University of Zagreb

FACULTY OF SCIENCE

DEPARTMENT OF BIOLOGY

Matko Bišćan

POTENTIAL OF PANNONIA PLAIN FOR WOLVES RECOLONIZATION: AN INTEGRATED APPROACH THROUGH MODELLING PREDICTIONS AND MONITORING OF THE RECOLONIZATION PROCESS

DOCTORAL THESIS

Zagreb, 2026

University of Zagreb

FACULTY OF SCIENCE

DEPARTMENT OF BIOLOGY

Matko Bišćan

POTENTIAL OF PANNONIA PLAIN FOR WOLVES RECOLONIZATION: AN INTEGRATED APPROACH THROUGH MODELLING PREDICTIONS AND MONITORING OF THE RECOLONIZATION PROCESS

DOCTORAL THESIS

Mentors:
Prof. Alessandro Massolo
Prof. Ivana Maguire

Zagreb, 2026

Sveučilište u Zagrebu

PRIRODOSLOVNO-MATEMATIČKI FAKULTET

BIOLOŠKI ODSJEK

Matko Bišćan

POTENCIJAL PANONSKE NIZINE ZA REKOLONIZACIJU VUKOVA - INTEGRIRANI PRISTUP MODELIRANJEM PREDVIĐANJA I PRAĆENJA PROCESA REKOLONIZACIJE

DOKTORSKI RAD

Mentori:
dr.sc. Alessandro Massolo, prof.
dr.sc. Ivana Maguire, prof.

Zagreb, 2026.

This doctoral thesis was prepared at the Department of Biology of the Faculty of Science, University of Zagreb, under the supervision of Prof. Alessandro Massolo, PhD, and Prof. Ivana Maguire, PhD, within the framework of the University Postgraduate Doctoral Study in Biology at the Department of Biology, Faculty of Science, University of Zagreb. It was carried out with the support of EKONERG – Energy and Environmental Protection Institute, Zagreb, where the author was employed during the doctoral research period.

University of Zagreb Doctoral Thesis

Faculty of Science

Department of Biology

POTENTIAL OF PANNONIA PLAIN FOR WOLVES RECOLONIZATION: AN INTEGRATED APPROACH THROUGH MODELLING PREDICTIONS AND MONITORING OF THE RECOLONIZATION PROCESS

MATKO BIŠĆAN

Department of Biology, Faculty of Science, University of Zagreb

The thesis aims to evaluate whether wolves could reestablish a viable population in the Pannonian part of Croatia by combining landscape and population modelling with empirical monitoring. It uses camera trap data from a global meta-analysis and ranger-based surveys to examine how large carnivores shape trophic structure in different contexts and to test the feasibility of camera trapping as a long-term monitoring tool. Results show that top-down effects of large carnivores as top predator on mesopredators and prey are generally weak and context dependent, indicating that wolf recolonization alone will not automatically restore "ideal" trophic pyramids. Spatially and temporally explicit models suggest that wolf recolonization in Pannonia is realistically possible, and could even unfold gradually through natural succession, particularly if major transport corridors and other barriers are mitigated, functional connectivity is improved and human-caused mortality is reduced as part of integrated, adaptive management. Overall, the thesis demonstrates that successful wolf return to the Pannonian Plain depends not only on ecological suitability, but on a broader rewilding framework that aligns habitat restoration, conflict mitigation and long term, camera trap-based monitoring in support of coexistence.

(144 pages, 183 references, original language: English)

Keywords: large carnivores, trophic structure, ecological connectivity, population dynamics, camera traps, adaptive management

Mentors: Alessandro Massolo, Prof. PhD

Ivana Maguire, Prof. PhD

Reviewers: Sven Jelaska, Prof. PhD

Duje Lisičić, Prof. PhD

Magda Sindičić, Prof. PhD

Sveučilište u Zagreb Doktorski rad

Prirodoslovno-matematički fakultet

Biološki odsjek

POTENCIJAL PANONSKE NIZINE ZA REKOLONIZACIJU VUKOVA - INTEGRIRANI PRISTUP MODELIRANJEM PREDVIĐANJA I PRAĆENJA PROCESA REKOLONIZACIJE

MATKO BIŠĆAN

Biološki odsjek, Prirodoslovno-matematički fakultet, Sveučilište u Zagrebu

Cilj ove disertacije je procijeniti mogu li vukovi ponovno uspostaviti održivu populaciju u panonskom dijelu Hrvatske kombiniranjem modeliranja ekosustava i populacijske dinamike s empirijskim monitoringom. U radu se koriste podaci s fotozamki iz globalne metaanalize te istraživanja koje su proveli čuvari prirode kako bi se ispitalo na koji način velike zvijeri oblikuju trofičku strukturu u različitim kontekstima te kako bi se provjerila izvedivost fotozamki kao alata za dugoročni monitoring. Rezultati pokazuju da su ″top-down″ učinci velikih zvijeri kao vršnih predatora na mezopredatore i plijen općenito slabi i ovisni o kontekstu, što upućuje na to da sama rekolonizacija vuka neće automatski obnoviti „idealne“ trofičke piramide. Prostorno i vremenski eksplicitni modeli ukazuju da je rekolonizacija vuka u Panoniji realno moguća, te da bi se mogla postupno odvijati prirodnom sukcesijom, osobito ako se ublaže utjecaji fragmentacija glavnih prometnica i drugih barijera, poboljša funkcionalna povezanost te smanji smrtnost uzrokovana čovjekom u sklopu integriranog, adaptivnog upravljanja. Sveukupno, disertacija pokazuje da uspješan povratak vuka u Panonsku nizinu ne ovisi samo o ekološkoj pogodnosti, nego o širem okviru obnove prirode koji usklađuje restauraciju staništa, smanjenje konflikata te dugoročni monitoring temeljen na fotozamkama u funkciji suživota.

(144 stranica, 183 literaturnih navoda, jezik izvornika: engleski)

Ključne riječi: velike zvijeri, trofička struktura, ekološka povezanost, populacijska dinamika, fotozamke, adaptivno upravljanje

Mentori: dr.sc. Alessandro Massolo, prof.

dr.sc. Ivana Maguire, prof.

Ocjenjivači: dr.sc. Sven Jelaska, prof.

dr.sc. Duje Lisičić, izv.prof.

dr.sc. Magda Sindičić, izv.prof.

ACKNOWLEDGEMENTS

I would also like to express my sincere gratitude to my supervisors, Prof. Alessandro Massolo and Prof. Ivana Maguire, for their continuous guidance and support throughout my doctoral studies. I am particularly thankful to Prof. Massolo for all his expert and critical insights that improved the scientific quality of this work, and to Prof. Maguire for her professional advice, unwavering patience, and encouragement. Her guidance often reminded me to persevere and helped me see that there was light at the end of the tunnel.

I would like to especially thank Dr. Dušan Jelić for his valuable advice, field knowledge, countless meetings, and for always finding time to discuss and support the development of this research. I am also grateful to BIOTA Ltd. for their institutional cooperation and scientific collaboration during this thesis.

I would like to express my deepest gratitude to EKONERG—Energy Research and Environmental Protection Institute Ltd., my employer, which financed and continuously supported my doctoral research. I am especially thankful to Maja Jerman Vranić and Dr. Vladimir Jelavić for their professional support, understanding, and flexibility—first as heads of the department in different periods, and always as colleagues who recognised the importance of this work and provided me with the time and encouragement needed to complete my PhD studies.

My heartfelt thanks go to the researchers and institutions who kindly provided access to their datasets included in the meta-analysis part of this research: Christopher Beirne (Asociación Conservación Osa, Costa Rica), Juliano A. Bogoni (Universidade do Estado de Mato Grosso, Brazil), Jedediah Brodie (University of Montana, USA), Zach J. Farris (Appalachian State University, Boone, NC, USA), Adrian Forsyth (Andes Amazon Fund, Washington, DC, USA), Hannah M. J. Hoskins (Joint Nature Conservation Committee, Peterborough, UK), Miha Krofel (University of Ljubljana, Slovenia), Babu Ram Lamichhane (Wild Care Nepal, Kathmandu, Nepal), Timothy G. O'Brien (Wildlife Conservation Society, Bronx, NY, USA), Neil Reid (Queen's University Belfast, UK), Francesco Rovero (University of Florence, Italy), Naresh Subedi (National Trust for Nature Conservation, Kathmandu, Nepal), Oliver R. Wearn (Zoological Society of London, UK), Andrew Whitworth (Asociación Conservación Osa, Costa Rica), as well as the Public Institution Nature Park Učka (Croatia), Public Institution

National Park Paklenica (Croatia), Public Institution National Park Risnjak (Croatia) and Public Institution Nature Park Papuk (Croatia). Their openness and scientific generosity made this work possible. I am also grateful to university students Mia Jakopović, Darija Jerčić, and Andrijana Čavlović for their committed help with data organisation and analysis related to this component of the study.

I am deeply thankful to my colleagues biologists and ecologists, as well as to my colleagues from the Faculty of Science and from EKONERG Ltd., for their collaboration, stimulating discussions, and all the practical help in the field and in the office. Their expertise, critical questions, and everyday support greatly enriched this work and made many demanding phases of the research more manageable and enjoyable.

I would like to express my deepest personal gratitude to my parents, who have, for as long as I can remember, supported me unconditionally and encouraged my curiosity about the world. They not only allowed me to freely choose my educational path, but actively nurtured it, often making personal sacrifices so that I could pursue opportunities that were far from guaranteed. Their faith in me, especially in moments when I doubted myself, has been a constant source of strength and motivation throughout this long journey.

I am equally grateful to my brother, sister and friends, whose humour, patience and steady belief in me helped to keep things in perspective and reminded me that life exists beyond deadlines, reviews and fieldwork. Their encouragement, messages, and shared moments of rest and celebration provided the balance I often needed.

Most of all, my heartfelt thanks go to my wife Lorena and our children, Lovro and Noa. Lorena has carried an enormous share of the everyday burdens so that I could dedicate myself to this work, and she has done so with incredible patience, love and understanding. She has been beside me through every setback and small victory, reassuring me when things seemed stuck and celebrating each step forward, no matter how small. Lovro and Noa have grown up alongside this PhD thesis, and their smiles, questions and hugs have given meaning to many late evenings and early mornings spent working. Knowing that they were watching me persevere has been one of my strongest motivations to continue. Without the unwavering love and support of my parents, my family, and especially Lorena, Lovro and Noa, this PhD thesis would simply not have been possible.

…

And finally, my gratitude extends beyond people—to nature itself, and to one creature that has guided both my research and my heart. And so, at the very end of this acknowledgment, I turn to you, Wolf.

Some call you a beast, others a guardian of the forest. But to me, you are a brother of the wild—a shadow moving through the misty paths of Velebit, a voice of freedom echoing across the valleys. Wherever you walk, the forest breathes deeper. Your howl breaks the silence and reminds us that wilderness still has a voice, that there is still hope for coexistence. You teach me that belonging means protecting, that true power lies not in control but in balance, and that home exists wherever we respect the rhythm of the earth.

Thank you, Wolf, for reminding me to remain humble before nature—for showing that every footprint, every breath, every heartbeat under the open sky matters. You challenge me to ask whether humankind is ready for coexistence, for acceptance, for a return to the wild spirit within itself.

I know you have not always been welcomed. You have been hunted, misunderstood, and wrongfully accused. Yet now, more than ever, we need you—your presence, your voice, your pack. Where wolves still roam, forests thrive and balance endures. Without you, nature grows quieter, emptier, poorer.

So, when I see your trace glimmering in the morning dew, I understand—your fate is bound to the fate of all wild things. You are the forest's warning and its promise. Losing you would mean losing the heartbeat of the living world.

I promise never to turn away—from you, or from nature. My vow belongs to both: to every tree, every river, every creature that shares this home. May we leave you, and nature, room to awaken once more—room for rewilding, to rebuild your forests, rivers, and kin. May we learn to trust you again, to follow, to grow, to breathe together. And as I look ahead, I dream of walking one day with my wife and sons through the same wild landscapes, knowing that you are still there - watching, guiding, living free.

Yes, that day will come. I am sure it will.

INFORMATION ABOUT THE MENTORS

Ivana Maguire (MBZ: 217830) is a full professor at the Department of Biology, Faculty of Science, University of Zagreb. After completing her degree in Biology at the Faculty of Science in 1993, she worked as a secondary school chemistry teacher, after which she enrolled in a master's program at the Université Catholique de Louvain-La-Neuve in Belgium. She began working at the Department of Biology in 1997 in the field of research related to the biology of freshwater crayfish, which was also the topic of her PhD, completed in 2002. Her scientific research includes various aspects of the study of freshwater crayfish of the family Astacidae. She participates in teaching various courses at the undergraduate, graduate and doctoral levels. She has also supervised 30 master's theses, 4 magisterial theses and 5 doctoral dissertations, as well as 4 student papers awarded the Rector's Award of the University of Zagreb. To date, she has actively participated in the implementation of 30 scientific projects, 12 of which she led. She has published more than 60 scientific papers in international peer-reviewed journals, actively participated in international scientific conferences with more than 93 contributions, and in national conferences with 44 contributions. So far, she has reviewed 68 scientific papers for various scientific journals and 2 scientific projects. As a member of the Editorial Board, she has contributed to the work of the scientific journal Natura Croatica and the journal Frontiers in Ecology and Evolution. She is a member of several national and international professional associations. She has participated in the organization of one national and seven international scientific conferences.

Alessandro Massolo is a senior researcher and university professor specializing in wildlife ecology, epidemiology and conservation biology. He has extensive international experience in academic research and teaching, with a particular focus on the ecology of medium and large mammals, human–wildlife interactions and disease transmission at the wildlife–human–domestic animal interface. His scientific work integrates field studies, spatial ecology, statistical modelling and risk assessment, often in interdisciplinary collaboration with veterinarians, public health specialists and conservation practitioners. He has participated in undergraduate, graduate and doctoral teaching, supervising numerous master's and doctoral students in ecology, wildlife management and related disciplines. He has been actively involved in national and international research projects, frequently in the role of principal investigator or key collaborator and has contributed to the development of applied tools and guidelines for wildlife monitoring and management. His publication record includes numerous articles in peer-reviewed international journals, as well as conference contributions and invited lectures. He regularly acts as a reviewer for scientific journals and research proposals and is a member of several professional and scientific associations in the fields of ecology, conservation and wildlife disease ecology.

TABLE OF CONTENTS

ABBREVIATIONS

The following abbreviations are used in this manuscript:

AIC	Akaike Information Criterion; model selection criterion balancing fit and complexity.
AICc	Corrected Akaike Information Criterion; AIC adjusted for small sample sizes.
BACI	Before–After Control–Impact.
P	Number of prey detections at a site.
QM	Test statistic for moderators; omnibus test of moderator effects.
QE	Test statistic for residual heterogeneity (Cochran's Q for errors).
PCA	Principal Component Analysis
RDI	Relative Detection Index; number of detections per 100 trap-nights.
REML	Restricted Maximum Likelihood; method for estimating parameters in random-effects models.
SCI	Sites of Community Importance
SD	Standard Deviation
SE	Standard Error
SPAs	Special Protection Areas
V	Number of mesopredator detections at a site.
σ^2	Between-study variance; variance component for random effects.

CHAPTER 1: GENERAL INTRODUCTION

1.1. BACKGROUND

1.1.1. LARGE CARNIVORES: GLOBAL CONTEXT

Out of total 245 carnivore species around the world, the 31 species (excluding marine species) have average body masses greater than 15 kg and are called large carnivores (Ripple et al., 2014). Today they have small population sizes (Mech and Boitani, 2003; IUCN 2020) and low population densities, while requiring extensive habitats, sufficient prey availability, and minimal human disturbance to maintain viable populations (Carbone et al., 1999; Cardillo et al., 2004; Cardillo et al., 2005). Major threats to large carnivore survival include habitat loss and fragmentation, and overhunting and poaching (Ripple et al., 2014; Wolf and Ripple, 2016). The higher extinction rate of large carnivores is also influenced by their morphological specialization necessary to attain large size, as predicted by evolutionary theory (Stanley, 1973). Due to anthropogenic and evolutionary pressure, large carnivore biodiversity loss can cause ″ecological extinctions″ which can disturb whole ecosystem. To be specific, if species loses its interaction strength due to rarity (Estes et al., 1989) it may cause weakening top-down control (Duffy, 2002) and increasing the importance of bottom-up relations in complex food web on trophic pyramid.

1.1.2. RECOLONIZATION PROCESSES AND MONITORING

Large carnivores are among the most controversial and challenging species to conserve, especially in human-dominated landscapes (Chapron, 2014). But, urbanization, depopulation of rural areas, efficiency improvement in agriculture and the transition to a post- industrial economy in Europe and North America has taken large areas of land out of human use that could be returned to a ″natural″ state (Gross, 2014). In Croatia, during the period 1991-2001, 500,000 persons were displaced due to the war, which is ~ 11.5% of the total population of Croatia (Nejašmić, 2014). This creates new opportunities for natural recolonization processes in Europe, including Croatia, as large carnivores are returning to areas of their historical range from which they were previously extirpated (Recio et al., 2021). This process is also associated with an increase in human–wildlife conflicts (Chapron et al., 2014). Also, anthropogenic barriers (like road network) over much of Europe may limit recolonization opportunities by edge effect and possibilities for ecosystem restoration (Ziółkowska, et al., 2016; D'Amico, et al., 2016). Where carnivores are recolonizing former ranges, they likely need (a) to reach ecologically functional densities (Soulé et al., 2005) and (b) time to trigger visible effects on lower trophic levels because ecological responses generally require long times to occur (Wilson el at., 2020). The effects of large carnivores on lower trophic levels can be determined through meta-analyses analysis of large data sets of species presence (Koricheva et al., 2013).

In this dissertation, an existing GIS-based spatial and temporal model is applied in combination with scenarios developed within this research to predict when and where large carnivores are likely to recolonize under different ecological and anthropogenic conditions. Such models have been widely used for species management (Adriaensen et al., 2003), including predicting wolf distribution in areas not yet recolonized in Western Europe (Marucco & McIntire, 2010). The results will support decision-making in management and conservation planning, including public education and the prevention of human–wildlife conflicts, thereby contributing to large carnivore population recovery and range expansion (Recio et al., 2021). Furthermore, given that camera trapping is currently the most common method for assessing mammalian species richness (Burton et al., 2015), it is important to evaluate its feasibility for monitoring the recolonization process.

1.1.3. THE GREY WOLF: BIOLOGY, ECOLOGY AND ROLE IN CROATIAN ECOSYSTEMS

The gray wolf (*Canis lupus*) is a mammal belonging to the order Carnivora and the family Canidae. Within the genus Canis, it is closely related to the coyote and jackals, while the domestic dog is considered a domesticated form of the wolf, often treated as Canis lupus familiaris. The gray wolf is the largest member of the dog family. An adult wolf is on average about 170 cm long from nose to tail, with a tail about 42 cm long and an average shoulder height of around 70 cm. In Croatia, wolves are typically gray, with somewhat darker backs and tails and lighter gray coloration toward the belly and legs; a dark stripe on the front of the foreleg is often visible. Wolves are highly adapted for long-distance movement and for capturing prey. They have relatively long legs, a narrow chest, strong jaws and 42 specialized teeth. Their senses of smell, hearing and sight are very well developed, which supports hunting, orientation and communication.

Wolves are social carnivores that usually live in packs. The pack is normally centered on one reproductive pair, while the other members are their offspring from different years. Pack life allows wolves to hunt larger prey, defend a territory and raise young cooperatively. The pack has a hierarchical social structure in which the dominant pair leads movement, hunting and reproduction. Most subordinate individuals do not reproduce, which acts as a natural mechanism of population regulation. Female wolves usually come into estrus once a year, from late January to April, with mating occurring during the third week of the heat period. Pregnancy lasts about 63 days, and pups are born in a den prepared in advance by the female. Litters usually contain 4–7 pups, which are blind and deaf at birth and depend first on milk and later on food brought by other pack members. As the pups grow, the pack uses rendezvous sites where adults return regularly. By their first winter, young wolves have already reached nearly adult size, and sexual maturity is usually achieved at around 22 months of age. Young wolves often disperse in their second or third year in search of a mate and a new territory.

The ecological niche of the wolf is that of a hunter of large mammals, especially wild ungulates. In Croatia, the most important natural prey species include red deer, roe deer, wild boar and, locally, chamois and mouflon. Diet differs regionally: in Gorski Kotar and Lika, wild ungulates made up 77.8% of wolf food, whereas in Dalmatia their share was only 13.3%, with livestock making up a much larger part of the diet because natural prey was less available there. This difference is one of the main reasons why wolf–human conflict has historically been strongest in Dalmatian pastoral landscapes. Wolves can live in many types of habitats as long as there is enough prey and sufficient cover, especially from human disturbance. In Croatia, mountainous forested regions such as Gorski Kotar and Lika provide the most favorable conditions because they combine forest cover, lower human density and the presence of major ungulate prey. Kusak also concluded that parts of the Pannonian macro-region, including Banovina and the forested hills of Slavonia, could potentially support wolves.

In contemporary Europe, wolves are structured into several main populations, including the Scandinavian, Karelian-Baltic, Central European, Carpathian, Dinaric-Balkan, Alpine-Italian and Iberian populations, with an overall abundance of roughly 12,000 individuals across the continent (Chapron et al., 2014). Croatia lies within the Dinaric-Balkan population, and historical data indicate that, hundred years ago, wolves inhabited the entire area of what is now Croatia (Štrbenac, 2010). Over the course of the 20th century, intensive hunting and organised eradication campaigns progressively reduced their range, so that by the mid-century they were still present in regions such as Banija, Turopolje and Žumberak (Huber et al., 1994). By the early 1990s, after decades of persecution, wolves persisted only in Gorski kotar and Lika (Frković et al., 1992). The wolf became legally protected in Croatia in 1995, which marked an important shift from earlier eradication policies toward conservation and management. After the 90s, their numbers increased, mostly because spreading to new habitats and reduction of hunting effort (Štrbenac, 2010). In 2001, the wolves settled in Gorski kotar, Lika and Dalmatia, and occasionally appeared in the Peripanonian area, on the southern slopes of Velebit, near Ravni Kotar, near Kastela and near Biokovo (Kusak, 2002). Between 2001 and 2008, wolves were established in the Banovina area, and in the Karlovac County, but not in Pannonia region, where they historically were present (Štrbenac, 2010).

Wolves' populations in Croatia are part of larger European regional Dinaric-Balkan population (Antolović, J. et al., 2006), therefore it is important to emphasize the central role of Pannonian Plain in reconnecting two European regional wolf populations, Dinaric-Balkan and Carpathian. The Pannonian Plain contains extensive semi-natural habitats in relatively good ecological condition, with abundant wild ungulate prey, major river systems and surrounding highland areas, while parts of Slavonia and the wider region are characterised by a relatively low human footprint due to long-term socio-economic change and rural depopulation (EEA, 2002). Although the Slavonian and Kordun Highlands are isolated and surrounded by open, human-modified habitats that wolves typically avoid, ongoing land abandonment and ecological succession are creating new areas of suitable habitat for wolves. Also, high habitat suitability zones for large carnivores are present in Pannonian Plain in Croatia (HAOP, 2016), and wolf were seen again in the Pannonian Plain during 2020 (Unpublished data, available from Papuk Nature Park). Therefore, the Pannonian Plain may be suitable for the recolonization process.

So, wolf, as large carnivore species, is keystone species (Carbone and Gittleman, 2002), but (anthropogenic) impact can affect its social structure and affect its role in ecosystem (Wallach et al., 2010). Even though large carnivores' top-down control is already known, their cascading effects onto other species still need to be studied (Prugh et al., 2009; Ripple et al., 2013; Ritchie and Johnson, 2009). It is therefore necessary to continue research into the general relationship between prey and predators because large carnivores have the dual role: (1) limiting large herbivores by predation, but also (2) limiting mesocarnivore species by intraguild competition, thus structuring one usually known linear food-chain into multiple food-web pathways (Ripple et al., 2014). Therefore, it is needed to start with analyses of trophic pyramid relations in Croatian ecosystems, which will be useful as initial step for analyzing and monitoring recolonization process of wolves in Pannonian Plain.

1.2. OBJECTIVES

1.2.1. GENERAL RESEARCH QUESTIONS

This thesis is structured around three main hypotheses that together address the ecological role of wolves as a top predator and the conditions for their successful recolonization. Each hypothesis focuses on a different but complementary level of inquiry: the ecological role of top predators (large carnivores) and their top-down effects, the feasibility of camera trapping for monitoring recolonization process and its effects, and the potential for future wolf recolonization of the Pannonian Plain under different management scenarios. Taken together, these hypotheses translate the overarching aim of the thesis into a set of testable propositions. They shape the overall study design, from the choice of focal ecosystems regarding feasibility of camera trapping for monitoring recolonization process and data to the statistical and modelling tools applied, and thus frame how the findings are interpreted in relation to large carnivore conservation, ecosystem functioning and management.

1.2.2. SPECIFIC RESEARCH HYPOTHESES

This doctoral thesis investigates the process of wolf recolonization in the Croatian part of Pannonian Plain and evaluates approaches for its monitoring and prediction. Specifically, it addresses three overarching questions: (1) To what extent can apex predators (large carnivores) exert top-down regulatory effects on trophic structure in systems where they are present? (2) Can camera trapping serve as a feasible tool for monitoring the progression of recolonization and its ecological effects? (3) Under which spatial, ecological, and management conditions can wolf recolonization of the Pannonian Plain occur within a decadal timeframe, particularly in relation to landscape connectivity and ecological barriers?

Hypothesis 1

> *The camera trapping might be used as a feasible monitoring tool to assess the evolution of the recolonization process and its effects: evaluation of camera-trap surveys conducted by protected-area staff to assess their applicability and cost-effectiveness for monitoring wildlife communities.*

The first part of this thesis examines whether camera-trap data collected by protected-area staff can provide a reliable and cost-effective basis for monitoring wildlife communities relevant to future recolonization processes. Using a case study from Paklenica National Park, camera-trap data collected by park rangers are analysed to assess data quality, consistency, and their suitability for ecological inference.

In addition, the financial feasibility of such monitoring is evaluated through a comparative cost analysis. The cost of conducting camera-trap surveys by external service providers was compared with the cost of surveys conducted by national park employees. Daily rates for external experts were obtained from three major Croatian companies conducting ecological surveys, while internal costs were derived from Paklenica National Park staff across four roles (ranger service officer, ranger service chief supervisor, senior adviser, and conservation manager). Survey effort was standardised by estimating the number of field days required based on a 15-day inspection interval per camera location, with additional days included for initial deployment. Total survey duration was then multiplied by daily rates to enable comparison between external and internal implementation.

This approach allows assessment of whether ranger-based monitoring can serve as a practical and economically viable tool for long-term camera-trap studies supporting recolonization monitoring.

Hypothesis 2

> *The top predator should have a regulatory effect on the trophic pyramid through top-down effects: meta-analysis of literature data on interactions among top predators (large carnivores), mesopredators, and prey monitored by camera traps to assess general trophic patterns.*

The second part of this thesis examines whether camera-trap data can be used to detect general top-down effects of large carnivores on mammal trophic structure across ecosystems. Focusing on studies that used camera traps to survey terrestrial mammals, a global synthesis quantifies how the relative representation of predators, prey, and scavengers varies with the presence and richness of top predators.

Species detections are classified into broad trophic levels to enable comparison of community structure among sites, and multivariate analyses are used to test whether systems with stronger large-carnivore assemblages show systematically different mesopredator–prey balances than systems where large carnivores are rare or absent.

In this way, the study evaluates the extent to which large carnivores exert top-down regulatory effects on trophic structure and assesses whether camera-trap datasets can provide a robust basis for detecting such patterns.

Hypothesis 3

> *The current situation in Pannonia Plain may be suitable for such recolonization to happen within a decade, particularly if actions to reduce ecological barriers as rivers and highways will be implemented: development of models using population dynamic modelling and gap analysis to predict the spatial and temporal patterns of the potential recolonization of wolves in the Pannonian Plain, and the possible outcomes of different management scenarios.*

The third part of this thesis will develop a spatially explicit population-dynamic model to forecast the recolonization of wolves in the Pannonian Plain, with a focus on Slavonia. The model will build on existing habitat-suitability assessments for large carnivores and incorporate key ecological and anthropogenic factors that influence wolf dispersal, survival and reproduction, including habitat quality, prey availability, human pressure and major landscape barriers such as rivers and transport infrastructure. By combining information on suitable habitat and connectivity with population-viability analysis, the model will explore how quickly and under which conditions wolves could establish a viable population in this region.

Different management and land-use scenarios will be simulated to evaluate how actions such as improving ecological connectivity, modifying prey densities, expanding protected areas or considering translocations might affect recolonization outcomes and extinction risk. The model will also draw on insights and parameters derived from camera-trap studies in Paklenica National Park and Papuk Nature Park to ensure that demographic assumptions are grounded in empirical data from Croatian wolf populations. Finally, the study will outline a monitoring framework based on camera trapping and associated statistical models to track the progress of recolonization and the associated changes in mammal communities, providing a practical tool to support adaptive management and coexistence planning in the Pannonian Plain.

CHAPTER 2: LITERATURE REVIEW

The recolonization of large carnivores into human-dominated landscapes raises intertwined ecological, methodological and management challenges, especially where apex predators return after long absences. Wolves, as wide-ranging apex predators, can strongly restructure mammal communities through consumptive and non-consumptive effects on prey and mesopredators, yet the strength and even direction of these effects varies across ecosystems as a function of productivity, habitat configuration and human pressure (Ripple et al., 2014; Ritchie & Johnson, 2009; Ford & Goheen, 2015). Documenting and interpreting such changes, and managing the associated social conflicts, requires monitoring tools that work across large spatial and temporal scales and governance frameworks that anticipate both ecological outcomes and societal constraints.

This chapter provides an integrated review of the ideas and evidence underpinning the three main hypotheses of this thesis. It first summarises current understanding of the ecological role of large carnivores and mesopredators, with particular emphasis on trophic cascades, mesopredator release and the context dependence of predator-mediated effects. It then examines camera trapping and meta-analysis as key tools for studying mammal communities and trophic interactions, before turning to the role of protected areas and ranger-based monitoring in generating long-term data on community dynamics. Finally, it reviews the literature on wolf recolonization, landscape connectivity and scenario-based management, with a focus on the Croatian context and the Pannonian Plain, where wolves are beginning to reappear in a mosaic, human-dominated landscape. Together, these sections establish the conceptual and empirical foundations for the subsequent chapters, which apply this framework at global, regional and local scales to assess the ecological consequences and management implications of wolf recovery.

2.1 THE ECOLOGICAL ROLE OF LARGE CARNIVORES AND MESOPREDATORS

Large carnivores are a small subset of the order Carnivora, which comprises 245 terrestrial species occupying nearly all major habitats on Earth (Ripple et al. 2014). Following criteria commonly used in the literature (Ripple et al. 2014), large carnivores can be defined as non-marine terrestrial species generally exceeding an average adult body mass of 15 kg and belonging to the families Canidae, Felidae, Mustelidae, Ursidae, and Hyaenidae. These species often occupy high trophic positions and can function as apex predators in many ecosystems, generally occur at low densities, have high energetic demands and require extensive home ranges, making them particularly vulnerable to habitat loss, persecution and prey depletion (Carbone et al. 1999; Cardillo et al. 2004, 2005; Mech & Boitani 2003). Consequently, many large carnivores are declining worldwide, both in distribution and abundance (Ripple et al. 2014). Yet, they remain key architects of food webs, because their strong consumptive and non-consumptive effects on large herbivores and smaller carnivores can restructure entire communities through trophic cascades and “landscapes of fear”, with far-reaching consequences for ecosystem structure and function (Schmitz et al. 2000; Estes et al. 2011; Ripple et al. 2014).

Classic population theory, from Malthus’ early ideas on density-dependent limits to growth through Verhulst’s logistic model and Lotka–Volterra predator–prey systems, provides the conceptual foundation for understanding how consumer–resource interactions shape population dynamics (Kingsland 1982). Mid-sized predators (which we operationally define here as mammalian carnivores with average body mass of roughly 1–15 kg, hereafter referred to as mesopredators) can increase in abundance or activity following changes in apex predator communities, sometimes contributing to strong impacts on smaller prey species (Soulé et al. 1988; Crooks & Soulé 1999; Ritchie & Johnson 2009). This body-mass range of mesopredators does not represent a universal definition of mesopredators but provides a consistent and transparent operational threshold for comparative analyses across systems. Many case studies support this idea: across continents, the removal of large carnivores has been associated with range expansions and density increases of mesopredators and concomitant prey collapses (Prugh et al. 2009; Ripple et al. 2014), whereas intact apex predator populations can suppress mesopredators and indirectly benefit vulnerable prey (Letnic et al. 2012). However, mesopredator release hypothesis is not universal and still a matter of debate. Context-dependent factors such as ecosystem primary productivity (which constrains prey availability), habitat change and human exploitation can modulate or obscure top-down effects, and outcomes may depend strongly on the composition, relative dominance and resource overlap of predators within the guild (Elmhagen & Rushton 2007; Ritchie & Johnson 2009). As a result, there is still considerable uncertainty about how general and predictable predator-mediated cascades are across ecosystems, and how variation in large-carnivore assemblage structure shapes food-web configuration (Ford & Goheen 2015; Jachowski et al. 2020). Consequently, evaluating mesopredator release across systems requires careful consideration of spatial and temporal context, as well as of variation in predator guild composition and the degree of resource overlap and competition among carnivore species.

A key knowledge gap concerns the role of apex predator richness and guild composition: rather than simply treating apex predator effects as present versus absent, this thesis explicitly considers differences among large-carnivore assemblage types and the relative dominance within large carnivore communities. Most empirical work has focused on single apex predator systems or on a small set of iconic case species, treating predator effects as largely binary and often lacking replication and controls (Ford & Goheen 2015). Yet carnivore assemblages frequently include several large predators that may interact via intraguild predation, competition or facilitation, and theory suggests that predator identity, richness and relative dominance can all modulate the strength and direction of trophic cascades (Griffin et al. 2013; Ripple et al. 2014). It therefore remains unclear whether the balance between mesopredators and prey in an ecosystem changes depending on how rich the large-carnivore assemblage is (in terms of the number of large-carnivore species present) and on whether these large-carnivore species are detected at similar frequencies or instead form a pattern where some are very frequently detected while others are only rarely recorded. For the purposes of this study, I refer to these very frequently detected species as dominant and to the rarely recorded species as rare. Addressing this question requires comparative analyses that move beyond ecological networks to encompass multiple predator configurations, habitats and regions.

These considerations are particularly relevant for systems in which apex predators are naturally recolonizing parts of their former range. Within this broader guild, grey wolves are a focal species of this thesis, because their ongoing and potential recolonization offers a rare opportunity to observe how changes in apex predator presence reshape mesopredator and prey communities in real time. Understanding the ecological role of wolves in such recolonizing systems requires not only a conceptual framework for predator–prey and intraguild interactions but also monitoring approaches that can quantify shifts in trophic structure across space and time, such as camera-trap surveys and their synthesis through meta-analysis. In the Croatian context, where wolves have recolonized parts of their former range but remain absent or only sporadically present in lowland regions like the Pannonian Plain, these questions are particularly pressing, as management decisions must anticipate both the ecological consequences and social implications of a future return. This thesis therefore uses wolves as a model apex predator to examine how large-carnivore guild structure, local community responses and landscape-level recolonization dynamics interact, with the goal of informing conservation planning in recolonizing landscapes.

2.2 CAMERA TRAPPING AND META-ANALYSIS AS TOOLS TO STUDY TROPHIC INTERACTIONS

In order to ensure the long-term survival of wild species and preserve habitats in a favourable condition, it is necessary to conduct systematic research that includes revision of the species richness lists, especially in protected areas. Efficient and reliable methods for assessment of species richness and abundance are crucial to determine conservation priorities and plan management strategies. The use of automatic cameras with infrared sensor triggered by ‘warm objects that are moving’ – animals is now a most frequently used technique to record species presence/richness, especially for medium- to large-sized mammals and terrestrial birds (Eymann et al., 2010; Norouzzadeh et al., 2018; Schneider et al., 2018). Camera traps offer a powerful, non-invasive tool for such comparative work, providing standardized data on occurrence, relative activity and co-detections of multiple species across broad spatial and temporal scales (Tobler et al. 2008; Chen et al., 2022). They can therefore provide not only basic information on species richness and occurrence, but also multi-species datasets that are suitable for analysing community structure and trophic interactions across space and time. These advantages are particularly relevant in protected areas, where long-term biodiversity monitoring is a central management objective and where camera traps can be deployed systematically across well-defined management units.

From an analytical perspective, camera-trap images and videos must be converted into comparable metrics before they can be used to study trophic interactions. Raw records are typically filtered into independent “events” (e.g. using a temporal threshold between consecutive images of the same species at the same station) and then aggregated as counts per species, station and unit of effort (such as trap-nights). These event-level data can be further summarised as detection rates, relative abundance indices or occupancy estimates, and grouped by trophic level (e.g. large carnivores, mesopredators, small and large prey) to derive ratios and indices that reflect community and pyramid structure. By applying consistent rules for event independence, effort standardisation and trophic classification across studies, camera-trap datasets become amenable to cross-site comparisons and to the calculation of effect sizes used in meta-analytical syntheses (e.g. log-ratios of mesopredator to prey detections or differences in detection rates between predator assemblage classes). This data-processing step is therefore critical for turning heterogeneous image collections into quantitative indicators of trophic interactions.

While individual camera-trap surveys can reveal local patterns in community structure and trophic interactions, their capacity to draw general conclusions is often limited to the specific landscapes where they were conducted. Despite being relatively easy and quick to deploy, camera-trap datasets have traditionally been analysed at the scale of individual studies or landscapes, which long limited inference about general patterns in trophic structure and carnivore effects across continents and ecosystem types. Recent pan-regional and global syntheses, however, show that large, harmonised camera-trap datasets can reveal broad-scale patterns in mammal responses to human activity and protection status (Chen et al., 2022; Burton et al., 2024), highlighting the growing potential of coordinated camera-trap networks for macroecological inference. To overcome these limitations and move from site-specific case studies to generalizable patterns, camera-trap data can be synthesised quantitatively across studies. Meta-analysis, understood as the quantitative synthesis of effect sizes across independent studies, provides a robust framework for pooling information from such heterogeneous systems, allowing estimation of overall relationships and formal tests of how these relationships vary among habitats and regions (Koricheva et al. 2013). Previous syntheses of predator effects, largely based on manipulative experiments rather than camera-trap surveys of mammal communities, suggest that predator richness can enhance prey suppression relative to average single-predator effects, and that the strength of both consumptive and non-lethal risk effects depends on predator identity, richness and environmental context (Griffin et al. 2013). However, these syntheses have relied predominantly on non-camera-trap data and have not integrated camera-trap surveys across multiple trophic networks and continents, nor explicitly contrasted systems differing in large-carnivore richness and dominance (Ahumada et al. 2011; Ahumada et al. 2013; Griffin et al. 2013; Steenweg et al. 2017). Global camera-trap syntheses can, in principle, quantify how the relative representation of different mammal trophic levels (small and large prey, mesopredators and large carnivores) varies with large-carnivore presence, richness and dominance, and thus test whether variation in predator guild structure is consistently associated with changes in mesopredator–prey ratios and trophic pyramid shape, providing a key tool for assessing how recolonizing apex predators such as wolves reshape mammal communities.

As the monitoring of mammalian species via camera traps is not so dependent on the environment to be sampled, constant assistance or even experienced field staff (Silveira et al., 2003), the question is whether protected areas' ranger service personnel can be an added value of the usual nature protection tool through baseline survey monitoring. Even with high initial costs of camera trapping, this method, compared to the line transects and track censuses, can be conducted more easily and with relatively low costs in a long term (Silveira et al., 2003). Camera trapping can be easily incorporated with regular ranger area control duties, thereby facilitating long-term data collection that can feed both local management and broader comparative analyses.

2.3 PROTECTED AREAS, RANGER-BASED MONITORING AND LOCAL TROPHIC DYNAMICS: THE PAKLENICA CASE

Protected areas are key arenas for long-term monitoring of mammal communities, where camera-trap networks and ranger-based data collection can be combined to track both biodiversity and trophic interactions over time. Rangers, as defined in this thesis, are mid-level protected-area staff whose primary responsibility is the on-the-ground implementation of management plans and policies developed by senior management in the main office. According to Howard (2014), particularly important roles of a ranger are ability to make correct decisions about resource allocations, acting as a mediator to manage community expectations and flexibility in policy implementation. Surprisingly, most identified skills were not the technical skills (i.e. managing plants or animals), but skills such as setting priorities, multitasking and communication. The role of rangers in protected areas mostly refers to two group activities, education/interpretation and law enforcement/conservation, but roles vary from one national park to another. Rangers in Croatia are mainly involved in park protection, performing emergency duties to protect people and the park itself, participating in search and rescue operations and conducting investigations into accidents, complaints and illegal activities according to the Croatian Nature Protection Act ("Official Gazette" No. 80/13, 15/18, 14/19, 127/19, 155/23.

Park ranger job qualifications vary depending on the country and the capacity in which rangers are hired. In Paklenica National Park (Paklenica NP), there are two levels of park rangers: ranger service officer and ranger service chief supervisor (Official Gazette, 2018). The required qualification for ranger service officer is completion of secondary education, while the qualification for ranger service chief supervisor is a bachelor's degree of biotechnical, natural, biomedical, technical or social orientation. Knowledge of work in the Geographic Information System (GIS) software is obligatory for both positions. In USA, minimal requirement is to possess some form of post-secondary education (Environmental Science, 2022). USA National Park Service requires a bachelor's degree related to the profession. The same requirements are in Australia (Parks Victoria, 2022) and South Africa (Shamwari, 2022). Further on, in Canada, while some positions require only a secondary school diploma, most ranger positions require a bachelor's degree or technical diploma in a field like conservation enforcement, natural resource management, outdoor education or forestry (Salazar, 2021). In Brazil, the requirements are slightly similar to those of Croatia; university degree is not obligatory, but it is recommended to study courses in the field of ecology, forestry and management during secondary education or coursework (Arnoni, 2018). In other European countries, the requirements are like those in Croatia. In Austria, university education is not compulsory, but it is necessary to complete two levels of training conducted by national parks (National Parks Austria, 2022). Most of the rangers in Germany are certified nature and landscape conservationists, whose requirement is to have a background of a so-called 'green' profession like forestry expert or agriculturist (Bundesverband Naturwacht, 2022). Also, in Germany, they have specialised bachelor's degree course 'Landscape Management and Nature Conservation', where students may choose the specialisation, protected area management. In addition to education, rangers have a very profound knowledge of the specific area (where animals are gathered, secret hideouts, waterholes, etc.) and/or have a long work experience within the protected area. During their regular field visits, they can collect large amounts of ecological data. In combination with the time spent working in the field (during regular visits), this can make them an invaluable 'tool' for biodiversity monitoring. Additionally, this may also be more cost effective for the management authority than hiring external professionals. Furthermore, protected areas often have an employed coordinator who has an ecological degree and can set up monitoring; so, rangers can do data collection.

In this context, Paklenica National Park (Paklenica NP) provides a concrete example of how camera trapping can be used to identify and characterise medium- to large-sized mammal communities, information that would form the baseline for monitoring wolf recolonisation in the Pannonian Plain. In Paklenica NP, a mammalian survey was therefore conducted entirely by rangers using camera traps. Rangers in the Paklenica NP, beside their usual roles, have also focused on collecting data from biomonitoring (flora and fauna), which they regularly report to the conservation manager. Over the past period, they have demonstrated excellent field survey skills and knowledge of different taxa, especially mammals. They initiated the purchase of camera traps and with their installation on well-set positions on trails and roads, numerous valuable data were recorded. This ranger-based camera-trap survey provided baseline information on medium- to large-sized mammals in the park and showed that ranger-led monitoring can be a cost-effective tool for assessing trophic structure in protected areas (Bišćan et al., 2022).

2.4 GLOBAL TROPHIC DYNAMICS OF LARGE-CARNIVORE GUILDS: INSIGHTS FROM A CAMERA-TRAP META-ANALYSIS

Local case studies show how camera-trap data can reveal predator–prey ratios, species-richness patterns across trophic levels and spatiotemporal niche partitioning within a single ecosystem. However, the strength and even the direction of predator-mediated effects are known to vary among systems, depending on factors such as productivity, habitat configuration and human pressure (Elmhagen & Rushton 2007; Ritchie & Johnson 2009). To assess whether patterns observed locally are part of more general trends, it is necessary to analyse camera-trap data across many ecosystems that differ in large-carnivore guild structure, mesopredator assemblages and prey communities (Elmhagen & Rushton 2007; Ritchie & Johnson 2009). Standardised global camera-trap studies have already shown that mammal communities exhibit broadly consistent trophic guild structures across tropical forests, and that these structures respond systematically to gradients of protection and human disturbance (Ahumada et al., 2011; Ahumada et al., 2013). By harmonising camera-trap protocols and metrics across continents, such initiatives demonstrate that relative representation of different trophic groups can be compared quantitatively among sites, providing a first step towards global assessments of food-web configuration.

At the same time, multi-site statistical approaches applied to camera-trap datasets have been used to infer predator–prey interactions and to test how strongly predators regulate prey across heterogeneous landscapes. Multi-site hierarchical co-abundance and occupancy models applied to camera-trap datasets now allow researchers to infer the strength and even the direction of predator–prey associations while accounting for imperfect detection and shared responses to environmental gradients (Amir et al., 2022). These findings echo broader evidence from mesopredator-release studies, where the consequences of changes in apex-predator assemblages depend on productivity, habitat structure and human impacts (Elmhagen & Rushton, 2007; Ritchie & Johnson, 2009).

Camera-trap studies focusing on large-carnivore guilds further show that prey availability and intraguild competition jointly regulate the spatiotemporal dynamics of predators, with temporal partitioning and spatial avoidance often mediating coexistence within carnivore communities (Cusack et al., 2021; Yarnell et al., 2021). Such work suggests that variation in large-carnivore richness and dominance can reshape not only mesopredator behaviour and abundance, but also overall trophic-level representation within mammal communities. Together, these global and regional analyses highlight both the potential and the current limitations of camera-trap syntheses for quantifying large-carnivore-driven trophic dynamics and underscore the need for comparative studies that explicitly link variation in large-carnivore guild structure to mesopredator–prey balance across ecosystems.

In this thesis, I analysed a global dataset of camera-trap surveys, allowing me to place local trophic patterns in a broader comparative context. This global perspective also underpins the later assessment of wolf recolonization in Croatia, where camera-trap monitoring is envisaged as a key tool for tracking both the return of wolves and the associated changes in mammal community structure.

2.5 WOLF RECOLONIZATION IN CROATIA: LANDSCAPE CONNECTIVITY AND MANAGEMENT PATHWAYS IN THE PANNONIAN PLAIN

Forecasting the spatiotemporal dynamics of recolonizing species presents a formidable challenge, as it is shaped by a multitude of factors ranging from indirect uncertainties to direct management interventions (Petracca et al. 2023; Coulson et al. 2001; Ellner et al. 2002; McCarthy et al. 2003). These influences include changes in habitat conditions, such as shifts in land use or climate patterns (Lawler et al. 2002; Abrahms et al. 2022), interspecific competition (Elbroch et al. 2015), the spread of diseases (Rhodes et al. 2011; Gordon et al. 2015), fluctuations in immigration or emigration (Lieury et al. 2016; Grauer et al. 2019), and active management actions (Saunders et al. 2018). Nevertheless, population projections remain a valuable tool for assessing how uncertainties affect species recolonization, supporting managers in their efforts to restore populations and clarify legal status (Morris & Doak 2002).

Building on these general challenges of forecasting recolonisation dynamics, ecological studies (Carroll et al. 2003; Oakleaf et al. 2006; Nelson et al. 2012) have identified several key factors linked to wolf occupancy and pack persistence, including increased forest cover, lower human population density, higher prey density, and reduced sheep density. Investigating the potential for species to return is also essential for preparing local communities, creating action plans and developing conflict-resolution strategies, particularly for large carnivores that have long been absent. Around the world, wolf recolonization has relied on a mix of traditional non-lethal methods, community-based conservation and technical solutions such as livestock guarding dogs, range riders, timed calving and electric fencing, often combined with stakeholder engagement, compensation schemes, cultural integration and structured dialogue projects (Distefano 2005; Bruns et al. 2020; European Commission 2023; Sonam et al. 2022; Hansen & Ejrnæs 2022; Ausband & Mech 2023). Drawing on these global experiences in wolf conservation and recolonization, it was assessed the potential for wolf recolonization in Croatia (Pannonia), where the species has experienced a complex history of decline and partial recovery across various regions.

Building on these global insights into recolonisation and coexistence, the Croatian case is particularly relevant because it already hosts three of the four European large carnivores: : the gray wolf (*Canis lupus*), the brown bear (*Ursus arctos*), and the Eurasian lynx (*Lynx lynx*). Historical information on wolf distribution and abundance in Croatia is primarily based on hunting records (Frković et al. 1992), management documents (Štrbenac et al. 2010) and expert reports (Kusak 2002), as systematic, standardized monitoring was not yet in place during most of the twentieth century. Wolf populations in Croatia began to decline in the late 19th century. Hunting records from 1894 show that at least one wolf was killed in each county that year, indicating that wolves once inhabited the entire territory of what is now the Republic of Croatia (Štrbenac et al. 2010). By the early 1990s, however, wolves survived only in Gorski Kotar and Lika (Frković et al. 1992), which together account for just 11% of Croatia's land area (Figure 1). After the 1990s, wolf numbers increased, most likely due to reduced hunting pressure (Štrbenac et al. 2010). In 2001, wolves recolonized southern Croatia (Dalmatia) and occasionally appeared further north on the southern slopes of the Velebit mountain range, as well as in the Peripannonian region, including Sisak-Moslavina County (Kusak 2002). Between 2001 and 2008, wolves established populations in central Croatia (the Banovina region) and in Karlovac County, but they did not return to the eastern part of the country (the Slavonia region, the Croatian segment of the Pannonian Basin), where they were historically present (Štrbenac et al. 2010).

Figure 1 Geographic regions (Velebit mountain, Dalmatia, Gorski Kotar, and Lika) and administrative divisions of Croatia (Karlovac County, Sisak-Moslavina County, Pannonian Plain within Croatia's boundaries, and Banovina) in relation to historical wolf distribution. The map displays a satellite imagery base with color-coded overlays highlighting the regions relevant to wolf distribution patterns (map prepared using QGIS software, version 3.32.3).

Against this historical backdrop of decline and partial recovery, Slavonia—the eastern part of Croatia that largely overlaps with the Croatian sector of the Pannonian Basin—emerges as a key region for considering future wolf recolonisation. Slavonia encompasses extensive semi-natural habitats that remain in relatively good ecological condition, characterized by abundant prey for wolves, major rivers and the Slavonian Highlands. The Pannonian Plain is a large lowland region in Central Europe that spans parts of Croatia, Hungary, Serbia, Romania, Austria and Slovakia and corresponds broadly to the former Roman province of Pannonia. Although the Slavonian Highlands are isolated and surrounded by human-modified open landscapes that wolves typically avoid, long-term socio-economic changes and rural depopulation have contributed to land abandonment and ecological succession, creating new, potentially suitable habitats for wolf recolonization (Leblond et al., 2016). Habitat suitability modelling has also identified several areas in Slavonia as highly suitable for large carnivores

(Kusak et al., 2016), and wolf sightings reported in Slavonia during 2020 (unpublished data from Papuk Nature Park; Doboš et al., 2023) further support these predictions.

Based on this evidence, it was hypothesized that Slavonia could be a suitable region for the establishment of a stable wolf population (Kusak et al. 2016). To test this, wolf recolonization trends in the area were predicted using the following methods: (i) applying an existing wolf population dynamics model to estimate potential recolonization outcomes under 11 different management and land-use scenarios; (ii) comparing scenario outcomes over 10, 30, and 100 years; and (iii) identifying potential conservation actions to reduce the risk of local extinction in recolonized areas.

In the context of this thesis, these scenario-based projections of wolf recolonization in Slavonia and the wider Pannonian Plain directly address Hypothesis 3 by evaluating how different management and land-use options may facilitate or hinder the establishment of a viable wolf population in this region.

CHAPTER 3: MATERIALS AND METHODS

Building on the conceptual framework and methodological insights developed in Chapter 2, the empirical part of this thesis is organised into three complementary research components that operationalise the literature-based insights and directly address Hypotheses 1–3. Together, these components translate the literature on large-carnivore guilds, mesopredator release and camera-trap monitoring into a concrete empirical design that links global patterns, a local case study and regional recolonization scenarios.

3.1 OVERALL STUDY DESIGN

This thesis combines three complementary research components to assess how camera-trap monitoring and large carnivores can be used to understand and manage mammal communities, and to evaluate the potential for wolf recolonization in the Pannonian Plain. Together, these components link feasibility assessment, global synthesis and forward-looking scenarios within a single analytical framework centred on large-carnivore guilds, trophic structure and camera-trap monitoring.

The first component (Hypothesis 1) evaluates whether camera-trap data collected by protected-area staff can provide a reliable and cost-effective basis for monitoring wildlife communities relevant to future recolonization processes. Using a case study from Paklenica National Park, ranger-based camera-trap data are analysed to assess data quality, consistency and their suitability for ecological inference. In parallel, a comparative cost analysis contrasts the expenses of externally contracted surveys with those conducted by park staff, in order to assess the practical and economic feasibility of long-term, ranger-led camera-trap monitoring.

The second component (Hypothesis 2) synthesises camera-trap studies of terrestrial mammals at a global scale to test whether variation in large-carnivore presence, richness and dominance is consistently associated with changes in the relative representation of mesopredators and prey across ecosystems. By compiling primary detection data from multiple continents and standardising them into common trophic metrics, this analysis evaluates the extent to which camera-trap datasets can provide a robust basis for detecting predator-mediated trophic patterns at broad spatial scales. These global results define the core response variables and guild definitions used throughout the thesis.

The third component (Hypothesis 3) develops a spatially explicit population-dynamic model to forecast the recolonization of wolves in the Pannonian Plain, with a focus on Slavonia. Building on existing habitat-suitability assessments and incorporating key ecological and anthropogenic factors—such as habitat quality, prey availability, human pressure and major landscape barriers—the model explores under which conditions wolves could establish a viable population in this largely lowland, currently wolf-free region. Different management and land-use scenarios are simulated to examine how measures that reduce ecological barriers or modify landscape connectivity may affect recolonization dynamics and extinction risk, and the model outlines a camera-trap-based monitoring framework for tracking these processes.

Across these three components, the thesis uses a consistent set of concepts—large-carnivore guild structure, mesopredator–prey balance and trophic-level representation—and a shared reliance on camera-trap data, ensuring that feasibility assessment, global synthesis and regional scenarios form an integrated whole rather than three independent studies.

3.3 PAKLENICA RANGER-BASED CAMERA TRAPPING (HYPOTHESIS 1)

3.3.1. STUDY AREA

Paklenica NP is part of the Velebit Mountain and one of the eight national parks of Croatia. The area consisting of Velika and Mala Paklenica was proclaimed a national park in 1949 due to its unique geomorphological structures and natural best-preserved forest complex in the territory of Dalmatia (Figure 2). The Paklenica NP extends on 95 km^2 and it includes the highest peaks of the Velebit Mountain, Vaganski vrh (1752 m a.s.l.) and Sveto brdo (1753 m a.s.l.). The relatively small area has an abundance of karstic geomorphological phenomena and forms (canyons), diverse flora and fauna, attractive landscapes and intact nature. Floristic features of the Paklenica NP are black pine forests and several types of beech forests. The area is characterised by four different habitat types: unforested and poorly overgrown areas, thermophilic oak, beech and fir forests, grassland/pastures and juniper shrubs (Figure 2). The various habitats in the Paklenica NP and its complex orography support a very diverse fauna. Birds are the most numerous groups of vertebrates, with 260 species recorded to date; also, 31 amphibian and reptile species have been recorded, of which 11 are snake species. Mammals are represented by 59 species in five different taxonomic orders (unpublished; available in ‘Paklenica National Park’ Public Institution, Table A1, Appendices). The most numerous mammalian order is Chiroptera with 24 species, followed by Rodentia (14 species), Carnivora (10 species), Eulipotyphla (six species) and Artiodactyla (five species). Out of 59 mammalian species recorded in the Paklenica NP, 42 species are protected under different categories. Twenty-one mammalian species are categorised by the International Union for Conservation of Nature global conservation categories for Croatia, 28 are in the Annex II and Annex IV of the Habitats Directive, 42 are in the Annex I and Annex II of the Bern Convention and four are under CITES Convention. Furthermore, 31 mammalian species are categorised as strictly protected species under Croatian legislation. Also, the Paklenica NP is part of Natura 2000 (network of nature protection areas in the territory of the European Union) as site HR2000871 Nacionalni Park Paklenica. Large carnivores (i.e. top predators) inhabiting the Paklenica NP are brown bear (*Ursus arctos* L), grey wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*). Mesopredators are golden jackal (*Canis aureus*), red fox (*Vulpes vulpes*), *Martes* sp., wild cat (*Felis silvestris*), European badger (*Meles meles*) and least weasel (*Mustela nivalis*). Medium- to large-sized mammalian prey species are roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), mouflon (*Ovis aries musimon*), chamois (*Rupicapra rupicapra*) and wild boar (*Sus scrofa*).

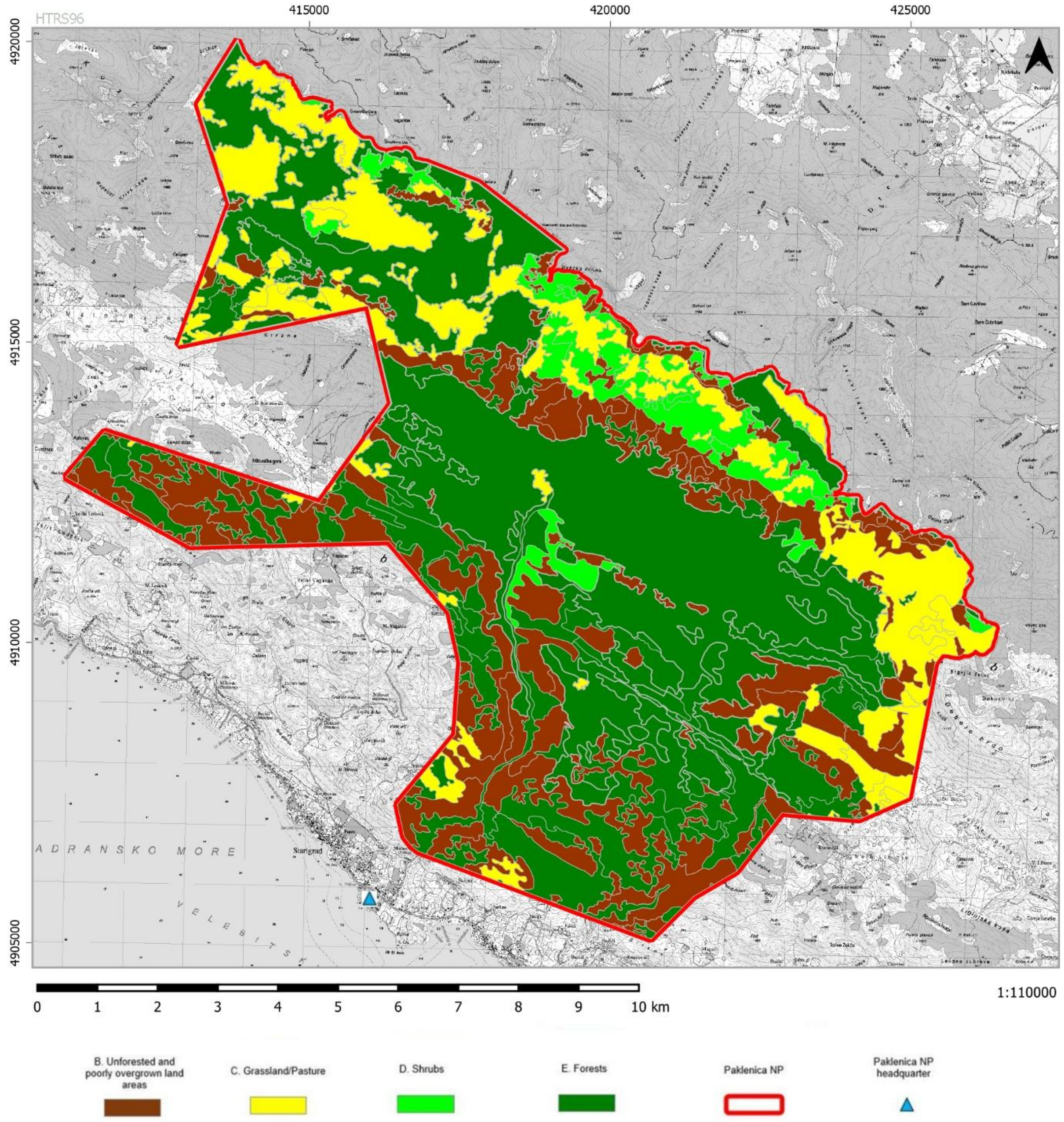

Figure 2 The habitat map of the Paklenica NP where camera trapping survey was conducted between 2011 and 2016. The map was produced by the author, while the habitat layers used in its preparation were derived from the 'Map of natural and semi-natural non-forest terrestrial and freshwater habitats of the Republic of Croatia' (Bardi et al., 2016). Map prepared using QGIS software (version 3.32.3).

3.3.2. CAMERA-TRAP DESIGN AND RANGER-BASED DATA COLLECTION

Camera surveys were performed between 2011 and 2016 at 22 camera sites (Table A2, Appendices), with one camera on each site. At every station the cameras recorded both still images and videos, and video clips varied in length depending on the model-specific settings used in a given year. Sites were chosen opportunistically, that is, on animal trails that are often used by park rangers, so that the care of the cameras could be incorporated into the usual work tasks of the rangers. Positions of camera traps are shown in Figure 3. Passive infrared heat- and motion-sensing cameras were used. Camera models were Cuddeback and SpyPoint Cellular Cameras. The trigger varied between 5 s, 30 s and 1 min. The video/picture set-up was also set differently, but the set-up of the video was dominant. Cameras were placed at locations designed to maximise chances of encountering medium- to large-sized mammalian species, including well-used animal trails, salt licks and small ponds. Each camera was fastened to a tree, 1 m above the ground, and focused to area without higher vegetation or onto an animal trail, to capture medium–large-sized mammalian species (Meek et al., 2014). Low-hanging branches and tall grass were trimmed at regular intervals to minimise camera misfires and provide an unobstructed view.

Cameras were installed at existing salt licks in 20% of the survey locations (N = XY), where salt is regularly provided for ungulates, which can substantially alter detection patterns by concentrating animal activity in space and time. In 20% of the locations (N=XY), camera traps were set next to small ponds, where regular use as watering sites can skew detections by drawing animals to a few focal points rather than reflecting their natural movement patterns.. If an attractant or water source was used, camera was directed to it. Cameras were checked once a month to change batteries and memory cards and to ensure proper functioning. All images were tagged with the time, date and temperature, while videos were only stamped with time and date.

Figure 3 Camera trapping sites at the Paklenica NP during 5-yearlong camera trapping surveys (2011 and 2016) The red line denotes the official boundary of Paklenica National Park, while the yellow polygon represents the minimum convex polygon (MCP) encompassing all camera locations.

Data from camera traps' memory cards was organised into folders, named by location and date, and stored on a central computer. Data spreadsheet was used for data entry, which was organised with 21 columns representing different data details (Table A3, Appendices). As the capture delay period differed among cameras (5 s, 30 s or 1 min, reflecting gradual improvements in field settings), all empty images and videos were removed prior to analysis. Independent events were then defined by discretising the time series: any record (image or video) with an animal detected by the sensor and documented by the camera was considered a separate event if it occurred at least 5 min after the previous record of the same species at the same camera station. This temporal threshold was applied to reduce pseudoreplication arising from animals remaining in front of the camera for extended periods, rather than to correct for differences in trigger speed, and is particularly important when cameras are placed on heterogeneous micro-locations (e.g. trails, salt licks, watering sites) that strongly influence local activity patterns. Camera trapping survey effort (number of 24-h operational camera trap nights) at each location was calculated from the date the camera was set until the date it was retrieved or, if the cameras malfunctioned, until the date stamped on the last picture taken.

For all photo captures, medium- to large-sized mammalian species determination was performed. The other groups of animals recorded on photos (Rodentia, Eulipotyphla, Chiroptera, *Martes* sp., Aves and Insecta) were not determined to the species level due to the camera traps setting methodology adapted to capture medium- to large-sized mammalian species. Mouse-like species (e.g. mice, rats, including all Eulipotyphla) were identified as ‘small mammals’ and all bats as Chiroptera. Furthermore, beech marten (*Martes foina*) and pine marten (*Martes martes*) were also not determined to species level because on most events, the species determination was not possible. So, ultimately, all these occurrences were classified as *Martes* sp. Also, species determination for insects and birds was not done, as they were identified in spreadsheet as Insecta and Aves. At last, there were also images of humans and domestic dogs, which were recorded as *Homo sapiens* and *Canis lupus familiaris*, respectively, while no vehicles were recorded.

Species richness index (SRI), defined here as the total number of mammal species detected per site, was calculated only for medium- to large-sized mammalian species. SRI was calculated as the sum of all recorded different species for each survey location and for the entire research area. SRI was also calculated for different habitats, substrates, temperature groups, seasons, day/night periods and photo/movie records. In order to analyse the time required to record all species of animals present in the study area, Pearson correlation was used. Thus, correlation was calculated between recorded SRI and camera trapping survey effort for each survey location. Calculation was done by the software Past, version 4.05.

3.3.3 DATA ANALYSIS: RANGER CONTRIBUTION

To quantify the financial aspect of the ranger service, a comparative analysis was done. The cost for conducting camera trapping surveys by external service was compared with the cost for conducting camera trapping surveys by nature park employees. Cost of a day of research conducted by external experts was collected from three biggest Croatian private companies that are conducting biological/ecological surveys. Cost per day of research conducted by the internal national park service was collected from the Paklenica NP. Their employees who can conduct camera trapping surveys are classified into four different categories: ranger service officer, ranger service chief supervisor, senior adviser and conservation manager. Further on, to calculate the number of days needed to conduct the camera-trapping survey in this case study in Paklenica NP, the camera-trapping survey effort for each location was divided by 30, reflecting the common practice of external service providers to inspect each site approximately once a month. The technical capacity of camera traps, however, would in many cases allow inspection intervals of 3–4 months, depending on site activity, camera specifications, SD-card capacity and battery life. Furthermore, the divided results (camera trapping survey effort for each survey location divided by 30) were increased by one additional day, which represents the first day of going to the survey location to set a camera trap. However, this assumption mainly applies to external survey teams travelling to the field, while for ranger staff, whose equipment is typically stored on-site, the required effort may be lower. Lastly, the divided results increased by one additional day were summed up for all survey locations together to calculate the total number of days needed to conduct this camera trapping survey. The summed days were then multiplied by the cost of a day of each type of researcher and compared with each other. Since this case study was conducted jointly by ranger service officers and ranger service chief supervisor, their cost was calculated as the mean value.

3.2 GLOBAL CAMERA-TRAP SYNTHESIS (HYPOTHESIS 2)

3.2.1 LITERATURE SEARCH

The methodological approach followed established guidelines for systematic reviews and meta-analyses in ecology to minimize subjectivity in study selection and data extraction (Koricheva et al. 2013). Because this research specifically focused on camera-trap data, only studies using camera traps to survey terrestrial mammals were considered for inclusion. All steps of the procedure, from the formulation of search strings to the final inclusion of studies, were predefined in a protocol developed prior to the literature search.

Because the primary objective of this research was to quantify how the presence and composition of large carnivores are associated with spatial variation in the structure of terrestrial trophic pyramids, particular emphasis was placed on camera trap studies reporting data for mammals in predator–prey contexts. To achieve this, a multi-tiered search strategy was implemented, combining broad keyword searches with successive screening of titles, abstracts and full texts across multiple scientific databases.

In the first step, it was conducted a broad keyword-based search to identify studies potentially containing data on predator–prey relationships in terrestrial mammal communities, including all literature published up to 1 January 2023. Systematic review of the scientific literature was conducted using Google Scholar. As this review (meta-analysis) was analysing linkage between large carnivore presence and the relative representation of different trophic levels (in particular mesopredators and their prey), the aim of this tier was to find papers that include camera trap data on the abundance of species in an area, namely mammals, with an emphasis on the relationship between prey and predators. The key words were *predator prey relationship, vertebrates, mammals, abundance, large carnivores.* To narrow the search for data and reduce the number of papers that do not contain the required data google scholar filter options were used: with all the words, with at least one of the words, with the exact phrase. In final search, as this meta-analysis was first focused on large carnivores, the phrase *˝large carnivores˝* was in filter *˝with the exact phrase˝, and phrase ˝predator prey relationship˝* was added to word *˝abundance˝* in filter *˝with all of the words˝*. In filter *˝with at least one of the words˝* were words *˝ terrestrial, mammal, vertebrate, predator˝*. Final phrase was - *abundance predator prey relationship terrestrial OR mammal OR vertebrate OR predator "large carnivores"*. Language was set to English. (Table A5-A7, Appendices).

In the second step, titles and abstracts of all retrieved records were screened to identify studies likely to include the required camera-trap data. An Excel spreadsheet was then created with the following categories: *Name, Title, Abstract, Comment, Link*. Categories *˝Title˝* and *˝Abstract˝* indicated whether the finding contained in its title or abstract information that would indicate that the finding had the necessary data for further analysis. ˝Name˝ was defined by the title of the finding, ˝Comment˝ contained my own notes regarding the possibility of obtaining the required data, and ˝Link˝ was a web link directing to the original source. Findings which had positive match for the *˝Abstract˝* (positive match means that *˝ Abstract˝* contains information that would indicate that the finding had the necessary data for further analysis), were further analysed.

In the third step, the full text of all potentially eligible papers was examined to confirm that they reported the specific camera-trap variables needed for the analyses, namely species-level detection data (identity of each mammal species), the number of recorded individuals or detections per species and camera-trap location, and the corresponding sampling effort (number of cameras and trap-nights) that could be assigned to trophic groups and spatial units. Full-text screening was conducted on all papers identified as potentially eligible in the previous step to determine whether they reported the camera-trap variables required for our analyses (e.g. species-specific detection data for large carnivores, mesopredators and prey, as well as sampling effort). For papers in which key raw data were incomplete or unclear, we contacted the original authors for clarification and to request additional datasets from the same projects or localities that were not retrieved in the initial literature search and included these datasets when sufficient information was provided.

To complement this process, it was then repeated the search using an additional literature database, applying the same keyword combinations and screening criteria. Since it is known that meta-analyses are of higher quality when two scientific literature search engines are used, we included Europe PCM search engine in addition to Google Scholar. The same keywords were used as in Google Scholar, and in tier 2, we identified 195 papers. Although many systematic reviews rely on citation databases such as Web of Science and Scopus, these platforms were not used in the search strategy. Instead, Google Scholar and Europe PMC were combined, as these sources provide better coverage of grey literature and technical reports (e.g. agency and NGO documents) in which camera-trap data are often reported. Nonetheless, it is acknowledged that no single combination of databases offers complete coverage and that some relevant studies may not have been captured by this search strategy.

Finally, a data-completeness filter was applied to retain only those studies and sites that, for large carnivores, mesopredators and prey, reported species identities, the number of recorded individuals (or detections) per species and camera-trap location, and the corresponding sampling effort, allowing mesopredator–prey detection ratios to be calculated consistently across assemblage types. After assembling the full set of papers, it was conducted a final screening step to ensure that each one contained the minimum information required to quantify the relationships among trophic levels. For every paper, it was checked whether data on the detection rates of all three focal groups were available, i.e. as counts of recorded individuals or detections per species and camera-trap location for large carnivores, mesopredators and prey. Findings for which any of these trophic levels were missing were excluded at this stage because they would not have allowed us to estimate mesopredator–prey detection ratios across different large-carnivore assemblage in a consistent way. This filtering step yielded the final set of study sites that entered the meta-analysis of mesopredator-to-prey detection ratios. In this meta-analysis, each paper represents a distinct camera-trap study, and each study site refers to a specific survey area reported within a paper; some papers report only one study site, whereas others include multiple study sites within the same publication.

3.2.2 DATA SOURCES AND EXTRACTION

In the next step, site-level camera-trap detection data from all eligible studies were compiled, and a common analytical framework for the global synthesis was defined. Because no previous work had reported quantitative response metrics (e.g. mesopredator–to–prey detection ratios) that directly matched our hypotheses and response metrics, suitable published estimates were rarely available. A global quantitative synthesis was therefore conducted using area-level primary data extracted from published and unpublished camera-trap studies, with a focus on spatial variation in mesopredator–prey detection ratios among sites. At each study site, the response metric was defined as the natural logarithm of the ratio between mesopredator detections and detections of their potential mammalian prey, whereas large carnivores were incorporated as explanatory variables describing predator guild structure, specifically large-carnivore richness, assemblage type and the relative dominance of frequently versus rarely detected large-carnivore species. Rather than relying on previously reported quantitative response metrics, raw detection data for mesopredators and prey were compiled for each study site, and a standardised mesopredator-to-prey detection ratio (expressed as its natural logarithm) was calculated using a consistent definition across all datasets. This approach allowed heterogeneous sources to be integrated within a formal meta-analytic framework while avoiding inconsistencies in reported metrics among studies. All quantitative response metrics were derived directly from primary detection counts, enabling a site-level quantitative synthesis across independent studies. Study identity was retained in the analyses to account for non-independence among sites originating from the same source. This method follows established practices in ecological meta-analysis where standardized response metrics are calculated from raw data when comparable published estimates are unavailable (Koricheva & Gurevitch 2014).

For each included study, species-level detection information and associated attributes were then systematically extracted into a structured dataset for analysis. Data extracted from 27 studies encompassing 57 independent sites were organized in an Excel spreadsheet. For each paper 28 attributes were extracted (Table A8, Appendices) and organized in columns with each row indicates one species per study.

3.2.3 FUNCTIONAL GROUPS AND COVARIATES

In these analyses, species at each site were aggregated into functional groups (Table A10, Appendices). Large carnivores were defined as non-marine mammalian predators with an average adult body mass greater than 15 kg (Ripple et al. 2014), and mesopredators as medium-sized mammalian carnivores of approximately 1–15 kg body mass, corresponding to the group labelled as small carnivores in our tables (Soulé et al. 1988). This 1–15 kg range represents an operational body-mass definition tailored to this global comparative dataset, rather than a universal or taxonomically fixed definition of mesopredators. For the purposes of this analysis, prey was classified as non-carnivorous terrestrial mammals and divided into small prey (Muridae and smaller species) and large prey (species larger than typical Muridae). During data preparation for the meta-analysis, preliminary explorations showed that the three original land-use classes (Natural, Seminatural, Anthropogenic) overlapped too much to be used reliably and were overly sensitive to the subjective judgment of the person compiling the dataset, because many sites had intermediate characteristics and could plausibly fall into more than one category. To reduce this potential for misclassification, study sites (i.e. sets of camera traps belonging to the same study area) were regrouped into two broader categories for analysis: "Natural", which retained all sites originally classified as natural, and "Human-modified", which combined sites originally classified as seminatural or anthropogenic, that is, all sites with notable human use or disturbance. After data extraction, the analysis proceeded in several steps to quantify how large-carnivore assemblages are associated with variation in mammal community composition, including both mesopredators and prey species, and to synthesise results across studies.

3.2.4 DATA PREPARATION AND SITE CLASSIFICATION

For each site, the total number of detections was first calculated, followed by the species richness index (defined here as the total number of mammal species detected per site - SRI) and the relative detection index. Detection data for each site were standardized to a common metric; namely, the Relative Detection Index (RDI), expressed as the number of detections per 100 trap-days. Subsequently, for each study site, the number of different species within each functional group (e.g., large carnivores - c, small carnivores - v, large prey - p, small prey - m) was calculated. All variables were then checked for consistency, missing data and apparent outliers before further analysis.

Afterward, large-carnivore species were analysed separately for each site to determine whether only one or multiple large-carnivore species were detected on site. In sites where more than one large-carnivore species was present, K-means clustering analysis (K = 2) was applied to species-level detection frequencies to identify locally dominant and locally rare species within each site. This unsupervised classification divided species based on their detection values into two clusters, minimizing within-group variation. Because camera-trap detection rates integrate both local density and activity, higher detection frequencies are expected for species that use space more intensively and are more likely to encounter prey and competitors, so our detection-based dominance categories provide a pragmatic proxy for ecological dominance (e.g. higher encounter and kill rates, stronger interference and spatial exclusion) within each local large-carnivore assemblage. Thus, for each site, every large-carnivore species was classified as either dominant or rare relative to the other large-carnivore species occurring at that site. Here, “Dominant” and “Rare” do not refer to global species status or to their hierarchy within the carnivore assemblage, but to their relative detection frequencies within each site-level large-carnivore assemblage, as determined by K-means clustering.

Based on this analysis, four groups of sites were defined: (i) A (Alone – one large-carnivore predator), only a single large-carnivore species was present at the site; (ii) D > R (Dominant > Rare), the number of dominant large-carnivore species at the site was greater than the number of rare species; (iii) R > D (Rare > Dominant), the number of rare large-carnivore species at the site was greater than the number of dominant species; (iv) D = R (Dominant = Rare), the number of dominant and rare large-carnivore species at the site was equal. Here, ‘dominant’ and ‘rare’ species follow the site-level classification derived from the K-means clustering of detection frequencies described above, where each large-carnivore species at a site was assigned to the dominant or rare group based on its relative detection rate within that local assemblage. Predator assemblage classification was based on large-carnivore community structure, with each site assigned to one of four large-carnivore assemblage categories based on the relative representation of dominant and rare large carnivore species, as stated before: (i) A, (ii) D>R, (iii) R>D, and (iv) D=R.

Quantitative response metrics were calculated at the site level as the natural logarithm of the mesopredator-to-prey detection ratio, with associated sampling variances defined so that sites with more detections contributed more precise estimates; full details of the response-metric calculation are provided below (see “Response metrics calculation”).

3.2.5 RESPONSE METRICS

Quantitative response metrics were calculated at the site level as the natural logarithm of the mesopredator-to-prey detection ratio, with associated sampling variances defined so that sites with more detections contributed more precise estimates. Response metrics calculation followed a log ratio approach, where mammal assemblage was quantified using the natural logarithm of the mesopredator-to-prey detection ratio:

$$y_i = \ln\left(\frac{V + 0.5}{P + 0.5}\right),$$

where V represents the total number of detections pooled across all mesopredator species at a given site, while P represents the total number of detections pooled across all prey species at that site. P was calculated as the sum of detections of large-prey and small-prey species (P = p + m, where p denotes detections of large prey and m denotes detections of small prey). Assessment of prey size structure was initially planned by comparing detection frequencies of small and large prey species along a prey-size gradient. However, camera traps are known to have limited detection efficiency for small mammals due to sensor height, body-size constraints and vegetation occlusion. In the compiled dataset, detections of small mammals (i.e. species that predominantly make up the small-prey guild in our classification) were available for only a subset (~35%) of sites and were still likely biased toward larger-bodied species within this group. Because detection processes were therefore not comparable across sites, analyses contrasting small versus large prey were not included as formal meta-analytic tests. Instead, the primary analyses focused on community axes for which camera-trap data provide more reliable and consistent detection, namely mesopredator–prey composition dependencies on large-carnivore groupings.

Because V and P are derived from camera-trap detections, this metric is a detection-based index that conflates true abundance, activity patterns, and detectability, rather than a direct estimate of population density or absolute mesopredator–prey ratios. A continuity correction of 0.5 was applied to accommodate zero counts and reduce bias associated with sparse data. Positive values of y_i indicate mesopredator-dominated assemblages, negative values indicate prey-dominated assemblages, and values near zero indicate similar detection frequencies of mesopredators and prey.

Sampling variances were approximated using:

$$v_i = \frac{1}{V + 0.5} + \frac{1}{P + 0.5},$$

which provides an appropriate variance estimator for log-transformed count ratios. These calculations were implemented in PAST 4.03. Response metrics therefore represent site-level mesopredator–prey ratios that are later related to predator assemblage class via meta-regression.

Sensitivity analysis was conducted to assess the robustness of results to the choice of continuity correction applied to zero-inflated count data; we conducted a sensitivity analysis using an alternative effect-size definition. In this analysis, site-level response metrics were calculated as the natural logarithm of the mesopredator-to-prey detection ratio with a stronger continuity correction, ln((V+1)/(P+1)), where V and P represent the number of mesopredator and prey detections, respectively. Corresponding sampling variances were estimated as 1/(V+1) + 1/(P+1). The sensitivity analysis was fitted using the same multilevel meta-analytic framework as the primary analysis, including large-carnivore assemblage class as a moderator and study identity as a random effect. Results from the sensitivity analysis were compared qualitatively and quantitatively with those of the primary analysis to evaluate the influence of low detection counts and zero inflation on model estimates.

3.2.6 META-ANALYTIC MODELLING AND VISUALISATION

To evaluate whether mammal community composition varies among study sites with different large-carnivore assemblages, a multilevel meta-analysis was conducted using camera-trap detection frequencies. Data were compiled from papers reporting site-level detections of mammal species recorded using camera traps. For each study site, species detections were aggregated into functional guilds, with mesopredators operationally defined as medium-sized carnivores and prey defined as non-carnivorous mammals, which were divided into small prey and large prey. For this meta-analysis, analyses were conducted at the study-site level, where each study site represents the spatial area within which camera traps were deployed and for which the original authors reported aggregated camera-trap results. Some papers report only one study site, whereas others include multiple study sites within the same publication. Mesopredator–prey detection ratios at each study site were then analysed in relation to differences in large-carnivore assemblage types among sites.

Response metrics were synthesised using multilevel random-effects meta-analytic models that account for among-study and among-site heterogeneity. Predator assemblage class (A, D>R, R>D, D=R) was included as a categorical moderator in the meta-analysis to test whether site-level mesopredator-to-prey ratios varied among assemblage types, i.e. predator class was evaluated via meta-regression rather than via pairwise treatment–reference contrasts (Viechtbauer 2010). Statistical analysis was based on multilevel random-effects meta-analytic models fitted with restricted maximum likelihood (REML). Large-carnivore assemblage category (A, D>R, R>D, D=R), describing differences in large-carnivore assemblage structure, was included as a fixed-effect moderator, while study identity was included as a random intercept to account for non-independence among sites originating from the same study. Residual heterogeneity was assessed using Cochran’s Q statistic, and the significance of the moderator was evaluated using Wald-type tests. Model fit and relative support for alternative specifications (e.g. with and without interaction terms) were compared using Akaike’s Information Criterion (AIC) and its small-sample correction (AICc). All analyses were conducted in R (ver. 4.5.1) using the metafor package.

Visualisation of raw site-level effects was used to complement the meta-analytic results and facilitate interpretation of underlying data patterns. Raw site-level effects were visualised across large-carnivore assemblage classes using boxplots and violin plots. Boxplots were used to summarise central tendency and dispersion of effect sizes within each predator assemblage class, while violin plots illustrated the full distribution and density of values. A horizontal reference line at zero was included in all plots to indicate equal mesopredator and prey detection frequencies, such that values above zero indicate relatively higher mesopredator detections than prey, whereas values below zero indicate relatively higher prey detections than mesopredators. These visualisations were intended to assess overlap among assemblage classes, identify potential outliers and evaluate whether patterns observed in the meta-analysis of mesopredator–prey ratios among large-carnivore assemblages were reflected in the raw, unweighted data.

Incorporating land-use context into the meta-analysis, it was assessed whether hypothesised top-down relationships between large-carnivore assemblage structure and mesopredator–prey community composition depend on human land use by extending the primary meta-analysis to include site-level land-use information. Each study site was classified according to land-use type as either natural or human-modified. Effect sizes were analysed using multilevel random-effects meta-analytic models fitted with restricted maximum likelihood (REML).

Two complementary models were evaluated. First, a main-effects model included predator assemblage class and land-use category as additive fixed effects, with study identity included as a random intercept to account for non-independence of sites within studies. Second, an interaction model additionally included the interaction between predator assemblage class and land-use category to explore whether predator effects differed between natural and human-modified landscapes. Residual heterogeneity was assessed using Cochran's Q statistic, and the overall significance of moderators was evaluated using Wald-type tests.

3.4 WOLF RECOLONIZATION MODELLING IN THE PANNONIAN PLAIN (HYPOTHESIS 3)

3.4.1 STUDY AREA

The Pannonian Basin, also referred to as the Pannonian Plain or Carpathian Basin, is a vast and relatively flat landform in Central Europe. This geomorphological unit extends across several countries, including Hungary, Croatia, Serbia, Slovakia, Austria, and Romania. In this study, the focus is on the Croatian portion of the Pannonian Basin and the adjacent Peripannonian area, which encompasses the region of Slavonia and parts of its neighboring territories (Figure 2). For the purposes of this research, the study area is designated as Slavonia. This region is bordered by the Drava River to the north, the Danube River to the east, the Sava River to the south, and the Moslavačka Gora hills to the west, covering approximately 15,000 km^2. Slavonia includes 12 Special Protection Areas (SPAs) established under the Bird Directive (2009/147/EC), 63 Sites of Community Importance (SCIs) under the Habitats Directive (92/43/EEC), and 52 areas protected by the Croatian Nature Protection Act ("Official Gazette" No. 80/13, 15/18, 14/19, 127/19, 155/23). The dominant habitats in this area are agricultural and forested landscapes, interspersed with patches of anthropogenic peri-urban environments (Figure 4). The forests are primarily composed of temperate broadleaf species, including mixed oak–hornbeam (*Quercus robur L., Carpinus betulus L.*) forests, pure hornbeam (*Carpinus betulus L.*) stands, Central European acidophilic cypress oak forests with common birch (*Betula pendula Roth.*) and Turkey oak (*Quercus cerris L.*), floodplain Hungarian oak (*Quercus frainetto Ten.*) forests, as well as mesophilic and neutrophilic pure beech (*Fagus sylvatica L.*) forests.

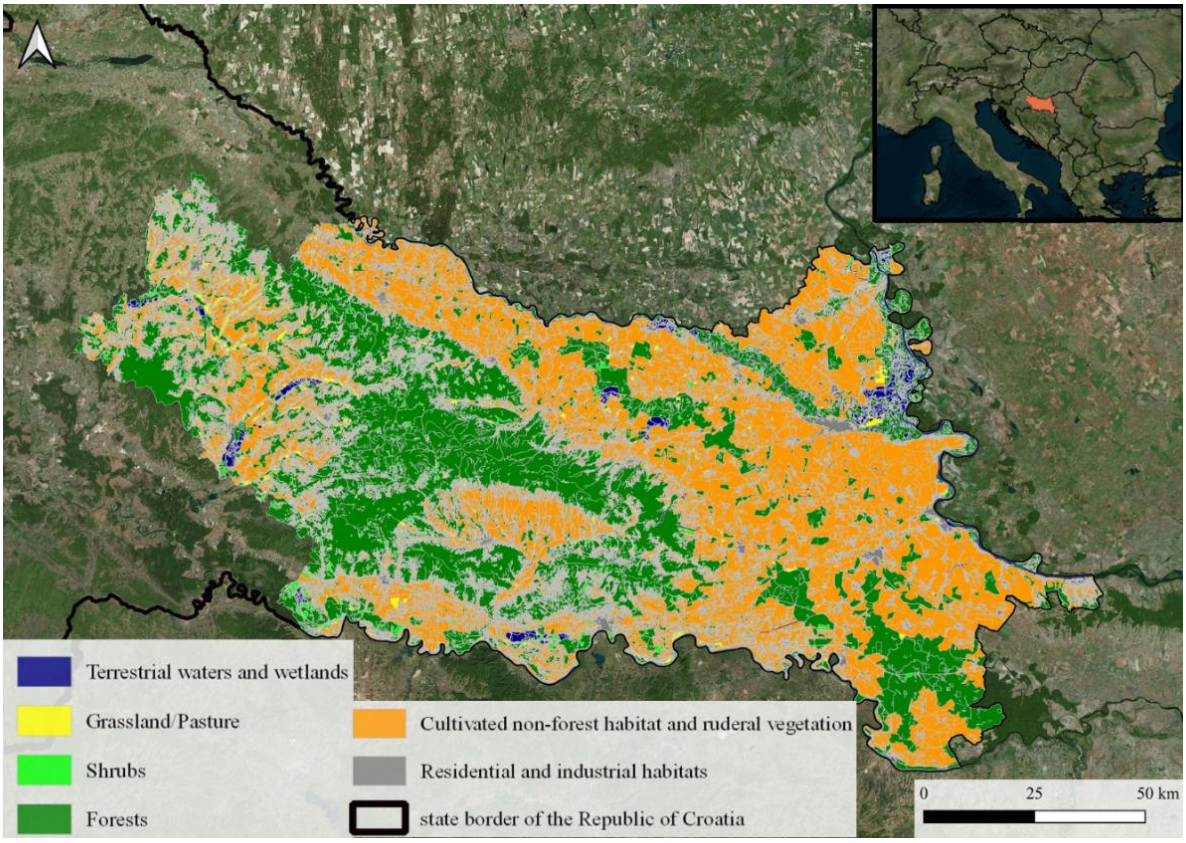

Figure 4 Land cover map of the Slavonia survey area (Croatia), illustrating the distribution of major habitat types. The study area is outlined by the national border of the Republic of Croatia (black line). Habitat categories depicted include forests (dark green), shrublands (light green), grasslands and pastures (yellow), cultivated non-forest habitats and ruderal vegetation (orange), residential and industrial areas (gray), and terrestrial waters and wetlands (dark blue). The map was produced by the author, while the habitat layers used in its preparation were derived from the 'Map of natural and semi-natural non-forest terrestrial and freshwater habitats of the Republic of Croatia' (Bardi et al., 2016). Map prepared using QGIS software (version 3.32.3).

There are currently no documented permanent wolf packs in the study area; however, researchers from the Papuk Nature Park Public Institution (unpublished data) have recorded the presence of at least one individual. The medium-sized carnivore guild in the region includes the golden jackal (*Canis aureus*), red fox (*Vulpes vulpes*), and badger (*Meles meles*; Doboš et al., 2023). Potential prey for wolves consists of roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), wild boar (*Sus scrofa*), and European hare (*Lepus europaeus*) (Doboš et al., 2023). In addition, several domestic species—such as cattle, horses, donkeys, goats, sheep, and pigs—are present; while these animals are not free-roaming, they graze in the area and may occasionally become prey for wolves.

To assess anthropogenic disturbance within the study area, changes in anthropogenic habitats—including residential and industrial zones (such as villages, cities, non-industrial, and industrial areas)—were evaluated using Croatia's habitat maps from 2004 (Antonić et al., 2005) and 2016 (Bardi et al., 2016) through GIS analysis in QGIS software (version 3.32.3).

3.4.2 PROJECTION MODEL

Combination of modeling approaches were employed for the Population and Habitat Viability Assessment (PHVA; Merli et al., 2023), with a primary focus on stochastic modeling techniques, supplemented by spatially explicit, demographic, catastrophic, and management models (Petracca et al., 2023). Key components of the stochastic models used in this research include the following: (i) Spatially Explicit Models: These models identify key habitats, assess habitat suitability for the species, and evaluate the impacts of habitat fragmentation and land-use changes. (ii) Demographic Models: These capture demographic variability at the population level, representing the structure and dynamics of the population based on characteristics such as age-specific survival and reproduction rates. (iii) Management and Conservation Models: These models evaluate scenarios involving harvesting, supplementation (such as translocations and reintroductions), habitat management, and other conservation interventions. (iv) Catastrophe Models: These simulate the frequency, severity, and types of catastrophic events (e.g., natural disasters and disease outbreaks) and their effects on the population. Importantly, our modeling approach is individual-based, meaning each animal in the population is simulated separately, with attributes such as age and sex. Genetic models were not included in this research due to insufficient available data. All simulations were conducted using VORTEX software, version 10.6.0 (Lacy & Pollak, 2023).

Vortex enables model parameterization and extinction probability prediction across 13 categories reflecting species ecology and management strategies: Scenario Settings, Species Description, State Variables, Reproductive System, Reproductive Rates, Mortality Rates, Catastrophes, Mate Monopolization, Initial Population Size, Carrying Capacity, Harvest, Supplementation, and Genetics. In all simulations, a population was considered to be extinct when the number of living individuals declined to zero and remained at that level by the end of the simulation time horizon. Parameters related to baseline population dynamics—Species Description, Reproductive System, Reproductive Rates, and Mortality Rates—were sourced from the existing literature (Štrbenac et al., 2010; Frković et al., 1992; Kusak, 2002; Platiša et al., 2011; Turinski, 2017; Wikenros et al., 2021). The remaining parameters, including Scenario Settings, Catastrophes, Initial Population Size, Carrying Capacity, Harvest, and Supplementation, were assigned predefined values for simulation purposes. For each scenario, estimates of population growth and extinction probability were generated, focusing primarily on changes in habitat carrying capacity while also incorporating variations modeled through the Vortex categories of Catastrophes, Harvest, and Supplementation. A detailed explanation of how these category values were defined and the specific scenarios in which they were applied is provided in the scenario description below.

All parameter values are reported in APPENDIX 12.

3.4.3 SCENARIOS

In this study, 11 different scenarios were modelled: a baseline scenario and 10 alternative scenarios, which were organized into three groups (

Table 1). Although there are no records of permanent wolf packs in the study area and only a single individual wolf has been observed, the initial population size set as a pair for all scenarios. The categories State Variables, Mate Monopolization, and Genetics were not explicitly modeled and were instead left at their default settings in all scenarios. For the Scenario Settings category, each simulation consisted of 1000 replicates and was run over three distinct timeframes: 10, 30, and 100 years.

The baseline scenario simulated the wolf population based solely on the carrying capacity of the modeled area. The remaining 10 scenarios were parameterized to reflect variations in catastrophes, carrying capacity, harvest levels, and supplementation efforts.

The first group of three scenarios represented adverse events—situations that could lead to a population decline relative to the baseline scenario. The second group comprised three scenarios involving an increased carrying capacity. The third group included four scenarios focused on supplementing the wolf population. Of the ten alternative scenarios depicting changes in population size, seven were designed as management interventions, while the remaining three addressed system uncertainty. All spatial analyses were performed using GIS in QGIS software (version 3.32.3).

*Table 1 Summary of 11 scenarios used to project the gray wolf population in the modelled area **

Scenario No.	**Scenario Name**	**Scenario Class**	**Description**	**Variable Vortex Categories**
1	Baseline	-	Population based on modeled area's carrying capacity, determined by habitat suitability map	Carrying Capacity
2	Disease	Uncertainty	50% population reduction over two six-month periods due to disease	Carrying Capacity and Catastrophes
3	Removals	Management	Annual removal of an animal due to human–wildlife conflicts	Carrying Capacity and Harvest
4	Illegal hunting	Uncertainty	Annual removal of two animals due to illegal hunting	Carrying Capacity and Harvest
5	Succession: Carrying capacity boost	Uncertainty	Increase in suitable habitat due to natural succession	Carrying Capacity
6	Forest Management: Carrying capacity boost	Management	Increase in suitable habitat due to alterations in forest management practices	Carrying Capacity
7	Hunting Management: Carrying capacity boost	Management	Increase in carrying capacity by modifying hunting management	Carrying Capacity
8	One-Region Corridor Enhancement: Immigration by existing corridors (Banovina)	Management	Supplementation with one male wolf from Banovina—enhancing existing corridors	Carrying Capacity and Supplementation
9	Corridor construction: Immigration by new corridors (Banovina) + succession	Management	Supplementation with one pair of wolves (male and female) from Banovina—creating new corridors with an increase in suitable habitats due to natural succession	Carrying Capacity and Supplementation
10	Two-Region Corridor Enhancement: Immigration by existing corridors (Banovina and Bosnia and Herzegovina)	Management	Supplementation with one male wolf from Banovina and one male wolf from Bosnia and Herzegovina—enhancing existing corridors from both regions	Carrying Capacity and Supplementation
11	Translocation: Translocation from Croatia	Management	Translocation of one male and one female wolf from another Croatian wolf population	Carrying Capacity and Supplementation

** Full details of all 11 scenarios are provided in Appendix A.*

The outcomes of these scenarios will be used to inform the design of camera-trap monitoring in the Pannonian Plain and to interpret expected changes in mesopredator–prey structure as wolves recolonize the region, in line with the broader framework developed in this thesis.

3.4.4 STATISTICAL ANALYSIS

To compare results across our modeled scenarios, the number of simulations in which populations went extinct (calculated as the inverse of survival rates) were analyzed from 1000 replicates over three time periods (10, 30, and 100 years). Data were generated annually for all 11 scenarios. First, we tested the extinction counts for normality using the Shapiro–Wilk test. Since the data violated parametric assumptions, non-parametric alternatives were employed (Constable et al., 1998). Kruskal–Wallis test was used followed by Dunn's post hoc tests to determine whether recolonization success (inverse of extinction counts) differed significantly between scenarios. These analyses were conducted for four datasets: the 10-year model, 30-year model, 100-year model, and a combined dataset incorporating all timeframes. Additionally, Principal Component Analysis (PCA) with a covariance matrix was performed on the combined dataset to identify potential groupings among scenarios based on extinction patterns (Jolliffe & Cadima, 2016). This approach allowed to reduce complex data into principal components, revealing which scenarios and timeframes contributed most significantly to species conservation. PCA was applied separately to the 10-year, 30-year, and 100-year datasets, as well as the combined dataset.

All analyses were performed using Past software (version 2024.5.0.2), while result visualizations were created with Microsoft Excel (version 365) and Statistica (version 13.3).

CHAPTER 4: RESULTS

4.1 PAKLENICA CASE STUDY (HYPOTHESIS 1)

4.1.1 CAMERA-TRAP DETECTIONS AND SPECIES RICHNESS

During the 5-year long camera trapping survey, total survey effort was 4474 camera days. Four locations had total survey efforts longer than 1 year and comprised 78% of the total survey effort, so the other 18 survey locations contained the remaining 22% of the total survey effort. All four of these long-term locations were salt-lick sites. Eleven locations had camera trapping survey efforts shorter than 2 months.

Fourteen mammalian species were recorded (Table A4) as follows: golden jackal (*Canus aureus*), grey wolf (*Canus lupus*), European roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), wild cat (*Felis silvestris*), European hare (*Lepus europaeus*), Eurasian lynx (*Lynx. lynx*), Eurasian badger (*Mles. meles*), northern chamois (*Rupicapra rupicapra*), Eurasian red squirrel (*Sciurus vulgaris*), wild boar (*Sus scrofa*), brown bear (*Ursus arctos*), red fox (*Vulpes vulpes*), and marten (*Martes* sp.). Furthermore, other determined groups were Chiroptera, Insecta and Rodentia. Regarding NATURA 2000 site HR2000871 Nacionalni park Paklenica, all medium–large mammalian key species were recorded during this survey.

In total, 16,289 events (photos/movies with animals) were recorded with 16,132 events (99.04%), where it was possible to determine the species, whereas in 157 events (0.96%), it was not possible to determine the species. In these 16,132 events, there were, in total, 31,727 recorded individual animals (because in some photos, there were groups with up to 14 animals). Ungulates were the most frequently recorded: northern chamois (9284 events, 64.31% of all photos/movies), red deer (2129 events, 14.75%), wild boar (1051 events, 7.28%) and European roe deer (998 events, 6.91%). On the other hand, the species with the lowest number of photos were predators: Eurasian lynx – 4 events, 0.03%, grey wolf – 3 events, 0.02% and golden jackal – 2 events, 0.01%. Not including humans, the species that were recorded at most survey locations were wild boar, roe deer and northern chamois (64% of all camera trapping locations). Carnivores were recorded at less than 50% of all camera trapping locations as follows: red fox – 8 (36%), brown bear – 7 (32%), *Martes* sp. (beech and pine marten) – 7 (32%), wild cat – 5 (23%), grey wolf – 3 (14%), Eurasian lynx – 3 (14%) and golden jackal – 1 (5%).

Average number of recorded animals per event was 1.96 (standard error [SE] = 0.0109). Ungulates had higher average numbers of recorded animals per event as follows: northern chamois – 2.24 (SE = 0.014), wild boar – 2.19 (SE = 0.057), red deer – 1.58 (SE = 0.020), European roe deer – 1.37 (SE = 0.017). They also had higher maximal number of recorded animals per event (wild boar – 14, northern chamois – 11, red deer – 6, European roe deer – 5) as they are usually in groups/herds, while most carnivores were recorded only solitary (Eurasian lynx, grey wolf, golden jackal, *Martes* sp.).

Due to camera trapping locations (Figure 3), three locations recorded the highest SRI with more than 10 different mammalian species, seven locations recorded between five and 10 different mammalian species, 10 locations recorded less than five different mammalian species, and two locations did not record any wildlife species (humans were only recorded). Regarding the SRI for locations during day period compared to during night period, higher values were recorded during night than during day period.

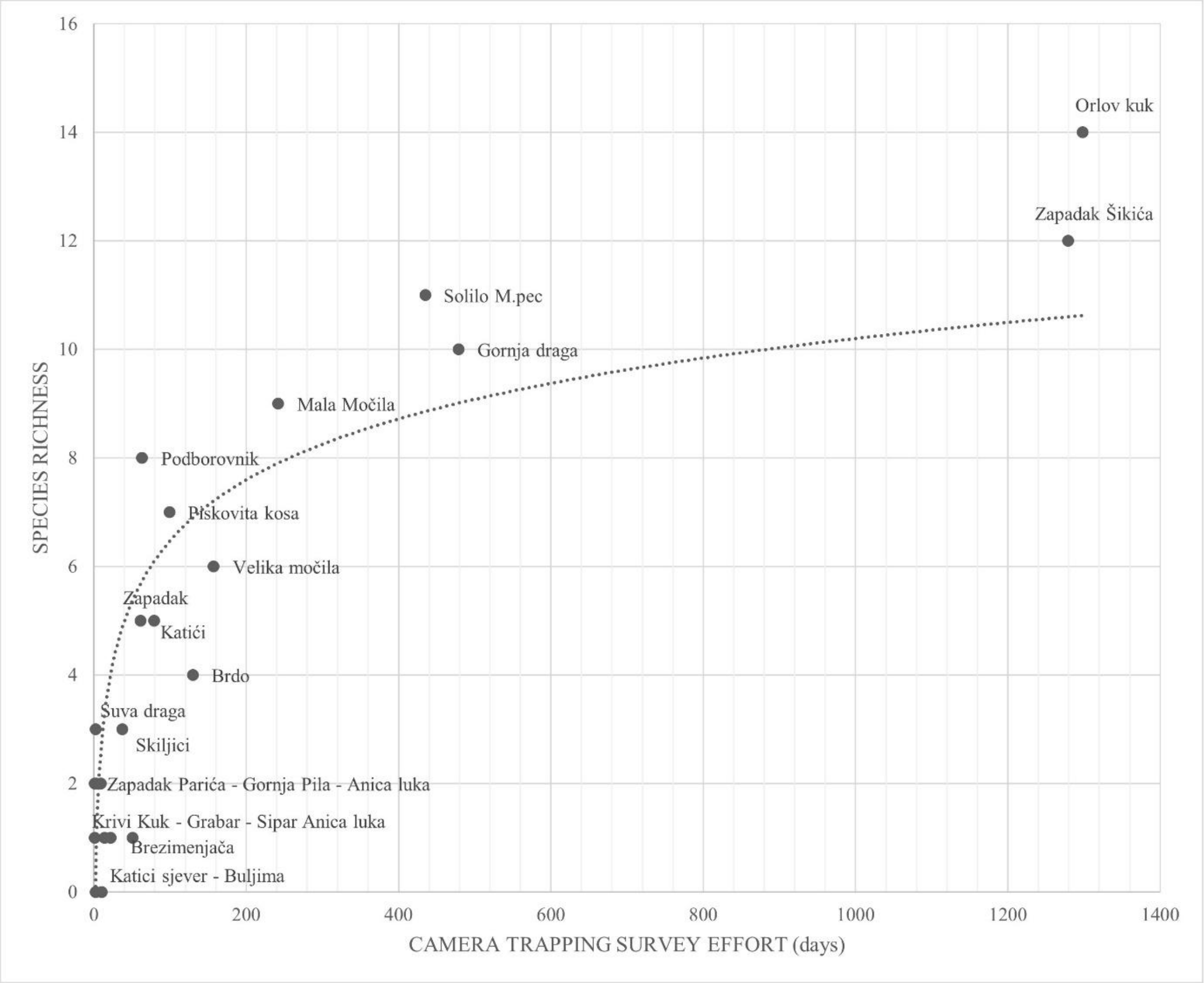

Figure 5 Species richness of the survey locations

Moreover, SRI was analysed regarding different habitats, substrates, temperatures, seasons and day/night periods, and the highest SRI values were found for semi-open karst habitat, stone substrate, temperature group 0–9°C, during autumn, during night and recorded on photo (Figure 6).

Figure 6 SRI distribution based on six different characteristics of the camera trapping locations: habitat, substrate, temperature group, seasons, day/night period, photo/movie

To analyse the time required to record all species of animals present in the study area, species richness was compared with camera trapping survey effort for each survey location. The correlation coefficient between the log subject variables was 0.901 ($P < 0.05$), which confirms that the two data sets are positively correlated. In the first 200 days, eight of 14 species were recorded (almost 60%); with a further doubling of the effort, a maximum of one additional species was detected (Figure 5, Figure 7). These additionally detected species were mostly elusive species that have been rarely recorded or large carnivore species that have low abundances as top predators. The same pattern can be seen analysing only top predator species records.

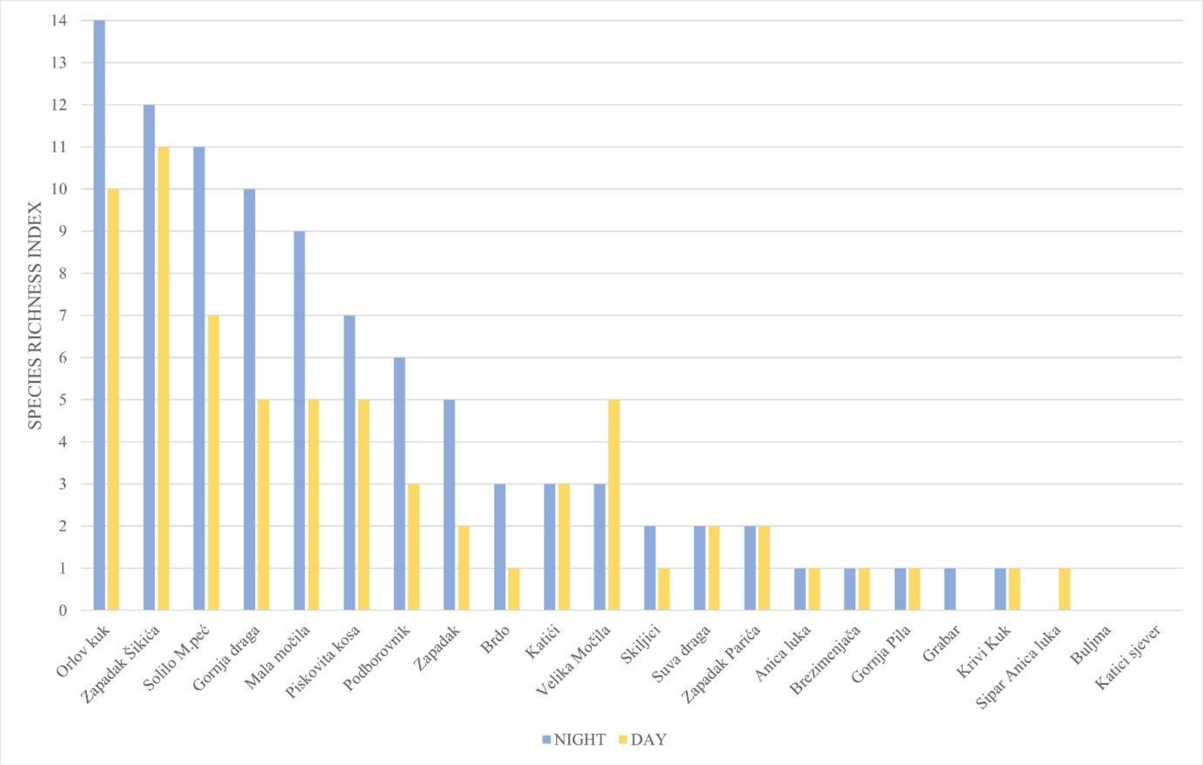

Figure 7 Comparison of the recorded species richness and camera trapping survey effort for each survey location

4.1.2 RANGER-BASED MONITORING OUTCOMES

Regarding the comparison of costs for conducting camera trapping survey by external service and internal national park service, the findings were as follows. External service costs varied from 200 € per day to 300 € per day; so, for further calculations, the mean value (250 € per day) was used. Internal Paklenica NP service costs varied significantly depending on the employment rank. The cost of the ranger service officer's working day was 33 € per day, ranger service chief supervisor's cost was 44 € per day, senior adviser's cost was 55 € per day and conservation manager's cost was 62 € per day. The calculated total number of days needed to conduct this camera trapping survey case study was 178 days. Therefore, the total cost of this research could be as follows according to the type of employee who could conduct the survey: external service – 44.500,00 €, ranger service officer – 5.874,00 €, ranger service chief supervisor – 7.832,00 €, senior adviser – 9.790,00 € and conservation manager – 11.036,00 €. The total cost of joint work by ranger service officers and ranger service chief supervisor was 13.706,00 €. External service had the highest cost price for conducting research, even four times higher than the cost of the Paklenica NP highest ranking employee, that is, conservation manager. Ranger service officer had the lowest cost for conducting research, around seven times lower than the external service cost. Ranger service chief supervisor's cost was 33%

higher than the ranger service officer's cost, senior adviser's cost was 67% higher and conservation manager's cost was 88% higher than the ranger service officer's cost. The total cost of joint work by ranger service officers and ranger service chief supervisor was approximately three times lower than the external service's cost.

4.2 GLOBAL META-ANALYSIS (HYPOTHESIS 2)

4.2.1 DATASET

The multi-tiered literature search produced a large initial pool of studies that was progressively narrowed to a final meta-analytic dataset. The keyword search (Tier 1) yielded between 151,000 records (for the phrase "mammals predator prey relationship") and 23,100 records (for "abundance large carnivorous vertebrate predator prey relationship"; Table A5, Appendices), and after refining the search syntax, the final search phrase ("abundance predator prey relationship terrestrial OR mammal OR vertebrate OR predator 'large carnivores'") returned 9,110 records (Table A6, Appendices). From these 9,110 records (Tier 2), 977 could be accessed and screened by title and abstract before the search engine stopped displaying additional results. Namely, 977 records correspond to the maximum number of Google Scholar results we were able to access and screen sequentially by title and abstract (we initially aimed for 1,000), because Google Scholar did not provide access to additional records beyond this range. These records were selected by following the default relevance ordering in Google Scholar, without applying any additional automated filtering tools. Of these, 184 records were classified as potentially eligible studies, meaning that, based on titles and abstracts, they appeared to use camera traps to sample terrestrial mammal communities and to report species-level detection data suitable for our analysis. The remaining records either did not rely on camera trapping or did not provide sufficient information on species detections and sampling effort to assess data suitability. Full-text assessment of the 184 potentially eligible studies (Tier 3) showed that only 22 contained the camera-trap data, i.e. species-level detections for large carnivores, mesopredators and prey, together with sampling effort per camera-trap site, required for the meta-analysis. For studies with incomplete raw data, author correspondence yielded a further 15 suitable datasets from additional localities that were not retrieved in the initial search, resulting in a total of 37 datasets used in the analyses. An additional search in Europe PMC (Tier 4) identified 195 records, of which 45 progressed to full-text assessment; however, the data required for quantitative analysis were publicly available or provided by authors upon request for only 7 of these papers. So, this study, during the pre-screening process, compiled data from 41 papers conducted at 87 independent study sites worldwide. After applying inclusion criteria and excluding study sites that did not provide data suitable for our analyses of mesopredator–prey ratios and large-carnivore assemblage structure, the final meta-analysis dataset (Tier 5) comprised 27 papers and 57 independent study sites with analysed camera-trap data (Table A8, Appendices). So, 30 study sites were excluded because they lacked detection data for one or more of the following groups: large carnivores, mesopredators and prey, resulting in the final dataset described below. Study sites without detection data for neither mesopredators nor prey were not used because the mesopredators–prey relationship was a prerequisite. Study sites without large carnivores were also excluded from the meta-analysis, because only three such sites were available compared with 57 sites with large carnivores, which was insufficient to robustly compare mesopredators–prey relationships in the presence versus the absence of large carnivores.

Finally, for this meta-analysis data were synthesized from 27 papers encompassing 57 independent study sites distributed across all continents except Antarctica, spanning 17 countries and thus providing a broad biogeographical basis for inference. Across all study studies, camera traps accumulated 257,291 sampling days (approximately 704 trap-years), corresponding on average to 4,513 sampling days per site (SE=1,746.95; Min=101, Max=99,241), while the surveyed area totalled 42,372 km^2, or on average 799 km^2 per site (SE=214.66; Min=1,3, Max=6400). In total, 305 mammal species were recorded, representing 20 orders and 66 families, with a mean of 21.59 species per site (SE=1,34; Min=6, Max=50). Species richness per site ranged from 4 species in, for example, the north-eastern Simpson Desert, Australia (Greenville et al., 2014), up to 50 species in the Kalabakan Forest Reserve, Malaysia (Wearn et al., 2017). Overall, the database comprised 993,729 independent detections. Independence of detections followed the criteria used in each original study, because raw time-stamp data were not available for redefining detection events. The database averaged 807.25 detections per site (SE=368.59; Min=1, Max=433,768), and detections were dominated by a few widespread species, with nine-banded armadillo (*Dasypus novemcinctus*), tayra (*Eira barbara*), South American coati (*Nasua nasua*) and wild boar (*Sus scrofa*) recorded at 22, 20, 19 and 19 sites, respectively. A large fraction of the recorded diversity was locally rare, with 106 species detected at only a single study site. Across all sites, the highest species richness recorded at any individual study site was 6 large carnivore species, 15 small carnivore species (mesopredators), 27 large prey species and 10 small prey species, with each of these maxima coming from a different study site.

4.2.2 *META-ANALYTIC RESULTS*

The multilevel meta-analysis showed that mesopredator–prey detection ratios did not significantly deviate from zero (Figure 8). Large-carnivore assemblage class, modelled as a categorical factor, did not significantly explain variation in these ratios (QM = 6.01, df = 4, p = 0.20; Table 2), indicating no clear overall association between large-carnivore assemblage structure and site-level mesopredator–prey balance. The model estimated a marginal negative overall effect (ln(V/P) = –0.185, SE = 0.142), indicating a non-significant tendency for prey detections to be higher than mesopredator detections across study sites (p = 0.196). No predator class significantly differed from the mesopredator-only reference category, though sites with equal detections of large carnivores and mesopredators (D=R) exhibited, although not significant, a tendency toward prey dominance (estimate = –0.307, p = 0.072). Land-use category (natural vs human-modified) was not a significant predictor of mesopredator–large prey balance (p = 0.287), and the interaction model showed no significant modification of predator effects by land use (QM = 8.77, p = 0.27). Overall, the multilevel random-effects models provided an adequate fit to the data, with no evidence of substantial unexplained heterogeneity.

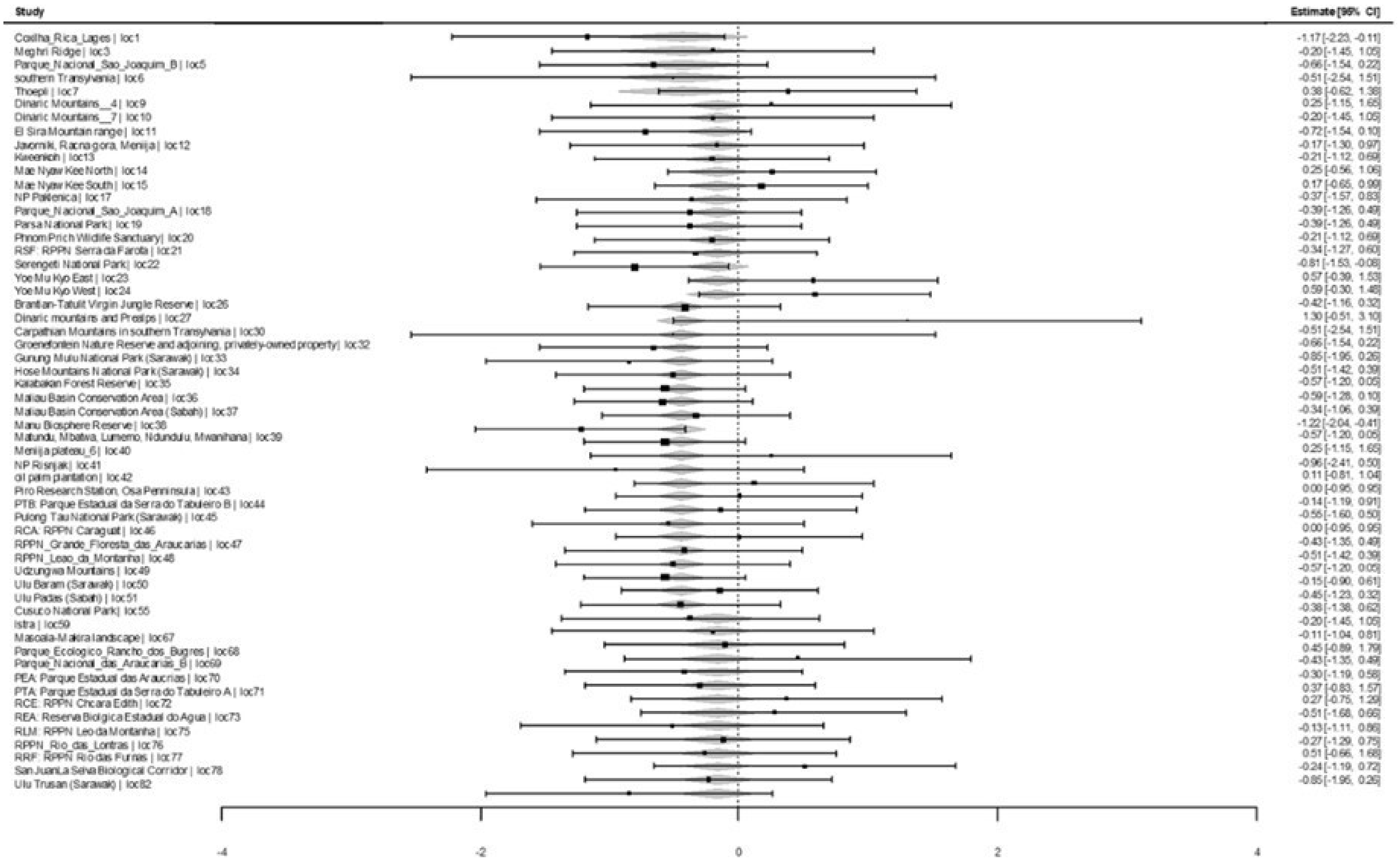

Figure 8 Forest plot showing site-level effect sizes expressed as the natural logarithm of the mesopredator-to-prey detection ratio (ln((V+0.5)/(P+0.5))). Square symbols represent individual study sites, with horizontal lines indicating 95% confidence intervals. The vertical dashed line at zero denotes equal mesopredator and prey detection frequencies. Negative values indicate prey-dominated assemblages, while positive values indicate mesopredator-dominated assemblages. Most site-level estimates overlap zero, indicating that only a few sites show statistically significant deviations from equal mesopredator and prey detections.

Site-level mesopredator–prey detection ratios were summarised using a forest plot (Figure 8), where each site's effect size, ln((V+0.5)/(P+0.5)), and 95% confidence interval were displayed relative to a reference line at zero indicating equal detection rates of mesopredators and prey. For each study, the grey shaded area depicts the distribution of the estimated effect size, while the square and horizontal line show the point estimate and its 95% confidence interval. As shown, most site-level estimates overlap zero and are distributed symmetrically around the null line, reflecting the lack of a strong consistent bias toward either mesopredator or prey dominance. Very low between-study variance (σ^2 close to zero) was estimated and the test for residual heterogeneity was not significant ($Q_E = 37.40$, df = 53, p = 0.95), suggesting that most variability in effect sizes is explained by sampling error rather than true between-study differences. This indicates that after accounting for sampling error, there was no detectable excess variability among sites – the estimated mesopredator–prey detection ratios were remarkably consistent across studies. The forest plot also showed substantial overlap in the large predator effect estimates among the different predator classes (with no class showing a distinct shift to the positive or negative side), which aligned with the non-significant moderator test.

Funnel plot of the site-level effect sizes from the meta-analysis is shown in Figure 9. Each point in the plot represents a study site's effect size (ln ratio of mesopredator to prey detections) plotted against its precision (inversely related to the variance or standard error). The dashed vertical line indicates the overall mean effect size (near zero). The points are dispersed in an approximately symmetrical funnel shape around the mean, with no conspicuous gap on one side of the mean. In other words, studies with higher precision (toward the top) cluster near the mean, and the spread of lower-precision studies (toward the bottom) is roughly balanced on both the left (negative) and right (positive) sides. This symmetry suggests an absence of strong publication bias or small study effects (e.g., no evidence that only studies showing a particular direction of effect were reported). The variability among low-precision sites appears random and is consistent with sampling uncertainty rather than systematically missing data or biases. This observation is in line with the high p-value for heterogeneity and supports the interpretation that the overall null result is not strongly driven by small-study effects.

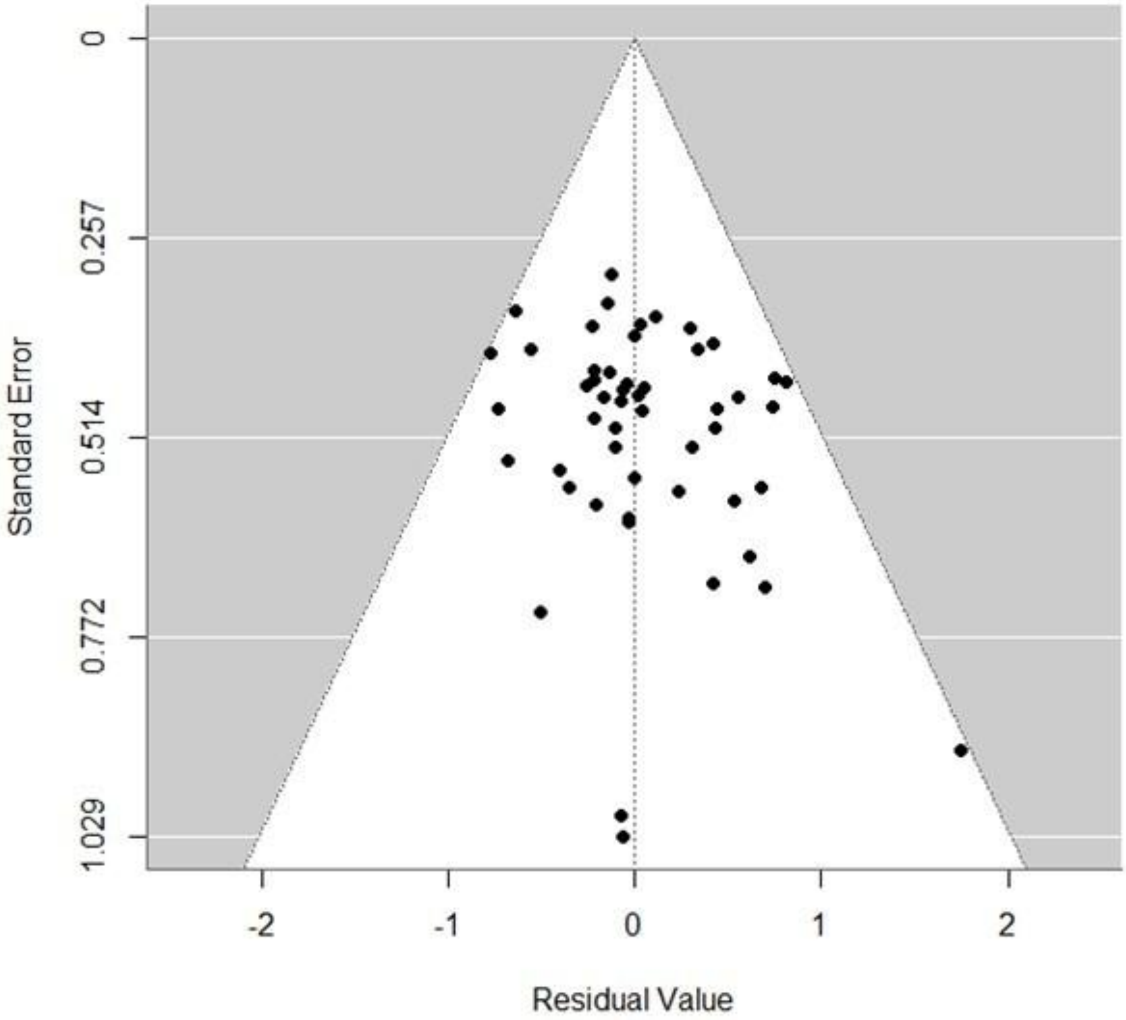

Figure 9 Funnel plot of site-level effect (ln((V+0.5)/(P+0.5))) against their precision. The symmetrical distribution of points around the pooled effect size suggests no evidence of small-site effects or systematic bias. Variation among low-precision sites is consistent with sampling uncertainty rather than selective reporting.

Violin plots of site-level mesopredator–prey detection ratios across predator assemblage classes (Figure 10) show broadly similar distributions, with most density concentrated below zero and no clear differences in mesopredator–prey balance among large-carnivore assemblage types.

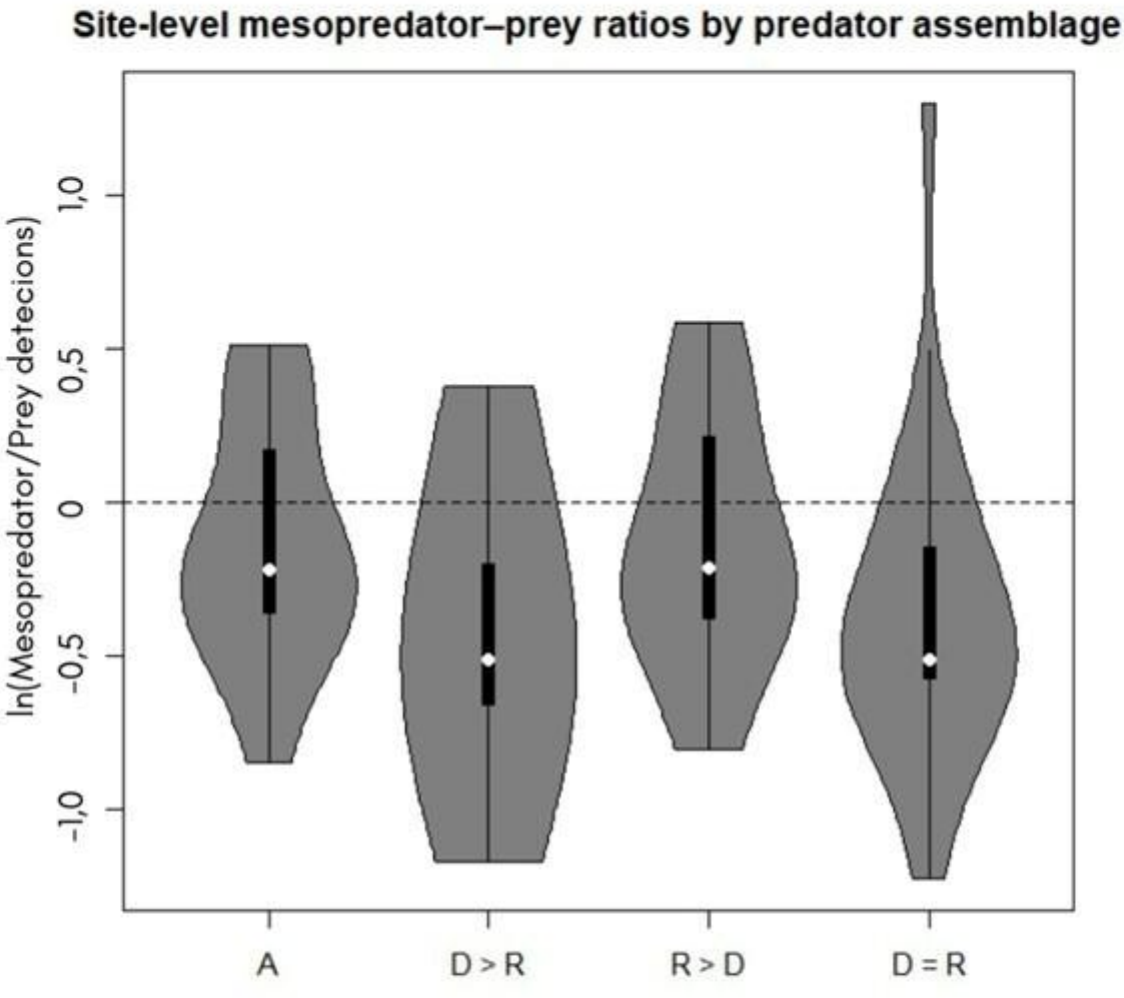

Figure 10 The Violin plots derived from site-level effect in the basic mesopredator-prey model for different large-carnivore assemblage classes (A, D>R, R>D and D=R). The response variable on the y-axis is the natural logarithm of the mesopredator-to-prey detection ratio, ln((V+0.5)/(P+0.5)), where V and P denote mesopredator and prey detections at each site, respectively. Assemblage classes describe variation in large-carnivore guild structure: A = sites with a single large-carnivore species, D>R = sites where the number of locally dominant large-carnivore species exceeds the number of locally rare species, R>D = sites with more locally rare than dominant large-carnivore species, and D=R = sites with equal numbers of dominant and rare large-carnivore species. The width of each violin represents the kernel density of site-level effect sizes within a given assemblage class; white diamonds indicate medians, bold vertical segments indicate interquartile ranges, and thin vertical lines indicate the full range of observed values.

Boxplots of site-level mesopredator–prey detection ratios across predator assemblage classes (Figure 11) indicate broadly overlapping distributions, with no class showing a pronounced shift toward either mesopredator or prey dominance.

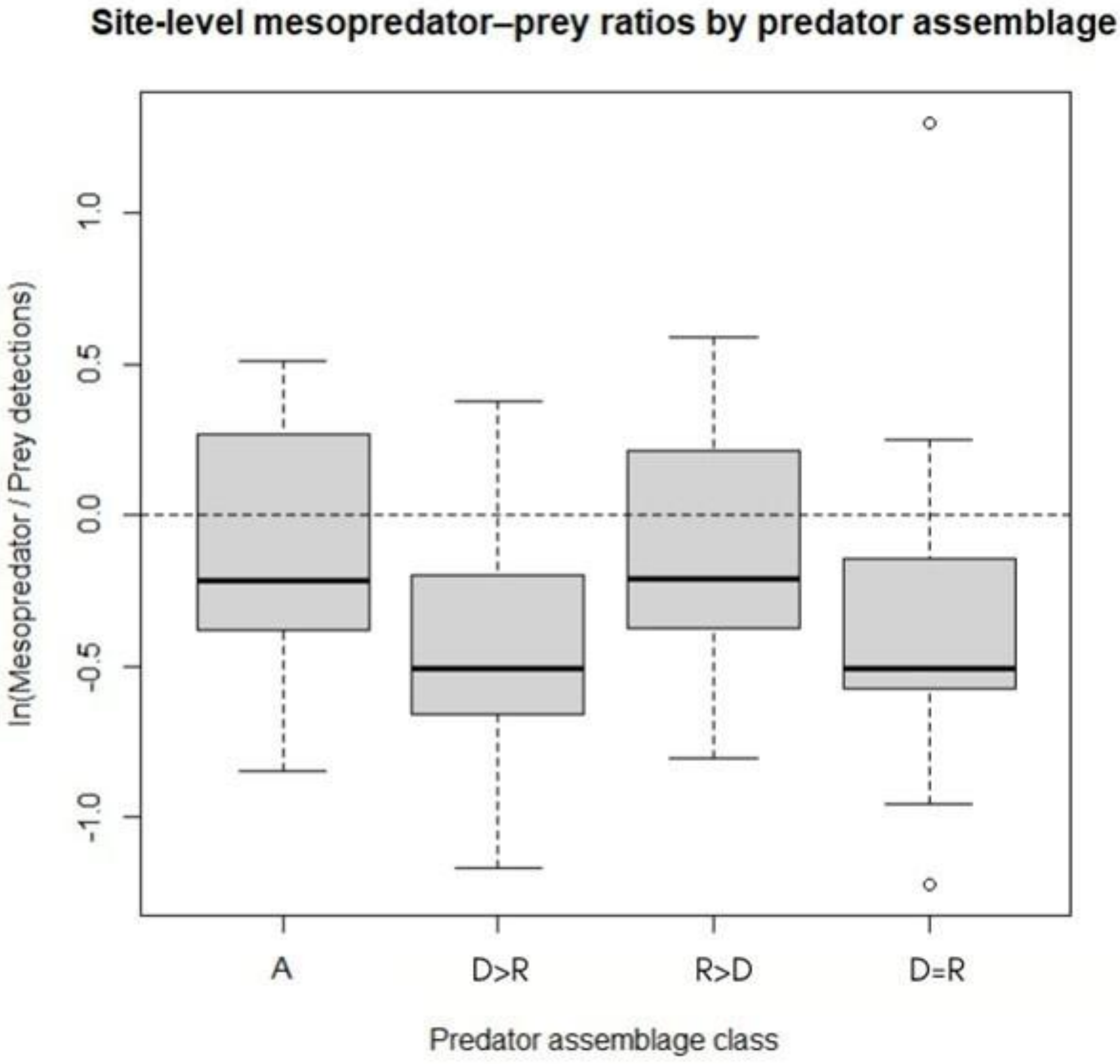

Figure 11 Boxplots of site-level mesopredator–prey effect sizes (ln((V+0.5)/(P+0.5))) across predator assemblage classes (A, D>R, R>D, D=R) The y-axis shows the natural logarithm of the mesopredator-to-prey detection ratio, where V and P are mesopredator and prey detections at each site, respectively. Predator assemblage classes (x-axis) describe differences in large-carnivore guild structure: A = sites with a single large-carnivore species; D>R = sites where the number of locally dominant large-carnivore species is greater than the number of locally rare species; R>D = sites with more locally rare than dominant large-carnivore species; and D=R = sites with equal numbers of dominant and rare large-carnivore species. The boxes show the interquartile range (25th–75th percentiles) of site-level mesopredator–prey effect sizes within each predator assemblage class, with horizontal lines indicating medians; whiskers extend to values within 1.5 times the interquartile range from the lower and upper

quartiles, and points beyond the whiskers represent outliers. Negative values indicate prey-dominated assemblages, whereas positive values indicate mesopredator-dominated assemblages.

Assemblage classes had all medians below zero and broadly overlapping interquartile ranges, reinforcing the lack of strong, systematic differences in mesopredator–prey balance among predator assemblage types.

Sensitivity analysis yielded qualitatively identical results to the main model (Figure A1, Appendices). The mean effect size was slightly attenuated (–0.238 vs –0.250), with similar variance patterns. Predator class remained a non-significant moderator (QM(df = 3) = 4.75, p = 0.1911), and residual heterogeneity was again negligible (QE p = 0.965). Model fit remained strong, with AIC = 66.90 and AICc = 68.17, suggesting that the model structure adequately captured variation without substantial overfitting.

Due to the limited and uneven detection of small mammals across study sites, no formal meta-analytic results are presented for prey size composition. Small mammal detections were absent or sparse at many sites, precluding robust comparison of small versus large prey detection ratios among large-carnivore assemblage classes. As outlined in the Methods, analyses and figures therefore focused on site-level mesopredator–prey detection ratios as the primary response, allowing us to evaluate how variation in large-carnivore assemblage structure relates to mesopredator–prey balance across sites.

Effects of predator assemblage structure and land use were evaluated across 57 sites, where mesopredator–prey detection ratios were generally negative, indicating prey-dominated assemblages. The main-effects meta-analysis revealed no significant residual heterogeneity after accounting for sampling variance (QE = 36.26, df = 52, p = 0.95), and no detectable between-study variance ($\sigma^2 = 0$). Model fit was strong (AIC = 72.74, AICc = 74.61), indicating that the inclusion of large-carnivore assemblage class and land-use predictors did not substantially overfit the data (Table 2). Furthermore, large-carnivore assemblage class did not significantly explain variation in mesopredator–prey ratios (QM = 6.01, df = 4, p = 0.20). Relative to sites with a single predator species, none of the predator assemblage classes differed significantly, although sites with equal numbers of dominant and rare predators (D=R) showed a marginal tendency toward lower mesopredator-to-prey ratios (estimate = −0.31, p = 0.07). Land-use category also had no significant main effect, with human-modified sites exhibiting slightly higher mesopredator–prey ratios than natural sites, but with wide confidence intervals overlapping zero.

Including the interaction between predator assemblage class and land-use category did not significantly improve model fit (QM = 8.77, df = 7, p = 0.27), and residual heterogeneity remained negligible (QE = 33.51, df = 49, p = 0.96). The model's AIC increased only slightly to 73.10 (AICc = 77.72), suggesting no meaningful improvement in fit by adding interaction terms.

In this model, the D=R class in natural sites exhibited a significantly lower mesopredator–prey ratio relative to single-predator sites (estimate = −0.44, p = 0.02), indicating stronger prey dominance. However, none of the interaction terms between predator assemblage class and human-modified land use were statistically significant, and confidence intervals were wide.

Overall, both models indicate substantial overlap in mesopredator–prey ratios among large-carnivore assemblage classes and land-use categories, with no consistent evidence that human modification alters the relationship between predator assemblage structure and community composition.

Table 2 Comparison summary of all meta-analysis models. k denotes the number of sites included in the model; σ^2 is the estimated between-study variance component; QE is Cochran's Q statistic for residual heterogeneity (with associated p-value); QM is the omnibus test statistic for moderators (with associated p-value); AIC and AICc are Akaike's Information Criterion and its small-sample correction; and "Notable effects" highlights predator assemblage classes with marginal or significant effects, classDeqR = sites with equal numbers of dominant and rare large-carnivore species.

Model	*k (sites)*	*σ^2*	*QE p-value*	*QM p-value*	*AIC*	*AICc*	*Notable Effects*
Main model (mesopredator vs prey)	57	0.001	0.9485 (QE(df = 53) = 37.3958,	0.1808 (QM(df = 3) = 4.8800)	72.37	73.65	classDeqR marginal (p=0.097)
Sensitivity analysis (ln(V+1)/(P+1))	57	0.001	0.9654	0.1911	66.9	68.17	classDeqR marginal (p=0.098)
*Mesopredator vs Large Prey**	57	0.001	0.9522	0.1983	72.74	74.61	classDeqR marginal (p=0.073)
Main effects: Predator class + land use	57	0.001	0.9522	0.1983	72.74	74.61	classDeqR marginal (p=0.073)

*Interaction: Predator class * land use*	57	0.001	0.9554	0.2697	73.1	77.72	classDeqR significant in natural land (p=0.02)

**'Mesopredator vs large prey' refers to an exploratory model where the response variable is the site-level ln(mesopredator / large-prey detections); small-prey detections were excluded from the denominator because their detection by camera traps was too sparse and uneven to support reliable small-to-large prey ratios across sites.*

4.3 WOLF RECOLONIZATION SCENARIOS (HYPOTHESIS 3)

4.3.1 BASELINE PROJECTIONS

This section is divided into three subsections, each corresponding to simulation results over 10-year, 30-year, and 100-year periods. Each subsection follows a consistent structure: to facilitate comparison, results for the baseline scenario are presented first, followed by outcomes for the remaining simulated scenarios. Comprehensive results and output summaries for all scenarios across all three timeframes are available in Appendices ().

Wolf population dynamics over a 10-year period across all scenarios was first examined as short-term extinction risks and growth trajectories. In the baseline scenario, the extinction probability was 0.26 (SE = 0.01, SD = 1.82), with a mean time to first extinction of 2.6 years (SE = 0.11, SD = 1.82). Surviving populations maintained an average of 14.1 individuals (SE = 0.13, SD = 3.58), consisting of 7 males and 7.1 females. Prior to reaching the carrying capacity limits, the mean population growth rate—expressed as the proportional increase—was 0.238 (SE = 0.003, SD = 0.271).

Then the simulations to 30 years were extended to evaluate medium-term differences in extinction probability and population size among scenarios. In the baseline scenario, the extinction probability was 0.29 (SE = 0.01), with a mean time to first extinction of 3.3 years (SE = 0.18, SD = 3.05). Surviving populations maintained an average of 15.7 individuals (SE = 0.06, SD = 1.56), comprising 7.8 males and 7.9 females. Prior to reaching the carrying capacity limits, the mean population growth rate—expressed as a proportional increase—was 0.2 (SE = 0.001, SD = 0.2).

Finally, 100-year simulations was analysed to characterise long-term extinction risks, population persistence, and the cumulative effects of different management and disturbance scenarios. In the baseline scenario, the extinction probability was 0.29 (SE = 0.01, SD = 7.29), with a mean time to first extinction of 3.9 years (SE = 0.46, SD = 7.74). Surviving populations maintained an average of 15.8 individuals (SE = 0.06, SD = 1.58), distributed as 7.8 males and 7.9 females. Prior to reaching the carrying capacity limits, the mean population growth rate—expressed as a proportional increase—was 0.20 (SE = 0.001, SD = 0.18).

4.3.2 EFFECTS OF ADVERSE EVENTS, CARRYING CAPACITY AND HARVEST

Over the 10-year timeframe, adverse events and changes in carrying capacity produced only modest differences in extinction probability and population size relative to the baseline scenario. Among scenarios in the “Adverse Events” group, Scenario 2 (“Disease”) showed the highest extinction probability across all scenarios at 0.32 (SE = 0.01, SD = 2.25). Scenarios 3 (“Removals”) and 4 (“Illegal Hunting”) shared identical extinction probabilities of 0.29 (SE = 0.01, SD = 2.13). The mean time to first extinction ranged from 2.7 years (“Illegal Hunting”, SE = 0.13, SD = 2.14) to 3 years (“Disease”, SE = 0.13, SD = 2.25). Surviving populations maintained an average of 13.5–13.8 individuals, with the lowest count in “Illegal Hunting” (SE = 0.12, SD = 3.25) and the highest in “Disease” (SE = 0.14, SD = 3.79). Sex ratios varied, with males numbering 6.3 (“Removals”) to 6.9 (“Disease”), and females numbering 6.8 (“Illegal Hunting”) to 7.5 (“Removals”). Prior to reaching the carrying capacity limits, the mean population growth rate in the baseline scenario spanned 0.194 (“Illegal Hunting”, SE = 0.03, SD = 0.28) to 0.226 (“Disease”, SE = 0.003, SD = 0.28). For scenarios in the “Carrying Capacity” group, all three scenarios (5: “Succession”, 6: “Forest Management”, and 7: “Hunting Management”) showed nearly identical extinction probabilities. Scenarios 5 and 6 had an extinction probability of 0.27, while Scenario 7 (“Hunting Management”) had a slightly higher probability of 0.28. The mean time to first extinction ranged from 2.8 years (“Forest Management”, SE = 0.12, SD = 1.93) to 3.1 years (“Succession”, SE = 0.14, SD = 2.29). Surviving populations maintained an average of 14.9–16.4 individuals, with the lowest count in “Forest Management” (SE = 0.14, SD = 3.88) and the highest in “Hunting Management” (SE = 0.16, SD = 4.41). Sex ratios varied, with males numbering 7.5 (“Forest Management”) to 8.2 (“Hunting Management”) and females numbering 7.6 (“Forest Management”) to 8.2 (“Hunting Management”). Prior to reaching the carrying capacity limits, the baseline scenario’s mean growth rate ranged from 0.224 (“Succession”, SE = 0.003, SD = 0.28) to 0.24 (“Hunting Management”, SE = 0.003, SD = 0.27).

Over a 30-year horizon, contrasts among adverse-event and carrying-capacity scenarios became more pronounced, revealing clearer divergences in extinction risk and mean population size. Within the “Adverse Events” group, the “Disease” scenario showed the highest probability of extinction among all scenarios at 0.32 (SE = 0.01). The “Removals” and “Illegal Hunting” scenarios followed with extinction probabilities of 0.28 (SE = 0.11) and 0.27 (SE = 0.01), respectively. The mean time to first extinction ranged from 3.1 years for “Illegal Hunting” (SE = 0.15, SD = 2.50) to 3.7 years for “Removals” (SE = 0.21, SD = 3.59). Surviving populations maintained an average of 14.9–15.4 individuals, with the lowest count in “Illegal Hunting” (SE = 0.06, SD = 1.51) and the highest in “Disease” (SE = 0.08, SD = 2.11). Sex ratios varied, with males numbering 6.5 (“Removals”) to 7.8 (“Disease”) and females numbering 7.4 (“Illegal Hunting”) to 8.6 (“Removals”). Prior to reaching the carrying capacity limits, the baseline scenario’s mean growth rate spanned 0.09 (“Illegal Hunting”, SE = 0.001, SD = 0.2) to 0.2 (“Disease”, SE = 0.001, SD = 0.23). Within the “Carrying Capacity” group, all three scenarios exhibited nearly identical extinction probabilities: 0.29 for “Succession” (SE = 0.01, SD = 0.22) and “Forest Management” (SE = 0.01, SD = 0.24) and 0.25 for “Hunting Management” (SE = 0.01, SD = 0.26). The mean time to first extinction ranged from 3.2 years (“Succession”, SE = 0.17, SD = 2.85) to 3.5 years (“Forest Management”, SE = 0.21, SD = 3.55). Surviving populations averaged 16.7–18.8 individuals, with the lowest count in “Forest Management” (SE = 0.06, SD = 1.67) and the highest in “Hunting Management” (SE = 0.06, SD = 1.60). Sex ratios varied slightly, with males numbering 8.3 (“Forest Management”) to 9.4 (“Hunting Management”) and females numbering 8.4 (“Forest Management”) to 9.4 (“Hunting Management”). Prior to reaching the carrying capacity limits, the baseline scenario’s mean growth rate spanned 0.213 (“Forest Management”, SE = 0.0014, SD = 0.2092) to 0.219 (“Hunting Management”, SE = 0.001, SD = 0.2).

Across the 100-year simulations, the long-term impacts of adverse events and alternative carrying-capacity trajectories were fully expressed, highlighting which scenarios most strongly increased extinction risk and reduced population persistence. Within the “Adverse Events” group, the “Removals” scenario showed the highest probability of extinction across all scenarios at 0.35 (SE = 0.02). The “Disease” and “Illegal Hunting” scenarios followed with identical extinction probabilities of 0.32 (SE = 0.01). The mean time to first extinction ranged from 4.1 years (“Illegal Hunting”, SE = 0.50, SD = 9.01) to 6.9 years (“Disease”, SE = 0.83, SD = 14.84). Surviving populations maintained an average of 14.8–15.5 individuals, with the lowest count in “Illegal Hunting” (SE = 0.06, SD = 1.64) and the highest in “Disease” (SE = 0.08, SD = 2.11). Sex ratios varied, with males numbering 6.5 (“Removals”) to 7.8 (“Disease”) and females numbering 7.3 (“Illegal Hunting”) to 8.7 (“Removals”). Prior to reaching the carrying capacity limits, the baseline scenario’s mean growth rate spanned 0.06 (“Illegal

Hunting", SE = 0.001, SD = 0.17) to 0.2 ("Disease", SE = 0.001, SD = 0.20). Within the "Carrying Capacity" group, extinction probabilities ranged from 0.26 ("Forest Management", SE = 0.01, SD = 0.31) to 0.30 ("Succession", SE = 0.01, SD = 0.2). The mean time to first extinction spanned 3.2 years ("Succession", SE = 0.18, SD = 3.05) to 3.7 years ("Forest Management", SE = 0.34, SD = 5.52). Surviving populations maintained an average of 16.8–18.9 individuals, with the lowest count in "Forest Management" (SE = 0.06, SD = 1.65) and the highest in "Hunting Management" (SE = 0.05, SD = 1.43). Sex ratios varied slightly, with males numbering 8.3 ("Forest Management") to 9.5 ("Hunting Management") and females numbering 8.5 ("Forest Management") to 9.4 ("Hunting Management"). Prior to reaching the carrying capacity limits, the baseline scenario's mean growth rate ranged from 0.21 ("Forest Management", SE = 0.001, SD = 0.18) to 0.214 ("Hunting Management", SE = 0.001, SD = 0.17).

4.3.3 SUPPLEMENTATION SCENARIOS

Over the 10-year period, supplementation scenarios already showed strong short-term benefits, substantially reducing extinction risk compared with the unsupplemented baseline. Within the "Population Supplementation" group, extinction probabilities ranged from 0 (in Scenario 9: Corridor Construction and Scenario 11: Translocation) to 0.28 (in Scenario 10: Two-Region Corridor Enhancement). In Scenario 9 ("Corridor Construction"), 18 simulations experienced extinction at least once, but each was followed by a successful recolonization, with no further extinction occurring thereafter. In Scenario 11 ("Translocation"), 15 simulations went extinct at least once, but 19 recolonizations were recorded, followed by four additional extinction events. The mean time to first extinction in this group ranged from 2.6 years for "Two-Region Corridor Enhancement" (SE = 0.11, SD = 1.88) to 2.9 years for "One-Region Corridor Enhancement" (SE = 0.17, SD = 2.03). The mean number of individuals in extant populations varied from 14.4 in "Two-Region Corridor Enhancement" (SE = 0.12, SD = 3.23) to 16.9 in "Corridor Construction" (SE = 0.04, SD = 1.36), with the number of males ranging from 7.2 to 8.5 and females from 7.2 to 8.4, depending on the scenario. When analyzing the entire period prior to reaching the carrying capacity, the mean population growth rate ranged from 0.23 in "Two-Region Corridor Enhancement" (SE = 0.003, SD = 0.27) to 0.32 in "Corridor Construction" (SE = 0.003, SD = 0.3).

Across 30 years, differences among supplementation strategies became clearer, with some scenarios nearly eliminating extinctions while others provided only partial improvement over the baseline. Within the “Population Supplementation” group, extinction probabilities ranged from 0, as seen in both the “Corridor Construction” and “Translocation” scenarios, to 0.29 in the “Two-Region Corridor Enhancement” scenario. In the “Corridor Construction” scenario, there were 16 simulations in which extinction occurred at least once; however, these were followed by 20 recolonizations, with 4 subsequent re-extinctions. In the “Translocation” scenario, 27 simulations experienced extinction at least once, but 28 recolonizations occurred, followed by 1 additional re-extinction. The mean time to first extinction in this group ranged from 2.9 years in the “One-Region Corridor Enhancement” scenario (SE = 0.17, SD = 2.20) to 3.6 years in the “Corridor Construction” scenario (SE = 0.64, SD = 2.55). The mean number of individuals in extant populations varied from 15.7 in the “Two-Region Corridor Enhancement” scenario (SE = 0.06, SD = 1.71) to 16.9 in the “Corridor Construction” scenario (SE = 0.04, SD = 1.40), with the number of males ranging from 7.9 to 8.4 and females ranging from 7.8 to 8.5, depending on the scenario. When analyzing the entire period before reaching carrying capacity truncation, the mean population growth rate ranged from 0.21 in the “Two-Region Corridor Enhancement” scenario (SE = 0.001, SD = 0.21) to 0.24 in the “Corridor Construction” scenario (SE = 0.001, SD = 0.21).

Over the full 100-year timeframe, supplementation scenarios revealed their long-term potential, with certain interventions maintaining stable wolf populations and preventing extinctions altogether. Within the “Population Supplementation” group, extinction probabilities ranged from 0 in both the “Corridor Construction” and “Translocation” scenarios to 0.29 in the “Two-Region Corridor Enhancement” scenario. In the “Corridor Construction” scenario, 16 simulations experienced extinction at least once, but these were followed by 19 recolonizations, with three subsequent re-extinctions. The “Translocation” scenario saw 19 simulations go extinct at least once, followed by 22 recolonizations and three additional re-extinctions. The mean time to first extinction ranged from 3.1 years in the “Translocation” scenario (SE = 0.34, SD = 1.49) to 3.9 years in the “Corridor Construction” scenario (SE = 1.35, SD = 5.39). The mean number of individuals in extant populations varied from 15.7 in the “Two-Region Corridor Enhancement” scenario (SE = 0.06, SD = 1.62) to 17.0 in the “Corridor Construction” scenario (SE = 0.04, SD = 1.32), with the number of males ranging from 7.9 to 8.6 and females ranging from 7.8 to 8.5, depending on the scenario. When analyzing the entire period before reaching carrying capacity truncation, the mean population growth rate ranged from 0.21 in the “Two-Region Corridor Enhancement” scenario (SE = 0.001, SD = 0.17) to 0.22 in the “Corridor Construction” scenario (SE = 0.001, SD = 0.18).

4.3.4 Comparative scenario performance and PCA

To compare extinction outcomes across all scenarios and timeframes, extinction counts were summarised visually and then tested for overall differences using non-parametric statistics. Figure 12 displays a box plot illustrating the distribution of the number of simulations in which populations became extinct across the 11 different scenarios.

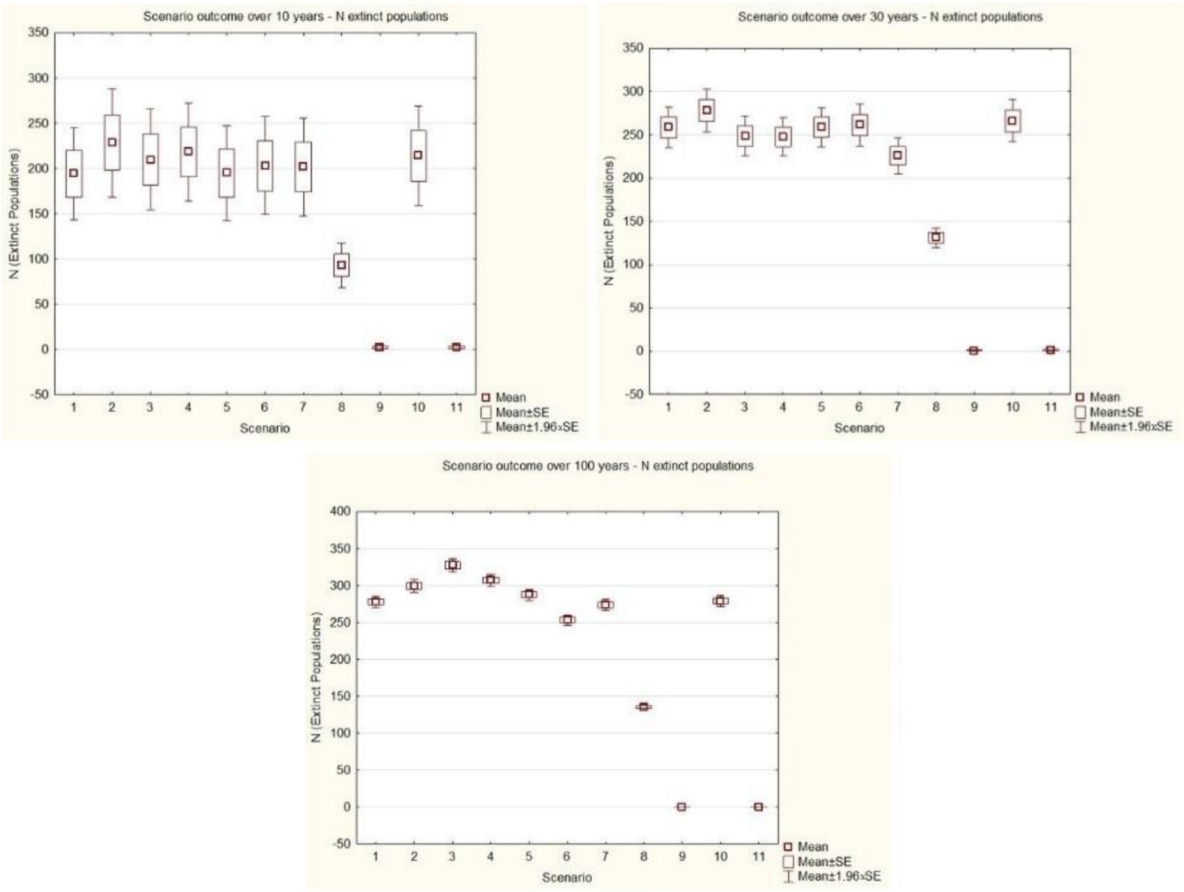

Figure 12 Box plots illustrate the distribution of the number of simulations in which populations became extinct across 11 different scenarios over the 10-, 30-, and 100-year periods. Red squares indicate the means, red boxes represent the mean ± standard error (SE), and whiskers show the mean ± 1.96 SE.

The Kruskal–Wallis test results revealed three distinct scenario groupings based on their impact on population extinction across 10-year, 30-year, and 100-year simulation periods, as well as in the combined dataset. Specifically, Scenarios 9 ("Corridor Construction") and 11 ("Translocation") exhibited the lowest extinction rates (0.00). Scenarios 1–7 showed similar patterns, with extinction occurring in 250–300 simulations on average, while Scenario 8 displayed intermediate values (mean ≈ 130 simulations) (Figure 13). This distribution pattern persisted across all timeframes—10-year, 30-year, 100-year —with scenario groupings remaining consistent regardless of temporal scale, as illustrated in Figure 13. Statistical analysis confirmed significant differences between scenarios in general across all model durations: 10-year (H(10, $N = 121$) = 53.71, $p < 0.001$), 30-year (H(10, $N = 341$) = 227.70, $p < 0.001$) and 100-year (H(10, $N = 1111$) = 963.89, $p < 0.001$), consistently showing the same pattern of scenario groupings regardless of the modeling timeframe. Dunn's post hoc tests highlighted significant differences ($p < 0.05$) between Scenarios 9/11 and all other scenarios, while no significant differences emerged among other scenario pairs.

Principal Component Analysis (PCA) was conducted to assess the relationships between scenarios, years, the number of simulations in which populations became extinct, and the mean size of extant populations, across four datasets: the 10-year, 30-year, and 100-year models, as well as the combined dataset of all the models. Detailed results are provided APPENDIX 13. The analysis resulted in three principal components for each dataset. The first two components (PC1 and PC2) together explained more than 99% of the variability across all time periods, while PC3 accounted for less than 0.1% of the variance. The loading matrix indicated that the number of extinct populations had the highest loading on PC1 (0.999), whereas the year variable had the highest loading on PC2 (0.997), demonstrating that these two variables were primarily responsible for the grouping of scenarios. The visualization of the PCA results for the combined dataset of all models revealed a clear clustering of scenarios into three distinct groups: scenarios 9 and 11 formed one cluster, Scenario 8 appeared as an isolated group, and the remaining scenarios clustered together. This pattern of scenario grouping remained consistent across all three individual datasets (10-, 30-, and 100-year models), as illustrated in Figure 13.

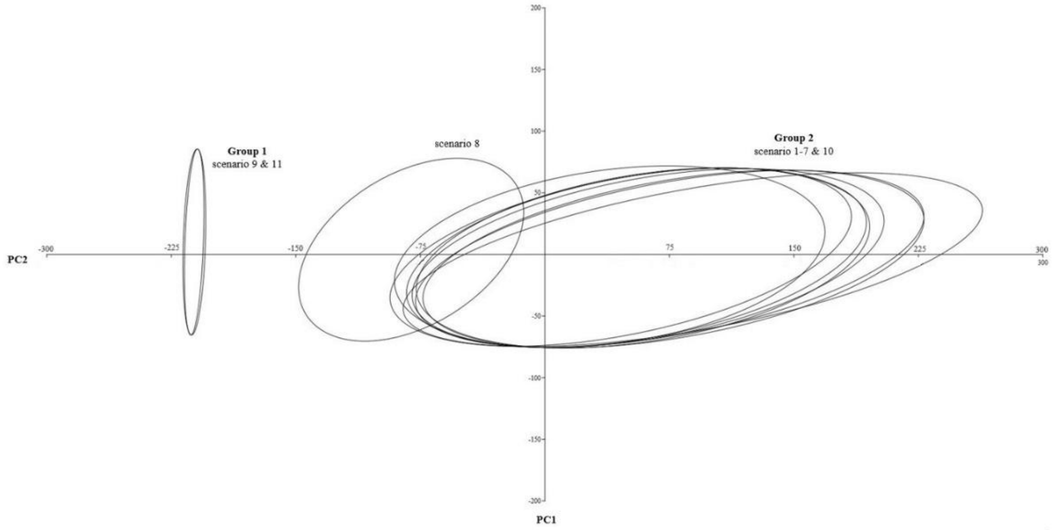

Figure 13 Principal Component Analysis (PCA) plot showing the distribution of scenarios along the first two principal components (PC1 and PC2) for the combined dataset (10-, 30-, and 100-year models). The plot reveals three distinct groupings: Group 1 (left) includes Scenarios 9 and 11, Scenario 8 (center) appears isolated, and Group 2 (right) clusters Scenarios 1–7 and 10. Ellipses around each point represent confidence regions for the scenarios.

CHAPTER 5: DISCUSSION

5.1 LOCAL CASE STUDY: PAKLENICA NP AND RANGER-BASED MONITORING (HYPOTHESIS 1)

Data gathered during this doctoral research has been published as the first peer-reviewed list of medium- to large-sized mammalian species for Paklenica National Park (Biscan et al., 2022), as no previous publication has addressed the park's mammalian diversity in this way. Considering unpublished data and grey literature available for the Paklenica NP, 15 medium–large-sized mammalian species (of 17 species previously recorded) have been recorded in this camera trapping survey, with no additional/new species. Out of 17 previously recorded species in the Paklenica NP, this survey did not record two mammalian species: mouflon (*Ovis musimon*) and weasel (*Mustela nivalis*) (unpublished; available in 'Paklenica National Park' Public Institution). Previous record of mouflon is probably the result of introduction by hunters; however, the reintroduced individuals did not create a stable population in the subject area and there was no subsequent reintroduction. On the other hand, weasel was probably not recorded during our survey because for small mustelids, camera trapping methodology needs adjustments; traps often fail to detect small and relatively fast-moving species due to the sensitivity of the passive infrared sensor (Mos, Hofmeester, 2020). Also, as Rodentia, Eulipotyphla, Chiroptera and Martes sp. were not determined to the species level, due to the camera setting methodology adapted to capture medium- to large-sized mammalian species, this survey did not record 12 previously noted species of Rodentia, two of Martes, six of Eulipotyphla and 24 of Chiroptera (unpublished; available in 'Paklenica National Park' Public Institution). Camera trapping can be also used for small mammals (Glen et al., 2013; De Bondi et al., 2010), but the set-up methodology is different than for medium/large mammals (Smith, Coulson, 2012). Of the medium-sized mammals from the order Rodentia, only *Lepus europaeus* and *Sciurus vulgaris* were determined to the species level.

All three large carnivore key species of Natura 2000 site NP Paklenica (brown bear, grey wolf and Eurasian lynx) were recorded during this survey. This Natura 2000 site is part of a larger continuous area, that is, large carnivore habitat in the Dinaric region, which extends through Croatia, Slovenia and Italy and includes 10 sites. All 10 Natura 2000 sites are characterised by similar wildlife, especially as habitats for all three large carnivores that are present in nature parks across the Alpine/Dinaric region. Furthermore, two Alpine national parks (Dolomiti

Bellunesi National Park, Italy and Triglav National Park, Slovenia) that are characterised by Alpine habitats and climate have similar mammalian diversity (unpublished: available for clarification in Dolomiti Bellunesi National Park, unpublished: available for clarification in Triglav National Park) as the Paklenica NP, which represents the Dinaric region, southern mountainous extension of the Alps.

To verify whether the obtained results could be improved by different camera trapping settings, future studies should consider placing camera traps at different heights from the ground and in more heterogeneous habitats. Attention should be paid to selecting locations that are not focused solely on resource hotspots such as salt licks and watering sites, as the use of such locations in this study introduced a bias by inflating the number of capture events for species attracted to these sites. Although baits, including lures and attractants, are widely used in association with camera traps to increase the probability of detecting a target species or a suite of species (du Preez et al., 2014), their use may further influence animal movement patterns and artificially increase the number of capture events for individuals or species attracted specifically to the bait. Consequently, baiting can exacerbate the discrepancy between detection rates and true relative abundance and should therefore be carefully considered when designing surveys and interpreting camera trapping results. Furthermore, Maffei & Noss (2008) recommend setting one camera per three to four home ranges in community where large carnivores are present, to avoid exaggerating the estimate. The camera should face a direction in relation to the expected animal travel and path of the sun. Also, it is needed to predict the vegetation growth because if we place the camera before the vegetation season and leave it there for a few months, the vegetation may grow so much that it will block camera traps and good results may not be obtained (Roveroa, 2013). Additionally, wind can move vegetation, which will trigger camera traps creating numerous blank photos. It is also important to use a very firm camera support because motion of the sensor may produce false triggers (Swann et al., 2004). Typical camera mode options include photos, video or both. Photos provide distinct points-in-time data that can be coded and analysed more easily than video, and, still images can be extracted from video files. Video footage is commonly used in bird nest research and in studying animal behaviour (Kross, Nelson, 2011) and predation (Reif, Tornberg, 2006).

Correlation between recorded species richness and camera trapping effort recorded in this study confirms the hypothesis that increasing the camera trapping survey effort increases the recorded species richness. However, the maximum of the recorded species richness still differs depending on which species is monitored, how large the habitat is and what is the number of cameras (Si et al., 2014). Also, this survey confirms that the recorded SRI may be different among different habitats, substrates, or temperature. In our survey, higher SRI values were recorded in the central part of the Paklenica NP, even though this could be a consequence of the number of cameras set in the central area versus peripheral parts of the NP. Keeping in mind what has been previously said, we cannot unequivocally conclude that a certain research area is richer in species diversity than another, because the camera trapping survey efforts were not uniform and were influenced by non-random camera placement at salt licks and watering sites. The concentration of cameras at these resource hotspots likely increased detectability for species that regularly use such sites, while underrepresenting species or individuals that avoid them, thereby introducing bias that confounds straightforward comparisons of species richness between areas.

Nevertheless, despite these limitations and sources of bias, this case study demonstrates that camera trapping can provide robust information on medium- to large-sized mammal communities in Paklenica NP and therefore represents a feasible tool for long-term monitoring of recolonization processes and their effects when appropriately designed and implemented. Since rangers have excellent knowledge of specific locations in protected areas and spend a large amount of time in the field, the question is whether they can be a valuable tool for monitoring the status of the wildlife species and habitats. Data collected through this camera trapping survey of mammals in the Paklenica NP, which was gathered by rangers, show similar biodiversity values as previous surveys conducted in the same area by ecologists (87.5% similarity). The reason for this is that rangers have a very profound knowledge of the specific area (where animals gather, their secret hideouts, waterholes, etc.) and/or have a long work experience within the protected area. Further, on analysing the costs for conducting camera trapping survey by external service and internal service, a significant difference was noted. From the cost analyses, the savings in financial resources are clearly visible if the research is conducted by internal ranger service. Therefore, the possibility that camera trap installation activities and further checks (battery change, data transfer) can be performed by internal ranger service rather than external service contributes to the added value of ranger service. Namely, this creates the possibility of conducting additional research in other areas of the ecology of protected areas, as less funding needs to be set aside for camera trapping surveys.

However, it should be emphasised that this case study refers to the cost ratios among the employment ranks in Croatia, where university degree is not a compulsory qualification for the ranger service officer position. Despite the different qualifications required for the position of ranger in other countries (USA, Canada, Australia, South Africa, Brazil, Germany, Austria), the difference between the costs of external service and internal ranger service is certainly lower. So, it is to be assumed that needs for financial resources allocation will be smaller for the internal ranger service than for the external service.

Certainly, it is necessary to continue research on the value of rangers in biodiversity monitoring, especially in relation to the accuracy and precision of data collected by internal and external services. As stated earlier, during this camera trapping survey 88% of previously recorded species were detected, that is, two species were not recorded; however, since we did not have a control group of researchers, we could not directly assess the accuracy of the data collected by Paklenica NP rangers. In future research, it would therefore be important to include a control group of other employees or external experts to allow rigorous comparison with internal rangers. For such comparative surveys, the same camera trapping methodology should be used, ideally with camera traps arranged in line transects (or another uniform design) with clearly defined distances between cameras, deployed simultaneously in all survey locations and using the same attractants. This would enable additional comparative analyses and provide more relevant and methodologically robust results regarding the effectiveness, accuracy and cost-efficiency of ranger-based monitoring programmes.

Ranger-based monitoring has recently received increasing attention in the global conservation literature, as protected areas worldwide seek cost-effective ways to collect reliable biodiversity and threat data. A recent synthesis by Kuiper et al. (2025) highlights that ranger-based monitoring has substantial potential to support biodiversity conservation and protected area management, particularly when ranger-collected data are systematically integrated into decision-making, supported by appropriate data management tools and clear monitoring objectives. This is consistent with the findings from Paklenica NP, where ranger-led camera trapping produced biodiversity results very similar to those of previous surveys conducted by ecologists, while substantially reducing overall costs. At the same time, Kuiper et al. (2025) emphasise several critical conditions that must be met for ranger-based monitoring to deliver reliable information, including adequate training, clear protocols, attention to biases in patrol coverage and detectability, and the capacity to analyse and use the data for management. These points mirror the methodological considerations raised in this study, such as the need to standardise camera placement, effort and the use of attractants, and the importance of explicitly addressing sources of bias such as resource hotspots (salt licks and watering sites). By aligning ranger-based monitoring in Paklenica NP with these best-practice recommendations, future surveys could further improve the accuracy and comparability of the collected data.

On the other hand, Dobson et al. (2020) argues that unstructured “messy” observational datasets can be highly valuable for conservation, but only if their biases, hidden costs and limitations are explicitly understood and managed. They conclude that such data are neither a cheap replacement for well-designed surveys nor inherently inferior; their usefulness depends on clear objectives, critical appraisal of the observation process and realistic assessment of the full costs of using them. Because messy data are strongly affected by observer behaviour, motivation and context, they often require complex analytical approaches and detailed metadata, which can make them expensive to process and hard to communicate. The authors emphasise that understanding and, where possible, shaping the observation process, as well as aligning the incentives of observers and decision-makers, is essential for improving both data quality and impact. Overall, they argue that messy data are here to stay in biodiversity conservation and sustainability science, and that a whole-system, adaptive-management perspective is needed to unlock their potential while avoiding misleading conclusions.

Complementing this perspective, global assessments of protected area staffing (Appleton et al., 2022) show that ranger services remain severely under-resourced relative to international biodiversity ambitions. Estimates based on data from more than 170 countries indicate that current protected area personnel, including rangers, are far below the levels needed to effectively manage existing protected and conserved areas. Current staffing levels are also insufficient to achieve targets such as the global “30 by 30” commitment, that is, effectively protecting 30% of the planet’s land area by 2030. This implies that substantial increases in the workforce and in support for that workforce are required. In the context of these pervasive staff shortages, the potential of ranger-led camera trapping in Paklenica NP illustrates both the potential and the practical constraints of relying on rangers to implement systematic camera trapping. While ranger-led surveys can generate robust data on medium- to large-sized mammals at relatively low financial cost, they also inevitably compete with rangers’ existing operational duties, which are already constrained by limited staffing and time. Any attempt to formalise ranger-based monitoring in Paklenica NP would therefore need to be accompanied by realistic planning of workloads, clear prioritisation of core tasks and, ideally, additional institutional support, so that the added responsibilities of camera trapping do not simply overburden a small team and undermine long-term sustainability of the programme.

In the context of this doctoral research, which addresses the potential recolonisation of wolves in Panonia (Papuk Nature Park), these findings have important practical implications. As Papuk is currently a protected area without an established wolf population, there is a timely opportunity to prepare internal services for systematic camera trapping of medium- to large-sized mammals before the top predator returns. Establishing a ranger-based camera trapping programme at this stage would provide a robust baseline on the composition, spatial distribution and relative activity of the mammal community in the absence of wolves, and would allow future surveys to document how recolonisation alters species occurrence and trophic interactions. In this sense, the Paklenica NP case study offers a transferable model for designing cost-effective, ranger-led monitoring frameworks that can support adaptive management in other protected areas, including Papuk, as they anticipate and respond to large carnivore recolonisation. Also, these insights from Paklenica NP provide a useful reference point for thinking about how and under what conditions ranger-based camera trapping can be integrated into routine management practice, and they directly inform the recommendations developed for establishing a similar baseline monitoring framework in Papuk.

5.2 GLOBAL META-ANALYSIS: LARGE CARNIVORES AND MESOPREDATOR–PREY BALANCE (HYPOTHESIS 2)

This meta-analysis revealed null or weak associations between large-carnivore assemblage structure and site-level mesopredator–prey detection ratios, providing little support for a generalized mesopredator release pattern across the sampled studies. Mesopredator release theory posits that removing or losing an apex predator can lead to a surge in mesopredator populations and heightened predation pressure on prey species, especially small and vulnerable prey (Ritchie & Johnson 2009). Importantly, this hypothesis was originally formulated to describe temporal changes in mesopredator populations following the reduction or loss of apex predators through time. By contrast, this analysis examines spatial variation in mesopredator–prey detection ratios among sites differing in large-carnivore assemblage structure, and therefore provides indirect, spatial evidence that can be more or less consistent with key predictions of the mesopredator release framework, rather than a direct temporal test of the hypothesis. Indeed, this trophic cascade mechanism has been documented across a variety of ecosystems: apex predator (i.e., large carnivore) declines are often associated with increases in midsized predators (i.e., mesopredators) and subsequent declines in their prey (Prug et al. 2009). For example, Crooks & Soulé (1999) observed that in southern California sage scrub fragments, the absence of coyotes (the apex predator) allowed smaller mesopredators such as cats, foxes, and raccoons to irrupt, which in turn dramatically reduced native bird populations and led to local extirpations of some bird species. Such case studies demonstrate the potential for powerful top-down cascades. However, recent work on Yellowstone challenges this narrative: by demonstrating that a widely cited claim of an exceptionally strong wolf-driven trophic cascade rested on tautological modelling and violated key analytical assumptions, MacNulty et al. (2025) reconciled those results with experimental evidence for only modest, spatially variable willow responses, reinforcing the view that large-carnivore cascades are often weaker and more constrained than iconic case studies suggest. In our synthesis of 57 camera-trap sites worldwide, we did not detect a consistent spatial pattern of mesopredator release or suppression. On the contrary, prey detections tended to exceed mesopredator detections in most sites across all predator assemblage classes, resulting in effect sizes that clustered near zero with no significant differences between predator assemblage classes. The very low between-study heterogeneity across 57 global sites is unusual for ecological meta-analyses and could reflect dominance of sampling error from sparse detections, compression of variability by our log-ratio metric, or genuinely weak and globally consistent mesopredator release, so it should be interpreted cautiously rather than as unequivocal evidence of universal trophic similarity. This suggests that variation in large-carnivore assemblage structure alone was not a dominant determinant of mesopredator–prey balance in the surveyed systems. Taken together, these findings suggest that mesopredator release does not emerge as a universal pattern in camera-trap mammal communities. Instead of a consistent shift toward mesopredator dominance in structurally simpler or functionally weaker large-carnivore assemblages, mesopredator–prey ratios remain broadly similar across predator assemblage types. This indicates that any top-down effects of predator richness and composition are strongly context dependent and intertwined with underlying environmental and resource gradients.

5.3 MECHANISMS AND LIMITATIONS UNDERLYING WEAK TOP-DOWN SIGNALS (HYPOTHESIS 2)

Why do large carnivore effects on mesopredator–prey balance appear weak? Mechanisms and limitations

Several non-mutually exclusive factors could help explain why we did not find strong evidence of mesopredator release across these diverse study systems. These include (i) ecological context dependence, (ii) human-mediated bottom-up control of prey populations and resources through hunting and land use, (iii) anthropogenic prey subsidies such as livestock, crops and refuse that decouple predators from wild prey, (iv) behavioural rather than purely numerical responses of mesopredators to large carnivores, (v) the counterbalancing direct and indirect effects of large carnivores on shared prey, and (vi) predominant bottom-up regulation of mammal communities, with strong top-down control emerging only under specific conditions.

First, the impact of large carnivores on mesopredators and prey likely varies with ecological context. Differences in habitat complexity, resource (prey) availability and overall predator community composition can modulate the strength of trophic cascades (Ritchie & Johnson 2009). In some environments, vegetation structure or prey refuges might buffer prey populations from mesopredator increases, for example when structural complexity and cover reduce encounter rates between predators and prey or provide effective escape microhabitats (Camacho 2014, Preiss Bloom et al. 2025). Conversely, the same habitat complexity can limit mesopredators even in systems with simplified or functionally weak large-carnivore guilds if refuges are more accessible to prey than to intermediate predators, or if complex vegetation interferes with mesopredator hunting efficiency (Boon et al. 2022, Preiss Bloom et al. 2025). Complex food webs with multiple predator species can also dilute or redirect large-carnivore effects. Alternative predators or competitors may partially fill the role of a missing or functionally weak large carnivore, dampening the expected release of a given mesopredator and generating variable net outcomes for shared prey (Sandom et al. 2013, Nishijima et al. 2014).

Second, human activities often intervene in predator–prey dynamics (Dorresteijn et al. 2015, Murphy et al. 2021). In many landscapes, humans act as an additional “super predator” or manager by controlling mesopredator populations (through culling, persecution or accidental road mortality) and by altering prey populations (e.g., via hunting or supplemental feeding), thereby modifying or overriding natural top-down pathways (Dorresteijn et al. 2015). Such influences can mask or counteract mesopredator release. For example, if large carnivores are strongly reduced or functionally absent but humans simultaneously suppress mesopredators or support prey through conservation actions, the net outcome may be neutral rather than an explosion of mesopredators. Conversely, human driven declines of large carnivores often coincide with habitat fragmentation and prey exploitation that confound simple cascade expectations (Dorresteijn et al. 2015, Murphy et al. 2021).

Third, mesopredators may respond to the presence of larger predators in ways that reduce direct encounters without necessarily disappearing from the landscape. Camera trap detection rates can be strongly influenced by shifts in behaviour and activity patterns. Mesopredators frequently adjust their temporal and spatial niches to avoid apex predators or dominant competitors, for example by becoming more nocturnal or reducing use of high-risk areas (Wang et al. 2015, Shores et al. 2019). Such behavioural plasticity means that apex predators can suppress mesopredator activity and alter their use of space—thereby reducing direct predation on prey—even when mesopredator numbers do not decline sharply, which in turn can produce only modest differences in detection ratios among different predator assemblage types (Gordon et al. 2015, Shores et al. 2019). In our data, this could translate to relatively modest differences in detection ratios among sites with different large-carnivore assemblage structures, as mesopredators persist but alter their behaviour to coexist with dominant large carnivores.

Finally, apex predators do not only influence ecosystems by controlling mesopredators; they also frequently prey on the same herbivores or smaller prey species that mesopredators exploit and can induce strong non consumptive "fear" responses in that prey (Gordon et al. 2015, Teckentrup 2020). An apex predator's presence might thus have mixed effects on prey populations: on one hand, it may relieve some predation pressure by keeping mesopredators in check (a positive indirect effect on prey), but on the other hand, the apex predator itself might hunt the prey or induce stress/fear in prey (a direct negative effect on prey). The net outcome for prey abundance or detection could be neutral if these opposing forces balance out. In terms of detection ratios, such combined consumptive and non-consumptive effects may allow apex predators to lower mesopredator activity yet also reduce prey numbers or visibility (Gordon et al. 2015), resulting in mesopredator–prey ratios that are not dramatically different among systems with different predator assemblage types. This counterbalancing of direct and indirect effects provides a plausible mechanistic explanation for the overall null pattern observed in our meta-analysis.

Furthermore, several methodological and data-related limitations need to be considered when interpreting these findings, particularly with respect to prey size structure and the context dependence of top-down effects across land-use gradients.

Prey size structure is often hypothesized to mediate indirect effects of predators on mammal communities. However, our ability to evaluate this mechanism was constrained by the limitations of camera-trap methodology. Small mammals are poorly detected by camera traps, and their recorded detections are strongly influenced by camera placement, habitat structure, and body size–dependent detectability (Glen et al. 2013). In our global dataset, small mammal data were available for only a minority of sites and were likely biased toward larger or more mobile species, making comparisons across sites unreliable. As a result, we did not attempt a formal meta-analysis of small versus large prey composition. Future studies integrating complementary sampling methods, such as live trapping or track-based surveys, would be required to robustly assess predator effects on prey size structure at broader spatial scales.

We found little evidence that predator assemblage structure alone is associated with systematic shifts in mesopredator–prey community balance at the global scale. Across both natural and human-modified landscapes, mesopredator–prey detection ratios were broadly similar, and predator assemblage class did not emerge as a strong predictor of community composition (AIC = 72.74 for the multivariate meta-analysis with 57 sites). Although mesopredator–prey ratios tended to be slightly higher in human-modified than in natural sites, this difference was not statistically significant. This outcome, together with the lack of significant interaction terms for predator assemblage by land use (despite somewhat lower mesopredator–prey ratios for D=R sites in natural landscapes), supports the view that top-down effects in terrestrial mammal communities are highly context dependent and often overridden by local ecological and environmental factors. It is also important to note that our inferences are based on camera-trap detections rather than true population densities, and detection rates are known to depend on survey design, habitat structure and species traits, which can obscure moderate changes in abundance or activity. In addition, the underlying studies are observational and highly heterogeneous in design, environmental context and human influence, so the meta-analytic "grand mean" effect is expected to be diluted when local responses vary in sign and magnitude, a pattern commonly reported in ecological meta-analyses of trophic interactions under strong contextual heterogeneity (Koricheva & Gurevitch 2014, Senior et al. 2016). It is also plausible that fine-scale mesopredator release occurs at the level of individual camera stations, particularly in highly human-modified areas with few large carnivores and many mesopredators, as reported by Vargas Soto et al. (2021), but that these local signals are diluted when detections are aggregated to the broader site level used in our meta-analysis.

Implications for the mesopredator-release concept

Considering these considerations, our results suggest that mesopredator release is not a ubiquitous or general consequence of variation in large-carnivore assemblage structure, but rather a context-dependent phenomenon. This conclusion is consistent with the findings of other syntheses – for example, Ritchie & Johnson (2009) noted that outcomes of predator removal or restoration vary widely with environmental context. Our broad-scale analysis reinforces that perspective: across many different sites and communities, we observed relatively consistent mesopredator–prey detection ratios, with prey generally dominating regardless of predator guild composition. In essence, simple top-down control by large carnivores, as reflected in different predator assemblage structures, did not consistently cascade to a strong mesopredator surge or prey collapse. Instead, ecological complexity and site-specific factors likely mediate these interactions, resulting in a subdued overall signal. This finding does not refute the mesopredator release hypothesis in particular instances; rather, it highlights that its manifestation is highly contingent on context. Our results therefore support a weaker formulation of the mesopredator-release concept, in which predator-mediated cascades can occur but are neither universal nor uniformly strong across systems, even where large-carnivore guilds differ strongly in richness or dominance structure (van Schaik et al. 2024).

Classic mesopredator release theory predicts stronger mesopredator dominance where large-carnivore guilds are strongly reduced or functionally weakened, particularly in human-modified landscapes (van Schaik et al. 2024). However, our global synthesis indicates that mesopredator–prey ratios remained broadly similar across predator assemblage types and land-use categories.

These findings highlight the limitations of using predator presence or assemblage composition alone to infer trophic regulation in heterogeneous landscapes. While local studies may detect strong mesopredator responses under specific conditions, our synthesis suggests that such effects are not generalizable across regions and land-use contexts. More broadly, they underscore that top-down control by carnivores is only one of several mechanisms shaping terrestrial mammal communities and that bottom-up resource limitation, habitat configuration and direct human impacts likely account for much of the apparent stability in mesopredator–prey ratios across contrasting predator guilds (Sandom et al. 2013, Dorresteijn et al. 2015, Mendoza & Araujo 2019,).

Implications for management and rewilding

From a conservation and wildlife management standpoint, our results imply that modifying predator assemblage structure (for example through large carnivore reintroduction, supplementation or continued suppression) may not universally produce large cascading effects on mesopredators and prey without the certain environmental conditions. Managers should therefore consider the broader ecosystem context – including habitat features, prey dynamics, and human influences – when predicting the outcomes of predator interventions. In practice, this means that predator-focused interventions need to be locally tailored, rather than transferred uncritically across systems, because the strength of top-down effects depends on primary productivity, habitat configuration, and the intensity of human pressures such as hunting or persecution (Mendoza & Araújo 2019). Management plans should explicitly account for resource productivity, landscape fragmentation, hunting regimes and the presence of other carnivores when forecasting mesopredator and prey responses (Sandom et al. 2013). For rewilding initiatives, this argues for combining the (re)establishment of apex predators with targeted measures on prey populations and habitats, such as improving habitat connectivity, reducing human-driven mortality, and securing corridors that allow dispersal from source populations (Carver et al. 2021). Spatially explicit planning of large-carnivore predator return can help anticipate these context-dependent outcomes and minimize conflicts. For example, modelling of wolf recolonization dynamics for Slavonia, Croatia, showed that scenarios combining increased habitat suitability, functional corridors and active population reinforcement produced the lowest extinction risk and the greatest potential for restoring wolves' ecological role in a human-dominated landscape (Biščan et al. 2025). Thus, the "roar" of large carnivores alone is not enough to rule; their ability to reshape trophic pyramids through changes in predator assemblage structure depends critically on environmental context, resource supply, habitat configuration and human pressures, all which management and rewilding plans must explicitly integrate.

5.4 WOLF RECOLONIZATION SCENARIOS IN SLAVONIA: MANAGEMENT IMPLICATIONS (HYPOTHESIS 3)

Eleven different scenarios were explored to evaluate the recolonization potential of wolves in Slavonia, considering habitat changes, immigration, translocation, harvest, and disease—within both managed and unmanaged contexts—using an existing population projection framework for wolves (Petracca et al., 2023).

The analyses showed that corridor construction and translocation contributed to optimal population viability, with zero recorded extinctions across all timeframes (10, 30, and 100 years). In contrast, the remaining scenarios exhibited significantly higher extinction risks, averaging over 27%—suggesting that passive or limited interventions may be inadequate for ensuring long-term persistence. Without corridor construction, only translocation consistently prevented extinction, while even other habitat-focused measures (e.g., increased carrying capacity) failed to do so. This underscores how habitat fragmentation constrains recolonization success and amplifies the impact of adverse events such as disease, illegal hunting, and human–wolf conflict. These findings highlight the critical importance of proactive, connectivity-enhancing strategies and point to the urgent need for more data on ecological, demographic, and health-related factors that shape recolonization dynamics. Certain model parameters—such as adjustments to carrying capacity and translocation success rates—were based on expert judgment due to limited empirical data, thereby introducing uncertainty that may affect the precision of the long-term projections. To improve model reliability and support more informed conservation decisions, future empirical studies should aim to validate and refine these parameters. In the following discussion, we analyze each scenario group in greater detail, examining their underlying assumptions, outcomes, and implications for conservation planning.

While the model produced various outputs, including survival rates and population sizes, extinction risk was considered the most relevant metric for assessing population viability and guiding conservation strategies. This is because recovery criteria inevitably involve normative decisions—such as defining what level of extinction risk is acceptable (Vucetich et al., 2006). Although neither U.S. nor EU legislation provides explicit quantitative thresholds for what constitutes an “acceptable” extinction risk, this study adopted a 10% threshold, consistent with recent approaches in species conservation planning (Carroll et al., 2019). Statistical analyses in this study revealed that extinction risk was the lowest—i.e., within an “acceptable” range—for two scenarios: Scenario 9 (Corridor Construction) and Scenario 11 (Translocation). A third scenario, Scenario 8 (One-Region Corridor Enhancement), approached the default threshold but did not match the performance of the top scenarios. Notably, Scenarios 9 and 11 exhibited statistically significant reductions in extinction events across all three modeled time periods (10, 30, and 100 years) when compared to other scenarios. The consistent effectiveness of these two scenarios over time underscores their robustness and long-term sustainability, positioning them as best-practice strategies for future management plans with the highest potential for ensuring wolf population persistence. Although Scenario 8 demonstrated a positive trend, further adjustments are needed for it to achieve outcomes comparable to the leading scenarios. Additionally, as the modeled time horizon increased, a greater number of scenarios showed statistically significant differences favoring population survival. This indicates that conservation measures tend to be more effective over extended periods. These findings underscore the importance of long-term implementation, with the most favorable outcomes occurring in the medium- (30 years) and long-term (100 years) projections. According to the literature, wolf populations in different regions have exhibited varying recovery timeframes following protection or reintroduction measures: 5–10 years in Yellowstone (Smith et al., 2003), 10–15 years in Poland (Smietana & Wajda, 1997) and the American Southwest (Bruskotter et al., 2014), 15–20 years in Scandinavia (Liberg et al., 2012), and 20–30 years in the Apennines (Mech & Boitani, 2003). Therefore, the effects of planned conservation measures require time to manifest. Future research should aim to establish standardized extinction risk thresholds across legislative frameworks and to identify key factors influencing corridor enhancement in order to improve the effectiveness of Scenario 8 and align its outcomes with those of the more successful Scenarios 9 and 11.

The time required to observe significant changes in wolf populations following recolonization efforts depends on various factors, including habitat quality, prey availability, human–wildlife interactions, and management strategies. As Scenarios 9 ("Corridor Construction") and 11 ("Translocation") involved the improvement and expansion of ecological corridors, the results suggest that habitat connectivity plays a crucial role in the successful recolonization of wolves within the study area. Habitat connectivity facilitates movement between suitable habitats, supports the maintenance of genetic diversity within populations (Fredrickson et al., 2003; Hedrick & Allendorf, 2004), and enhances survival and range expansion by providing access to essential resources such as prey and shelter (Berger et al., 2007; Ripple & Beschta, 2012). In the study area, the primary barrier to habitat connectivity is the highway. However, spatial analysis conducted in this study identified 27 existing highway structures (e.g., underpasses) that could facilitate wolf recolonization from the Banovina region toward Slavonia (Figure 5). Among these, eight highway structures are likely passable for wolves in their current state with only minor design adjustments, while an additional five could become suitable with more substantial modifications. Although baseline scenario modeling indicates that the study area has the capacity to support a wolf population for a limited period, there is currently no established population in Slavonia, as wolves were historically extirpated from the region (Štrbenac et al., 2010). A likely reason for the absence of natural recolonization is the presence of highways, which are not fully passable for wolves due to inadequate infrastructure. These highways have effectively isolated the Slavonia region (the modeled area) from Banovina, where a stable wolf population currently exists. Additional contributing factors may include illegal hunting, competition with other predators (likely golden jackals; Ćirović et al., 2017), limited prey availability, and broader human–wildlife conflicts. As an initial step, it is essential to modify existing highway structures to function as wildlife passages. Such interventions could mitigate the effects of habitat fragmentation and create the conditions necessary for wolf recolonization in adjacent habitats. The most plausible dispersal route for wolves would likely originate in Banovina, potentially serving as a source population for establishing new packs in Slavonia. In subsequent phases of this research, in addition to recommending modifications to existing highway infrastructure, it will be crucial to assess the entire potential corridor between Banovina and Slavonia. This assessment should aim to identify and enhance specific areas, or habitat features that may currently act as barriers to the wolf movement. Attention should be given to the availability of small, forested patches that can serve as resting sites, which have been shown to facilitate long-distance wolf dispersal (Torretta et al., 2023). In line with our findings and the identification of 27 existing highway structures (Figure 14), we recommend prioritizing a detailed spatial analysis to determine the most suitable sites for the construction or adaptation of wildlife crossings. Although eight of these structures appear potentially suitable with only minor modifications, selecting strategic locations—based on criteria such as proximity to core habitats, existing landscape permeability, and minimal human disturbance—is critical for effective mitigation planning. Accordingly, future research should focus on developing a corridor suitability model that incorporates landscape connectivity metrics and on mapping priority sites for crossing enhancement or new construction. This spatial planning effort should be accompanied by updated maps highlighting high-potential dispersal zones and key crossing points. Such tools would not only guide infrastructure adaptations but also support evidence-based conservation policymaking and implementation at national and regional levels. On the other hand, population supplementation through translocation can enhance genetic diversity (Fredrickson et al., 2003; Hedrick & Allendorf, 2004), facilitate population recovery by enabling wolves to recolonize their historical range more rapidly (Ripple & Beschta, 2012; Fredrickson et al., 2003), and compensate for natural losses caused by mortality, dispersal (emigration), and inter-pack competition (Tallmon et al., 2004). Given Slavonia's potential connectivity with the Banovina wolf population, mitigating habitat fragmentation—particularly caused by highways—should be prioritized over direct translocation efforts. Establishing a continuous habitat link between these two suitable areas would allow for ongoing population renewal and genetic exchange without the need for active animal translocation. The findings of this study align with the principles of trophic rewilding and reflect successful wolf recolonization patterns observed across North America and Europe (Smith et al., 2010; Vila et al., 2003; Wabakken et al., 2001; Chapron et al., 2014).

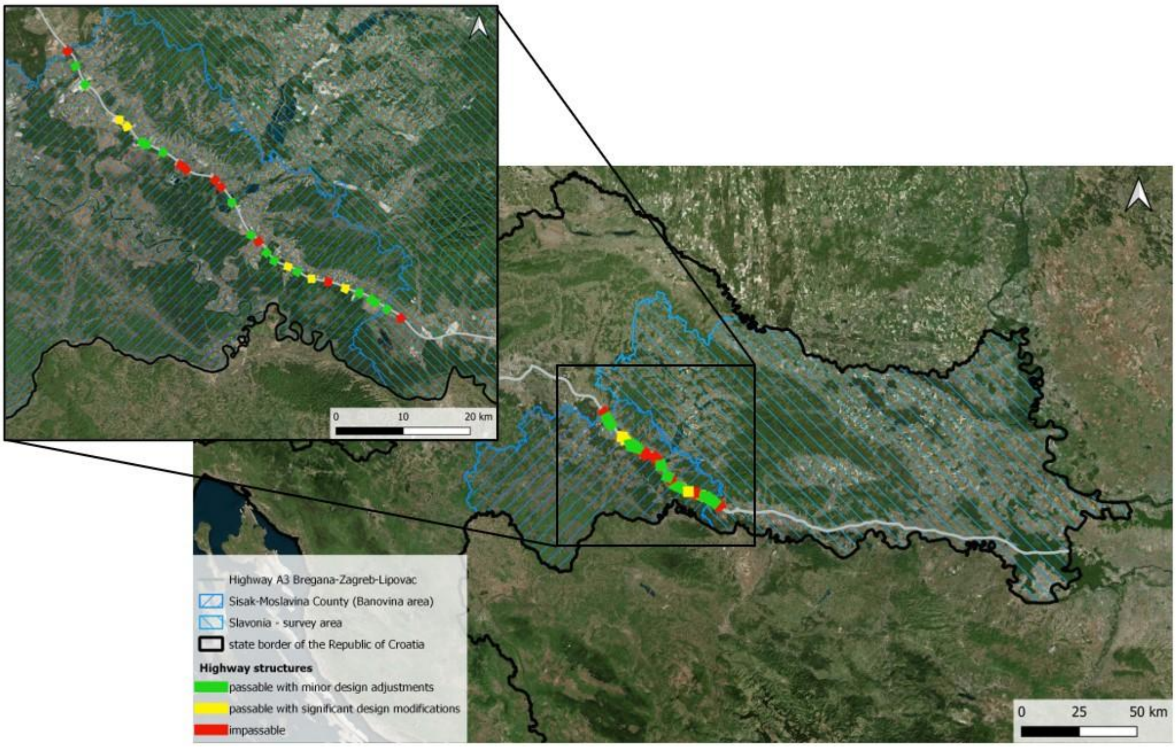

Figure 14 Results of the spatial analysis of potential wolf corridors along the A3 highway (Bregana–Zagreb–Lipovac) between the Banovina and Slavonia regions in Croatia. The main map displays the study area within Croatia's national borders (black line), highlighting Sisak-Moslavina County (Banovina area) and the Slavonia survey area with blue hatching. Highway structures are classified into three categories: passable with minor design adjustments (green markers), passable with significant design modifications (yellow markers), and impassable (red markers). The inset map (top left) provides a detailed view of a 20 km corridor segment, showing the distribution of passage structures.

The remaining seven scenarios modeled in this study exhibited extinction risks exceeding 27%. Diseases can not only cause direct mortality but also indirectly reduce recolonization rates, particularly among juveniles (Mech et al., 2008; Almberg et al., 2009). Additionally, research from Minnesota indicates that natural wolf mortality rates are significantly lower than human-caused mortality (Oliynyk, 2023). Illegal wolf hunting results in ecosystem disruption, the fragmentation of family groups, interference with reproduction, and reduced population growth (Liberg et al., 2020; Nowak et al., 2021). Wolves inhabiting German military training areas demonstrated higher survival rates compared to those in similar habitats outside these areas (Reinhardt et al., 2019), suggesting that illegal killings may be influenced by land ownership, with hunting practices potentially functioning as population regulators. If this pattern continues, the future distribution and abundance of European wolves may be driven more by mortality-related source–sink dynamics than by habitat availability alone. The removal of a dominant wolf during human–wildlife conflicts destabilize packs, causing increased stress, territorial instability, and decreased reproductive success (Liberg et al., 2020; Sunde et al., 2021). In Croatia and Bosnia and Herzegovina, 96.5% of wolf deaths between 1986 and 2001 were human-caused, primarily from shooting (91.6%) and traffic incidents (8.4%)—predominantly affecting young individuals, with an average age at death of only 1.9 years. Only a single case (1.2%) was attributed to natural causes (intraspecific aggression), and two cases (2.3%) remained of unknown cause (Kusak, 2002). In wolf populations that are not heavily impacted by human activities, up to 65–70% of wolf mortality is due to intraspecific aggression (Mech et al., 1998; Peterson, 1995), suggesting that mortality patterns in Croatia deviate significantly from natural dynamics. Therefore, future research should focus on identifying effective measures to reduce wolf mortality caused by human activities.

Beyond direct human-caused mortality, additional emerging threats to wolf survival have been documented. In Italy, widespread exposure to anticoagulant rodenticides has been detected in wolf carcasses, posing a significant conservation concern (Musto et al., 2024). Similarly, parasitic infections should not be overlooked. Studies from France and Italy suggest that parasite invasions in wolves may be linked to environmental contamination from domestic dog feces, as well as factors such as diet composition and wolf population density (Molnar et al., 2019). These conditions can facilitate the transmission of pathogens or parasites, such as Echinococcus or Toxocara, especially in areas with high densities of free-ranging dogs or substantial human disturbance. Furthermore, our model does not incorporate genetic variability or inbreeding dynamics due to limited empirical data. Nevertheless, genetic threats—including wolf–dog hybridization—pose significant risks to the genetic integrity and long-term viability of wolf populations in the region. A Croatian study (Kusak et al., 2018) using microsatellites, mitochondrial DNA, and Y-chromosome markers combined with phenotypic data found that 2.8% of the tested wild canids were confirmed hybrids. All hybrids were detected in Dalmatia—an area characterized by high anthropogenic disturbance and recent wolf recolonization. These hybrids are the result of mating between female wolves and male dogs. Notably, hybrids tend to be more synanthropic and are more prone to attacking livestock, potentially exacerbating human–wildlife conflicts (Cusdin & Greenwood, 2000). Although toxicological, parasitological, and genetic data are currently lacking for Croatia, including the Slavonia region, these issues should be addressed in future necropsy and monitoring protocols. Given the likelihood of similar ecological interactions being observed in neighboring countries—such as environmental pollution, proximity to human settlements, and the presence of free-ranging dogs, future research should not only monitor dispersal and habitat connectivity but also systematically assess body condition, causes of mortality, parasite loads, toxicological exposure, and signs of hybridization in recolonizing individuals. While no hybrid cases have yet been recorded in Slavonia, the risk persists due to shared ecological conditions and the absence of a stable wolf population. Therefore, ongoing genetic monitoring is essential to prevent hybrid establishment, safeguard the species' genetic integrity, and inform long-term conservation and recolonization strategies. Integrative health and genetic assessments are critical for accurately evaluating population viability and should be prioritized alongside spatial and demographic analyses. Although adverse scenarios predict high extinction risks, even habitat enlargement scenarios (i.e., increased carrying capacity) entail significant extinction risks. Despite changes in hunting regulations, forest management, or natural succession—all contributing to expanded wolf habitats compared to the baseline scenario—the risk of extinction remains unacceptably high. This aligns with previous findings showing that a limited habitat size increases resource competition, reduces prey availability, and restricts space for breeding (Kittle, 2014). Therefore, it can be concluded that the presence and spatial arrangement of wolf habitats—characterized by a minimal poaching risk and sufficient size to support breeding territories connected by corridors—are likely critical for population persistence.

Beyond the impacts identified in this study, research by Carricondo-Sanchez et al. (2020) has highlighted several additional significant factors that could influence the success of wolf recolonization, including altered prey behavior and human-related activities. Deer, as a primary prey species, may become more cautious and avoid areas frequently used by wolves. Such behavioral changes can substantially affect the spatial distribution and movement patterns of prey populations, thereby influencing wolf recolonization dynamics (Wójcicki & Borowski, 2023). Anthropogenic factors, such as human activities and landscape modifications, also play a crucial role in shaping wolf behavior and distribution. Understanding how human presence impacts wolves is essential for developing effective conservation and recolonization strategies. In the context of the study area, further urbanization and the abandonment of rural lands are expected. Given that wolves have been absent from the region for approximately a century and that livestock farms are currently not adapted to predator presence, an increase in human–wolf conflicts can be anticipated once wolves begin to recolonize the area. Therefore, preparing local communities through education and inclusive engagement is vital to mitigate potential conflicts and promote coexistence. Additionally, it is important to acknowledge the growing focus within the scientific community on climate change-driven impacts. Changes in habitat suitability and prey availability due to climate change pose significant challenges for wolf recolonization (Merli et al., 2023). Predictions for the Slavonia region indicate shifts in forest ecosystems (Ugarković et al., 2016), suggesting a transition from one forest type to another. Nonetheless, forests—a critical habitat for wolves—are expected to remain prevalent within the study area.

Lastly, it is important to discuss the crucial factors for the successful recolonization of wolves: sociopolitical factors including human–wolf conflict, public perception, and policy interventions. While this aspect could not be directly modeled in this research, the authors emphasize that effectively managing people's attitudes and implementing adaptive policy interventions are indispensable for successful recolonization efforts when planning wolf recolonization in an area (Niemiec et al., 2022). Human–wolf conflicts arise from various factors, including livestock predation, competition for game species, and concerns about potential direct attacks on humans (Rodríguez-Recio et al., 2022). Media coverage and outreach campaigns play a significant role in shaping public opinion. Bišćan and Damjanović (2022) analyzed media portrayals of wolves in the Croatian daily press from 2012 to 2022. Their findings showed that 56% of the coverage depicted wolves negatively, while only 39% included input from large-animal experts. This raises important questions about why wolves are often portrayed negatively and how many reported incidents are genuinely attributable to wolves. Furthermore, a comprehensive analysis (Bombieri et al., 2023) of 5440 large carnivore attacks worldwide from 1950 to 2019 reveals that the socioeconomic context significantly influences the occurrence of such incidents. In high-income countries, recreational activities are the primary risk factor, whereas in low-income countries, attacks are more often linked to livelihood activities. Their findings highlight the predominance of bear attacks in Europe, while wolf attacks remain rare and typically involve scenarios with dogs or injured animals. While acknowledging the potential risks associated with wolf encounters, it is important to put the data into context. In Europe and North America, only eleven recorded wolf attacks resulting in two fatalities occurred over an 18-year period. Given the estimated populations of approximately 60,000 wolves in North America and 15,000 in Europe coexisting with hundreds of millions of people, the risk of a wolf attack, although present, is statistically negligible (Linnell et al., 2021). In Montana, USA, wolf populations grew from 2007 to 2020 before stabilizing, while incidents of livestock predation by wolves remained minimal throughout this period (Wilson, 2023). Moreover, understanding local coexistence narratives is crucial for developing effective management plans for wolf recolonization. Pettersson et al. (2023)

identified three key discourses: the wolf protectionist discourse, which prioritizes wolf autonomy through the strict regulation of human activities; the traditional use discourse, emphasizing human-centered control over wolf populations; and the pragmatic discourse, which advocates balancing conservation goals with local priorities and the equitable sharing of costs and benefits. Integrating these perspectives is essential, as spatial and temporal models underscore the importance of collaboration, trust-building, and inclusive strategies. Educating communities about the ecological role of wolves and proactively mitigating conflicts remain vital in areas with potential wolf recolonization. Equally important are stakeholder involvement and adaptive management strategies, which complement ecological data to ensure long-term success.

CHAPTER 6: CONCLUSION

6.1. CONCLUSIONS

Large predators play a key role in regulating ecosystems and have inspired fear and awe in humans since ancient times. Wolves, in particular, are deeply entangled with our cultural history, at once feared, persecuted and turned into our closest animal companions through domestication. After centuries of systematic reduction of large carnivores, including wolves, modern conservation, urbanisation and rural abandonment have created conditions for their renewed expansion in parts of Europe. Against this backdrop, this doctoral thesis addressed a simple but consequential question: can wolves recolonise parts of the Pannonian Plain where they were once present but are now absent—and if so, under which ecological and management scenarios?

The first component of this thesis, a ranger-based camera-trapping survey in Paklenica National Park (Hypothesis 1), evaluated whether camera trapping conducted by protected-area staff can serve as a feasible, cost-effective tool for monitoring wildlife communities and recolonisation dynamics. The survey showed that rangers, when equipped with clear protocols and basic training, can implement standardised camera-trapping methods and generate biodiversity metrics that are comparable to those from previous ecologist-led studies, while substantially reducing financial and logistical demands. At the same time, the results highlighted important limitations, including non-uniform survey designs, camera placement concentrated at salt licks and watering sites, and the absence of a parallel control survey by external researchers, all of which introduce bias and constrain the strength of inferences. Overall, Hypothesis 1 is supported in the sense that ranger-based camera trapping represents a practical and scalable monitoring approach, but its reliability depends on continued methodological refinement, workload planning and institutional support. This demonstrates that trained protected-area staff can reliably implement standardised camera-trapping protocols and generate robust, cost-effective information on carnivore–prey communities, providing a practical template for monitoring in other protected areas such as Papuk Nature Park.

The second component, a global meta-analysis of camera-trap studies (Hypothesis 2), examined whether large carnivores exert a general regulatory effect on mammal communities through top-down control detectable in mesopredator–prey detection ratios. Contrary to the simple expectation of a strong, consistent signal of mesopredator release in the absence of top predators, the analysis yielded mixed results, with detection ratios showing no uniform deviations from zero across predator assemblages or land-use categories. These findings suggest that top-down effects of large carnivores, as reflected in camera-trap detections, are weak to moderate and highly context dependent, being mediated by habitat structure, prey availability, predator guild composition and human pressures, as well as methodological constraints such as under-detection of small mammals and heterogeneous survey designs. In this sense, Hypothesis 2 is only partially supported: while large carnivores do influence lower trophic levels, their effects do not translate into a strong, generalisable global pattern in camera-trap detection ratios. This underscores the need for carefully designed local studies—such as future monitoring in Papuk Nature Park—to clarify how context-dependent trophic dynamics unfold during wolf recolonisation.

Building on these empirical insights into trophic structure and monitoring, the third and central component of the thesis focused on forecasting how wolf recolonization could unfold in the Pannonian Plain under different management conditions (Hypothesis 3). Using a spatially and temporally explicit population-dynamic model parameterised with data from Croatian wolf populations and complementary estimates from the wider European literature, 11 scenarios were explored, grouped into adverse events, increased carrying capacity and population supplementation. Across all simulated timeframes (10, 30 and 100 years), baseline and adverse-event scenarios were associated with substantial long-term extinction risk, and scenarios representing disease outbreaks, illegal hunting or removal of problem individuals led to rapid declines. Increasing carrying capacity alone only moderately reduced extinction risk and was insufficient to secure long-term population viability without improved connectivity or reduced human-caused mortality. By contrast, supplementation scenarios involving corridor construction and/or translocation had the lowest extinction probabilities and maintained viable populations over 100-year horizons, with spatial analysis identifying existing highway structures that could facilitate wolf movement between Banovina and Slavonia. These findings support Hypothesis 3: successful wolf recolonization of the Pannonian Plain is feasible, but only under clearly defined ecological and management conditions that secure functional connectivity and limit adverse anthropogenic pressures.

When interpreted together, the Paklenica case study, the global meta-analysis and the Pannonian modelling clarify what an integrated approach to wolf conservation and recolonisation must entail. First, because the synthesis of camera-trap studies showed that top-down effects on mammal communities are highly context dependent, conservation and rewilding strategies in the Pannonian Plain cannot rely on wolf recovery alone to deliver predictable mesopredator suppression or prey restoration. Second, the demonstrated capacity of ranger-based camera-trap networks to generate high-quality data provides a realistic basis for tracking demographic and ecological responses over time, including the progression of the recolonisation process itself, and for informing adaptive management of corridors, hunting regimes and conflict-mitigation measures. Third, since the modelling indicates that a viable wolf population could, under favourable conditions, establish itself "on its own" and that recolonisation of the Pannonian Plain is plausible within the coming decades if connectivity is maintained, anthropogenic pressures are reduced and long-term camera-trap monitoring is embedded in adaptive management, it is essential to initiate proactive planning for wolf–human coexistence in Pannonia rather than waiting for conflicts to emerge.

6.2. LIMITATIONS AND RECOMMENDATIONS

This thesis, like any empirical work in complex real-world ecosystems, has some inherent limitations when interpreting its findings. The global camera-trap meta-analysis relies on published studies that differ in design, effort and reporting, and that use detections rather than true population densities, which inevitably smooths over part of the fine-scale ecological variation. The Paklenica case study focuses on a single protected area, with heterogeneous camera effort and non-random placement at resource hotspots such as salt licks and watering sites, so the number of events recorded for each species is subject to spatial bias and does not allow for more complex ecological conclusions to be drawn with confidence. Regarding the recolonization model for the Pannonian Plain, it is important to recognise that the ecosystem is shaped by many ecological and sociological factors that could further refine both the model and the set of scenarios and thus yield more precise projections. In its current form, the model explores a limited number of carefully selected "what-if" scenarios and should therefore be interpreted primarily as a structured exploration rather than as a precise forecast, to be updated as new data become available. Nevertheless, the results clearly indicate the general direction and types of scenarios under which viable wolf populations in the Pannonian Plain are most likely to be achieved.

These limitations point directly toward priorities for future research and management in the Pannonian Plain. At the methodological level, camera-trap studies aimed at inferring trophic interactions would benefit from more harmonised survey designs and reporting standards, including consistent information on camera placement, spacing, effort and detectability, as well as complementary methods for small mammals. Integrating camera-trap data with independent estimates of occupancy or density would help bridge the gap between detection rates and true demographic responses of predators and prey. In protected areas such as Papuk and along key Pannonian corridors, ranger-based camera-trap networks should be expanded and standardised, so that they can function as a long-term backbone for monitoring wolf presence, prey communities and human activity. In parallel, further work is needed to refine and extend the recolonization model by incorporating updated demographic parameters, explicit measures of corridor quality, and a more detailed representation of conflict drivers such as livestock practices, hunting regimes and attitudes toward large carnivores.

From a management perspective, future efforts in Pannonia should prioritise: (i) safeguarding and improving ecological connectivity between Banovina, Papuk and other suitable habitats, with particular emphasis on adapting existing highway structures and planning new wildlife crossings; (ii) incorporating ranger-based camera-trap monitoring into routine management to provide early-warning indicators of wolf expansion, conflict hotspots and changes in prey populations; and (iii) integrating social-science research on risk perception, tolerance and governance into conservation planning, so that corridor construction, conflict-mitigation measures and possible translocations are co-designed with local communities. Taken together, these steps would strengthen the evidence base, reduce key uncertainties and ensure that any future recolonization of the Pannonian Plain by wolves unfolds within a framework that is ecologically effective and socially acceptable.

CITED REFERENCES

1. Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of least-cost modelling as a functional landscape model. Landscape and Urban Planning, 64, 233–247.

2. Ahumada, J. A., Hurtado, J., & Lizcano, D. (2013). Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: A tool for conservation. PLoS ONE, 8(9), e73707.

3. Ahumada, J. A., Silva, C. E. F., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., McWilliam, A., Mugerwa, B., O'Brien, T., Rovero, F., Sheil, D., Spironello, W. R., Winarni, N., & Andelman, S. J. (2011). Community structure and diversity of tropical forest mammals: Data from a global camera trap network. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1578), 2703–2711.

4. Almberg, E. S., Mech, L. D., Smith, D. W., Sheldon, J. W., & Crabtree, R. L. (2009). A serological survey of infectious disease in Yellowstone National Park's canid community. PLoS ONE, 4, e7042.

5. Almpanidou, V., Mazaris, A. D., Mertzanis, Y., Avraam, I., Antoniou, I., Pantis, J. D., & Sgardelis, S. P. (2020). Landscape connectivity and suitable habitat analysis for wolves (Canis lupus L.) in the Eastern Pyrenees. Sustainability, 12, 5762.

6. Antolović, J., Frković, A., Grubešić, M., Holcer, D., Vuković, M., Flajšman, E., Grgurev, M., Hamidović, D., Pavlinić, I., & Tvrtković, N. (2006). Crvena knjiga sisavaca Hrvatske [Red data book of mammals of Croatia]. Ministarstvo kulture, Državni zavod za zaštitu prirode. [In Croatian]

7. Antonić, O., Kušan, V., Jelaska, S., Bukovec, D., Križan, J., Bakran-Petricioli, T., Gottstein-Matočec, S., Pernar, R., Hećimović, Ž., Janeković, I. (2005). Kartiranje staništa Republike Hrvatske (2000.–2004.) [Habitat mapping of the Republic of Croatia (2000–2004)]. Drypis, 1(1).

8. Appleton, M. R., Courtiol, A., Emerton, L., Slade, J. L., Tilker, A., Warr, L. C., Álvarez Malvido, M., Barborak, J. R., de Bruin, L., Chapple, R., Daltry, J. C., Hadley, N. P., Jordan,

C. A., Rousset, F., Singh, R., Sterling, E. J., Wessling, E. G., & Long, B. (2022). Protected area personnel and ranger numbers are insufficient to deliver global expectations. Nature Sustainability, 5, 1100–1110.

9. Arnoni, H. (2018). Como se tornar um guarda-florestal? Super Interessante. https://super.abril.com.br/mundo-estranho/como-se-tornar-um-guarda-florestal/
10. Ausband, D. E., & Mech, L. D. (2023). The challenges of success: Future wolf conservation and management in the United States. BioScience, 73, 587–591.
11. Amir, Z., Sovie, A. R., & Luskin, M. S. (2022). Inferring predator–prey interactions from camera traps: A Bayesian co-abundance modeling approach. Ecology and Evolution, 12(12), e9627.
12. Bardi, A., Papini, P., Quaglino, E., Biondi, E., Topić, J., Milović, M., Pandža, M., Kaligarič, M., Oriolo, G., Roland, V. (2016). Karta prirodnih i poluprirodnih ne-šumskih kopnenih i slatkovodnih staništa Republike Hrvatske [Map of natural and semi-natural non-forest terrestrial and freshwater habitats of the Republic of Croatia]. Ministarstvo zaštite okoliša i energetike.
13. Berger, K. M., Gese, E. M., & Berger, J. (2007). Carnivore repatriation and holarctic prey: Narrowing the deficit in ecological effectiveness. Conservation Biology, 21, 1105–1116.
14. Bišćan, M., & Damjanović, I. (2022). The Big Bad Wolf—The perception of media-mediated messages. In Book of abstracts (pp. 169–170). Croatian Association of Nature and Environmental Protection Experts (HUSZPO).
15. Bišćan, M., Jelić, D., Maguire, I., & Massolo, A. (2025). Modeling wolf, Canis lupus, recolonization dynamics to plan conservation actions ahead: Will the “Big Bad Wolves” howl again in Slavonia, Croatia? Diversity, 17(7), 461.
16. Blanco, J. C., Cortés, Y., & Virgós, E. (2005). Wolf response to two kinds of barriers in an agricultural habitat in Spain. Canadian Journal of Zoology, 83, 312–323.
17. Bombieri, G., Penteriani, V., Almasieh, K., Ambarlı, H., Ashrafzadeh, M. R., Das, C. S., Dharaiya, N., Hoogesteijn, R., Hoogesteijn, A., Ikanda, D., Kabir, M., Krofel, M., Licoppe, A., Linnell, J. D. C., López-Bao, J. V., Majic, A., Mann, C. L., Miller, J. R. B., Mukeka, J. M., Muthoni, F., Odden, J., Ordiz, A., Patterson, B. D., Persson, J., Rigg, R., Sergio, F.,

Valente, R., Zarco-González, M. M., Zimmermann, B., & Delgado, M. del M. (2023). A worldwide perspective on large carnivore attacks on humans. PLoS Biology, 21, e3001946.

18. Boon, J. S., Keith, S. A., Exton, D. A., & Field, R. (2023). The role of refuges in biological invasions: A systematic review. Global Ecology and Biogeography, 32, 123–138.
19. Bruns, A., Waltert, M., & Khorozyan, I. (2020). The effectiveness of livestock protection measures against wolves (Canis lupus) and implications for their co-existence with humans. Global Ecology and Conservation, 21, e00868.
20. Bruskotter, J. T., Vucetich, J. A., Enzler, S. A., Treves, A., & Nelson, M. P. (2014). Removing protections for wolves and the future of the U.S. Endangered Species Act (1973). Conservation Letters, 7, 401–407.
21. Bundesverband Naturwacht. (2022). Germany's rangers. https://www.bundesverband-naturwacht.de/?lang=en
22. Burton, A. C., Beirne, C., Gaynor, K. M., Sun, C., Granados, A., Allen, M. L., Alston, J. M., Alvarenga, G. C., Álvarez Calderón, F. S., Amir, Z., Anhalt-Depies, C., Appel, C., Arroyo-Arce, S., Balme, G., Bar-Massada, A., Barcelos, D., Barr, E., Barthelmess, E. L., Baruzzi, C., Basak, S. M., Beenaerts, N., Belmaker, J., Belova, O., Bezarević, B., … Kays, R. (2024). Mammal responses to global changes in human activity vary by trophic group and landscape. Nature Ecology & Evolution, 8(5), 924–935. https://doi.org/10.1038/s41559-024-02363-2
23. Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology, 52(3), 675–685. https://doi.org/10.1111/1365-2664.12432
24. Camacho, C. (2014). "Bodyguard" plants: Predator escape performance influences microhabitat choice by nightjars. Behavioural Processes, 103, 101–110.
25. Carbone, C., & Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. Science, 295, 2273–2276. https://doi.org/10.1126/science.1067994

26. Carbone, C., Mace, G. M., Roberts, S. C., & Macdonald, D. W. (1999). Energetic constraints on the diet of terrestrial carnivores. Nature, 402, 286–288.

27. Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L., & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. Science, 309, 1239–1241.

28. Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., & Mace, G. M. (2004). Human population density and extinction risk in the world's carnivores. PLoS Biology, 2, e197.

29. Carricondo-Sanchez, D., Zimmermann, B., Wabakken, P., Eriksen, A., Milleret, C., Ordiz, A., Sanz-Pérez, A., & Wikenros, C. (2020). Wolves at the door? Factors influencing the individual behavior of wolves in relation to anthropogenic features. Biological Conservation, 244, 108514.

30. Carroll, C., Lacy, R. C., Fredrickson, R. J., Rohlf, D. J., Hendricks, S. A., & Phillips, M. K. (2019). Biological and sociopolitical sources of uncertainty in population viability analysis for endangered species recovery planning. Scientific Reports, 9, 10130.

31. Carroll, C., Phillips, M. K., Schumaker, N. H., & Smith, D. W. (2003). Impacts of landscape change on wolf restoration success: Planning a reintroduction program based on static and dynamic spatial models. Conservation Biology, 17, 536–548.

32. Carver, S., Convery, I., Hawkins, S., Beyers, R., Eagle, A., Kun, Z., Van Maanen, E., Cao, Y., Fisher, M., Edwards, S. R., Nelson, C., Gann, G. D., Shurter, S., Aguilar, K., Andrade, A., Ripple, W. J., Davis, J., Sinclair, A., Bekoff, M., Noss, R., Foreman, D., Pettersson, H., Root-Bernstein, M., Svenning, J.-C., Taylor, P., Wynne-Jones, S., Watson Featherstone, A., Navarro, L. M., Aykroyd, T., Parfitt, A., & Soulé, M. (2021). Guiding principles for rewilding. Conservation Biology, 35, 188–198.

33. Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin,

E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. Science, 346, 1517–1520.

34. Chapron, G., Wikenros, C., Liberg, O., Wabakken, P., Flagstad, Ø., Milleret, C., Månsson, J., Svensson, L., Zimmermann, B., Åkesson, M., & Sand, H. (2021). Estimating wolf (Canis lupus) population size from number of packs and an individual-based model. Ecology and Evolution, 11, 11739–11748.

35. Chen, C., Brodie, J. F., Kays, R., Davies, T. J., Liu, R., Fisher, J. T., Ahumada, J., McShea, W., Sheil, D., Agwanda, B., Andrianarisoa, M. H., Appleton, R. D., Bitariho, R., Espinosa, S., Grigione, M. M., Helgen, K. M., Hubbard, A., Hurtado, C. M., Jansen, P. A., Jiang, X., Jones, A., Kalies, E. L., Kiebou-Opepa, C., Li, X., Lima, M., Meyer, E., Miller, A. B., Murphy, T., Piana, R., Quan, R.-C., Rota, C. T., Rovero, F., Santos, F., Schuttler, S. G., Uduman, A., van Bommel, J., Young, H., & Burton, A. C. (2022). Global camera trap synthesis highlights the importance of protected areas in maintaining mammal diversity. Conservation Letters, 15(2), e12865.

36. Corlett, R. T. (2016). Restoration, reintroduction, and rewilding in a changing world. Trends in Ecology & Evolution, 31, 453–462.

37. Ćirović, D., Jurišić, A., & Kovačić, D. (2017). Golden jackal expansion in Europe: A case of mesopredator release. Italian Journal of Mammalogy, 28, 9–15.

38. Constable, P., Hinchcliff, K., Demma, N., Callahan, M., & Dale, B. (1998). Serum biochemistry of captive and free-ranging gray wolves (Canis lupus). Journal of Zoo and Wildlife Medicine, 29, 435–440.

39. Coulson, T., Mace, G. M., Hudson, E., & Possingham, H. (2001). The use and abuse of population viability analysis. Trends in Ecology & Evolution, 16, 219–221.

40. Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. Nature, 400, 563–566.

41. Cusdin, P. A., & Greenwood, A. G. (2000). The keeping of wolf-hybrids in Great Britain. Department of the Environment, Transport and the Regions; Royal Society for the Prevention of Cruelty to Animals.

42. Davis, R. S., Yarnell, R. W., Gentle, L. K., Uzal, A., Mgoola, W. O., & Stone, E. L. (2021). Prey availability and intraguild competition regulate the spatiotemporal dynamics of a modified large carnivore guild. Ecology and Evolution, 11(14), 7890–7905.

43. De Bondi, N., White, J. G., Stevens, M., & Cooke, R. (2010). A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. Wildlife Research, 37(6), 456–465.

44. Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R. R., Shin, Y.-J., Visseren-Hamakers, I. J., Willis, K. J., Zayas, C. N., Lonsdale, M., Larigauderie, A., Toivonen, T., van der Wal, H., Watson, R. T., Wu, J., Díaz-Reviriego, I., Pascual, U., Soberón, J., Essen, C. von, Figueroa, V. E., & Pires, A. P. F. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. Science, 366(6471), eaax3100.

45. Distefano, E. (2005). Human–wildlife conflict worldwide: Collection of case studies, analysis of management strategies and good practices. Food and Agriculture Organization of the United Nations.

46. Doboš, M., Pavić, G., Kukić, G., Sikora, Č., Jušić, K., & Jelić, D. (2023). Istraživanje faune na Papuku pomoću fotozamki (siječanj 2022.–ožujak 2023.) [Fauna research on Papuk using camera traps (January 2022–March 2023)]. Javna ustanova Park prirode Papuk.

47. Dobson, A. D. M., Milner-Gulland, E. J., Aebischer, N. J., Beale, C. M., Brozovic, R., Coals, P., Critchlow, R., Dancer, A., Greve, M., Hinsley, A., Ibbett, H., Johnston, A., Kuiper, T., Le Comber, S., Mahood, S. P., Moore, J. F., Nilsen, E. B., Pocock, M. J. O., Quinn, A., Travers, H., Wilfred, P., Wright, J., & Keane, A. (2020). Making messy data work for conservation. One Earth, 2(5), 455–465.

48. Dorresteijn, I., Schultner, J., Nimmo, D. G., Fischer, J., Hanspach, J., Kuemmerle, T., Kehoe, L., & Ritchie, E. G. (2015). Incorporating anthropogenic effects into trophic ecology: Predator–prey interactions in a human dominated landscape. Proceedings of the Royal Society B: Biological Sciences, 282(1814), 20151602.

49. Du Preez, B., Loveridge, A., & Macdonald, D. (2014). To bait or not to bait: A comparison of camera-trapping methods for estimating leopard Panthera pardus density. Biological Conservation, 176, 153–161.

50. Duffy, J. E. (2002). Biodiversity and ecosystem function: The consumer connection. Oikos, 99, 201–219.

51. D'Amico, M., Periquet, S., Román, J., & Revilla, E. (2016). Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. Journal of Applied Ecology, 53, 181–190.

52. Elbroch, L. M., Lendrum, P. E., Newby, J., Quigley, H., & Thompson, D. J. (2015). Recolonizing wolves influence the realized niche of resident cougars. Zoological Studies, 54, 41.

53. Ellner, S. P., Fieberg, J., Ludwig, D., & Wilcox, C. (2002). Precision of population viability analysis. Conservation Biology, 16, 258–261.

54. Elmhagen, B., & Rushton, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: Top down or bottom up? Ecology Letters, 10, 197–206.

55. Environmental Science. (2022). What is a park ranger? https://www.environmentalscience.org/career/park-ranger

56. Estes, J. A., Duggins, D. O., & Rathbun, G. B. (1989). The ecology of extinctions in kelp forest communities. Conservation Biology, 3, 252–264.

57. Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M. E., & Wardle, D. A. (2011). Trophic downgrading of planet Earth. Science, 333(6040), 301–306.

58. Eymann, J., Degreef, J., Häuser, C., Monje, J. C., Samyn, Y., & Vandenspiegel, D. (2010). Manual on field recording techniques and protocols for All Taxa Biodiversity Inventories and Monitoring. Abc Taxa.
59. European Commission. (2023). The situation of the wolf (Canis lupus) in the European Union (European Commission Report). European Commission.
60. European Environment Agency. (2002). The Pannonian region. In Europe's biodiversity: Biogeographical regions and seas (pp. 1–6). European Environment Agency
61. Ford, A. T., & Goheen, J. R. (2015). Trophic cascades by large carnivores: A case for strong inference and mechanism. Trends in Ecology & Evolution, 30(12), 725–735.
62. Fredrickson, R. J., Hedrick, P. W., & Wayne, R. K. (2003). Genetic rescue of an insular population of large mammals. Proceedings of the Royal Society B: Biological Sciences, 270, 91–97.
63. Frković, A., Ruff, R., Cicnjak, L., & Huber, D. (1992). Wolf mortality during 1946–86 in Gorski kotar, Croatia. In Proceedings of the 18th IUGB Congress (pp. 353–358).
64. Glen, A. S., Cockburn, S., Nichols, M., Ekanayake, J., & Warburton, B. (2013). Optimising camera traps for monitoring small mammals. PLOS ONE, 8(6), e67940.
65. Gompper, M. E., Ray, J. C., Groff, C., & Berger, J. (2002). A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin, 30, 962–973.
66. Gordon, C. E., Feit, A., Grüber, J., & Letnic, M. (2015). Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. Proceedings of the Royal Society B: Biological Sciences, 282(1802), 20142870.
67. Gordon, C. H., Banyard, A. C., Hussein, A., Laurenson, M. K., Malcolm, J. R., Marino, J., Regassa, F., Stewart, A. M. E., Fooks, A. R., & Sillero-Zubiri, C. (2015). Canine distemper in endangered Ethiopian wolves. Emerging Infectious Diseases, 21, 824–832.
68. Grauer, J. A., Gilbert, J. H., Woodford, J. E., Eklund, D., Anderson, S., & Pauli, J. N. (2019). Modest immigration can rescue a reintroduced carnivore population. Journal of Wildlife Management, 83, 567–576.

69. Greenville, A. C., Wardle, G. M., Tamayo, B., & Dickman, C. R. (2014). Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. Oecologia, 175(4), 1349–1358.

70. Griffin, J. N., Byrnes, J. E. K., & Cardinale, B. J. (2013). Effects of predator richness on prey suppression: A meta-analysis. Ecology, 94(10), 2180–2187.

71. Gross, M. (2014). How wild do you want to go? Current Biology, 24, R1067–R1070.

72. Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica, 4(1), 9.

73. Hansen, S. S., & Ejrnæs, R. (2022). Mediating human–wolves conflicts through dialogue, joint fact-finding and empowerment. Frontiers in Environmental Science, 10, 826351.

74. Hedrick, P. W., & Allendorf, F. W. (2004). Genetically effective population size of large mammals: An assessment of estimators. Conservation Genetics, 5, 467–483.

75. Howard, J. L. (2014). Managing the natural environment: The role of park rangers and the skills they need. Rural Society, 22(3), 242–250.

76. International Union for Conservation of Nature. (2020). The IUCN Red List of Threatened Species. https://www.iucnredlist.org

77. Jachowski, D. S., Butler, A., Eng, R. Y. Y., Gigliotti, L., Harris, S., & Williams, A. (2020). Identifying mesopredator release in multi-predator systems: A review of evidence from North America. Mammal Review, 50(4), 367–381.

78. Jeremić, J., Kusak, J., Huber, Đ., Štrbenac, A., & Korša, A. (2017). Report on the status of wolf populations in Croatia in 2016. Croatian Agency for the Environment and Nature.

79. Jolliffe, I. T., & Cadima, J. (2016). Principal component analysis: A review and recent developments. Philosophical Transactions of the Royal Society A, 374, 20150202.

80. Kajgana, I. (2015). Utjecaj čovjeka na aktivnost velikih sisavaca na području Zrinskog gorja [Influence of humans on the activity of large mammals in the Zrinska Gora area] (Diplomski rad). Sveučilište u Zagrebu, Prirodoslovno-matematički fakultet.

81. Kingsland, S. E. (1982). The refractory model: The logistic curve and the history of population ecology. The Quarterly Review of Biology, 57(1), 29–52.

82. Kittle, A. (2014). The influence of prey availability, habitat attributes and other factors on space use by social carnivores (Doctoral dissertation). University of Guelph.

83. Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C., & Ronkainen, S. (2006). Dispersal in an expanding wolf population in Finland. Journal of Mammalogy, 87, 281–287.

84. Kojola, I., Hallikainen, V., Mikkola, K., Gurarie, E., Heikkinen, S., Kaartinen, S., Nikula, A., & Nivala, V. (2016). Wolf visitations close to human residences in Finland: The role of age, residence density, and time of day. Biological Conservation, 198, 9–14.

85. Koricheva, J., & Gurevitch, J. (2014). Uses and misuses of meta-analysis in plant ecology. Journal of Ecology, 102(4), 828–844.

86. Koricheva, J., Gurevitch, J., & Mengersen, K. (Eds.). (2013). Handbook of meta-analysis in ecology and evolution. Princeton University Press.

87. Kross, S. M., & Nelson, X. J. (2011). A portable low-cost remote videography system for monitoring wildlife. Methods in Ecology and Evolution, 2(2), 191–196.

88. Kuiper, T., Dancer, A., Beale, C. M., Ghoddousi, A., Ibbett, H., Joanny, L., Keane, A., Kavhu, B., Makaza, D., Milner-Gulland, E. J., Moore, J. F., & Xu, L. (2025). Unlocking the value of ranger-based monitoring for biodiversity conservation and protected area management. Conservation Letters, 18(1), e13082.

89. Kusak, J. (2002). Conditions for life of wolves (Canis lupus L.) in Croatia (Doctoral dissertation). University of Zagreb.

90. Kusak, J., Fabbri, E., Galov, A., Gomerčić, T., Arbanasić, H., Caniglia, R., Galaverni, M., Reljić, S., Huber, Đ., & Randi, E. (2018). Wolf–dog hybridization in Croatia. Veterinarski Arhiv, 88, 375–395.

91. Kusak, J., Huber, Đ., Trenc, N., & Desnica, S. (2016). Stručni priručnik za procjenu utjecaja zahvata na velike zvijeri pojedinačno te u sklopu planskih dokumenata [Expert manual for assessing impacts of projects on large carnivores individually and within planning documents]. Agencija za zaštitu okoliša.

92. Lacy, R. C., & Pollak, J. P. (2023). Vortex: A stochastic simulation of the extinction process (Version 10.6.0). Chicago Zoological Society.

93. Lawler, J. J., Campbell, S. P., Guerry, A. D., Kolozsvary, M. B., O’Connor, R. J., & Seward, L. C. N. (2002). The scope and treatment of threats in endangered species recovery plans. Ecological Applications, 12, 663–667.

94. Leblond, M., St-Laurent, M. H., & Côté, S. D. (2016). Wolf habitat selection is shaped by human activities in a highly managed boreal forest. Forest Ecology and Management, 276, 125–131.

95. Letnic, M., Ritchie, E. G., & Dickman, C. R. (2012). Top predators as biodiversity regulators: The dingo Canis lupus dingo as a case study. Biological Reviews, 87(2), 390–413.

96. Liberg, O., Chapron, G., Wabakken, P., Pedersen, H. C., Thompson Hobbs, N., & Sand, H. (2012). Shoot, shovel and shut up: Cryptic poaching slows restoration of a large carnivore in Europe. Proceedings of the Royal Society B: Biological Sciences, 279, 910–915.

97. Liberg, O., Suutarinen, J., Åkesson, M., Andrén, H., Wabakken, P., Wikenros, C., & Sand, H. (2020). Poaching-related disappearance rate of wolves in Sweden was positively related to population size and negatively to legal culling. Biological Conservation, 243, 108456.

98. Lieury, N., Besnard, A., Ponchon, C., Ravayrol, A., & Millon, A. (2016). Geographically isolated but demographically connected: Immigration supports efficient conservation actions in the recovery of a range-margin population of the Bonelli’s eagle in France. Biological Conservation, 195, 272–278.

99. Linnell, J. D. C., Kovtun, E., & Rouart, I. (2021). Wolf attacks on humans: An update for 2002–2020 (NINA Report 1944). Norwegian Institute for Nature Research.

100. MacNulty, D. R., Cooper, D., Procko, M., & Clark-Wolf, T. J. (2025). Flawed analysis invalidates claim of a strong Yellowstone trophic cascade after wolf reintroduction: A comment on Ripple et al. (2025). Global Ecology and Conservation, 63, e03899.

101. Maffei, L., & Noss, A. (2008). How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. Biotropica, 40(1), 71–75.

102.Marucco, F., & McIntire, E. J. B. (2010). Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: Wolves in the Italian Alps. Journal of Applied Ecology, 47, 789–798.

103.McCarthy, M. A., Andelman, S. J., & Possingham, H. P. (2003). Reliability of relative predictions in population viability analysis. Conservation Biology, 17, 982–989.

104.Mech, L. D., Adams, L. G., Meier, T. J., Burch, J. W., & Dale, B. W. (1998). The wolves of Denali. University of Minnesota Press.

105.Mech, L. D., & Boitani, L. (2003). Wolf–prey relations. In L. D. Mech & L. Boitani (Eds.), Wolves: Behavior, ecology, and conservation. University of Chicago Press.

106.Mech, L. D., & Boitani, L. (2003). Wolves: Behavior, ecology, and conservation. University of Chicago Press.

107.Mech, L. D., Goyal, S. M., Paul, W. J., & Newton, W. E. (2008). Demographic effects of canine parvovirus on a free-ranging wolf population. Journal of Wildlife Diseases, 44, 824–836.

108.Meek, P., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D. E., Tobler, M., & Townsend, S. (2014). Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation, 23(9), 2321–2343.

109.Mendoza, M., & Araújo, M. B. (2019). Climate shapes mammal community trophic structures and humans simplify them. Nature Communications, 10, 5197.

110.Merli, E., Mattioli, L., Bassi, E., Bongi, P., Berzi, D., Ciuti, F., Luccarini, S., Morimando, F., Viviani, V., Caniglia, R., Galaverni, M., Fabbri, E., Scandura, M., & Apollonio, M. (2023). Estimating wolf population size and dynamics by field monitoring and demographic models: Implications for management and conservation. Animals, 13, 1735.

111.Morris, W. F., & Doak, D. F. (2002). Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer Associates.

112.Mos, J., & Hofmeester, T. R. (2020). The Mostela: An adjusted camera trapping device as a promising non-invasive tool to study and monitor small mustelids. Mammal Research, 65(4), 843–853.

113. Musto, C., Gazzola, A., Milanesi, P., Ghidini, A., Pizzi, R., Apollonio, M., & Bassi, E. (2024). First evidence of widespread positivity to anticoagulant rodenticides in grey wolves (Canis lupus). Science of the Total Environment, 915, 169990.

114. National Parks Austria. (2022). Become a ranger: How it works. https://www.nationalparksaustria.at/en/2758.html

115. Nejašmić, I. (2014). Iseljavanje iz Hrvatske od 1900. do 2001.: Demografske posljedice stoljetnog procesa. Migracijske i etničke teme, 30, 405–435. [In Croatian]

116. Nelson, A., Kauffman, K., Middleton, A., Jimenez, M. D., McWhirter, D. E., Barber, J., & Gerow, K. (2012). Elk migration patterns and human activity influence wolf habitat use in the Greater Yellowstone Ecosystem. Ecological Applications, 22, 2293–2307.

117. Niemiec, R., Berl, R. E. W., Gonzalez, M., Teel, T. L., Salerno, J., Breck, S., Camara, C., Collins, M., Scholtz, C., Hoag, D., & Crooks, K. R. (2022). Rapid changes in public perception toward a conservation initiative. Conservation Science and Practice, 4, e12632.

118. Nishijima, S., Takimoto, G., & Miyashita, T. (2014). Roles of alternative prey for mesopredators on trophic cascades in intraguild predation systems: A theoretical perspective. The American Naturalist, 183, 625–637.

119. Norouzzadeh, M. S., Nguyen, A., Kosmala, M., Swanson, A., Palmer, M. S., Packer, C., & Clune, J. (2018). Automatically identifying, counting, and describing wild animals in camera-trap images with deep learning. Proceedings of the National Academy of Sciences, 115(25), E5716–E5725.

120. Oakleaf, J. K., Mack, C., Murray, D. L., & Henger, C. S. (2006). Habitat selection by recolonizing wolves in the northern Rocky Mountains of the United States. Journal of Wildlife Management, 70, 554–563.

121. Official Gazette. (2018). Pravilnik o unutarnjem redu u Nacionalnom parku „Paklenica” (No. 76/00, 70/05, 80/13, 15/18). Narodne novine.

122. Oliynyk, R. T. (2023). Human-caused wolf mortality persists for years after discontinuation of hunting. Scientific Reports, 13, 13853.

123. Parks Victoria. (2022). Becoming a park ranger. https://www.parks.vic.gov.au/get-into-nature/careers/becoming-a-park-ranger

124. Petracca, L. S., Converse, S. J., Maletzke, B. T., & Gardner, B. (2023). Forecasting dynamics of a recolonizing wolf population under different management strategies. Animal Conservation. https://doi.org/10.1111/acv.70019

125. Peterson, R. (1995). Wolves as interspecific competitors in canid ecology. In L. N. Carbyn, S. H. Frits, & D. R. Seip (Eds.), Ecology and conservation of wolves in a changing world (Occasional Publication No. 35, pp. 315–323). Canadian Circumpolar Institute.

126. Platiša, M., Pintar, I., & Kusak, J. (2011). Tjelesne osobine sivog vuka (Canis lupus L.) [Body characteristics of the gray wolf (Canis lupus L.)]. Veterinar, 49(1).

127. Preiss Bloom, S., Shamon, H., Amir, Z., Ben Ami, D., & Dayan, T. (2025). Human disturbance thresholds determine the ecological role of an apex predator. Scientific Reports, 15, 37604.

128. Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The rise of the mesopredator. BioScience, 59(9), 779–791.

129. Recio, M. R., Singer, A., Wabakken, P., & Sand, H. (2020). Agent-based models predict patterns and identify constraints of large carnivore recolonizations: A case study of wolves in Scandinavia. Biological Conservation, 251, 108752.

130. Reed, D. H., O'Grady, J. J., Ballou, J. D., & Frankham, R. (2003). The frequency and severity of catastrophic die-offs in vertebrates. Animal Conservation, 6, 109–114.

131. Reif, V., & Tornberg, R. (2006). Using time-lapse digital video recording for a nesting study of birds of prey. European Journal of Wildlife Research, 52(4), 251–258.

132. Reinhardt, I., Kluth, G., Nowak, C., Szentiks, C. A., Krone, O., Ansorge, H., & Mueller, T. (2019). Military training areas facilitate the recolonization of wolves in Germany. Conservation Letters, 12, e12635.

133. Rhodes, J. R., Ng, C. F., de Villiers, D. L., Preece, H. J., McAlpine, C. A., & Possingham, H. P. (2011). Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. Biological Conservation, 144, 1081–1088.

134. Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. Biological Conservation, 145, 205–213.

135. Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. Science, 343(6167), 1241484.

136. Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters, 12(9), 982–998.

137. Rodríguez-Recio, M., Wikenros, C., Zimmermann, B., & Sand, H. (2022). Rewilding by wolf recolonization, consequences for ungulate populations and game hunting. Biology, 11, 317.

138. Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). Which camera trap type and how many do I need? A review of camera features and study designs for a range of wildlife research applications. Hystrix, 24(2), 148–156.

139. Salazar, A. (2021). How do you become a park ranger in Canada? Cube Toronto. https://cubetoronto.com/canada/how-do-you-become-a-park-ranger-in-canada/

140. Sandom, C., Dalby, L., Fløjgaard, C., Kissling, W. D., Lenoir, J., Sandel, B., Trøjelsgaard, K., Ejrnæs, R., & Svenning, J.-C. (2013). Mammal predator and prey species richness are strongly linked at macroscales. Ecology, 94(5), 1112–1122.

141. Saunders, S. P., Cuthbert, F. J., & Zipkin, E. F. (2018). Evaluating population viability and efficacy of conservation management using integrated population models. Journal of Applied Ecology, 55, 1380–1392.

142. Schmitz, O. J., Hambäck, P. A., & Beckerman, A. P. (2000). Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. The American Naturalist, 155(2), 141–153.

143. Schneider, S., Taylor, G. W., Linquist, S. S., & Kremer, S. C. (2018). Past, present, and future approaches using computer vision for animal re-identification from camera trap data. Methods in Ecology and Evolution, 10(4), 461–470.

144. Searle, C. E., Smit, J. B., Cusack, J. J., Strampelli, P., Grau, A., Mkuburo, L., Macdonald, D. W., Loveridge, A. J., & Dickman, A. J. (2021). Temporal partitioning and

spatiotemporal avoidance among large carnivores in a human-impacted African landscape. PLOS ONE, 16(9), e0256876.

145. Senior, A. M., Grueber, C. E., Kamiya, T., Lagisz, M., O'Dwyer, K., Santos, E. S. A., & Nakagawa, S. (2016). Heterogeneity in ecological and evolutionary meta-analyses: Its magnitude and implications. Ecology, 97(12), 3293–3299.

146. Shamwari. (2022). How to become a game ranger or field guide. https://www.shamwari.com/how-to-become-a-game-ranger-or-field-guide/

147. Si, X., Kays, R., & Ding, P. (2014). How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. PeerJ, 2, e374.

148. Silveira, L., Jácomo, A. T. A., & Diniz-Filho, J. A. F. (2003). Camera trap, line transect census and track surveys: A comparative evaluation. Biological Conservation, 114(3), 351–355.

149. Soulé, M. E., Estes, J. A., Miller, B., & Honnold, D. L. (2005). Strongly interacting species: Conservation policy, management, and ethics. BioScience, 55, 168–176.

150. Stanley, S. M. (1973). An explanation for Cope's rule. Evolution, 27, 1–26.

151. Štrbenac, A., Kusak, J., Huber, Đ., Jeremić, J., Oković, P., Majić-Skrbinšek, A., Vukšić, I., Katušić, L., Desnica, S., Gomerčić, T., Bišćan, A., Zec, D., & Grubešić, M. (2010). Plan upravljanja vukom u Republici Hrvatskoj za razdoblje od 2010. do 2015. [Wolf management plan in the Republic of Croatia for the period 2010–2015]. Ministarstvo kulture, Državni zavod za zaštitu prirode. [In Croatian]

152. Shores, C. R., Dellinger, J. A., Newkirk, E. S., Kachel, S. M., & Wirsing, A. J. (2019). Mesopredators change temporal activity in response to a recolonizing apex predator. Behavioral Ecology, 30(5), 1324–1335.

153. Smith, D. W., Drummer, T. D., Murphy, K. M., & Guernsey, D. S. (2010). Survival of colonizing wolves in the Northern Rocky Mountains of the United States, 1982–2004. Journal of Wildlife Management, 74, 620–634.

154. Smith, D. W., Peterson, R. O., & Houston, D. B. (2003). Yellowstone after wolves. BioScience, 53, 330–340.

155. Smith, J. K., & Coulson, G. (2012). A comparison of vertical and horizontal camera trap orientations for detection of potoroos and bandicoots. Australian Mammalogy, 34(2), 196–201.

156. Smietana, W., & Wajda, W. (1997). Wolf number changes in Bieszczady National Park, Poland. Acta Theriologica, 42, 241–252.

157. Sonam, K., Dorjay, R., Lamo, S., & Bijoor, A. (2022). A community-based conservation initiative for wolves in the Ladakh Trans-Himalaya, India. Frontiers in Ecology and Evolution, 10, 809817.

158. Soulé, M. E., Bolger, D. T., Alberts, A. C., Wright, J., Sorice, M., & Hill, S. (1988). Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology, 2(1), 75–92.

159. Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., Townsend, S. E., Carbone, C., Rowcliffe, J. M., Whittington, J., Brodie, J., Royle, J. A., Switalski, A., Clevenger, A. P., Heim, N., & Rich, L. N. (2017). Scaling-up camera traps: Monitoring the planet's biodiversity with networks of remote sensors. Frontiers in Ecology and the Environment, 15(1), 26–34.

160. Štrbenac, A., Kusak, J., Huber, Đ., Jeremić, J., Oković, P., Majić-Skrbinšek, A., Vukšić, I., Katušić, L., Desnica, S., Gomerčić, T., Bišćan, A. (2010). Plan upravljanja vukom u Republici Hrvatskoj za razdoblje od 2010. do 2015 [Wolf management plan in the Republic of Croatia for the period 2010–2015]. Ministarstvo kulture; Državni zavod za zaštitu prirode.

161. Sunde, P., Collet, S., Nowak, C., Thomsen, P. F., Hansen, M. M., Schulz, B., Matzen, J., Michler, F.-U., Vedel-Smith, C., & Olsen, K. (2021). Where have all the young wolves gone? Traffic and cryptic mortality create a wolf population sink in Denmark and northernmost Germany. Conservation Letters, 14, e12812.

162. Swann, D., Hass, C., Dalton, D. C., & Wolf, S. A. (2004). Infrared-triggered cameras for detecting wildlife: An evaluation and review. Wildlife Society Bulletin, 32(2), 357–365.

163. Tallmon, D. A., Luikart, G., & Waples, R. S. (2004). The alluring simplicity and complex reality of genetic rescue. Trends in Ecology & Evolution, 23, 9–14.

164. Teckentrup, L. (2020). Understanding predator–prey interactions: Fear effects and community structure (Doctoral dissertation). University of Potsdam.

165. Tobler, M. W., Carrillo-Percastegui, S. E., Pitman, R. L., Mares, R., & Powell, G. (2008). An evaluation of camera traps for inventorying large and medium-sized terrestrial rainforest mammals. Animal Conservation, 11, 169–178.

166. Torretta, E., Corradini, A., Pedrotti, L., Bani, L., Bisi, F., & Dondina, O. (2023). Hide-and-seek in a highly human-dominated landscape: Insights into movement patterns and selection of resting sites of rehabilitated wolves (Canis lupus) in northern Italy. Animals, 13, 46.

167. Turinski, I. (2017). Međudjelovanje velikih predatora Hrvatske—Eurazijskog risa (Lynx lynx L.) i sivog vuka (Canis lupus L.)—kroz odnose predacije i kompeticije [Interactions of large predators in Croatia—Eurasian lynx and gray wolf—through predation and competition] (Diplomski rad). Sveučilište Josipa Jurja Strossmayera u Osijeku, Odjel za biologiju.

168. Ugarković, D., Tikvić, I., Mikac, S., Stankić, I., & Balta, D. (2016). The influence of changing climate extremes on the ecological niche of pedunculate oak in Croatia. South-East European Forestry, 7, 143–148.

169. van Schaik, T., van Kuijk, M., & Sterck, E. H. M. (2024). Understanding mesopredator responses to changes in apex predator populations in Europe: Implications for the mesopredator release hypothesis. Mammal Review, 54(3), e12357.

170. Vargas Soto, J. S., Beirne, C., Whitworth, A., Cruz Diaz, J. C., Flatt, E., Pillco-Huarcaya, R., Olson, E. R., Azofeifa, A., Saborío-R., G., Salom-Pérez, R., Espinoza-Muñoz, D., Hay, L., Whittaker, L., Roldán, C., Bedoya-Arrieta, R., Broadbent, E. N., & Molnár, P. K. (2022). Human disturbance and shifts in vertebrate community composition in a biodiversity hotspot. Conservation Biology, 36(2), e13813.

171. Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. Journal of Statistical Software, 36(3), 1–48.

172. Vila, C., Sundqvist, A. K., Flagstad, O., Seddon, J., Björnerfeldt, S., Kojola, I., Casulli, A., Sand, H., Wabakken, P., & Ellegren, H. (2003). Rescue of a severely bottlenecked wolf

(Canis lupus) population by a single immigrant. Proceedings of the Royal Society of London B, 270, 91–97.

173. Vucetich, J. A., Nelson, M. P., & Phillips, M. K. (2006). The normative dimension and legal meaning of endangered and recovery in the U.S. Endangered Species Act. Conservation Biology, 20, 1383–1390.

174. Wabakken, M. J., Svensson, L., & Maartmann, E. (2001). The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. Canadian Journal of Zoology, 79, 710–725.

175. Wallach, A. D., Johnson, C. N., Ritchie, E. G., & O'Neill, A. J. (2010). Predator control promotes invasive-dominated ecological states. Ecology Letters, 13, 1008–1018.

176. Wang, Y., Allen, M. L., & Wilmers, C. C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation, 190, 23–33.

177. Wearn, O. R., Rowcliffe, J. M., Carbone, C., Pfeifer, M., Bernard, H., & Ewers, R. M. (2017). Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. Biological Conservation, 212(Part A), 162–171.

178. Wikenros, C., Gicquel, M., Zimmermann, B., Flagstad, Ø., & Åkesson, M. (2021). Age at first reproduction in wolves: Different patterns of density dependence for females and males. Proceedings of the Royal Society B, 288, 20210207.

179. Wilson, S. M. (2023). Living with predators: A 20-year case study in the Blackfoot River watershed of Montana. In L. B. McNew, D. K. Dahlgren, & J. L. Beck (Eds.), Rangeland wildlife ecology and conservation (pp. 347–360). Springer.

180. Wilson, M. W., Ridlon, A. D., Gaynor, K. M., Gaines, S. D., Stier, A. C., & Halpern, B. S. (2020). Ecological impacts of human-induced animal behaviour change. Ecology Letters, 23, 1522–1536.

181. Wójcicki, A., & Borowski, Z. (2023). The presence of wolves leads to spatial differentiation in deer browsing pressure on forest regeneration. Scientific Reports, 13, 17245.

182. Wolf, C., & Ripple, W. J. (2016). Prey depletion as a threat to the world's large carnivores. Royal Society Open Science, 3, 160252. https://doi.org/10.1098/rsos.160252

183. Ziółkowska, E., Perzanowski, K., Bleyhl, B., Ostapowicz, K., & Kuemmerle, T. (2016). Understanding unexpected reintroduction outcomes: Why aren't European bison colonizing suitable habitat in the Carpathians? Biological Conservation, 195, 106–117.

APPENDICES

APPENDIX 1: Table A1. List of mammals in the Paklenica NP with information regarding species recorded during camera trapping survey 2011–2016.

APPENDIX 2: Table A2. Camera trapping sites at the Paklenica NP during camera trapping survey with starting date, ending date and days in total for an interval

APPENDIX 3: Table A3. Data spreadsheet organisation

APPENDIX 4: Table A4. Species recorded during camera trapping survey for each camera trapping site at the Paklenica NP

APPENDIX 5: Table A5 Pre-Initial search using filters for keywords to audit search relevance and applicability

APPENDIX 6: Table A6 Initial search using filters for keywords to audit search relevance and applicability

APPENDIX 7: Table A7 Final search using filters for keywords to audit search relevance and applicability

APPENDIX 8: Table A8 Overview of studies and sites included in the meta-analysis

APPENDIX 9: Table A9 Data extracting categories

APPENDIX 10: Table A10 List of species and associated classification into the functional groups

APPENDIX 11: Figure A11 Forest plot from the sensitivity analysis using an alternative continuity correction

APPENDIX 12: Detailed description of each simulation scenario, outlining the assumptions, parameter adjustments, and the rationale behind their design.

APPENDIX 13: Principal component analysis (PCA) results showing eigenvalues, explained variance, and variable loadings for four datasets: 10-year model, 30-year model, 100-year model and the combined dataset of all models for years (all) , the number of extinct populations and mean size od extanta populations.

APPENDIX 1:

Table A1. List of mammals in the Paklenica NP with information regarding species recorded during camera trapping survey 2011–2016.

Order	**Binomial name**	**English name**	**Conservation status**					**Ct 2011–2016**	**No. of events**
			CRD	**HD**	**BERN**	**CITES**	**SPS**		
Artiodactyla	*Capreolus capreolus*	Roe deer			III			+	998
	Cervus elaphus	Red deer			III			+	2129
	Ovis musimon	Mouflon			III				-
	Rupicapra rupicapra	Chamois	RE	II, IV, V*	III		+	+	9284
	Sus scrofa	Wild boar						+	1051
Carnivora	*Canis aureus*	Golden jackal		V				+	2
	Canis lupus	Grey wolf	NT	II, IV, V	II	A	+	+	3
	Felis sylvestris	Wildcat		IV	II	II, A	+	+	20
	Lynx lynx	Eurasian lynx	RE	II, IV	III	II, A	+	+	4
	Martes foina	Beech marten			III			+	22
	Martes martes	European pine marten		V	III			+	
	Meles meles	European badger			III			+	436
	Mustela nivalis	Least weasel			III				-
	Ursus arctos	Brown bear	NT	II, IV	II	II, A	+	+	101
	Vulpes vulpes	Red fox						+	68
Chiroptera	*Barbastella barbastellus*	Western barbastelle	DD	II, IV	II		+		-
	Eptesicus serotinus	Serotine bat		IV	II		+		-
	Hypsugo savii	Savi's pipistrelle		IV	II		+		-
	Miniopterus schreibersii	Common bent-wing bat	EN	II, IV	II		+		-
	Myotis alcathoe	Alcathoe bat					+		-

Table A1. (continued) List of mammals in the Paklenica NP with information regarding species recorded during camera trapping survey 2011–2016.

Order	**Binomial name**	**English name**	**Conservation status**					**Ct 2011–2016**	**No. of events**
			CRD	**HD**	**BERN**	**CITES**	**SPS**		
Chiroptera	*Myotis aurascens*	Whiskered bat					+	-	-
	Myotis bechsteinii	Bechstein's bat	VU	II, IV	II		+	-	-
	Myotis emarginatus	Geoffroy's bat	NT	II, IV	II		+	-	-
Eulipotyphla	*Myotis myotis*	Greater mouse-eared bat	NT	II, IV	II		+	-	-
	Myotis mystacinus	Whiskered bat		IV	II		+	-	-
	Myotis nattereri	Natterer's bat		IV	II		+	-	-
	Nyctalus leisleri	Lesser noctule	NT	IV	II		+	-	-
	Nyctalus noctule	Common noctule		IV	II		+	-	-
	Pipistrellus kuhlii	Kuhl's pipistrelle		IV	II		+	-	-
	Pipistrellus nathusii	Nathusius's pipistrelle		IV	II		+	-	-
	Pipistrellus pipistrellus	Common pipistrelle		IV	II		+	-	-
	Pipistrellus pygmaeus	Soprano pipistrelle					+	-	-
	Plecotus auritus	Brown long-eared bat		IV	II		+	-	-
	Plecotus kolombatovici	Kolombatovic's long-eared bat	DD				+	-	-
	Rhinolophus euryale	Mediterranean horseshoe bat	VU	II, IV	II		+	-	-
	Rhinolophus ferrumequinum	Greater horseshoe bat	NT	II, IV	II		+	-	-
	Rhinolophus hipposideros	Lesser horseshoe bat	NT	II, IV	II		+	-	-
	Tadarida teniotis	European free-tailed bat		IV	II		+	-	-
	Vespertilio murinus	Parti-coloured bat		IV	II		+	-	-

Table A1. (continued) List of mammals in the Paklenica NP with information regarding species recorded during camera trapping survey 2011–2016.

Order	**Binomial name**	**English name**	**Conservation status**					**Ct 2011–2016**	**No. of events**
			CRD	**HD**	**BERN**	**CITES**	**SPS**		
Eulipotyphla	*Crocidura suaveolens*	Lesser white-toothed shrew			III				-
	Erinaceus concolor	Southern white-breasted hedgehog							-
	Sorex alpinus	Alpine shrew			III				-
	Sorex araneus	Common shrew			III				-
	Suncus etruscus	Etruscan shrew			III				-
	Talpa europea	European mole							-
Rodentia	*Apodemus epimelas*	Western broad-toothed field mouse							-
	Apodemus flavicollis	Yellow-necked mouse							-
	Apodemus sylvaticus	Wood mouse							-
	Chionomys nivalis	European snow vole	NT		III				-
	Clethrionomys glareolus	Bank vole							-
	Dinaromys bogdanovi	Balkan snow vole	DD				+		-
	Dryomys nitedula	Forest dormouse	NT	IV	III		+		-
	Eliomys quercinus	Garden dormouse	NT		III				-
	Lepus europaeus	European hare	NT		III			+	306
	Microtus multiplex liechtenstein	Alpine pine vole							-
	Mus domesticus	Western European house mouse							-
	Glis glis	Glis glis	LC		III				-
	Rattus rattus	Black rat							-
	Sciurus vulgaris	Red squirrel	NT		III			+	1

Table A1. (continued) List of mammals in the Paklenica NP with information regarding species recorded during camera trapping survey 2011–2016.

Notes: *Only *R. rupicapra balcanica*

Conservation status: CRD = Croatian Red Book (IUCN category: EX – extinct, EW – extinct in the wild, CR – critically endangered, EN – endangered, VU – vulnerable, NT – near threatened, LC – least concern, DD – data deficient, NE – not evaluated, NR – not recognised); HD = the Annexes of the EU Directive of the Conservation of Natural Habitats and of Wild Fauna and Flora (Habitats Directive); Bern = the Convention on the Conservation of Natural Habitats and of Wild Fauna and Wild Flora; CITES = the Convention on International Trade in Endangered Species of Wild Fauna and Flora; SPS = Croatian Ordinance on strictly protected species (OG, 144/13, 73/16)

CT 2011–2016 = camera trapping survey during 2011–2016 (+ = species recorded during survey)

APPENDIX 2:

Table A2. Camera trapping sites at the Paklenica NP during camera trapping survey with starting date, ending date and days in total for an interval

1. Anica luka												🟩																																																													-	1
2. Brdo																									🟩	🟩	🟩	🟩	🟩																	🟩	🟩																											-	130
3. Brezimenjaća																																																																		🟩	🟩	🟩					-	51
4. Buljma																																														🟩																											-	2
5. Gornja draga																																					🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩						🟩	🟩	🟩														salt	479
6. Gornja Pila																																																															🟩										ponds	3
7. Grabar																																														🟩																											-	14
8. Katići																																																	🟩				🟩											🟩	🟩	🟩							ponds	79
9. Katici sjever																																																🟩																									-	10
10. Krivi Kuk																																																																							🟩		-	22
11. Mala Moćila																																																							🟩	🟩	🟩	🟩	🟩	🟩								🟩	🟩	🟩	🟩		corn	242
12. Orlov kuk																									🟩	🟩	🟩	🟩	🟩	🟩		🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩		🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	salt	1298
13. Piskovita kosa												🟩																																																	🟩	🟩								🟩	🟩	🟩			-	99
14. Podborovnik										🟩																																					🟩	🟩	🟩																									-	63
15. Sipar Anica luka																										🟩																																															-	1
16. Skiljici																																				🟩																																					salt	2
17. Solilo M.pec										🟩	🟩																🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩			🟩	🟩																														salt	435
18. Suha draga																																																					🟩	🟩	🟩																				-	37
19. Velika moćila								🟩			🟩																																									🟩	🟩	🟩									🟩		🟩	🟩	🟩						-	157
20. Zapadak								🟩	🟩	🟩		🟩																																																													pond	61
21. Zapadak Parića																																																														🟩											ponds	9
22. Zapadak Šikića																										🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩		🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩		🟩	🟩	🟩	🟩	salt, pond, corn	1279

APPENDIX 3:

Table A3. Data spreadsheet organisation

Column name	Column meaning
Folder no.	Name of the folder (e.g. 1.Podborovnik-solilo M.pec 17.-19.11.2011)
ID no.	Name of the photo/video (e.g. PICT0001)
Photo/video	p = photo; m = video
Day	Day when the photo/video was taken
Month	Month when the photo/video was taken
Year	Year when the photo/video was taken
Time	Time when the photo/video was taken
Duration	Duration of the video (in seconds)
Temp	Temperature when the photo/video was taken (°C)
Night/day	n = night; d = day
Habitat	Habitat type where the camera was set (m = open meadow; k = semi-open karts habitat; v = low vegetation (bushes) up to 1.5 m; y = young forests; o = old forest [trunk thicker than approx. 30 cm])
Substrate	Substrate type where the camera was set (1 = stone; 2 = soil; 3 = sand; 4 = gravel; 5 = leaf litter)
Species	Latin name of the species – photocaptures of animals for which it was not possible to clearly determine the species (C category during assessment = safety assessment of species determination) were recorded as – ('dash')
Abundance	Abundance of the animals for each species on photo/video
Assessment	Safety assessment of species determination (A = 100% sure; B = maybe, but not sure; C = do not know species)
Species type	m = small prey (all Muridae); p = prey (larger than Muridae); v = small carnivore (everything smaller than large carnivores); c = large carnivore (bear, wolf, lynx, jackal); s = scavengers
Lure type	For example, salt, carcass (species), pond, etc.
Location	Location of the camera trap
Type of protection	Type of the area protection (n = non-protected area; if protected area, then write a name of the protected area [e.g. NP Paklenica])
County	Camera trap area county name
State	Camera trap area state name

APPENDIX 4:

Table A4. Species recorded during camera trapping survey for each camera trapping site at the Paklenica NP (locations 1–10).

Location		**1. Anica luka**	**2. Brdo**	**3. Brezimenjača**	**4. Buljma**	**5. Gornja draga**	**6. Gornja Pila**	**7. Grabar**	**8. Katići**	**9. Katici sjever**	**10. Krivi Kuk**
From–to (intervals)		01.12.2011–01.12.2011	29.01.2013–11.05.2013; 25.10.2014–20.11.2014	27.06.2016–16.08.2016.	28.10.2014–29.10.2014.	18.01.2014–26.03.2015; 23.09.2015–07.11.2015	17.03.2016–19.03.2016	12.10.2014–14.10.2014	01.01.2015–10.01.2015; 11.05.2015–17.05.2015; 17.04.2016–17.06.2016	05.12.2014–14.12.2014	09.11.2016–30.11.2016
Total duration	Years					1					
	Months		4	1		3			2		
	Days	1	10	21	2	25	3	14	18	10	22
	Days sum	1	130	51	2	479	3	14	79	10	22
Species records	*Sus scrofa*			+		+	+	+	+		
	Capreolus capreolus					+	+		+		
	Rupicapra rupicapra	+	+			+			+		+
	Cervus elaphus					+			+		
	Lepus europaeus		+			+					
	Vulpes vulpes	+				+					
	Ursus arctos		+			+					
	Meles meles		+			+					
	Martes sp.					+					
	Felis silvestris								+		
	Canis lupus										
	Rodentia										
	Lynx lynx					+					
	Canis aureus										
	Sciurus vulgaris										
	Homo sapiens		+		+	+		+	+	+	
	Aves		+			+					
	Canis lupus familiaris										
	Chiroptera										
	Insecta										

Table A4. (continued) Species recorded during camera trapping survey for each camera trapping site at the Paklenica NP (locations 11–18).

Location		**11. Mala Močila**	**12. Orlov kuk**	**13. Piskovita kosa**	**14. Podborovnik**	**15. Sipar Anica luka**	**16. Skiljici**	**17. Solilo M.pec**	**18. Suha draga**
From–to (intervals)		08.07.2015– 24.12.2015; 24.08.2016– 03.11.2016.	18.01.2013– 03.06.2013; 20.08.2013– 17.02.2016; 06.04.2016– 10.12.2016	08.12.2011– 11.12.2011; 24.11.2015– 23.12.2015; 24.08.2016– 27.10.2016	18.10.2011– 26.10.2011; 14.11.2014– 06.01.2015	04.02.2013– 04.02.2013	30.12.2013– 31.12.2013	22.10.2011– 15.11.2011; 12.03.2013– 23.03.2014; 04.06.2014– 06.07.2014	30.05.2015– 05.07.2015
Total duration	Years		2					1	
	Months	7	18	3	3			2	1
	Days	28	21	8	3	1	2	10	6
	Days sum	242	1298	99	63	1	2	435	37
Species records	*Sus scrofa*	+	+	+	+			+	
	Capreolus capreolus	+	+	+	+		+	+	+
	Rupicapra rupicapra		+	+	+	+	+	+	+
	Cervus elaphus	+	+	+	+			+	
	Lepus europaeus	+	+	+	+			+	+
	Vulpes vulpes	+	+	+	+				
	Ursus arctos	+	+					+	
	Meles meles	+	+	+				+	
	Martes sp.	+	+		+			+	
	Felis silvestris	+	+					+	
	Canis lupus		+		+				
	Rodentia		+					+	
	Lynx lynx		+				+		
	Canis aureus		+						
	Sciurus vulgaris							+	
	Homo sapiens	+	+		+	+	+	+	+
	Aves					+			
	Canis lupus familiaris								
	Chiroptera								
	Insecta								

Table A4. (continued) Species recorded during camera trapping survey for each camera trapping site at the Paklenica NP (locations 19–22).

Location		**19. Velika močila**	**20. Zapadak**	**21. Zapadak Parića**	**22. Zapadak Šikića**	**Total no. of locations**
From–to (intervals)		01.08.2011–02.08.2011; 23.11.2011–27.11.2011; 23.04.2015–30.06.2015; 17.03.2016; 03.05.2016–21.07.2016	24.08.2011–08.09.2011; 09.11.2011–23.12.2011	10.02.2016–19.02.2016	17.02.2013–25.06.2014; 17.08.2014–05.07.2016; 10.09.2016–20.09.2016; 07.10.2016–30.12.2016	
Total duration	Years				2	**6**
	Months	5	2		18	**69**
	Days	5	1	9	3	**233**
	Days sum	157	61	9	1279	**4474**
Species records	*Sus scrofa*	+	+	+	+	**14**
	Capreolus capreolus	+	+	+	+	**14**
	Rupicapra rupicapra	+			+	**14**
	Cervus elaphus	+	+		+	**10**
	Lepus europaeus	+			+	**10**
	Vulpes vulpes		+		+	**8**
	Ursus arctos	+			+	**7**
	Meles meles				+	**7**
	Martes sp.		+		+	**7**
	Felis silvestris				+	**5**
	Canis lupus				+	**3**
	Rodentia				+	**3**
	Lynx lynx					**3**
	Canis aureus					**1**
	Sciurus vulgaris					**1**
	Homo sapiens	+	+		+	**16**
	Aves				+	**4**
	Canis lupus familiaris				+	**1**
	Chiroptera				+	**1**
	Insecta				+	**1**

APPENDIX 5:

Table A5 Pre-Initial search using filters for keywords to audit search relevance and applicability

1	2	3	4	5	6	7	number of results
mammals	predator	prey	relationship				151,000
presence	large	carnivores					126,000
abundance	large	carnivores					109,000
large	carnivores	predator	prey				69,100
presence	large	carnivores	predator	prey			65,300
large	carnivores	predator	prey	relationship			58,500
abundance	large	carnivores	predator	prey			58,400
abundance	terrestrial	carnivores					55,800
carnivores	predator	prey	relationship				52,200
abundance	carnivores	predator	prey				50,700
large	carnivorous	predator	prey				48,400
abundance	large	carnivores	europe				48,000
presence	large	carnivores	predator	prey	relationship		46,500
mammals	carnivores	predator	prey	relationship			42,400
abundance	large	carnivores	predator	prey	relationship		42,000
large	carnivorous	predator	prey	relationship			40,600
abundance	carnivores	predator	prey	relationship			38,300
carnivorous	predator	prey	relationship				37,500
abundance	wolf	predator	prey	relationship			36,000
abundance	large	carnivorous	vertebrate				30,000
abundance	large	carnivores	europe	predator	prey		29,800
abundance	terrestrial	carnivores	predator	prey			28,400
abundance	canis	lupus					27,100
abundance	large	carnivores	europe	predator	prey	relationship	27,100
abundance	terrestrial	carnivores	predator	prey	relationship		25,700
abundance	large	carnivorous	vertebrate	predator	prey		24,300
presence	mammal	carnivore	predator	prey	relationship		24,200

presence	mammalian	carnivore	predator	prey	relationship		23,300
abundance	large	carnivorous	vertebrate	predator	prey	relationship	23,100

APPENDIX 6:

Table A6 Initial search using filters for keywords to audit search relevance and applicability

with **all** of the words	with **at least one** of the words	with the **exact phrase**	**number of results**
abundance	carnivores OR vertebrates	"predator prey relationship"	2,060
abundance	carnivores OR mammals	"predator prey relationship"	2,660
abundance	carnivores OR terrestrial	"predator prey relationship"	2,690
abundance	vertebrates OR mammals	"predator prey relationship"	2,790
abundance	vertebrates OR terrestrial	"predator prey relationship"	2,800
abundance	carnivores OR vertebrates OR mammals	"predator prey relationship"	3,100
abundance	carnivores OR vertebrates OR terrestrial	"predator prey relationship"	3,230
abundance	mammals OR terrestrial	"predator prey relationship"	3,370
abundance	carnivores OR mammals OR terrestrial	"predator prey relationship"	3,610
abundance	carnivorus OR vertebrates OR mammals OR terrestrial	"predator prey relationship"	3,660
abundance	vertebrates OR mammals OR terrestrial	"predator prey relationship"	3,670
abundance	carnivores OR vertebrates OR mammals OR terrestrial	"predator prey relationship"	3,880
abundance	carnivores OR predator OR vertebrates OR mammals OR terrestrial	"predator prey relationship"	6,840

APPENDIX 7:
Table A7 Final search using filters for keywords to audit search relevance and applicability

with **all** of the words (AND)	with **at least one** of the words (OR)	with the **exact phrase**	**number of results**
abundance predator prey relationship	terrestrial mammal vertebrate predator	large carnivores	9,110

APPENDIX 8:

Table A8 Overview of studies and sites included in the meta-analysis

Locality	**Name / reference**
Google Scholar	
Gunung Mulu National Park (Sarawak)	Brodie, J. F., & Giordano, A. J. (2013). Lack of trophic release with large mammal predators and prey in Borneo. Biological Conservation, 163, 58–67.
Hose Mountains National Park (Sarawak)	Brodie, J. F., & Giordano, A. J. (2013). Lack of trophic release with large mammal predators and prey in Borneo. Biological Conservation, 163, 58–67.
Maliau Basin Conservation Area (Sabah)	Brodie, J. F., & Giordano, A. J. (2013). Lack of trophic release with large mammal predators and prey in Borneo. Biological Conservation, 163, 58–67.
Pulong Tau National Park (Sarawak)	Brodie, J. F., & Giordano, A. J. (2013). Lack of trophic release with large mammal predators and prey in Borneo. Biological Conservation, 163, 58–67.
Ulu Baram (Sarawak)	Brodie, J. F., & Giordano, A. J. (2013). Lack of trophic release with large mammal predators and prey in Borneo. Biological Conservation, 163, 58–67.
Ulu Padas (Sabah)	Brodie, J. F., & Giordano, A. J. (2013). Lack of trophic release with large mammal predators and prey in Borneo. Biological Conservation, 163, 58–67.
Ulu Trusan (Sarawak)	Brodie, J. F., & Giordano, A. J. (2013). Lack of trophic release with large mammal predators and prey in Borneo. Biological Conservation, 163, 58–67.
Meghri Ridge	Avgan, B., Zimmermann, F., & Aghayan, S. (2014). Presence–absence surveys of prey and their use in predicting leopard (Panthera pardus) densities: A case study from Armenia. Journal of Zoology, 294, 77–86.
Serengeti National Park	Swanson, A., Caro, T., Davies-Mostert, H., Mills, M. G. L., Macdonald, D. W., Borner, M., et al. (2016). In the absence of a “landscape of fear”: How lions, hyenas, and cheetahs coexist. Ecology and Evolution, 6, 8534–8545.
Masoala-Makira landscape	Gerber, B. D., Karpanty, S. M., & Randrianantenaina, J. (2015). Hunting, exotic carnivores, and habitat loss: Anthropogenic effects on a native carnivore community, Madagascar. PLOS ONE, 10(9), e0136456.
San Juan–La Selva Biological Corridor	Medellín, R. A., Chetkiewicz, C.-L. B., Rabinowitz, A., Redford, K. H., Robinson, J. G., Sanderson, E. W., & Taber, A. (2000). Integrating occupancy modeling and camera-trap data to estimate medium and large mammal detection and richness in a Central American biological corridor. Biological Conservation, 95, 1–14.ncr-journal.bear-land
Groenefontein Nature Reserve and adjoining private property	Meek, P. D., Ballard, G.-A., Claridge, A., Kays, R., Moseby, K., O’Brien, T., … Woods, J. (2014). The road less travelled: Assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. Wildlife Research, 41, 394–409.bioone
Phnom Prich Wildlife Sanctuary	Gray, T. N. E., Phan, C., Long, B., & Pinn, T. (2012). Habitat preferences and activity patterns of the larger mammal community in Phnom Prich Wildlife Sanctuary, Cambodia. Raffles Bulletin of Zoology, 60, 403–410.felinosdoaguai
foothills of the Carpathian Mountains in southern Transylvania	Popescu, V. D., Artelle, K. A., Pop, M. I., Manolache, S., Rozylowicz, L., & Macdonald, D. W. (2016). Incorporating anthropogenic effects into trophic ecology: Predator–prey interactions in a human-dominated landscape. Proceedings of the Royal Society B, 283, 20161528.bioone
RSF: RPPN Serra da Farofa	Bogoni, J. A., Cherem, J. J., Giehl, E. L. H., Oliveira-Santos, L. G. R., Castilho, P. V., Picinatto-Filho, V., et al. (2016). Landscape features lead to shifts in communities of medium- to large-bodied mammals in subtropical Atlantic Forest. Journal of Mammalogy, 97(3), 713–725.bioone
PTB: Parque Estadual da Serra do Tabuleiro B	Bogoni, J. A., Cherem, J. J., Giehl, E. L. H., Oliveira-Santos, L. G. R., Castilho, P. V., Picinatto-Filho, V., et al. (2016). Landscape features lead to shifts in communities of medium- to large-bodied mammals in subtropical Atlantic Forest. Journal of Mammalogy, 97(3), 713–725.bioone

Table A8 (continued) Overview of studies and sites included in the meta-analysis

Locality	**Name / reference**
PEA: Parque Estadual das Araucárias	Bogoni, J. A., Cherem, J. J., Giehl, E. L. H., Oliveira-Santos, L. G. R., Castilho, P. V., Picinatto-Filho, V., et al. (2016). Landscape features lead to shifts in communities of medium- to large-bodied mammals in subtropical Atlantic Forest. Journal of Mammalogy, 97(3), 713–725.bioone
RCE: RPPN Chácara Edith	Bogoni, J. A., Cherem, J. J., Giehl, E. L. H., Oliveira-Santos, L. G. R., Castilho, P. V., Picinatto-Filho, V., et al. (2016). Landscape features lead to shifts in communities of medium- to large-bodied mammals in subtropical Atlantic Forest. Journal of Mammalogy, 97(3), 713–725.bioone
RLM: RPPN Leão da Montanha	Bogoni, J. A., Cherem, J. J., Giehl, E. L. H., Oliveira-Santos, L. G. R., Castilho, P. V., Picinatto-Filho, V., et al. (2016). Landscape features lead to shifts in communities of medium- to large-bodied mammals in subtropical Atlantic Forest. Journal of Mammalogy, 97(3), 713–725.bioone
RRF: RPPN Rio das Furnas	Bogoni, J. A., Cherem, J. J., Giehl, E. L. H., Oliveira-Santos, L. G. R., Castilho, P. V., Picinatto-Filho, V., et al. (2016). Landscape features lead to shifts in communities of medium- to large-bodied mammals in subtropical Atlantic Forest. Journal of Mammalogy, 97(3), 713–725.bioone
PTA: Parque Estadual da Serra do Tabuleiro A	Bogoni, J. A., Cherem, J. J., Giehl, E. L. H., Oliveira-Santos, L. G. R., Castilho, P. V., Picinatto-Filho, V., et al. (2016). Landscape features lead to shifts in communities of medium- to large-bodied mammals in subtropical Atlantic Forest. Journal of Mammalogy, 97(3), 713–725.bioone
REA: Reserva Biológica Estadual do Aguaí	Bogoni, J. A., Cherem, J. J., Giehl, E. L. H., Oliveira-Santos, L. G. R., Castilho, P. V., Picinatto-Filho, V., et al. (2016). Landscape features lead to shifts in communities of medium- to large-bodied mammals in subtropical Atlantic Forest. Journal of Mammalogy, 97(3), 713–725.bioone
RPPN_Rio_das_Lontras	Bogoni, J. A., Hernández, M. I. M., & da Silva, P. G. (2016). Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. Biodiversity and Conservation, 25, 1661–1675.agris.fao
Parque_Ecologico_Rancho_dos_Bugres	Santos, M. E. B., Bogoni, J. A., & Farias, P. M. (2018). Mamíferos de médio e grande porte do Parque Ecologico Rancho dos Bugres, Sul do Brasil. Revista Brasileira de Zoociências, 19(3), 23–37.felinosdoaguai
Coxilha_Rica_Lages	Bogoni, J. A., Batista, G. O., Graipel, M. E., & Peroni, N. (2020). Good times, bad times: Resource pulses influence mammal diversity in meridional Brazilian highlands. Science of the Total Environment, 708, 134837.felinosdoaguai+1
Parque_Nacional_Sao_Joaquim_B	Bogoni, J. A., Batista, G. O., Graipel, M. E., & Peroni, N. (2020). Good times, bad times: Resource pulses influence mammal diversity in meridional Brazilian highlands. Science of the Total Environment, 708, 134837.felinosdoaguai+1
Parque_Nacional_Sao_Joaquim_A	Bogoni, J. A., Batista, G. O., Graipel, M. E., & Peroni, N. (2020). Good times, bad times: Resource pulses influence mammal diversity in meridional Brazilian highlands. Science of the Total Environment, 708, 134837.felinosdoaguai+1
RPPN_Grande_Floresta_das_Araucarias	Bogoni, J. A., Batista, G. O., Graipel, M. E., & Peroni, N. (2020). Good times, bad times: Resource pulses influence mammal diversity in meridional Brazilian highlands. Science of the Total Environment, 708, 134837.felinosdoaguai+1
RPPN_Leao_da_Montanha	Bogoni, J. A., Batista, G. O., Graipel, M. E., & Peroni, N. (2020). Good times, bad times: Resource pulses influence mammal diversity in meridional Brazilian highlands. Science of the Total Environment, 708, 134837.felinosdoaguai+1

Table A8 (continued) Overview of studies and sites included in the meta-analysis

Locality	**Name / reference**
Parque_Nacional_das_Araucarias_B	Bogoni, J. A., Batista, G. O., Graipel, M. E., & Peroni, N. (2020). Good times, bad times: Resource pulses influence mammal diversity in meridional Brazilian highlands. Science of the Total Environment, 708, 134837.felinosdoaguai+1
Google scholar - given contacts	
Matundu, Mbatwa, Lumemo, Ndundulu, Mwanihana	Cavada, N., Havmøller, R. W., Rovero, F., Scharff, N., & Svenning, J.-C. (2019). A landscape-scale assessment of tropical mammals reveals the effects of habitat and anthropogenic disturbance on community occupancy. PLOS ONE, 14(4), e0215682.
Javorniki, Racna gora, Menišija	Krofel, M. (unpublished data). Camera-trap study of medium- and large-sized mammals in the Dinaric Mountains and Prealps.
Dinaric Mountains__4	Krofel, M. (unpublished data). Camera-trap study of medium- and large-sized mammals in the Dinaric Mountains and Prealps.
Dinaric mountains and Prealps	Krofel, M. (unpublished data). Camera-trap study of medium- and large-sized mammals in the Dinaric Mountains and Prealps.
Menišija plateau_6	Krofel, M. (unpublished data). Camera-trap study of medium- and large-sized mammals in the Dinaric Mountains and Prealps.
Dinaric Mountains__7	Fležar, U., Jerina, K., Pokorny, B., & Krofel, M. (2019). Free food for everyone: Artificial feeding of brown bears provides food for many non-target species. European Journal of Wildlife Research, 65, 24.dinalpbear+1
Thoepli	Gray, T. N. E., Prum, S., Pin, C., & Phan, C. (2017). First structured camera-trap surveys in Karen State, Myanmar, reveal high diversity of globally threatened mammals. Oryx, 51(4), 1–9.news.mongabay+1
Kweenkoh	Gray, T. N. E., Prum, S., Pin, C., & Phan, C. (2017). First structured camera-trap surveys in Karen State, Myanmar, reveal high diversity of globally threatened mammals. Oryx, 51(4), 1–9.news.mongabay+1
Mae Nyaw Kee North	Gray, T. N. E., Prum, S., Pin, C., & Phan, C. (2017). First structured camera-trap surveys in Karen State, Myanmar, reveal high diversity of globally threatened mammals. Oryx, 51(4), 1–9.news.mongabay+1
Mae Nyaw Kee South	Gray, T. N. E., Prum, S., Pin, C., & Phan, C. (2017). First structured camera-trap surveys in Karen State, Myanmar, reveal high diversity of globally threatened mammals. Oryx, 51(4), 1–9.news.mongabay+1
Yoe Mu Kyo East	Gray, T. N. E., Prum, S., Pin, C., & Phan, C. (2017). First structured camera-trap surveys in Karen State, Myanmar, reveal high diversity of globally threatened mammals. Oryx, 51(4), 1–9.news.mongabay+1
Yoe Mu Kyo West	Gray, T. N. E., Prum, S., Pin, C., & Phan, C. (2017). First structured camera-trap surveys in Karen State, Myanmar, reveal high diversity of globally threatened mammals. Oryx, 51(4), 1–9.news.mongabay+1
El Sira Mountain range	Whitworth, A., Villacampa, J., Brown, A., Huarcaya, R. P., Downie, R., & MacLeod, R. (2020). Camera trapping reveals a diverse and unique high-elevation mammal community under threat from habitat loss and hunting in the Sira Communal Reserve, Peru. Oryx, 54(4), 545–555.cambridge
Piro Research Station, Osa Penninsula	Thorstrom, R., & Holmes, R. T. (2001). Secondary forest is utilized by Great Curassows (Crax rubra) and Great Tinamous (Tinamus major) in the absence of hunting. Ornitología Neotropical, 12, 1–8.oipub
Manu Biosphere Reserve	Whitworth, A., Brown, A., Huarcaya, R. P., Cuthbert, R. J., & MacLeod, R. (2019). Human disturbance impacts on rainforest mammals are most notable in the canopy, especially for larger-bodied species. Diversity and Distributions, 25(6), 1166–1178.onlinelibrary.wiley
Udzungwa Mountains	Henschel, P., Cushman, S. A., Maliti, H., Mwamkala, L., & Caro, T. (2019). Reserve size and anthropogenic disturbance affect the density of an African leopard (Panthera pardus) meta-population. PLOS ONE, 14(6), e0209541.journals.plos
NP Paklenica	Public Institution Paklenica National Park. (unpublished data). Camera-trap survey of medium- and large-sized mammals in Paklenica National Park.
Cusuco National Park	Reid, N. (unpublished data). Camera-trap study of mammals in Cusuco National Park, Honduras.
Brantian-Tatulit Virgin Jungle Reserve	Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., et al. (2017). Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. Biological Conservation, 212, 162–171.eprints.ncl

Table A8 (continued) Overview of studies and sites included in the meta-analysis

Locality	**Name / reference**
Kalabakan Forest Reserve	Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., et al. (2017). Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. Biological Conservation, 212, 162–171.eprints.ncl
Maliau Basin Conservation Area	Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., et al. (2017). Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. Biological Conservation, 212, 162–171.eprints.ncl
oil palm plantation	Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., et al. (2017). Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. Biological Conservation, 212, 162–171.eprints.ncl
Istra	Public Institution Nature Park Učka. (unpublished data). Camera-trap survey of mammals in Istria (Nature Park Učka and surroundings).
Parsa National Park	Karki, J. B., Jhala, Y. V., Jnawali, S. R., Acharya, K. P., & Yumnam, B. (2015). Rapid recovery of tigers Panthera tigris in Parsa Wildlife Reserve, Nepal. Oryx, 49(1), 1–9.journals.plos
NP Risnjak	Public Institution Risnjak National Park. (unpublished data). Camera-trap survey of medium- and large-sized mammals in Risnjak National Park.
Europe PCM	
southern Transylvania	Dorresteijn, I., Loos, J., Hanspach, J., & Fischer, J. (2015). Incorporating anthropogenic effects into trophic ecology: Predator–prey interactions in a human-dominated landscape. Proceedings of the Royal Society B: Biological Sciences, 282(1814), 20151602.

APPENDIX 9:

Table A9 Data extracting categories (for papers that included multiple study sites, the listed variables (Number of species, Species in article, Order, Family, Species type, No. of individuals or detections, No. of individuals or detections per km, Study area (km²), Data collecting period, Data from, Data to, Sampling effort) were recorded separately for each study site, so each site is represented by a distinct row with a complete set of information for all listed categories.)

Attribute name	**Attribute meaning**
No.	*Number of article - internal mark*
Name	*Article title*
data / no data	*Required data available or not*
Publ year	*Article publication year*
Number of species	*Survey species number*
Species in article	*Scientific species name*
Order	*Scientific species order*
Family	*Scientific species family*
Species type	*m = small prey (all Muridae); p = prey (larger than Muridae); v = small carnivore (everything smaller than large carnivores); c = large carnivore*
No. of individuals (or detections)	*number of animals per survey in events*
No. of individuals or detections / km	*number of animals per survey in events divided by survey area*
Study area (km^2)	*Survey area*
Data collecting period	*Survey duration*
Data from	*Survey start date (month and year)*
Data to	*Survey end date (month and year)*
Sampling effort	*Number of camera-days*
Locality	*Local site name*
Country	*Survey country*
Continent	*Survey continent*
X	*X coordinate*
Y	*Y coordinate*
Altitude	*Survey altitude*
Habitat	*Survey habitats*
Natural, Seminatural, Anthropogenic**	*Sites were classified into three land-use categories—natural, semi-natural and anthropogenic—using the formal protection status of each area together with the original authors' qualitative descriptions of degradation and human activity.*
Type of data	*Type of survey data - camera traps*
Further notes	*Internal comments of research author (Matko Bišćan)*

***During data preparation for the meta-analysis, preliminary data screening showed that the three original land-use classes overlapped too much to be used reliably and were overly sensitive to the subjective judgment of the person compiling the dataset, because many sites had intermediate characteristics and could plausibly fall into more than one category. To reduce this potential for misclassification, sites were therefore regrouped into two broader categories for analysis: "natural", comprising areas with no or negligible human activities, and "Human-modified", comprising all sites with notable human use or disturbance.*

APPENDIX 10:

Table A10 List of species and associated classification into the functional groups. Functional group: large carnivores – c, small carnivores – v, large prey – p, and small prey – m.

Species in article	**Order**	**Family**	**Functional group**
Acinonyx jubatus	Carnivora	Felidae	c
Canis aureus	Carnivora	Canidae	c
Canis dingo	Carnivora	Canidae	c
Canis latrans	Carnivora	Canidae	c
Canis lupus	Carnivora	Canidae	c
Canis lupus familiaris	Carnivora	Canidae	c
Canis mesomelas	Carnivora	Canidae	c
Crocuta crocuta	Carnivora	Hyaenidae	c
Cuon alpinus	Carnivora	Canidae	c
Helarctos malayanus	Carnivora	Ursidae	c
Herpailurus yagouaroundi	Carnivora	Felidae	c
Hyaena hyaena	Carnivora	Hyaenidae	c
Lycalopex gymnocercus	Carnivora	Felidae	c
Lynx lynx	Carnivora	Felidae	c
Melursus ursinus	Carnivora	Ursidae	c
Neofelis diardi	Carnivora	Felidae	c
Neofelis nebulosa	Carnivora	Felidae	c
Panthera leo	Carnivora	Felidae	c
Panthera onca	Carnivora	Felidae	c
Panthera pardus	Carnivora	Felidae	c
Panthera tigris	Carnivora	Felidae	c
Panthera tigris altaica	Carnivora	Felidae	c
Panthera tigris sondaica	Carnivora	Felidae	c
Panthera tigris sumatrae	Carnivora	Felidae	c
Panthera uncia	Carnivora	Felidae	c
Puma concolor	Carnivora	Felidae	c
Tremarctos ornatus	Carnivora	Ursidae	c
Ursus arctos	Carnivora	Ursidae	c
Ursus malayanus	Carnivora	Ursidae	c
Ursus thibetanus	Carnivora	Ursidae	c
Amblonyx cinereus	Carnivora	Mustelidae	v
Aonyx capensis	Carnivora	Mustelidae	v
Arctictis binturong	Carnivora	Viverridae	v
Arctonyx collaris	Carnivora	Mustelidae	v
Atelocynus microtis	Carnivora	Canidae	v
Atilax paludinosus	Carnivora	Herpestidae	v
Bdeogale crasicauda	Carnivora	Herpestidae	v
Caracal caracal	Carnivora	Felidae	v
Catopuma badia	Carnivora	Felidae	v
Catopuma temminckii	Carnivora	Felidae	v
Cerdocyon thous	Carnivora	Canidae	v
Chironectes minimus	Didelphimorphia	Didelphidae	v
Civettictis civetta	Carnivora	Viverridae	v

Table A10 (continued) List of species and associated classification into the functional groups

Species in article	Order	Family	Species type
Conepatus semistriatus	Carnivora	Mephitidae	v
Cryptoprocta ferox	Carnivora	Eupleridae	v
Didelphis albiventris	Didelphimorphia	Didelphidae	v
Diplogale hosei	Carnivora	Viverridae	v
Eira barbara	Carnivora	Mustelidae	v
Eupleres goudotii	Carnivora	Eupleridae	v
Felis catus	Carnivora	Felidae	v
Felis chaus	Carnivora	Felidae	v
Felis silvestris	Carnivora	Felidae	v
Fossa fossana	Carnivora	Eupleridae	v
Galerella pulverulenta	Carnivora	Herpestidae	v
Galerella sanguinea	Carnivora	Herpestidae	v
Galictis cuja	Carnivora	Mustelidae	v
Galictis vittata	Carnivora	Mustela	v
Galidia elegans	Carnivora	Eupleridae	v
Galidictis fasciata	Carnivora	Eupleridae	v
Genetta genetta	Carnivora	Viverridae	v
Genetta maculata	Carnivora	Viverridae	v
Genetta servalina lowei	Carnivora	Viverridae	v
Helogale parvula	Carnivora	Herpestidae	v
Hemigalus derbyanus	Carnivora	Viverridae	v
Herpestes brachyurus	Carnivora	Herpestidae	v
Herpestes javanicus	Carnivora	Herpestidae	v
Herpestes semitorquatus	Carnivora	Herpestidae	v
Herpestes urva	Carnivora	Herpestidae	v
Ichneumia albicauda	Carnivora	Herpestidae	v
Ictonyx striatus	Carnivora	Mustelidae	v
Leopardus guttulus	Carnivora	Felidae	v
Leopardus pardalis	Carnivora	Felidae	v
Leopardus tigrinus	Carnivora	Felidae	v
Leopardus wiedii	Carnivora	Felidae	v
Leptailurus serval	Carnivora	Felidae	v
Lontra longicaudis	Carnivora	Mustelidae	v
Lutra lutra	Carnivora	Mustelidae	v
Martes flavigula	Carnivora	Mustelidae	v
Martes foina	Carnivora	Mustelidae	v
Martes martes	Carnivora	Mustelidae	v
Meles meles	Carnivora	Mustelidae	v
Mellivora capensis	Carnivora	Mustelidae	v
Mephitis mephitis	Carnivora	Mephitidae	v
Mungos mungo	Carnivora	Herpestidae	v
Mustela erminea	Carnivora	Mustelidae	v
Mustela frenata	Carnivora	Mustelidae	v
Mustela nudipes	Carnivora	Mustelidae	v

Table A10 (continued) List of species and associated classification into the functional groups

Species in article	Order	Family	Species type
Mustela putorius	Carnivora	Mustelidae	v
Mustela strigidorsa	Carnivora	Mustelidae	v
Mydaus javanensis	Carnivora	Mephitidae	v
Nasua narica	Carnivora	Procyonidae	v
Nasua nasua	Carnivora	Procyonidae	v
Nyctereutes procyonoides	Carnivora	Canidae	v
Otocyon megalotis	Carnivora	Canidae	v
Paguma larvata	Carnivora	Viverridae	v
Paradoxurus hermaphroditus	Carnivora	Viverridae	v
Pardofelis marmorata	Carnivora	Felidae	v
Prionailurus bengalensis	Carnivora	Felidae	v
Prionailurus planiceps	Carnivora	Felidae	v
Prionodon linsang	Carnivora	Prionodontidae	v
Prionodon pardicolor	Carnivora	Prionodontidae	v
Procyon cancrivorus	Carnivora	Procyonidae	v
Procyon lotor	Carnivora	Procyonidae	v
Proteles cristata	Carnivora	Hyaenidae	v
Puma yagouaroundi	Carnivora	Felidae	v
Rhynchogale melleri	Carnivora	Herpestidae	v
Viverra megaspila	Carnivora	Viverridae	v
Viverra tangalunga	Carnivora	Viverridae	v
Viverra zibetha	Carnivora	Viverridae	v
Viverricula indica	Carnivora	Viverridae	v
Vulpes vulpes	Carnivora	Canidae	v
Aepyceros melampus	Artiodactyla	Bovidae	p
Alcelaphus buselaphus	Artiodactyla	Bovidae	p
Alces alces	Artiodactyla	Cervidae	p
Axis axis	Artiodactyla	Cervidae	p
Bassaricyon alleni	Carnivora	Procyonidae	p
Bison bonasus	Artiodactyla	Bovidae	p
Bos gaurus	Artiodactyla	Bovidae	p
Bos javanicus	Artiodactyla	Bovidae	p
Bos taurus	Artiodactyla	Bovidae	p
Bos taurus indicus	Artiodactyla	Bovidae	p
Boselaphus tragocamelus	Artiodactyla	Bovidae	p
Bradypus variegatus	Pilosa	Bradypodidae	p
Bubalus bubalis	Artiodactyla	Bovidae	p
Cabassous tatouay	Cingulata	Chlamyphoridae	p
Cabassous unicinctus	Cingulata	Dasypodidae	p
Callosciurus adamsi	Rodentia	Sciuridae	p
Callosciurus notatus	Rodentia	Sciuridae	p
Callosciurus prevostii	Rodentia	Sciuridae	p
Caluromys lanatus	Didelphimorphia	Didelphidae	p
Capra aegagrus	Artiodactyla	Bovidae	p

Table A10 (continued) List of species and associated classification into the functional groups

Species in article	Order	Family	Species type
Capra sibirica	Artiodactyla	Bovidae	p
Capreolus capreolus	Artiodactyla	Cervidae	p
Capricornis milneedwardsii	Artiodactyla	Bovidae	p
Capricornis sumatraensis	Artiodactyla	Bovidae	p
Cavia aperea	Rodentia	Caviidae	p
Cephalopachus bancanus	Primates	Tarsiidae	p
Cephalophus harveyi	Artiodactyla	Bovidae	p
Cephalophus spadix	Artiodactyla	Bovidae	p
Cercocebus sanjei	Primates	Cercopithecidae	p
Cercopithecus mitis	Primates	Cercopithecidae	p
Cervus elaphus	Artiodactyla	Cervidae	p
Cervus nippon	Artiodactyla	Cervidae	p
Cervus unicolor	Artiodactyla	Cervidae	p
Chlorocebus pygerythrus	Primates	Cercopithecidae	p
Choloepus hoffmanni	Pilosa	Megalonychidae	p
Coendou bicolor	Rodentia	Erethizontidae	p
Coendou ichillus	Rodentia	Erethizontidae	p
Coendou spinosus	Rodentia	Erethizontidae	p
Conepatus chinga	Carnivora	Mephitidae	p
Connochaetes taurinus	Artiodactyla	Bovidae	p
Cuniculus paca	Rodentia	Cuniculidae	p
Cyclopes didactylus	Pilosa	Cyclopedidae	p
Damaliscus lunatus jimela	Artiodactyla	Bovidae	p
Dasyprocta azarae	Rodentia	Dasyproctidae	p
Dasyprocta punctata	Rodentia	Dasyproctidae	p
Dasyprocta variegata	Rodentia	Dasyproctidae	p
Dasypus novemcinctus	Cingulata	Dasypodidae	p
Dasypus septemcinctus	Cingulata	Dasypodidae	p
Daubentonia madagascariensis	Primates	Daubentoniidae	p
Dendrohyrax validus	Hyracoidea	Procaviidae	p
Didelphis aurita	Didelphimorphia	Didelphidae	p
Didelphis marsupialis	Didelphimorphia	Didelphidae	p
Didelphis pernigra	Didelphimorphia	Didelphidae	p
Dinomys branickii	Rodentia	Dinomyidae	p
Echinosorex gymnura	Eulipotyphla	Erinaceidae	p
Elephas maximus	Proboscidea	Elephantidae	p
Equus asinus	Perissodactyla	Equidae	p
Equus caballus	Perissodactyla	Equidae	p
Equus quagga	Perissodactyla	Equidae	p
Erethizon dorsatum	Rodentia	Hystricidae	p
Eudorcas thomsonii	Artiodactyla	Bovidae	p
Euphractus sexcinctus	Cingulata	Chlamyphoridae	p
Exilisciurus exilis	Rodentia	Sciuridae	p
Giraffa camelopardalis	Artiodactyla	Giraffidae	p

Table A10 (continued) List of species and associated classification into the functional groups

Species in article	Order	Family	Species type
Gracilinanus microtarsus	Didelphimorphia	Didelphidae	p
Guerlinguetus ingrami	Rodentia	Sciuridae	p
Hippopotamus amphibius	Artiodactyla	Hippopotamidae	p
Hippotragus niger	Artiodactyla	Bovidae	p
Hydrochoerus hydrochaeris	Rodentia	Caviidae	p
Hyemoschus aquaticus	Artiodactyla	Tragulidae	p
Hylobates muelleri	Primates	Hylobatidae	p
Hystrix africaeaustralis	Rodentia	Hystricidae	p
Hystrix brachyura	Rodentia	Hystricidae	p
Hystrix crassispinis	Rodentia	Hystricidae	p
Hystrix cristata	Rodentia	Hystricidae	p
Hystrix indica	Rodentia	Hystricidae	p
Kobus ellipsiprymnus	Artiodactyla	Bovidae	p
Lariscus hosei	Rodentia	Sciuridae	p
Lariscus insignis	Rodentia	Sciuridae	p
Lepus capensis	Lagomorpha	Leporidae	p
Lepus europaeus	Lagomorpha	Leporidae	p
Lepus microtis	Lagomorpha	Leporidae	p
Lepus peguensis	Lagomorpha	Leporidae	p
Loxodonta africana	Proboscidea	Elephantidae	p
Macaca arctoides	Primates	Cercopithecidae	p
Macaca fascicularis	Primates	Cercopithecidae	p
Macaca leonina	Primates	Cercopithecidae	p
Macaca mulatta	Primates	Cercopithecidae	p
Macaca nemestrina	Primates	Cercopithecidae	p
Madoqua kirkii thomasii	Artiodactyla	Bovidae	p
Manis javanica	Pholidota	Manidae	p
Mazama americana	Artiodactyla	Cervidae	p
Mazama gouazoubira	Artiodactyla	Cervidae	p
Mazama nana	Artiodactyla	Cervidae	p
Meleagris gallopavo	Galliformes	Phasianidae	p
Menetes berdmorei	Rodentia	Sciuridae	p
Metachirus nudicaudatus	Didelphimorphia	Didelphidae	p
Microcebus murinus	Primates	Cheirogaleidae	p
Microsciurus flaviventer	Rodentia	Sciuridae	p
Muntiacus atherodes	Artiodactyla	Cervidae	p
Muntiacus muntjak	Artiodactyla	Cervidae	p
Myocastor coypus	Rodentia	Echimyidae	p
Myoprocta pratti	Rodentia	Dasyproctidae	p
Myrmecophaga tridactyla	Pilosa	Myrmecophagidae	p
Nandinia binotata	Carnivora	Nandiniidae	p
Nanger granti	Artiodactyla	Bovidae	p
Neotragus moschatus	Artiodactyla	Bovidae	p
Odocoileus virginianus	Artiodactyla	Bovidae	p

Table A10 (continued) List of species and associated classification into the functional groups

Species in article	Order	Family	Species type
Oreotragus oreotragus	Artiodactyla	Bovidae	p
Orycteropus afer	Tubulidentata	Orycteropodidae	p
Ovis ammon	Artiodactyla	Bovidae	p
Ovis vignei	Artiodactyla	Bovidae	p
Papio cynocephalus	Primates	Cercopithecidae	p
Papio hamadryas	Primates	Cercopithecidae	p
Paraxerus vexillarius	Rodentia	Sciuridae	p
Pecari tajacu	Artiodactyla	Tayassuidae	p
Pelea capreolus	Artiodactyla	Bovidae	p
Petaurista elegans	Rodentia	Sciuridae	p
Phacochoerus africanus	Artiodactyla	Suidae	p
Philander frenatus	Didelphimorphia	Didelphidae	p
Philantomba monticola	Artiodactyla	Bovidae	p
Pongo pygmaeus	Primates	Hominidae	p
Potamochoerus larvatus	Artiodactyla	Suidae	p
Potos flavus	Procyonidae	Carnivora	p
Presbytis frontata	Primates	Cercopithecidae	p
Presbytis hosei	Primates	Cercopithecidae	p
Presbytis rubicunda	Primates	Cercopithecidae	p
Priodontes maximus	Cingulata	Dasypodidae	p
Pronolagus saundersiae	Lagomorpha	Leporidae	p
Propithecus candidus	Primates	Indriidae	p
Ptilocercus lowii	Scandentia	Ptilocercidae	p
Raphicerus campestris	Artiodactyla	Bovidae	p
Raphicerus melanotis	Artiodactyla	Bovidae	p
Rheithrosciurus macrotis	Rodentia	Sciuridae	p
Rupicapra rupicapra	Artiodactyla	Capridae	p
Rusa unicolor	Artiodactyla	Cervidae	p
Sapajus nigritus	Primates	Cebidae	p
Sciurus niger	Rodentia	Sciuridae	p
Sciurus carolinensis	Rodentia	Sciuridae	p
Sciurus spadiceus	Rodentia	Sciuridae	p
Sciurus vulgaris	Rodentia	Sciuridae	p
Setifer setosus	Afrosoricida	Tenrecidae	p
Smutsia temminckii	Pholidota	Manidae	p
Sundasciurus hippurus	Rodentia	Sciuridae	p
Sundasciurus lowii	Rodentia	Sciuridae	p
Sundasciurus tenuis	Rodentia	Sciuridae	p
Sus barbatus	Artiodactyla	Suidae	p
Sus scrofa	Artiodactyla	Suidae	p
Sus scrofa cristatus	Artiodactyla	Suidae	p
Sus scrofa vittatus	Artiodactyla	Suidae	p
Sylvicapra grimmia	Artiodactyla	Bovidae	p
Sylvilagus brasiliensis	Lagomorpha	Leporidae	p

Table A10 (continued) List of species and associated classification into the functional groups

Species in article	Order	Family	Species type
Sylvilagus floridanus	Lagomorpha	Leporidae	p
Syncerus caffer	Artiodactyla	Bovidae	p
Tamandua mexicana	Pilosa	Myrmecophagidae	p
Tamandua tetradactyla	Pilosa	Myrmecophagidae	p
Tapirus bairdii	Perissodactyla	Tapiridae	p
Tapirus indicus	Perissodactyla	Tapiridae	p
Tapirus terrestris	Perissodactyla	Tapiridae	p
Taurotragus oryx	Artiodactyla	Bovidae	p
Tayassu pecari	Artiodactyla	Tayassuidae	p
Tenrec ecaudatus	Afrosoricida	Tenrecidae	p
Tetracerus quadricornis	Artiodactyla	Bovidae	p
Thryonomys swinderianus	Rodentia	Thryonomyidae	p
Trachypithecus phayrei	Primates	Cercopithecidae	p
Tragelaphus oryx	Artiodactyla	Bovidae	p
Tragelaphus scriptus	Artiodactyla	Bovidae	p
Tragelaphus strepsiceros	Artiodactyla	Bovidae	p
Tragelaphus sylvaticus	Artiodactyla	Bovidae	p
Tragulus kanchil	Artiodactyla	Tragulidae	p
Tragulus napu	Artiodactyla	Tragulidae	p
Trichys fasciculata	Rodentia	Hystricidae	p
Tupaia dorsalis	Scandentia	Tupaiidae	p
Tupaia gracilis	Scandentia	Tupaiidae	p
Tupaia tana	Scandentia	Tupaiidae	p
Xerus princeps	Rodentia	Sciuridae	p
Cricetomys gambianus	Rodentia	Nesomyidae	m
Dendrogale murina	Scandentia	Tupaiidae	m
Glis glis	Rodentia	Gliridae	m
Hemicentetes semispinosus	Afrosoricida	Tenrecidae	m
Leopoldamys sabanus	Rodentia	Muridae	m
Lepus nigricollis	Lagomorpha	Leporidae	m
Maxomys ochraceiventer	Rodentia	Muridae	m
Maxomys whiteheadi	Rodentia	Muridae	m
Microgale soricoides	Afrosoricida	Tenrecidae	m
Petrodromus tetradactylus	Macroscelidea	Macroscelididae	m
Rattus rattus	Rodentia	Muridae	m
Rattus satarae	Rodentia	Muridae	m
Rhynchocyon cirnei	Macroscelidea	Macroscelididae	m
Rhynchocyon udzungwensis	Macroscelidea	Macroscelididae	m
Suncus murinus	Eulipotyphla	Soricidae	m
Sundamys muelleri	Rodentia	Muridae	m
Tokudaia muenninki	Rodentia	Echimyidae	m
Tupaia minor	Scandentia	Tupaiidae	m

APPENDIX 11:

Figure A1 Forest plot from the sensitivity analysis using an alternative continuity correction (ln((V+1)/(P+1))). Effect sizes and confidence intervals are qualitatively similar to the main analysis, with a slight compression toward zero. The consistency of patterns across continuity corrections indicates that results are robust to zero inflation and not driven by rare detection events.

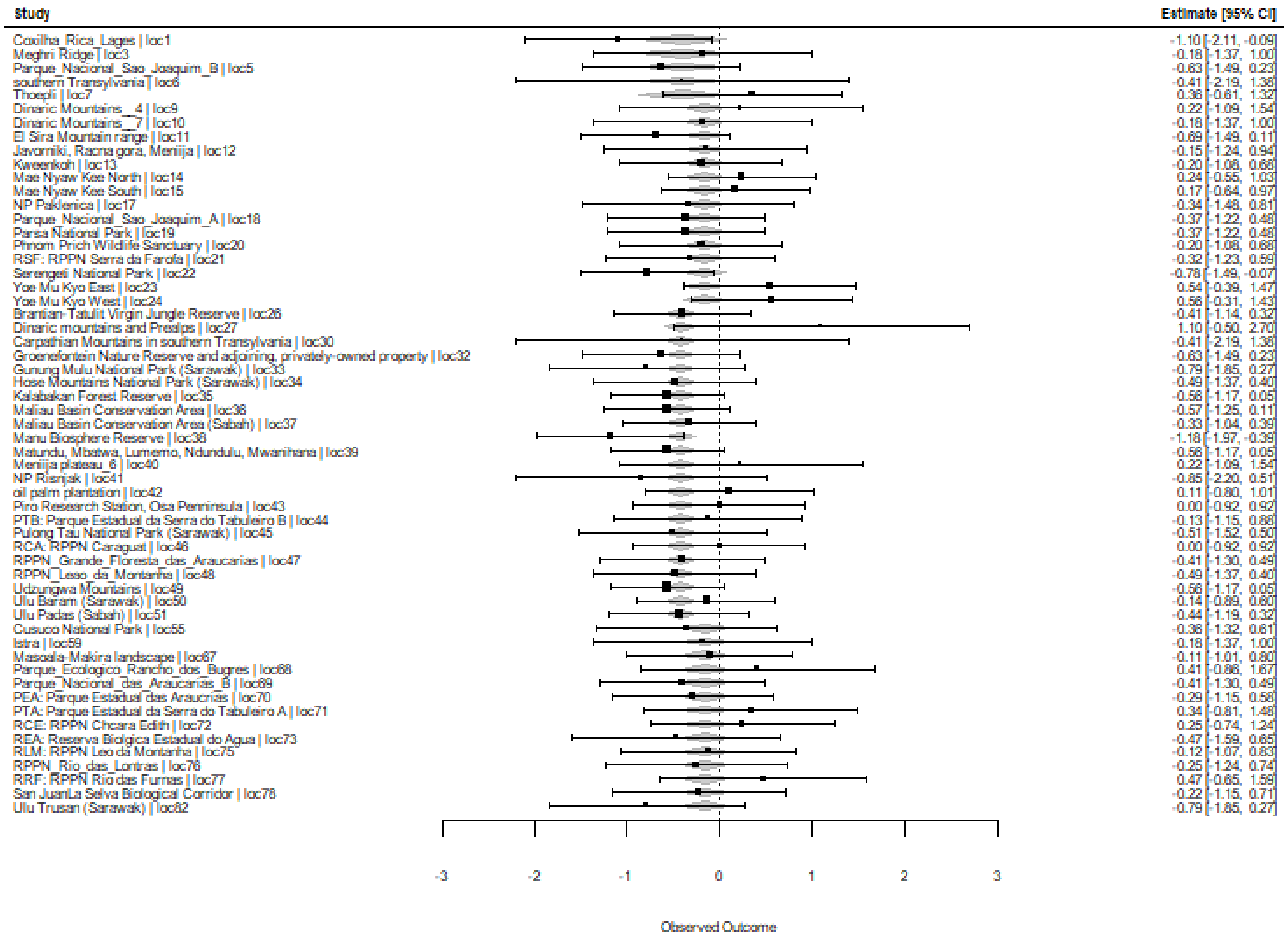

Figure A1 Forest plot from the sensitivity analysis using an alternative continuity correction (ln((V+1)/(P+1))). Effect sizes and confidence intervals are qualitatively similar to the main analysis, with a slight compression toward zero. The consistency of patterns across continuity corrections indicates that results are robust to zero inflation and not driven by rare detection events.

APPENDIX 12:

Detailed description of each simulation scenario, outlining the assumptions, parameter adjustments, and the rationale behind their design.

Baseline scenario (S1)

The baseline scenario (Scenario 1) modelled the wolf population according to the carrying capacity of the study area. This carrying capacity estimate was based on a habitat suitability map for wolves (Kusak et al. 2016), which classified areas into categories 7, 8, and 9—where category 9 represents the highest suitability (Figure A2). Within the study area, these combined categories cover a total of 1076 km^2. Based on the literature (Jeremić et al. 2017), we calculated the baseline carrying capacity for wolves in this area to be 16 individuals, which was used as the initial population size to start the model.

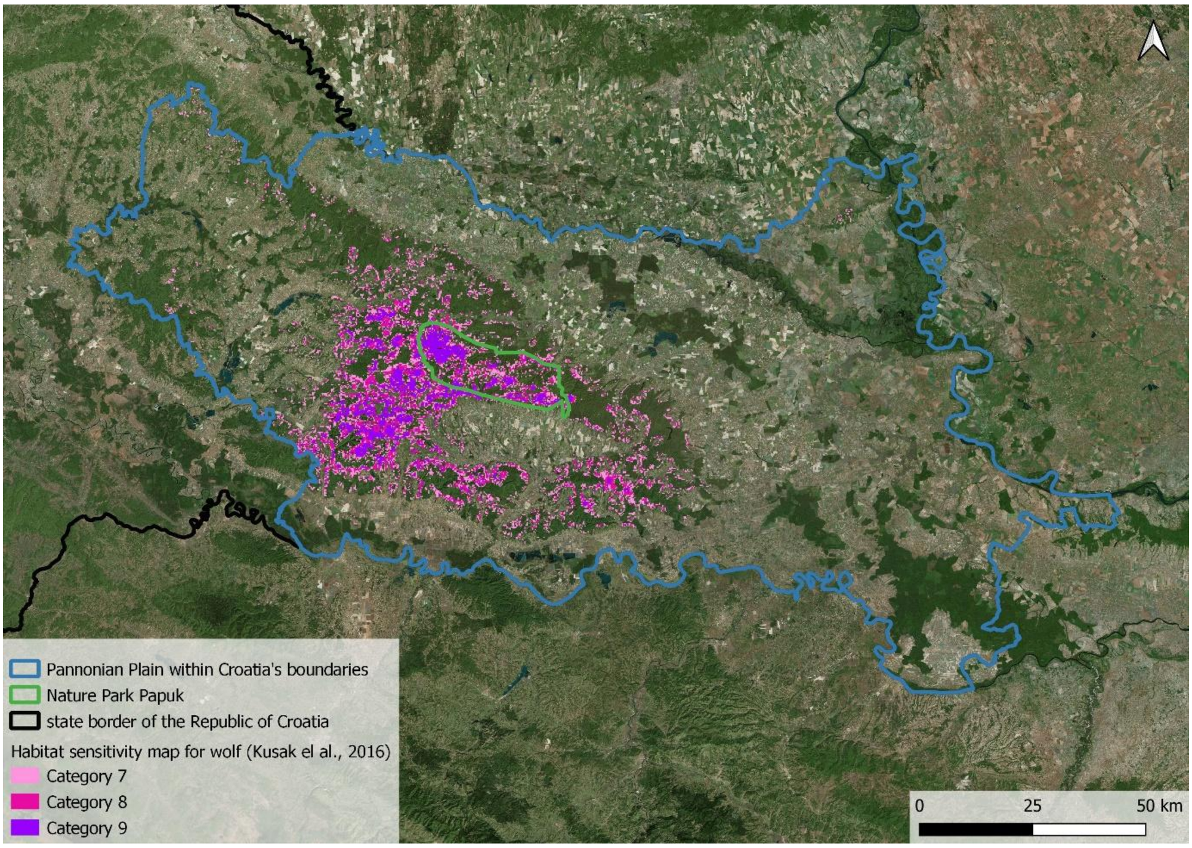

Figure A2. Habitat suitability map for wolves in Slavonia. The study area is outlined by the Republic of Croatia's state border (black line) and the Slavonia survey area (blue line). Habitat suitability categories (Kusak et al. 2016) are shown in ascending order of habitat quality: category 7 (light pink), category 8 (medium pink), and category 9 (dark purple). Nature Park Papuk is also indicated.

Group 1—Adverse events scenarios (S2–S4)

The first group of modelled scenarios (Scenarios 2–4) represents adverse events that could reduce the population compared to the baseline scenario. For all these scenarios, the carrying capacity remained the same as in the baseline—16 individuals. Scenario 2 ("Disease") anticipated a 50% population reduction. This scenario maintained the baseline carrying capacity but incorporated the risk of a catastrophic disease outbreak, with a survival rate of 0.5. Disease outbreaks, such as those caused by canine parvovirus or distemper, were assumed to occur randomly between year 1 and the end of the simulation. Based on the literature (Reed et al. 2003), the modelled frequency was 14% per generation, corresponding to a 0.14 probability over a 100-year period. Scenario 3 ("Removals") involved the annual removal of one individual (harvest = 1 animal per year) to simulate removals resulting from livestock attacks, settlement intrusions, aggressive behaviour towards people, or a lack of fear of humans. The literature [86] suggests that male wolves may approach residential areas more frequently than females, so this scenario modelled the removal of one male. Scenario 4 ("Illegal Hunting") simulated the poaching of two male wolves per year (harvest = 2 males).

Group 2—Carrying capacity scenarios (S5–S7)

The second group of scenarios (Scenarios 5–7) involves increasing the carrying capacity. All three use the wolf habitat suitability map as the baseline. Scenario 5 ("Succession") analysed changes in forest habitat area across three reference years (2012, 2015, and 2018). Data on forest and non-forest areas (broadleaved and coniferous forests) were obtained from the Copernicus High-Resolution Layer Forest Type. The baseline year, 2012, corresponds to the wolf habitat suitability map, while the other two years came from the Copernicus cadastre. The analysis showed that forest habitats within suitability categories 7, 8, and 9 expanded to 1183 km^2—an increase of 107 km^2. Based on previous studies [84], the baseline carrying capacity for wolves in Scenario 5 was calculated as 18 individuals, which also served as the initial population size for the model. Scenario 6 ("Forest Management") simulated the effects of changing forest management practices to retain mature forests for longer periods. The aim was to delay final felling by 20 years, thereby increasing the extent of older forests suitable for wolves. In this scenario, forest areas were upgraded from habitat suitability category 6 to 7, from 7 to 8, and from 8 to 9, including the existing area in category 9. This was based on the 2004 Croatian forest habitat map (Antonić et al. 2005), which underpinned the wolf habitat suitability map. The Papuk Nature Park was selected as the study area for this scenario, given that its protected status facilitates implementing such management changes. The analysis indicated an increase to 1116 km^2 in categories 7, 8, and 9—an increase of 40 km^2. Following [84], the carrying capacity for Scenario 6 was set at 17 wolves, which was also used as the initial population size. Scenario 7 (“Hunting Management”) modelled an increase in the carrying capacity by reducing hunting quotas for wolf prey. The hunting grounds in the study area were analysed by calculating the percentage of each hunting ground covered by suitable wolf habitat (categories 7, 8, and 9). Hunting grounds where over 50% of the area fell within these categories were identified, covering 55% of all suitable habitats in the study area. We hypothesized that reducing the hunting quota for wolf prey by 20% in these grounds would lead to a corresponding 20% increase in the wolf carrying capacity. Based on this assumption, the baseline carrying capacity for wolves in Scenario 7 was calculated to be 19 individuals.

Group 3—Population supplementation scenarios (S8–S11)

The third group of scenarios (Scenarios 8–11) focuses on wolf population supplementation. The analysis centred on existing overpasses and underpasses, as well as potential modifications to highways, aimed at mitigating their barrier effect that separates the continuous wolf population in Banovina from the study area in Slavonia. These highway structures were initially identified using the Digital Orthophoto map (accessed via http://geoportal.dgu.hr/wms, accessed on 17 July 2023) through GIS analysis. Field visits were then conducted to verify these findings, followed by further GIS analysis to evaluate potential connecting corridors between Banovina and Slavonia using habitat maps from 2004 (Antonić et al. 2005) and 2016 (Bardi et al. 2016). A total of 27 existing highway overpasses and underpasses were identified as potential pathways to support wolf recolonization from Banovina to Slavonia. These structures were categorized into three groups: impassable, potentially passable with significant design modifications, and potentially passable with minor design adjustments. They are considered potentially passable because, although not originally designed for large mammals, many include bridges and smaller overpasses over watercourses whose dimensions may still allow large mammals to cross. Of these, eight highway structures are potentially passable for wolves in their current state with only minor adjustments needed, while an additional five could be made suitable with more substantial design modifications. Accordingly, Scenario 8 (“One-Region Corridor Enhancement”) modelled the supplementation of the baseline Slavonian population with a single male wolf migrating from Banovina. The supplementation focused on a male wolf because males outnumber females among long-distance dispersers (Linnell et al. 2021) and males tend to disperse more frequently than females (Wilson, 2023). Scenario 9

("Corridor Construction") involved supplementing the baseline Slavonian population with a pair of wolves from Banovina by improving existing highway structures to make them passable for wolves and potentially constructing new crossings. Scenario 10 ("Banovina and Bosnia and Herzegovina") modelled the supplementation of the baseline Slavonian population with one male wolf from Banovina and one male wolf from Bosnia and Herzegovina, facilitated by enhancing existing highway structures to allow passage from both regions. Supplementation from Bosnia and Herzegovina is potentially more challenging because Slavonia (Croatia) and Bosnia and Herzegovina are separated not only by the highway mentioned earlier but also by the Sava River. In this scenario, wolves would need to either swim across the Sava River or use a bridge, then cross the highway. While the analysis of existing highway structures suggests crossing the highway is possible, crossing the Sava River remains uncertain. Although Blanco et al. (2005) suggested that it might be feasible, this scenario was modelled as an additional, though unlikely, possibility. Scenario 11 ("Translocation") represented the supplementation of the baseline Slavonian population with a pair of wolves translocated from a nearby Croatian region where wolves are continuously present. The carrying capacity for Scenarios 8 through 11 remained the same as in the baseline scenario.

APPENDIX 13:

Principal component analysis (PCA) results showing eigenvalues, explained variance, and variable loadings for four datasets: 10-year model, 30-year model, 100-year model and the combined dataset of all models for years (all) , the number of extinct populations and mean size od extanta populations.

Table A11. Principal component analysis (PCA) results showing eigenvalues, explained variance, and variable loadings for four datasets: 10-year model, 30-year model, 100-year model and the combined dataset of all models for years (all) , the number of extinct populations and mean size od extanta populations.

Time Period	**Component**	**Eigenvalue**	**Variance**	**Loading**		
			(%)	**Year**	**N (Extinct Population)**	**Mean size (extant populations)**
All	PC1	14333.800	94.087	0.048	0.999	0.008
	PC2	890.921	5.848	0.997	-0.048	0.060
	PC3	9.872	0.065	-0.060	-0.005	0.998
10-year	PC1	12604.500	99.794	0.015	1.000	0.012
	PC2	25.601	0.203	0.523	-0.018	0.852
	PC3	0.392	0.003	0.852	-0.006	-0.523
30-year	PC1	13245.400	99.323	-0.022	1.000	-0.011
	PC2	83.713	0.628	0.932	0.025	0.361
	PC3	6.594	0.049	-0.361	0.002	0.933
100-year	PC1	14398.900	94.443	0.029	1.000	0.003
	PC2	840.885	5.515	0.999	-0.029	0.041
	PC3	6.285	0.041	-0.042	-0.002	0.999

CURRICULUM VITAE

Matko Bišćan enrolled in the undergraduate programme in Environmental Science at the Faculty of Science, University of Zagreb, in 2009, where he obtained a bachelor's degree in Environmental science. He completed his graduate studies in Ecology at the Department of Biology, Faculty of Science, in 2012, earning a master's degree in Ecology and Nature Protection. Since 2014, he has been employed at EKONERG – Energy and Environmental Protection Institute Ltd., where he works as a senior expert, team leader and team member on numerous projects in nature conservation and environmental impact assessments. His research focuses on large carnivore ecology, trophic interactions, ecological connectivity and coexistence, with a particular emphasis on wolf recolonization dynamics in Croatia and the wider Pannonian region. He is the first author of a scientific paper on modelling wolf recolonization to support proactive conservation planning in Slavonia, published in Diversity (https://doi.org/10.3390/d17070461), and first author of an article on the role of protected area rangers in biodiversity monitoring, published in Ekológia (Bratislava - https://doi.org/10.2478/eko-2022-0019). In addition, he has contributed as author or co-author to several conference presentations and abstracts on rewilding, wetland and river revitalisation, innovative baseline assessment methods in environmental impact studies, and habitat diversity analysis in protected areas. He continuously advances his expertise through professional seminars and international workshops and is fluent in English.

Scientific publications, participation in international/national conferences, technical reports:

- Bišćan, M., Jelić, D., Maguire, I., & Massolo, A. (2025). Modelling wolf (*Canis lupus*) recolonization dynamics to plan conservation actions ahead: Will the "big bad wolves" howl again in Slavonia, Croatia? Diversity, 17(7), 461. https://doi.org/10.3390/d17070461
- Bišćan, M., Lukač, G., Špalj, F., Blagajac, R., Jelić, D., Maguire, I., & Massolo, A. (2022). The value of protected areas ranger service personnel for biodiversity monitoring: Case study in Paklenica National Park (Croatia). Ekológia (Bratislava), 41(2), 157–174. https://doi.org/10.2478/eko-2022-0019
- Bišćan, M., Stanec Svedrović, D., Ruždjak, D., Marković, B., Lubura Matković, T., Ričković, V., & Vidaković Šutić, R. (2022). Is there any hope for the wetlands? Revitalization of the middle Danube region. In O. Antonić, N. Mikulić, & M.

Celinšćank (Eds.), Book of abstracts (pp. 109–110). Zagreb: Croatian Association of Experts in Nature and Environmental Protection. (oral presentation, international peer review, scientific abstract)

- Bišćan, M., & Damjanović, I. (2022). The Big Bad Wolf – the perception of media-mediated messages. In O. Antonić, N. Mikulić, & M. Celinšćank (Eds.), Book of abstracts (pp. 169–170). Zagreb: Croatian Association of Experts in Nature and Environmental Protection. (poster, international peer review, scientific abstract)
- Bišćan, M., Lukač, G., Špalj, F., Jelić, D., Maguire, I., & Massolo, A. (2021). Važnost čuvara prirode javnih ustanova zaštićenih područja prirode u monitoringu bioraznolikosti: na primjeru istraživanja sisavaca pomoću fotozamki na području Nacionalnog parka Paklenica (Hrvatska) [The importance of protected area rangers for biodiversity monitoring: A camera-trap case study of mammals in Paklenica National Park, Croatia]. In M. Đaković et al. (Eds.), Symposium of Doctoral Students of the Faculty of Science – Book of abstracts (pp. 154–155). Zagreb: Faculty of Science, University of Zagreb. (oral presentation, peer-reviewed, scientific abstract)
- Bišćan, M., & Damjanović, I. (2021). Je li Kopački rit spreman za ReWilding? [Is Kopački rit ready for rewilding?]. In S. Ozimec et al. (Eds.), Proceedings of the 10th symposium with international participation "Kopački rit – yesterday, today, tomorrow" (pp. 24–27). Osijek: Public Institution Nature Park Kopački rit. (poster, international peer review, scientific abstract)
- Bišćan, M., Marković, K., Marković, B., Bušić, P., Kotaran Munda, M., & Vidaković Šutić, R. (2019). Revitalizacija rukavaca na rijeci Dravi u sklopu DRAVA LIFE projekta [Backwater revitalisation on the Drava River within the DRAVA LIFE project]. In Book of abstracts (pp. 673–682). Opatija, Croatia. (oral presentation, national peer review, scientific abstract)
- Bišćan, M., Marković, K., Marković, B., Bušić, P., Kotaran Munda, M., & Vidaković Šutić, R. (2019). Projekti revitalizacije i "divlje prirode" – izazovi budućnosti i mogućnosti suživota [Revitalisation and "wild nature" projects – future challenges and opportunities for coexistence]. In Book of abstracts (pp. 82–88). Vodice, Croatia. (oral presentation, national peer review, scientific abstract)
- Bišćan, M., Marković, B., Vucić, M., & Jelić, D. (2019). Inovativna metoda procjene nultog stanja vrsta korištena za potrebe postupka procjene utjecaja na okoliš [An innovative method for baseline assessment of species for environmental impact

assessment]. In Book of abstracts (pp. 20–24). Vodice, Croatia. (oral presentation, national peer review, scientific abstract)

- Bišćan, M., Radović, A., & Jelaska, S. D. (2012). Usporedba stanišne raznolikosti zaštićenih područja u ovisnosti o prostornoj i tematskoj razlučivosti podloga [Comparison of habitat diversity in protected areas depending on spatial and thematic resolution of input layers]. In S. D. Jelaska et al. (Eds.), 11th Croatian Biological Congress: Book of abstracts (pp. 186–187). Zagreb: Croatian Biological Society 1885. (oral presentation, national peer review, scientific abstract)
- Bišćan, M., Vucić, M., & Jelić, D. (2019). Survey of medium and large mammal populations in the Papuk Nature Park area (Technical report; Document ID 2019-3-2802-1). BIOTA Ltd., for the Public Institution Papuk Nature Park, Zagreb, Croatia (technical report)