_terrain:rest_of_year	-2.84E-05	1.43E-04	-0.199	0.842
forest:human_modification:rest_of_year	-4.43E-04	0.001	-0.441	0.66
rugged_terrain:human_modification:rest_of_year	-2.70E-05	2.46E-04	-0.11	0.912

Rugged terrain: Landscape scale

Term	Estimate	SE	T-statistic	p value
Intercept	31.4	13.7	2.29	0.0222
forest	-0.856	0.191	-4.48	8.72E-06
rugged_terrain	1.07	0.106	10.1	1.10E-22
human_modification	-0.297	0.346	-0.857	0.391
forest:rugged_terrain	-7.60E-05	0.00116	-0.0655	0.948
forest:human_modification	0.0134	0.00587	2.28	0.0231
rugged_terrain:human_modification	0.00386	0.00197	1.96	0.05

Rugged terrain: Home range scale

Term	Estimate	SE	T-statistic	p value
Intercept	161	11.5	14	1.47E-41
forest	-1.67	0.156	-10.7	1.04E-25
rugged_terrain	0.478	0.0733	6.52	1.03E-10
human_modification	0.929	0.393	2.36	0.0183
night	-27.3	17.3	-1.57	0.116
forest:rugged_terrain	0.00583	8.27E-04	7.05	2.94E-12
forest:human_modification	-0.0254	0.00561	-4.52	6.73E-06

rugged_terrain:human_modification	0.00827	0.0014	5.9	4.63E-09
forest:night	0.39	0.231	1.69	0.092
rugged_terrain:night	-0.0185	0.113	-0.164	0.87
human_modification:night	-0.473	0.654	-0.723	0.47
forest:rugged_terrain:night	-0.00101	0.00127	-0.794	0.427
forest:human_modification:night	0.00457	0.00919	0.498	0.619
rugged_terrain:human_modification:night	0.00112	0.00221	0.506	0.613
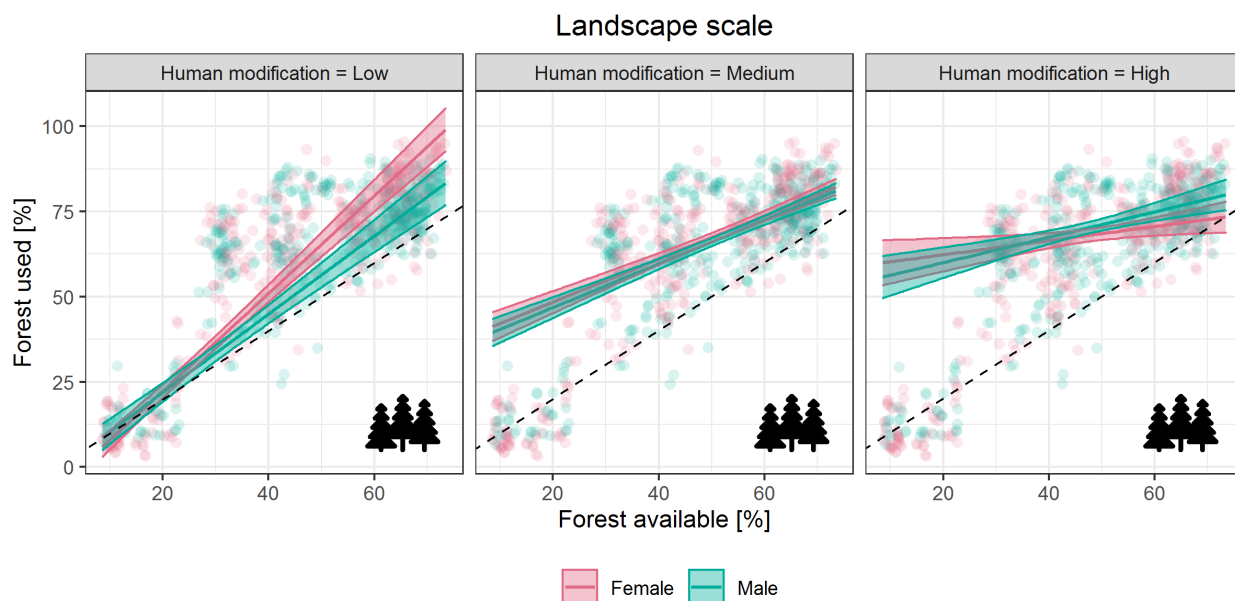
Figure SI V-3: Functional responses of forest use at the landscape scale (i.e., home range placement) depending on human modification and sex. Dashed diagonal lines indicate use proportional to availability. Low, medium, and high levels of human modification correspond to 10th, 50th and 90th percentile values in our dataset. Marginal model effects with 95% confidence intervals and partial residuals are colored by sex. Other variables are kept at their mean values for computing marginal effects.
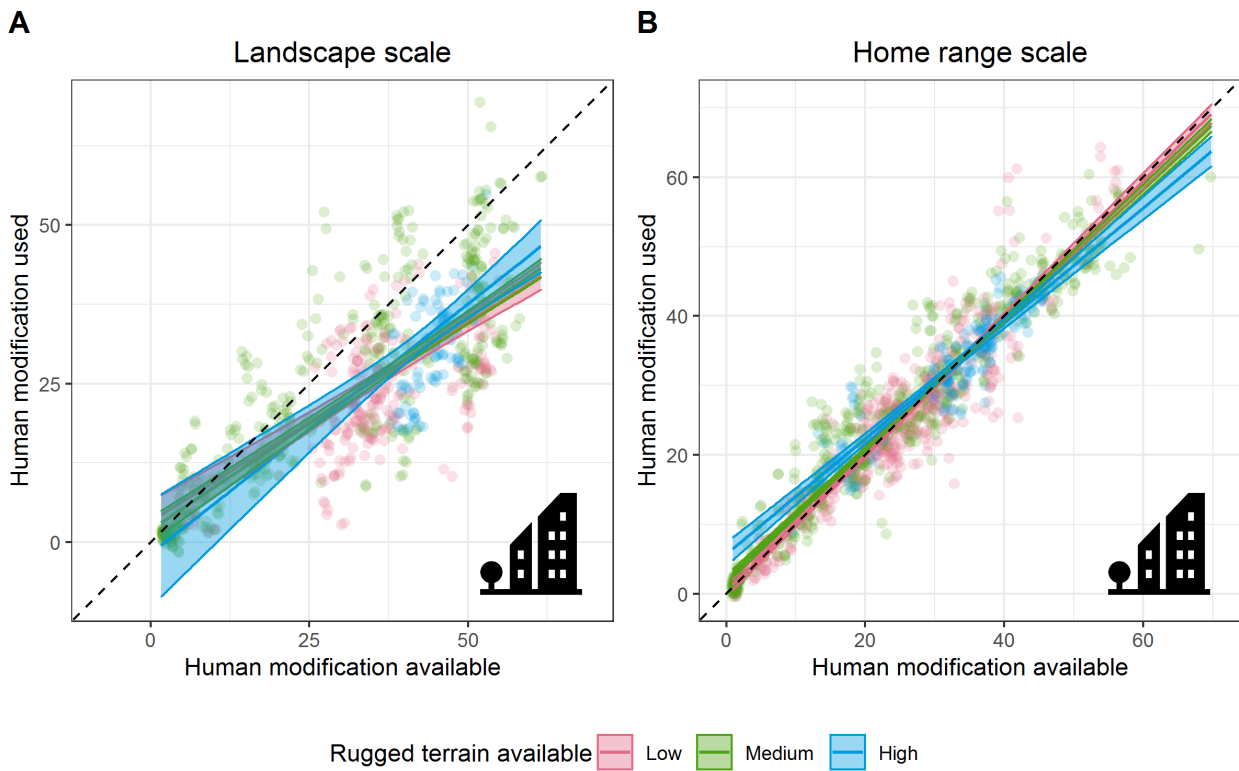
Figure SI V-4: Association of lynx with different levels of the human modification index (Kennedy et al., 2019) with varying availability of rugged terrain. Plots show functional responses in habitat use (i.e., use in dependence on availability), with dashed diagonal lines indicating proportional use. Marginal model effects with 95% confidence intervals and partial residuals for low, medium, and high levels of rugged terrain (10th, 50th and 90th percentile in our dataset) are highlighted in different colors. Other variables are kept at their mean values for computing marginal effects. In contrast to the effect of forest on human modification use (see Figure V-4), no clear effect of rugged terrain was detected.

Chapter VI:
Synthesis

1   Summary and main conclusions

The growing availability of satellite image and animal tracking data is opening new opportunities for advancing habitat modeling and thereby improve our capacity to assess wildlife habitat use and suitability across space and time. Yet, much of this potential has remained untapped, since approaches making full use of these data sources in habitat models have been lacking. Specifically, regarding the use of satellite imagery, approaches have been missing for linking habitat models to the full potential of global, free and multi-decadal satellite image archives for monitoring spatiotemporal habitat dynamics (Coops and Wulder, 2019; Randin et al., 2020). Concerning the use of animal tracking data, a central challenge lies in developing approaches that allow to capture and reveal the context-dependency of wildlife habitat use, for example when integrating tracking datasets across large spatial extents and wildlife populations (Northrup et al., 2022). In this thesis, I aimed to develop approaches for harnessing the potential of big satellite image and animal tracking data in habitat models. Specifically, my goal was to address the abovementioned research gaps by developing and advancing approaches for (1) the direct use of Landsat time series in habitat models for characterizing wildlife habitat dynamics and (2) integrating animal tracking datasets across wildlife populations for assessing habitat suitability and variation in habitat use over large spatial extents. Applying these approaches to different mammal species in Europe, my research also provided important new ecological insights about large mammal behavior, habitat use and distribution, thus offering potentially valuable information and datasets for wildlife management and conservation planning.

My thesis contributes to the larger goal of harnessing the potential of big satellite image and animal tracking data for habitat modeling in different ways. The individual research chapters (chapters II-V) focus on habitat modeling at different spatial and temporal scales (ranging from fine spatial and temporal resolutions to large-area and long-term assessments; see Figure I-2) and relate to both sides of the modeling equation of habitat models (i.e., satellite-based variables as predictors and animal tracking data as a response variable in habitat models). The first two research chapters focus on approaches for deriving satellite-based predictor variables from Landsat time series for characterizing spatiotemporal habitat dynamics continuously and at fine scales. In chapter II, I developed an approach for using Landsat-based spectral-temporal metrics in habitat models as *habitat metrics*. Building on this, in chapter III I extended the approach for reconstructing long-term habitat dynamics

using harmonized, annual time series of Landsat-based metrics. The latter two research chapters of the thesis focus on approaches for integrating animal tracking datasets across wildlife populations to assess habitat suitability and use over large spatial extents. In chapter IV, I compared modeling approaches for incorporating regional variation in habitat use in large-area habitat assessments. Finally, in chapter V, I assessed continental-scale variation in habitat use by Eurasian lynx, extending a modeling approach for characterizing functional responses (i.e., environmentally related variation) in habitat use. Together, the insights gained from the individual research chapters allowed me to answer the two overarching research questions.

Research question 1: *What is the potential of using Landsat imagery in habitat models for characterizing wildlife habitat across space and time?*

The first two research chapters (chapters II and III) showed that spectral-temporal metrics offer an effective approach for deriving change-sensitive and consistent predictor variables from Landsat time series that enable a continuous monitoring of wildlife habitat dynamics across space and time. In chapter II, I found that a suite of spectral-temporal metrics, categorized into habitat metrics characterizing different aspects of large mammal habitats, improved the performance of habitat models for three large mammal species (Eurasian lynx, red deer, and roe deer) when compared to the use of land-cover maps. The finding that performance increases were particularly high for seasonal habitat models differentiating between summer and winter habitat use highlighted the potential of spectral-temporal metrics for capturing intra-annual variation in habitat conditions. Moreover, habitat metrics allowed to characterize fine-scale spatial variation in habitat suitability related to forest structure (i.e., forest type and age classes), demonstrating that the direct use of continuous satellite-based variables in habitat models allows adding more nuance to habitat assessments by describing gradients in suitability within land-cover types.

Chapter III showed that spectral-temporal metrics harbor great potential for reconstructing long-term habitat dynamics. Using annual time series of metrics and linking them to a time series of animal tracking data allowed for detailed reconstructions of habitat suitability dynamics for deer caused by forest disturbance and recovery. The results of this chapter also underscore the importance of ensuring temporal consistency when working with time series of satellite-based variables in habitat models, as the harmonization of metric time series through a time series segmentation algorithm improved the robustness of the habitat reconstructions. Specifically, habitat time series were less affected by satellite observation

density and habitat models were more transferable in time than when using raw, unharmonized metric time series. The habitat time series provided novel insights into long-term responses by deer to forest disturbance, highlighting long-lasting impacts of forest disturbances on deer habitat suitability. More broadly, the findings of this chapter demonstrate the great potential of linking habitat models to the unique temporal depth of the Landsat image archive for assessing long-term habitat dynamics, allowing to improve the understanding of responses by animals to landscape dynamics.

While highlighting several clear advantages of spectral-temporal metrics, my research also revealed some of their limitations as predictors variables in habitat models. First, although metrics derived from multi-spectral satellite imagery can be linked to different habitat aspects by using specific spectral indices, as done in chapter II, a set of spectral-temporal metrics remains a complex and high-dimensional dataset that is challenging to interpret. In comparison, categorical or continuous map products (e.g., land-cover maps or forest age maps, respectively), which can be derived by integrating satellite imagery and ground-truth reference data in predictive models, can offer easier interpretable variables. The sometimes indirect and correlative relationships between satellite-based metrics and wildlife habitat use can hamper the interpretation of species' responses in habitat models, as well as potentially limit their transferability across space and time. As a second potential limitation, spectral-temporal metrics are less effective than abovementioned map products at summarizing habitat conditions at broad scales. For example, while the share of forest cover provides an ecologically meaningful characterization of habitat conditions at the scale of large mammal home ranges (as used in chapters IV and V), summarizing spectral-temporal metrics across large areas leads to an averaging-out of fine-scale variation and hence a loss of information.

Despite these limitations, my research showed that linking habitat models to the Landsat satellite image archive through the use of spectral-temporal metrics as predictor variables allows to strongly boost their capacity for monitoring wildlife habitat dynamics. The main strengths of spectral-temporal metrics lie in their ability to capture fine-scale spatial variation in habitat characteristics, their capacity for describing temporal variation in habitat conditions (both in terms of seasonal variability as well as for reconstructing long-term dynamics), and finally, in the possibility to derive these metrics directly from image data without the need of reference datasets. Given the global, free, and multi-decadal availability of the Landsat image record as well as the possibility to generate spectral-temporal metrics automatically (e.g., using cloud-computing platforms such as the Google Earth Engine), the

approaches developed in my thesis offer widely applicable and cost-effective methods for improving habitat models.

Research question 2: *How can animal tracking data be integrated across wildlife populations for large-area assessments of habitat suitability and use?*

Chapters IV and V highlighted the importance of considering environmentally related variation in habitat use (also referred to as *functional responses*; Mysterud & Ims, 1998) when combining animal tracking datasets across multiple populations in large-area assessments of habitat suitability and use. The comparison of different approaches for integrating tracking datasets for large-area habitat mapping (chapter IV) showed that incorporating non-stationarity (i.e., regional variation) in habitat selection improved the predictive performance of habitat models, particularly when variation in habitat use was modeled as a function of environmental variation between study sites rather than spatial proximity. The findings of this chapter also revealed that the choice of modeling approach used to integrate tracking datasets can affect habitat mapping results: Both global approaches pooling all tracking datasets for model training as well as local approaches combining the predictions of site-specific models were able to achieve accurate habitat predictions, but habitat patch maps derived from global and local approaches showed considerable differences, pointing to a need for assessing the impacts of modeling choices on mapping results and hence potential conservation recommendations.

Chapter V demonstrated that the combination of tracking datasets across several populations of the same species opens opportunities for advancing our understanding of the adaptive capacity of wildlife to human pressures. The continental-scale assessment of functional responses by lynx, the first such analysis for any large carnivore at this scale, provided new insights into how lynx adjust their habitat use in response to varying human pressure and under different environmental settings, particularly highlighting the importance of refuge habitats for lynx (i.e., forest cover and rugged terrain) in this context. Extending the previously used univariate approach based on regressing habitat use against habitat availability (Holbrook et al., 2019) to a multivariate approach capturing the interactive effects of multiple factors on functional responses was important to allow understanding how human pressure and refuge habitat availability interact in shaping lynx habitat use at a continental scale. This highlights the importance of treating variation in habitat use as a function of multiple habitat factors when integrating tracking datasets across wildlife populations (Matthiopoulos et al., 2011; Northrup et al., 2022). In addition, the results of

chapter V also revealed considerable diurnal and seasonal variation in lynx habitat use, underscoring that also temporal variation in habitat use should be considered in large-area assessments of habitat use.

Although relating variation in lynx habitat use to gradients in environmental conditions and human pressure proved effective for modeling habitat use in both studies, other factors influencing habitat use might be important to consider when integrating tracking datasets across wildlife populations. Specifically, factors such as genetic variation, population density and species interactions might be important to consider in order to understand and predict variation in habitat use across populations (Smith et al., 2019; van Beest et al., 2014; Wisz et al., 2013). The incorporation of these factors in habitat models is, however, often made difficult because of the lack of appropriate datasets.

In sum, both chapters showed that accounting for context-dependency and specifically environmentally related variation in habitat use is critically important when analyzing wildlife habitat use across large spatial extents. As demonstrated by my research, functional responses in habitat use (i.e., relating variation in habitat use to broad-scale habitat availability) are a powerful and widely applicable analytical concept useful for both explaining variation in habitat use across environmental gradients as well as for generating more accurate and transferable predictions of habitat suitability (Holbrook et al., 2019; Matthiopoulos et al., 2011). By reflecting the environmental context-dependency of habitat use, the fundamental trade-off between the specificity and generality of habitat models (i.e., capturing local variation versus ensuring overall transferability) can, at least partially, be overcome (Paton and Matthiopoulos, 2016). More broadly, both studies demonstrate the large potential of integrating animal tracking datasets across populations for advancing our understanding of wildlife habitat distributions and habitat use.

2   Cross-cutting insights

In addition to answering the two overarching research questions, the research of this thesis yielded more general insights on opportunities and challenges of harnessing big satellite image and animal tracking data for habitat modeling. Specifically, four cross-cutting insights emerged from my thesis.

First, my findings underscore the importance of moving beyond static descriptions of wildlife habitat in habitat models (Franklin, 2010). Both habitat conditions (i.e., the

environmental characteristics of wildlife habitats) as well as habitat use (i.e., species' responses to habitat conditions) often are highly dynamic across space and time. As shown in this thesis, both satellite imagery and animal tracking data are potentially powerful tools for capturing these dynamics in habitat models. While satellite-based predictor variables allow describing temporal dynamics in habitat conditions at different scales (e.g., intra-annual habitat variation in chapter II and disturbance-related long-term dynamics in chapter III), animal tracking data reflects variation in habitat use across time (e.g., diurnal and seasonal habitat use patterns in chapters II, III, and V) and space (e.g., environmentally related variation in habitat use in chapters IV and V). Given adequate approaches for deriving predictor variables and for modeling species' responses, the integration of satellite image and animal tracking data thus will help moving towards *dynamic habitat models* that will improve our understanding of habitat distributions and species' ecology.

Second, my findings showed that habitat modeling should consider the hierarchical, scale-dependent nature of habitat use. The selection of habitats by animals is a multi-scale process, in which broad-scale selection patterns (i.e., the selection of home ranges within the wider landscape) constrain fine-scale habitat use (i.e., movements within home ranges; Mayor et al., 2009). A proper understanding of species' habitat use thus requires approaches that allow analyzing habitat use across multiple scales, as I used in this thesis for the scale-integrated modeling of lynx habitat in chapter IV as well as for the assessment of functional responses by lynx across scales in chapter V. Animal tracking offers a particularly powerful source of information in this context, as dense time series of animal locations provided by tracking datasets can easily be summarized at different scales for characterizing habitat use (e.g., by deriving home ranges for describing broad-scale use and using individual locations for characterizing fine-scale use; DeCesare et al., 2012).

Third, related to the scale-dependency of habitat use, my thesis also highlights the importance of matching the spatiotemporal scale of environmental predictor variables with the habitat use patterns of interest. This principle is reflected throughout all research chapters of my thesis, for example in using spectral-temporal metrics capturing intra-annual variability in habitat conditions for seasonal habitat modeling in chapter II, in temporally matching time series of deer tracking data with Landsat time series characterizing forest disturbance and recovery dynamics in chapter III, and in deriving environmental variables at different spatial scales for the scale-integrated habitat modeling and the assessment of functional responses across scales in chapters IV and V. In this context, Landsat-based spectral-temporal metrics are particularly powerful for capturing both seasonal and long-

term temporal variation in habitat use, while in the spatial domain, they are most suited for characterizing fine-scale habitat use. More broadly, my research demonstrates that the combination of satellite image and animal tracking data allows for a large flexibility in characterizing habitat suitability and use across different spatial and temporal scales.

Finally, my findings underscore the importance of evaluating the spatial and temporal transferability of habitat models based on satellite image and animal tracking data. As habitat models rely on correlative relationships between environmental variables and habitat use patterns, which in turn may fail to properly capture underlying processes, they are prone to issues regarding model transferability (Yates et al., 2018). Importantly, the findings of my thesis demonstrate that methods for ensuring consistency in satellite-based predictor variables (e.g., the harmonization of metric time series in chapter III), matching variables on habitat use and environmental predictors (e.g., the multi-temporal habitat modeling approach in chapter III) as well as approaches for considering context-dependence in habitat models (incorporating environmentally related variation in large-area habitat models in chapter IV) can help to improve the transferability of habitat models. This demonstrates that adequate approaches for the use of satellite image and animal tracking data can allow for more robust and transferable habitat models that help reliably assessing habitat suitability and use across space and time.

3   Implications for wildlife conservation and management

Several findings of this thesis have implications for the conservation and management of large mammals in Europe and elsewhere, given the novel insights provided into the ecology of two of most widespread and abundant large ungulate species (red deer and roe deer) as well as a regionally threatened, but recovering large carnivore (Eurasian lynx). Chapter III showed that forest disturbances can lead to long-lasting and strong improvements in habitat suitability for deer, particularly red deer. As forest disturbances have strongly increased in Europe and elsewhere (Millar and Stephenson, 2015; Senf et al., 2018) and are projected to further increase because of climate change (Seidl et al., 2017), they are an increasingly important driver of habitat dynamics for large mammals. Regarding deer and other large herbivores, this trend has the potential to increase conflicts with forestry, as the concentration of deer browsing in forest gaps opened by disturbance can inhibit forest regeneration (Kuijper et al., 2009; Tremblay et al., 2007). Deer overabundance already is regionally leading to considerable negative economic and ecological effects on forests (Côté et al.,

2004). Considering forest disturbance impacts on ungulate habitat suitability, browsing behavior as well as potential impacts on population dynamics (Gaillard et al., 2003) thus will be increasingly important in the management of ungulate populations, for example when setting hunting quotas. Approaches for the satellite-based monitoring of disturbance-related habitat dynamics, as developed in this thesis, could be highly useful for informing wildlife management in this context.

The findings of chapters IV and V provide important information for the conservation of Eurasian lynx. Specifically, the assessment of potential habitat suitability across the European continent in chapter IV highlighted large areas of unoccupied but suitable lynx habitat, indicating considerable potential for further range expansions. The habitat suitability maps provide the first continental-scale, yet high-resolution dataset on lynx habitat, offering an important basis for evaluating the potential of reintroductions or assessing habitat connectivity between populations. In fact, the maps are already used by the World Wide Fund For Nature (WWF) for an assessment of lynx habitat availability and connectivity in Belgium. Such assessments are particularly important in the case of the Eurasian lynx in Europe, as the success of recolonization through natural dispersal by this species so far has been limited (Bonn Lynx Expert Group, 2021; Linnell et al., 2009).

In addition, chapter V revealed a remarkable capacity by lynx to adapt to human pressures by adjusting its habitat use. Yet, the findings also highlighted that the availability of refuge habitats enabling lynx to avoid human pressure (e.g., forests and rugged terrain) are critically important to allow them to persist in human-dominated landscapes. This underscores that maintaining such refuges, particularly also beyond protected areas (e.g., military training grounds; Reinhardt et al., 2019) should be a central goal for large carnivore conservation and restoration efforts in human-dominated landscapes. Overall, the findings of both chapters support the view that neither habitat availability (Magg et al., 2016), nor the flexibility of lynx to adapt to co-occurring in human-dominated landscapes (Bouyer et al., 2015a), but rather human-caused mortality (e.g., through poaching, legal hunting, and vehicle collisions) will likely remain to most crucial limiting factor for further population recoveries and range expansions of lynx in Europe (Heurich et al., 2018).

4   Further research and outlook

This thesis helped advancing approaches for harnessing the potential of big satellite image and animal tracking data in habitat models. Yet, some open questions remain, and my findings can form the basis for new research avenues.

While the Landsat archive will remain unparalleled in its potential for assessing long-term habitat changes, an increasing number and diversity of satellite sensors is available that can be used for deriving predictor variables for habitat modeling. Adapting metric-based compositing approaches as used in this thesis also for other types of sensors, such as radar (e.g., Sentinel 1; Bae et al., 2019), space-borne lidar (e.g., GEDI; Burns et al., 2020), hyperspectral (e.g., EnMap; Leitão et al., 2015) or very high-resolution sensors (e.g., 3m PlanetScope imagery; Wicaksono & Lazuardi, 2018) could allow for improved characterizations of certain habitat characteristics. For example, radar and lidar data is better suited for capturing vertical habitat structure (e.g., forest height) than optical imagery (Hyde et al., 2006), which is an important habitat feature for many wildlife species (Culbert et al., 2013). Similarly, satellite time series simultaneously offering high spatial and temporal resolutions, available for example from PlanetScope imagery or through the fusion of Landsat and Sentinel 2 imagery (Claverie et al., 2018) will allow to better match the spatiotemporal resolution of habitat characterizations with fine-scale movement decisions by animals, as modeled in approaches such as step-selection functions (Thurfjell et al., 2014). In sum, the growing availability of satellite image data is continuously enhancing the potential of satellite-based variables for habitat modeling (He et al., 2015; Leitão and Santos, 2019).

For the analyses conducted for this thesis, I made use of a cloud-computing platform for generating environmental predictor variables (i.e., the Google Earth Engine; Gorelick et al., 2017) as well as a continental-scale tracking database for characterizing wildlife habitat use (i.e., the EUROLYNX database; Heurich et al., 2021). This enabled modeling habitat suitability and use across large spatial extents and at fine spatial and temporal scales. A further integration of satellite image and animal tracking data sources in online, cloud-computing infrastructures has enormous potential to advance the combined use of these datasets for habitat modeling. Linking publicly available satellite image archives with open animal tracking databases (e.g., Movebank; Kranstauber et al., 2011) in cloud-computing platforms that offer tools for processing satellite imagery as well as habitat modeling would open numerous possibilities for further up-scaling habitat models, potentially allowing for global, multi-species and near real-time habitat assessments (Crego et al., 2022).

The findings of Chapter III demonstrated the large potential of linking habitat models with long-term satellite image records for continuously mapping dynamics in habitat suitability. Linking such habitat time series derived from satellite-based habitat modeling to data on population dynamics (i.e., changes in the distribution and abundance of species) is another promising potential research avenue. How to infer population dynamics from habitat modeling is an active field of research (Matthiopoulos et al., 2019, 2015). Establishing a clearer link between mapped habitat changes and distribution and abundance dynamics would strongly boost the potential of habitat modeling as a tool for biodiversity monitoring, for example in the context of operationalizing the monitoring of Essential Biodiversity Variables on species' populations (Jetz et al., 2019; Kissling et al., 2018).

My research highlighted the importance of considering context-dependency in wildlife habitat use when applying habitat models, particularly also when integrating wildlife datasets across large geographic extents, environmental gradients and across different populations of the same species. While the approaches used in this thesis mainly focused on environmentally related variation in habitat use (i.e., functional responses in habitat use; chapters IV and V), other potential sources of variation can be incorporated in habitat modeling. For example, genetic variation, species interactions, and population density constitute other potentially important drivers of variation in habitat use across populations (Avgar et al., 2020; Fletcher, 2007). Methods to account for these phenomena in habitat models have been proposed (Smith et al., 2019; van Beest et al., 2014; Wisz et al., 2013). Developing modeling approaches that allow disentangling the influence of several different sources of variation in habitat use (e.g., individual-level variation, environmental variation, genetic variation, species interactions, and population density) could help further improve the ability of habitat models to predict habitat suitability robustly across space and time and will lead to a better understanding of what drives variation in habitat use by wildlife.

Overall, the new wealth of information offered by big satellite image and animal tracking data has already led to an emergence of a new generation of habitat models that allows to better understand wildlife behavior and provide more accurate information on species' habitats and their dynamics (Neumann et al., 2015; Randin et al., 2020). The further integration of these data sources and the advancement of approaches for harnessing their potential in habitat models will continue to improve our ability to monitor and understand biodiversity dynamics and thus, more generally, support efforts to restore and safeguard biodiversity across the globe.

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Eidesstattliche Erklärung

Hiermit erkläre ich, die vorliegende Dissertation selbstständig und ohne Verwendung unerlaubter Hilfe angefertigt zu haben. Die aus fremden Quellen direkt oder indirekt übernommenen Inhalte sind als solche kenntlich gemacht. Die Dissertation wird erstmalig und nur an der Humboldt-Universität zu Berlin eingereicht. Weiterhin erkläre ich, nicht bereits einen Doktortitel im Fach Geographie zu besitzen. Die dem Verfahren zu Grunde liegende Promotionsordnung ist mir bekannt.

Julian Oeser

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